The role of the sandprawn, *Callichirus kraussi*, as an ecosystem engineer in a temporarily open/closed Eastern Cape estuary, South Africa.

By

Cuma Njozela

Submitted in fulfillment for the degree of

Master of Science at Rhodes University

July 2012

Supervisor: Prof PW Froneman

DECLARATION

This thesis has not been submitted to any university other than Rhodes University, Grahamstown, South Africa. The work presented is that of the author.

ABSTRACT

The role of the sandprawn, *Callichirus* (=*Callianassa) kraussi* (Stebbing), as an ecosystem engineer was assessed in the lower reach of the temporarily open/closed Kasouga Estuary situated along the Eastern Cape coastline of southern Africa over the period April 2010 to June 2011. The study comprised two distinct components, a field study and a caging experiment. The field study assessed the correlation between sand prawn densities and selected physico-chemical (organic content of the sediment and bioturbation) and biological (microphytobenthic algal concentrations and macrobenthic abundance and biomass) variables in 50 quadrants in the lower reach of the estuary. Densities of the sand prawn within the quadrants ranged from 0 to 156 ind m^{-2} (mean = 37 ind m^{-2}). There were no significant correlations between the densities of the sandprawn and the estimates of the organic content of the sediment and the abundance and biomass of the macrofauna ($P > 0.05$ in all cases). Numerical analyses failed to identify any effect of the sandprawn density on the macrofaunal community structure. The rate of bioturbation was, however, strongly correlated to the sand prawn density. Similarly, the microphytobenthic alga concentrations were significantly negatively correlated to the sand prawn densities (($P < 0.05$). The absence of any distinct impact of the sandprawn on the macrobenthic community structure appeared to be related to their low densities in the lower reach of the estuary during the study.

To better understand the role of the sandprawn as an ecosystem engineer, a caging experiment was conducted using inclusion and exclusion treatments (n= 5 for each treatment). Densities of the sandprawn in the inclusion treatments (80 ind m^{-2}) were in the range of the natural densities within the estuary. The experiment was conducted over a period of 18 weeks in the lower reach of the estuary during summer. The presence of the sandprawn, *C kraussi*, contributed to a significant decrease in the microphytobenthic algal concentrations and the abundance and biomass of the macrofauna ($P < 0.05$ in all cases). The decrease in the microphytobenthic algal concentrations in the presence of the sandprawn appeared to be related to the res-suspension of the sediments (bioturbation) generated by the burrowing and feeding activities of the sandprawn. The observed decrease in macrofaunal abundances and biomass in the inclusion treatments appeared to be mediated by both the decreased food availability (mainly the microphytobenthic algae) and the burial of organisms within the sediments. Numerical analysis indicated that the sandprawn did, however, not contribute to a change in the species composition of the macrofauna. Results of the current study indicate that *C.kraussi* plays an important role in structuring the invertebrate community and energy flow within temporarily/open closed Kasouga Estuary.

ACKNOWLEDGMENTS

I firstly thank my supervisor, Professor P.W. Froneman for the trust and confidence he showed in me by agreeing to be my supervisor at the eleventh hour. I also extend my gratitude to him for providing additional financial support so that my extended stay in Grahamstown would be a pleasant one. Finally, I would also like to thank the National Research Foundation (NRF) and Rhodes University for providing funds and facilities to conduct this research

TABLE OF CONTENTS

CHAPTER 1:

CHAPTER 2:

CHAPTER 3

CHAPTER 4:

CHAPTER 5:

CHAPTER 6:

LIST OF FIGURE LEGENDS

LIST OF TABLE LEGENDS

CHAPTER 1

General Introduction

1.1. Ecosystems engineers

The term “system engineer” was first proposed by Lawton and Jones (1993). Although the concept had been recognized by Darwin in 1881, there had been no unifying concept that examined the relationship between the resource use of individuals, the dynamics of population and communities and the biogeochemical processes of ecosystems (Jones *et.al.,* 1994). At the time of its first usage, the concept was acclaimed as a pioneering effort to link species with the ecosystem through physical consequences of biological activity (Jones *et al.,* 1994). The concept of ecosystem engineering describes the aspects of the relationships between organisms and their environment which are not directly trophic or competitive (Jones *et al.,* 1994). Instead, it encompasses physical properties that are brought about by organisms called system engineers. These processes aid in the modification, maintenance and the creation of new habitats (Jones *et al*., 1994).

Jones *et al* (1994) identified two kinds of engineering species, “autogenic” and “allogenic” ecosystem engineers. Autogenic engineers impact on the habitat in which they live through their own physical structures and are an integral part of the ecosystem. Allogenic engineers modulate resources from one physical state to another through their behavior and activities (Jones *et al.,* 1994). Whilst the effects of ecosystem engineers on the associated community can be equally dramatic to those of keystone species, critical interactions of the allogenic engineers are usually regarded as trophic. The phenomena of physical and keystone species are synonymous, even though they are intrinsically linked (Jones *et al.*, 1994). Jones *et al.* (1997a) later refined the notion of ecosystem engineering by distinguishing, and by exploring probable net effects of physical ecosystem engineers on species diversity and abundances, and upon populations, community and ecosystem stability.

Ecosystem engineers tend to be most dominant in stressful environments (Jones *et al.*, 1997b), and consequently, both autogenic and allogenic ecosystem engineers can have a striking presence in many coastal ecosystems (Pillay and Branch 2011). Benthic ecosystem engineers can be divided into epibenthic and endobenthic organisms depending on whether they spend most of their time above or below the sediment. Many endobenthic macroinvertebrate species modify the sedimentary habitat through their feeding and burrowing activities (Gacia *et al.*, 2003; Bouma *et al.*, 2006). Endobenthic bottom dwelling species affect a number of resource flows through bioturbation and bio-irrigation. Epibenthic ecosystem engineers affect local hydrodynamics and thereby often affect local sediment dynamics and particle trapping (Gacia *et al*., 2003; Bouma *et al*., 2006).

Other trophic relations, habitat modification by ecosystem engineers tend to constitute a positive feedback on conspecifics (Cuddington and Hastings, 2004). These positive feedbacks generally require a minimal threshold to be surpassed before becoming effective (Bouma *et al.*, 2009). As a result, isolated individuals of autogenic engineers often come and go. However, once several individuals manage to establish themselves, they systematically succeed in modifying the environment to their own advantage and patches of marsh plants, meadows of seagrass or beds of suspension feeders are known to persist over long periods of time (van Wesenbeeck *et al.*, 2008). The same kind of positive feedback mechanisms and threshold appear to apply to allogenic ecosystem engineers. For example, the bioturbating activities of lugworms contribute to the maintenance of their sandy habitat by preventing a succession of muddy bottoms (Volkenborn *et al*., 2007). In stressful environments such as the sea-shore, the combination of thresholds and positive feedback dynamics may induce alternative stable state dynamics (van der Heide *et al*., 2007). This results in large characteristics stands dominated by a principal autogenic or allogenic ecosystem engineer, which generates a modified environment that can provide habitat for other species.

Autogenic ecosystem engineers support an often diverse assemblage of smaller organisms (Volkenborn and Reise, 2006; Heide *et al*., 2007). These organisms may be sessile as is the autogenic engineer itself or tend to constitute a burden, such as fouling algae and barnacles rather than feeding on the principal ecosystem engineer. Allogenic infaunal ecosystem engineers like lugworms may by joint irrigation facilitate other infauna and may also accommodate inmates in their burrows (Volkenborn and Reise, 2006).

Due to their functional characteristics, ecosystem engineers can exert a strong influence on ecosystem properties that exceeds what may be taken based on their abundance alone (Hooper *et al*., 2005). Biodiversity is lowest where productivity is maximal or where stress in the form of physical conditions, disturbance or predation is high (Jones *et al*., 1997a). In areas with high productivity, the diversity is determined by competition processes. Hence, if ecosystem engineers modify the productivity, this may also explain their effect on biodiversity. The significance of ecosystem engineering tends to increase in stressful environments (Jones *et al.,* 1997b), and the decrease in biodiversity of aquatic organisms in the down shore direction may be mitigated by ecosystem engineering at sediment shores (Bertness, 2007).

1.2. Bioturbation

Bioturbation are the activities undertaken by organisms that disturb or rework the sediments (Flach and Tamaki, 2001). Bioturbation has significant effects on the physical properties of the sediment, as well as on the flora and fauna of that particular habitat (Flach and Tamaki, 2001). Bioturbation by callianassid sandprawns affects the sediment composition through vertical and horizontal mixing of layers, by selective expulsion of particular grain sizes from burrows and by the removal of organic material from superficial sediment (Flach and Tamaki, 2001; Pillay and Branch, 2011). It also enhances nutrient and gaseous flux between the sediment and water column. Bioturbation also facilitates oxygen penetration into the sediment to depths of up to 1m (Murphy and Kremer, 1992).

Sediment reworking by callianassid sand prawns is also highly influential in structuring soft-bottom communities, including demonstrable effects on bacteria, microalgae and meiofauna (Branch and Pringle, 1987; Pillay, 2006; Pillay and Branch 2011), macrofauna (Berkenbusch *et al.*, 2000; Siebert and Branch, 2005a; Pillay and Branch 2011) and seagrasses of estuarine ecosystems (Siebert and Branch, 2006). Many of these effects arise through the turnover of sediment from burrows to the sediment-water interface, which deposits an unconsolidated and highly erodible surface layer (Aller and Dodge, 1974; Pillay and Branch 2011) that has cascading effects on community structure and function.

Mobility permits escape from burial by bioturbation, but it incurs metabolic costs, because of the energy spent overcoming burial and lost feeding time (Pillay *et al*., 2007a). Brenchley (1981) hypothesized that the susceptibility of organisms to bioturbation depends on mobility. Densities of sedentary tube builders, like the spionid polycheate *Rhynchospio arenicola* and the tenaid *Leptochelia dubia,* are significantly reduced by the bioturbative activities of the mud shrimp *Upogebia pugettensis*, the lugworm *Arenicola marina* and the sand dollar *Dendrester exentricus* (Brenchley, 1981; Siebert and Branch, 2007). In contrast, mobile organisms, including surface suspension-feeding and burrowing bivalves and polychaetes, seemed unaffected by bioturbation. The mobility hypothesis is mostly used to explain the relative effects of bioturbation by sandprawns on the macrofauna with different powers of mobility (Siebert and Branch, 2007). Nonetheless, even if organisms are mobile, it is likely that evasion of disturbance by bioturbation will carry a metabolic cost. For example, a study conducted by Pillay *et al*. (2007b) in Durban Bay, South Africa, showed that even though the gastropod, *Nassarius krassianus,* could survive the bioturbative effects of the sandprawn, *Callichirus kraussi*, its consumption of microalgae was reduced. If sustained this would limit growth, reproduction and survival and ultimately to emigration to avoid areas bioturbated by *C.kraussi*. This is reflected by the documented scarcity of *N.kraussianus* in areas characterized by elevated abundances of the sandprawn. (Pillay *et al*., 2007c).

1.3. The sandprawn: *Callichirus kraussi*

The sandprawn, *Callichirus* (= *Callianassa) kraussi* (Stebbing), is a conspicuous component of the macrofauna in temporarily open/closed (TOCEs) and permanently open estuaries (POEs) and marine embayments along the South African coastline (Whitfield, 1992) (Table 1.1). According to Siebert and Branch (2005), *C.kraussi* is a permanent member of the benthos and can attain densities > 350 ind.m^{-2} (Table 1.1). The sandprawn is able to complete its life cycle within estuaries. It has an abbreviated larval life without planktonic stages (Forbes, 1973). The larvae of *C.kraussi* remain protected within the parent burrow, although occasionally they may be recorded in the water column (Forbes, 1973). Adult sand prawns are able to tolerate salinity values of as low as 1 (Practical Salinity Units (PSU)), but successful development of eggs and larval stages require salinity values > 20 (Forbes, 1978). Populations occurring in waters where salinity values are permanently < 17 are not self-maintaining and must be recruited from elsewhere (Forbes, 1978). Forbes (1980) recorded annual migrations of post-larvae into the temporarily open/closed Swartvlei and East Kleinemonde systems and suggested that these life stages act as the dispersal phase in this species allowing it to spread into areas where it is otherwise unable to breed successfully.

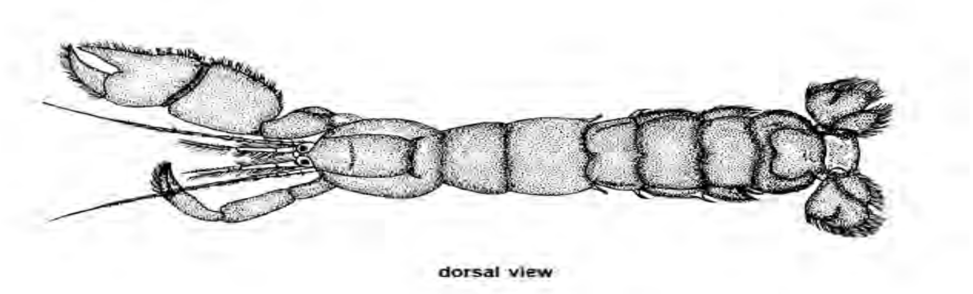


Figure 1.1. Dorsal view of a of the sandprawn *Callianassa krauissi* (Stebbing).

Vorsatz (1999) investigated *C.kraussi* life history strategies in the laboratory and recorded larval development times of 14-15 days at a salinity of 16 and a temperature of 16°C. At

28˚C, larval development occurred at a lower salinity threshold than those reported by Forbes (1978). The sandprawns collected by Vorsatz (1999) had embryos with well developed eyespots and most of the development of larvae had taken place at an estuary where salinity values were >20. Two to three months after hatching, the juveniles form surface openings to their own burrows. They achieve this by burrowing laterally from the parent burrow (Forbes, 1973). According to Forbes (1977), the peak in breeding occurs in austral winter, between the months of May and August. A secondary minor breeding peak also occurs in the summer, during November to December. Both sexes live for about 2 years. The females hatch between winter and spring. They then breed in the following summer at an approximate age of between 16-18 months; with carapace length of 8mm. Males reach a carapace length 8-9 mm in their first year. They attain a maximum carapace length of 11-13 mm by 18 months. This is ultimately followed by their death in the winter of their second year (Forbes, 1977).

Table 1.1. Estimates of the abundance of the sandprawn, *Callichirus kraussi,* in selected shallow water coastal environments and estuaries in along the southern African coastline.

Location	**Sandprawn abundance (ind.m^{-2})**	**Source**
Kasouga Estuary, Eastern Cape.	0-156	This study
Great Brak Estuary, Western Cape.	22-419	DWAF (2001)
Langebaan Lagoon, Western Cape.	2-602	Nel, (2006)
Swartkops Estuary, Eastern Cape.	>400	Hanekom, (1980)
Durban Bay, KwaZulu-Natal.	0-264	Pillay *et al.* (20027)

The burrowing activities of sandprawns have been demonstrated to have a significant influence on estuarine ecosystem structure and function (Rowden and Jones, 1993). Callianasid sandprawns bring the sediment into the surface where they deposit it in volcano-like mounds (Forbes 1977; Rowden and Jones, 1993; Pillay *et al*. 2007a). Adult sand prawns have the potential to influence the settlement and recruitment of numerous estuarine species, as the burrowing influences adult characteristics (Pillay *et al*., 2007; Pillay and Branch, 2011). As the sandprawn expel sediment from their burrows to the sediment surface, they disturb/or bury the microbial biofilms which play a key role in marine ecosystems by binding the topmost sediment layer and promoting lamina flow of water over the sediment bed, serving as food sources for adult and larval invertebrates and providing cues for the settlement of the invertebrate larvae (Pillay *et al*., 2007a). The densities of *C.kraussi* and biofilm concentrations correlate strongly with juveniles (Pillay *et al*., 2007a). Where there is an absence or scarcity of *C.kraussi*, the biomass of microalgae, bacteria, extracellular polymeric substances (EPS) and the number of recruits is ≈ 2-4 times greater than in areas with dense populations of *C.kraussi*. These trends are also mirrored by species richness and diversity values with almost as twice as many juvenile taxa recorded in areas with low densities of *C.kraussi* (Pillay *et al*., 2007b). The macrofaunal assemblages in areas of high densities of *C.kraussi* are therefore, fundamentally different to areas with low densities and are characterized by low species richness, diversity and abundance of macrofauna (Siebert and Branch, 2005). As a consequence, *C kraussi* can be considered as an important autogenic ecosystem engineer in estuaries and in shallow marine environments (Pillay and Branch 2011).

1.4. Temporarily open/closed estuaries

The total estuarine area in South Africa is about 600 km^2 of which about 200 km^2 is found along the Cape coastline (Tupie *et al*., 2002). Variations in climate, topography and catchment geology give rise to a wide variety of estuary types along the southern African coastline (Whitfield 1998). Whitfield *et al.* (2009) identified five types of estuary along the southern African coastline, permanently open; river mouths; estuarine lakes/bays and temporarily open/closed estuaries (TOCEs). Of the total number of estuaries, ≈ 73% of all estuaries along the southern African coastline are categorized as temporarily open/closed estuaries (TOCEs) (Whitfield, 2000). These estuaries are separated from the sea for the better part of the year, because a sand bar forms in the mouth area as a result of low river flow and long shore winds (Whitfield *et al*., 2008). During periods of high rainfall in the catchment area, the water levels in these estuaries may rise sufficiently high to breach the sand bar (Whitfield, 1992; Wooldridge and McGwynne, 1996). This corresponds to a period of estuarine water outflow into the marine environment. Thereafter, tidal conditions will predominate until the estuary closes off from the sea. During the subsequent closed period, seawater inflow is provided by overwash during spring tides or during severe storms (Perissinotto *et al*, 2000; Whitfield *et al*., 2008).

Temporarily open/closed estuaries are characterized by the virtual absence of any horizontal or vertical patterns during the closed in the physico-chemical variables of the system (Henninger *et al.*, 2008; Whitfield *et al*., 2008; 2012) which can amongst others be attributed to the small catchment area (generally < 100 km^2) which limits the inflow of freshwater into the system and, the coastal winds which facilitate the horizontal and vertical mixing of the water column (Froneman, 2002b). The absence of any horizontal and vertical patterns in physico-chemical variables during the closed phase of the estuary contributes to the virtual absence in spatial patterns in the biology of these systems (Whitfield *et al.*, 2008).

Several investigations have shown that overtopping and breaching events play an important role in structuring the invertebrate and vertebrate (fish and flying birds) communities within these systems (Vorwerk *et al*., 2003; Froneman, 2004; Perissinotto *et al*., 2004; Allan and Froneman, 2004; Whitfield *et al*., 2008). The outflow of estuarine water following breaching events coincides with a decline in the abundances and biomass of fauna within the estuary presumably as the biomass-rich waters are exported to the marine environment (Froneman, 2004; Allan and Froneman, 2008; Whitfield *et al*., 2008). The decrease in abundance and biomass values can also be attributed to the loss of habitats by removal of submerged macrophytes within the littoral zone that acts as a refuge (Henninger *et al*., 2008). The open phase is, however, characterized by the recruitment of marine breeding invertebrate and vertebrate species into the estuary (Kemp and Froneman, 2004). The recruitment coincides with a dramatic change in species diversity and community structure within these systems (Froneman, 2004; Kemp and Froneman, 2004; Bernard and Froneman, 2005; Whitfield *et al*., 2008). The limited accessibility of marine species to complete their life cycles within estuaries probably manifests itself in the numerical dominance of the estuarine endemic component within temporarily open/closed systems. Thus, unlike the permanently open estuaries, the distribution of macrobenthos within TOCEs may be independent of salinity (Boesach, 1977).

1.5 Aims and objectives

Numerous studies have demonstrated that callianassid prawns can be considered as important ecosystem engineers in large permanently open estuaries and in shallow marine environments both within southern Africa (Branch and Sieburth, 1997; Forbes, 1977; Pillay et al. 2007a; Pillay and Branch 2011) and in shallow coastal systems in the northern hemisphere (Rowden and Jones, 1993). Densities of sandprawn within southern Africa TOCEs can at times, attain levels equivalent to their larger permanently open counter parts within the same geographic region (Teske *et al.*, 2001; Table 1.1). To date, no studies have been conducted on the role of the sandprawn as an ecosystem engineer within southern African TOCEs. The aim of this study was to assess the role of the sand prawn *Callichirus kraussi*, as an ecosystems engineer in a small TOCE along the Eastern Cape coastline of South Africa. This thesis comprises two distinct components. The first component comprised a field study that examined the impact of the sandprawn, *C.kraussi*, on selected physico-chemical and biological variables in the lower reach of the temporarily open/closed Kasouga Estuary located on the Eastern Cape coastline of South Africa. The second component involved experiment manipulation (using caging experiments) in an attempt to better assess the role of sandprawn, *C.kraussi*, as an ecosystem engineer in the lower reach of the estuary.

CHAPTER 2

Study site

This study was restricted to the temporarily open/closed Kasouga Estuary located along the south-east coastline of the Eastern Cape Province, between the coastal towns of Kenton-on-Sea and Port Alfred (Figure 2.1). The Kasouga Estuary is regarded as being in excellent condition as there are minimal anthropogenic impacts (Whitfield, 2000). Below, a brief summary of the hydrological and climatic conditions along the Eastern Cape coastline of southern Africa and a description of the Kasouga Estuary are presented.

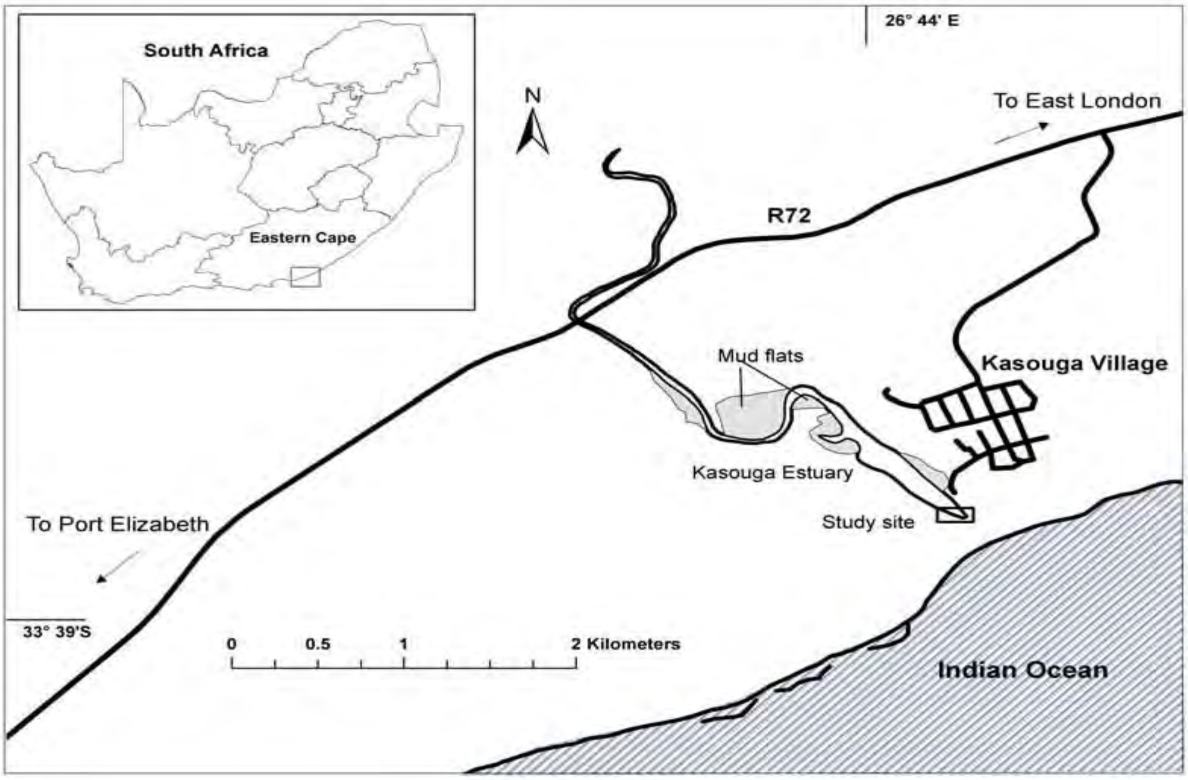


Figure 2.1. Geographical location of the temporarily open/closed Kasouga Estuary located on the south-east coastline of southern Africa (After Froneman *et al.*, 2012).

2.2. COASTAL AND CLIMATIC CONDITIONS

The coast of the Eastern Cape is bordered by the Indian Ocean, with the tropical Agulhas Current flowing alongside the continental shelf in a south-westerly direction (Ross, 1988). The Agulhas Current is the dominant factor influencing the climate of South Africa's south-east coastline (Stone *et al*., 1988). The Agulhas Current forms part of the South Indian Ocean Gyre, which has its warm waters originating from both the Equatorial Current flowing through the Mozambique Channel as a series of eddies, and the water flowing down the east coast of Madagascar (Ross, 1988). The warm strong surface current contributes to a subtropical climate regime along the coastline (according to the Koppen system of climate identification). The air temperature ranges from 10°C to 22°C, with an annual rainfall of at least 600mm (Lubke, 1998). The coastal town of Port Alfred, which is located about 20km west of the Kasouga Estuary, has a well established weather station and gives a good indication of the temperature and rainfall for the coastal region.

During the period 2000 to 2011, rainfall in Port Alfred area occurred throughout the year and received about 485mm per year. The lowest rainfall was recorded in July (25mm) and the highest in late summer, March (56mm) (www.saexplorer.co.za/south-africa/climte/port_alfred.asp). The mean monthly rainfall at the Port Alfred weather station is indicated in Figure 2.2.

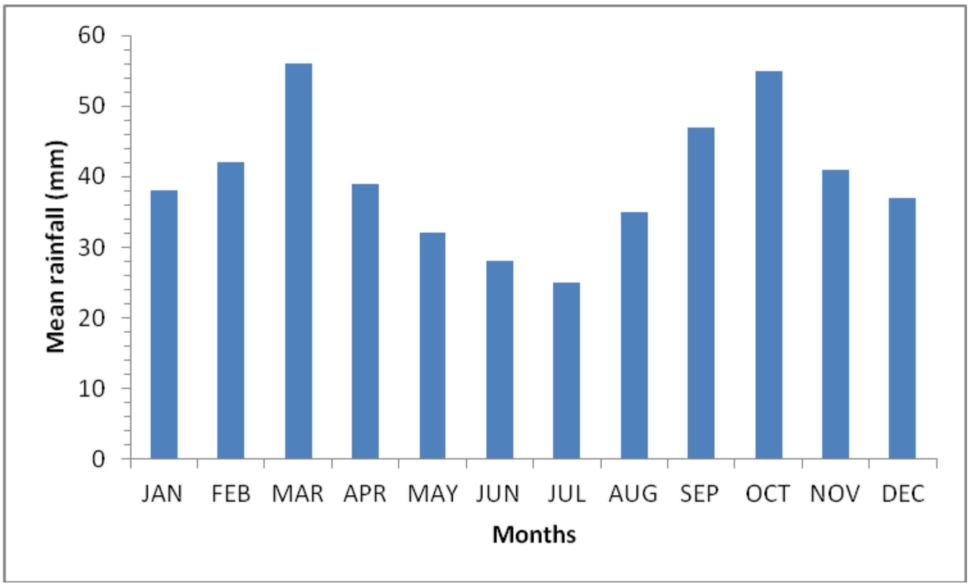


Figure 2.2. Mean annual rainfall (mm) at the Port Alfred weather station over the period 2000 to 2011.(www.saexplorer.co.za/south-africa/climate/port_alfred.asp).

The Agulhas Current is narrow (≈100 km wide) and is fast flowing and has an average velocity of 1m.s^{-1} and frequently reaches 2m.s^{-1} at its core (Ross, 1988; Lutjeharms, 1998). The surface temperature varies seasonally between 22°C and 27°C (Ross, 1998). Due to the widening of the continental shelf, the Agulhas Current diverges from the coast between East London and Port Elizabeth (Lutjeharms *et al.*, 2000). The Agulhas Current is closest to the South African coastline at East London (≈170km north-east of the Kasouga Estuary), and veers off the coast near Port Elizabeth (≈180km south -west of the Kasouga Estuary), where its flow is less concentrated and slower (Stone, 1988). Owing to retroflection, a counter-current develops offshore and once again the water circulates in an eastward direction. The retroflective currents cause rapid changes in sea temperature. In winter, a temperature difference of as much as 10°C between inshore water and the warm Agulhas Current waters further offshore can be recorded (Stone, 1988).

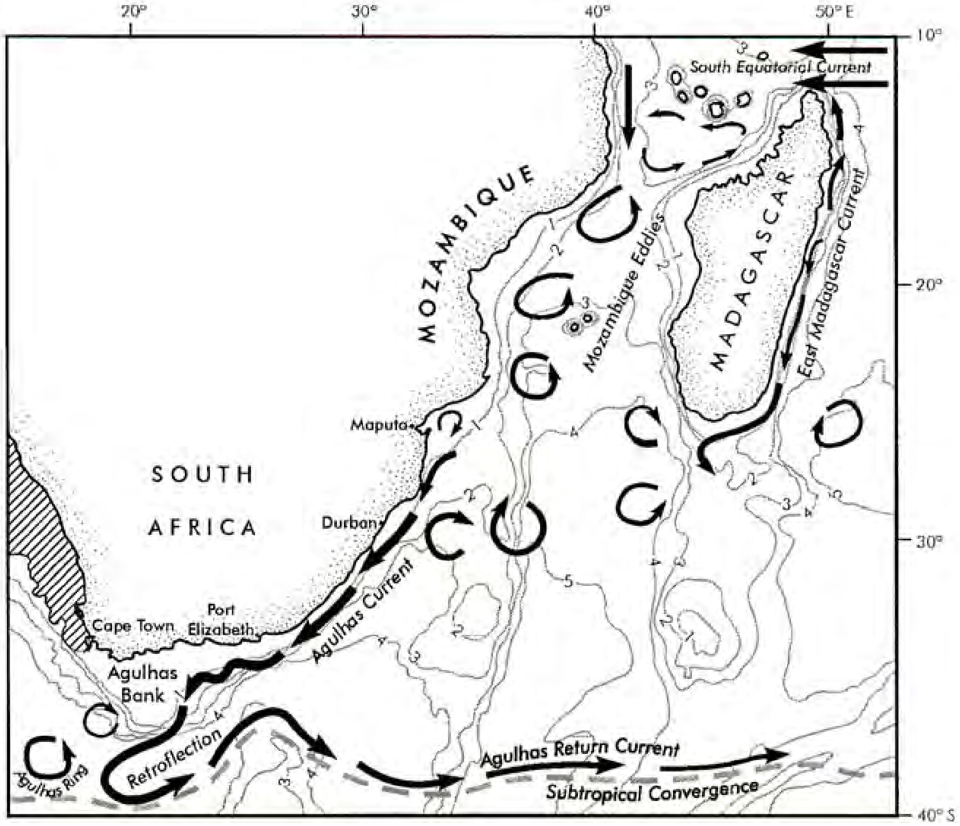


Figure 2.3. Schematic representation of the flow direction and hydrological features of the Agulhas Current along the southeastern seaboard of southern Africa. (After Lutjeharms 2005).

The Port Alfred upwelling cell moves parallel to the Agulhas Current and causes rapid changes of the sea temperature. This is caused by a lift in of the cold deep water from the Southern Indian Central Water onto the continental shelf (Lutjeharms, 1998). The surface layers of the water are affected by the wind, which may be warm, when a thin layer of Agulhas Current water covers the cold upwelled water when blowing from the south-west, and when the wind swings to the north-east, the layer of the sun-warmed water is displaced to expose the cold upwelled water (Lutjeharms, 1998). The atmospheric circulation and Agulhas Current, with associated upwellings, and eddies influence the periods of rainfall and storm waves which batter the south-eastern Cape coastline, result in greater than average rainfall (>100mm) and mouth breaching events (Wooldridge and McGwynne, 1996; Perissinotto *et al*., 2000, Froneman, 2004a). These breaching events cause rapid outflow of estuarine water, and the removal of submerged vegetation, both of which affect the populations of estuarine fauna (Vorwerk *et al*., 2008).

2.3. THE STUDY ESTUARY

The Kasouga Estuary (33˚39 ’S; 26˚44’E) is classified as a medium-sized temporarily open/closed estuary and is located≈ 20 km west of Port Alfred and ≈ 15 km east of Kenton - on-Sea (Figure 2.1). During the closed phase, it has a surface area of ≈ 22 ha (Froneman, 2003). The estuary is navigable for approximately 2.5 km and its widest part is about 150 m. The Kasouga Estuary is mostly shallow and its depth in the main channel ranges between 0.5 m to 2 m (Froneman, 2002). The catchment area of this estuary is about 39 km^2, and is mostly used for cattle farming. The stream and river valleys within the catchment area are relatively undisturbed and are covered by Valley Bushveld vegetation (Froneman, 2004).

Depending on the rainfall received within the catchment area, the average monthly water temperature and salinity levels in the estuary range between 10˚C to 30˚C and from 0 to 40 (practical salinity units), respectively. During drought conditions salinities may >40 (Froneman, 2004). Mouth-opening events occur during or shortly after high rainfall events (rainfall > 100 mm). The mouth of the estuary rapidly closes off (usually < 2 weeks) from the sea due to extensive sandbar development caused by a long-shore drift. During the subsequent closed period, seawater inflow into the estuary occurs during peak spring tides and severe winter storms. The Kasouga Estuary during a closed phase has a well-mixed water column (Froneman, 2003).

Over the past decade numerous studies have been conducted on the biology of the temporarily open/closed Kasouga Estuary (see for example Froneman, 2003; 2006; Froneman and Henninger 2008). These studies have largely focused on the trophodynamics of both the zooplankton and hyperbenthos within the estuary (Froneman and Henninger, 2008). Only a single study has investigated the macrobenthic community structure within the system (Teske and Wooldridge 2001). Results of this study indicate that the lower reach of the macrobenthic community is comprised mainly of the sandprawn, *C.kraussi*, the amphipods *Exosphaeroma hylocetes* and *Grandiedirella lignorum* and polychaetes. Shifts in the macrobenthic community structure within the system have been linked to amongst others, mouth phase, freshwater inflow, sediment grain size and the organic content of the sediments (Teske and Wooldridge 2001; 2003; 2004).

CHAPTER 3

The role of the sandprawn, *Callichirus kraussi*, as an ecosystem engineer in the temporarily open/closed Kasouga Estuary: a field study

3.1. Introduction

Investigations in South Africa have shown that the sandprawn, *Callichirus* (=*Callianassa) kraussi,* has substantial effects on the fauna and flora of estuaries and lagoons because of its high sediment turnover rates (Branch and Pringle, 1987; Siebert and Branch, 2005; Pillay and Branch 2011). Sediment reworking by callianassids is highly influential in structuring soft-bottom dwelling communities, including demonstrable effects on bacteria, microalgae and meiofauna (Branch and Pringle, 1987; Pillay, 2006), macrofauna (Berkenbusch *et al.,* 2000; Siebert and Branch, 2005a,b) and seagrasses (Siebert and Branch, 2006). Many of these effects arise through the turnover of sediment from burrows to the sediment-water interface, which deposits an unconsolidated and highly erodible surface layer that has cascading effects on community structure and function (Aller and Dodge, 1974).

The susceptibility of organisms to the effects of bioturbation is, however, strongly dependant on their mobility (Pillay and Branch 2011). This is referred to as the mobility hypothesis Densities of sedentary tube builders are significantly reduced by the activities of ecosystem engineers. In contrast, although mobile organisms are able to escape burial due to bioturbation, they incur metabolic costs because of the energy they use to overcome burial and by also by losing feeding time (Pillay *et al.*, 2007a). Pillay *et al.* (2007a) demonstrated that even though the gastropod *Nassarius kraussianus,* survived the bioturbative effects of *C.kraussi*, its consumption of microalgal food was reduced. If sustained, this could limit the growth, reproduction and survival, or lead to its emigration to areas less bioturbated by *C.kraussi*. This is reflected by the scarcity of *N.kraussianus* in areas where there is an abundance of *C.kraussi* (Pillay *et al.*, 2007a).

Densities of sandprawns within TOCEs can attain levels equivalent to those recorded in large permanently open estuaries within the same geographic area (Table 1.1). These data would suggest that sandprawns may play an important role is structuring the macrobenthic communities within these systems. This study aimed to examine the impact of the sand prawn, *C.kraussi*, on selected physico-chemical and biological variables in the lower reaches of the temporarily open/closed Kasouga Estuary.

3.2. Materials and Methods

The field study was restricted to the lower reaches of the temporarily open/closed Kasouga Estuary (33°39′11″S, 26°44′01″E), located along the coast of the Eastern Cape Province, South Africa. A detailed description of the estuary is presented in Chapter 2.

A total of fifty, 25X25cm quadrats were randomly occupied in the lower reach of the Kasouga Estuary corresponding to that region where maximum sand prawn densities were recorded. The study took place over the period 10 to 13 April 2011. Within each quadrat, the bioturbation, the percentage organic matter of the sediment, microphytobenthic chl-a concentrations and the sand prawn and epi- and infaunal abundances were determined as described below.

3.2.1. Sediment bioturbation

Centrifuge tubes (aperture area = 0.78cm^2, length = 10cm, with bottom 2cm tapered) were employed as sediment traps to estimate the bioturbation created by *C. kraussi* within each quadrant. The aspect ratio (length/diameter) of each centrifuge tube was 10:1, considered as the optimum value to prevent re-suspension of trapped sediment (Ellis *et al.*, 2002). The tubes were buried with ~ 2cm of the tube protruding above the sediment surface. After 1 hour the tubes were sealed. The sediment in each tube was extracted and dried at 60°C for 24 hours before being weighed. The amount of sediment within each trap was used as an index of sediment erodability (bioturbation), expressed as g.cm^{-2}.hr^{-1}.

3.2.2. Microphytobenthic chl-a concentrations

Microphytobenthic chl-a concentrations were determined by collecting a surface sample of sediment in a test tube {10cm long and 1cm diameter) within each of the quadrants. The tubes were kept in the dark, inside a cooler box until their return to the laboratory and then maintained in the freezer for 24 hours at -20°C together with 30ml 90% acetone per sample until processing. Chlorophyll-a (Chl-a) concentrations were then determined flourometrically employing Turner 10 AU fluorometer before and after acidification (Holm-Hansen and Riemann, 1978). Chl-a concentrations were expressed as µg chl-a cm^{-2}.

3.2.3. Sediment Organic Matter

Sediment Organic Matter (SOM) was determined from sediment samples collected in a similar manner to that to that described above. The sediment was dried in a 60°C oven for 48 hours, after which it was weighed and organic matter combusted at 450°C for 5 hours. SOM concentrations were then calculated as the difference between pre-combusted and combusted weights and expressed as percentage organic matter present. The percentage data arcsine transformation was employed, which was worked out as follows:-

(a) $x\% = x/100 = 0.0x$

(b) $\sin^{-1}\sqrt{0.0x}$

3.2.4. Macrobenthic abundances and biomass

The estimates of the epi- and infaunal abundances and biomass were determined from sediment samples collected within the quadrats using a Van-Veen Grab (dimensions 25X25X30cm). The sediment collected was gently filtered through a 1000µm mesh to remove all macrobenthic organisms. Samples were collected were preserved in 10% formalin and transported back to the laboratory. In the laboratory, the total macrobenthic abundances, biomass and species composition were determined by examining the entire sample. Species were identified using the keys of Day (1969) and Branch *et al.* (1994). Biomass was calculated as wet weight after removing all excess water by blotting. The total biomass of the macrobenthos within each sample was then determined using a Sartorius microbalance. Results were expressed as ind.m^{-2} and biomass mg wwt. m^{-2}.

3.2.5. Statistical Analyses

Numerical Analyses

Spatial patterns in macrobenthic community structure in the different quadrats were analysed using the statistical package, PRIMER (Plymouth Routines in Multivariate Ecological Research) (Clarke and Warwick 1994). To evaluate potential groupings in community structure between the different quadrats, a hierarchical cluster analysis was employed. Species abundance data were log transformed in order to reduce the bias due to highly abundant species (Legendre and Legendre 1983) and the Bray-Curtis similarity measure applied after which a dendrogram was plotted using complete linkage. To test for differences between observed groupings, the one-way ANOSIM procedure (a program of PRIMER) was employed, after Field *et al*. (1982). To identify which species were responsible for the observed groupings, the SIMPER analysis was used and species, which contributed 5% or more to the observed groups were listed.

3.2.6. Statistical analyses

Relationships between the selected physico-chemical (bioturbation and organic content of the sediment) and biological variables (microphytobenthic algal concentrations and the macrobenthic abundances and biomass) and the sandprawn densities in the different quadrants were assessed using Pearson Correlation analyses. The analyses were conducted using the statistical package, Excel, version 6.0. Sandprawns abundances were log transformed and a scatter chart (M.S.Excel) was employed to compare the values of sandprawns with the values of bioturbation, microphytobenthic algal concentrations, arcsine transformed sediment organic matter, log transformed macrobenthic abundances and macrobenthic biomass.

3.3. Results

3.3.1. Sandprawn abundances

The abundances of sandprawns within the various quadrats occupied in the lower reaches of the estuary ranged from 0 to156 ind.m^{-2}. The total length of the sandprawns in the different quadrants ranged from 28 to 55 mm, total length (TL).

3.3.2. Sediment bioturbation

The estimates of sediment bioturbation in the quadrats ranged from 0.01 to 0.46 g.cm^{-2}.h^{-1} and demonstrated a strong positive significant correlation (R^2 = 0.62; $P < 0.05$) with an increase in the abundances of the sandprawn (Figure. 3.1)

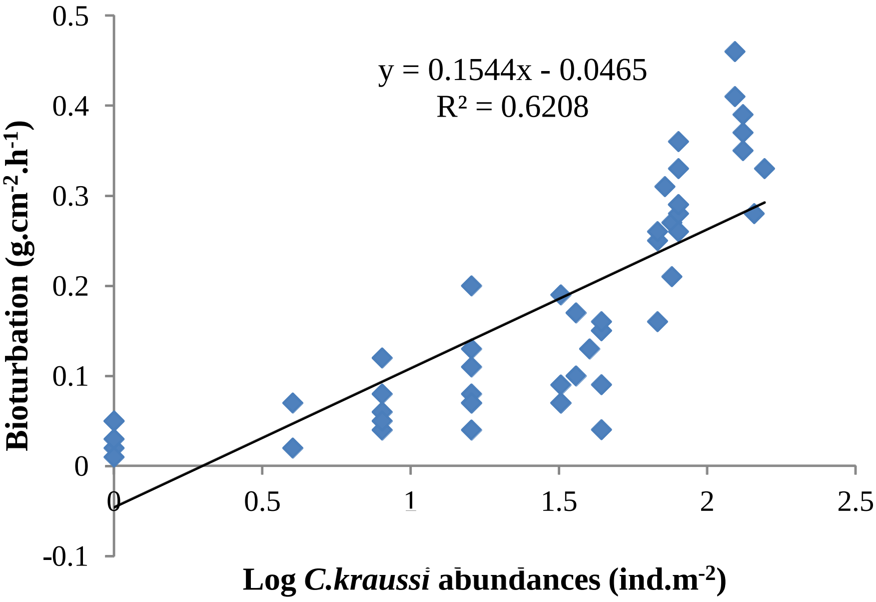


Figure. 3.1. The relationship between *C.kraussi* abundances and sediment bioturbation.

3.3. Microphytobenthic algal concentrations

Total microphytobenthic algal concentrations in the different quadrants ranged from 0.04 to 2.31µg chl-a.cm^{-2} and demonstrated a significant negative correlation (R^2 = 0.34; $P < 0.05$) with the increase in the abundance of the sandprawn (Figure.3.2).

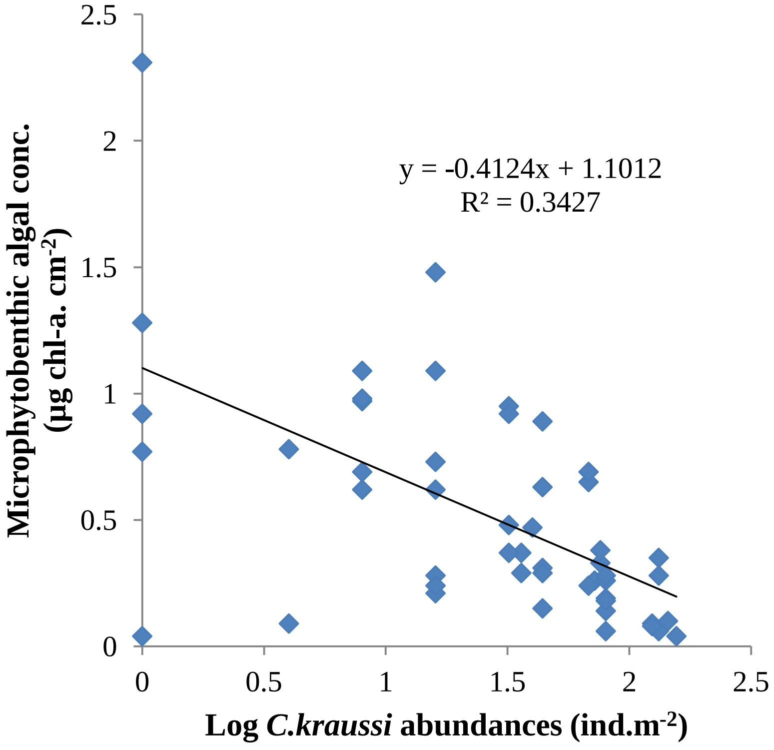


Figure. 3.2. Microphytobenthic chl-concentrations in the various quadrats with different densities of the sandprawn in the lower reaches of the temporarily open/closed Kasouga Estuary on the Eastern Cape coastline of South Africa.

3.3.5. Sediment Organic matter

The percentage organic matter of the sediment in the different quadrats ranged from 0.29 to 3.87% and demonstrated a weak, non-significant correlation ($R^2 = 0.10$; $P > 0.05$) with the abundances of sandprawn (Figure 3.3).

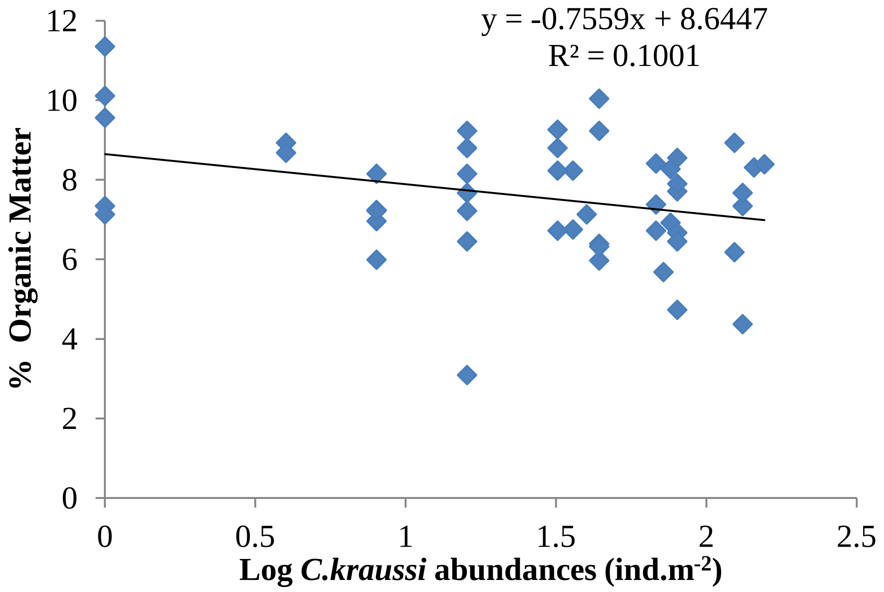


Figure 3.3. The percentage organic matter in the sediments in the quadrants with different densities of the sandprawn in the lower reaches of the temporarily open/closed Kasouga Estuary located on the Eastern Cape coastline of South Africa

3.3.6. Macrobenthos abundances and biomass

The total macrobenthos abundances in the quadrats varied from 419 to 7913 ind.m^{-2} and again demonstrated a weak, non-significant correlation ($R^2 = 0.0045$; $P > 0.05$) with the abundances of the sandprawn within the region of study (Figure 3.4A). The macrobenthic biomass in the different samples ranged from 2.9 to 19.57 gwwt.m^{-2} and also demonstrated a weak, non-significant correlation ($R^2 = 0.04$; $P > 0.05$) with the abundances of the sandprawn (Figure 3.4B).

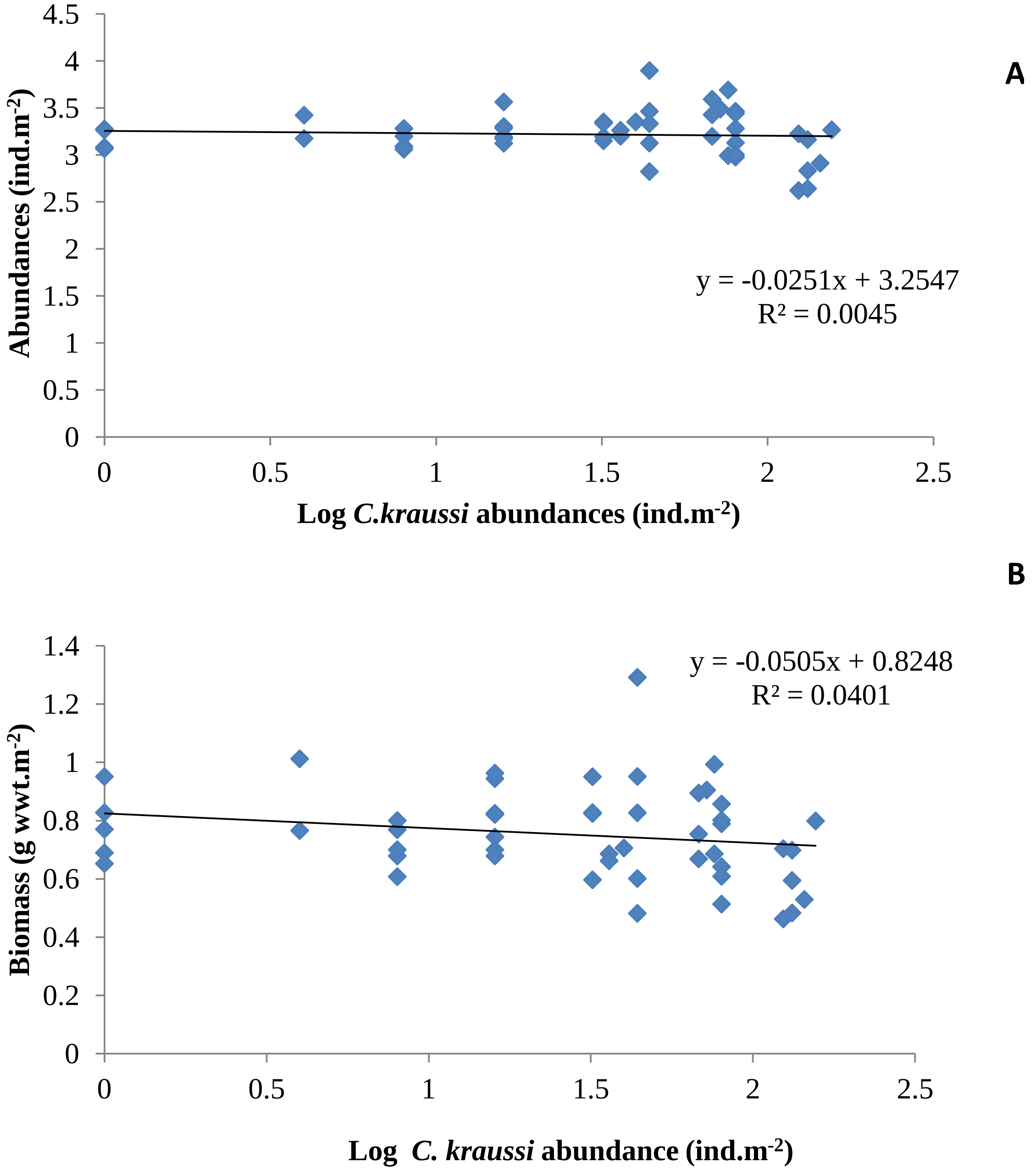


Figure. 3.4. The relationship between the abundance (A) and biomass (B) of the macrobenthic and sandprawn densities in the lower reaches of the temporarily open/closed Kasouga Estuary located on the Eastern Cape coastline of South Africa.

3.3.6. Numerical analysis

Results of the hierarchical cluster analyses indicated the presence of four distinct grouping of quadrats, designated Group 1 to 4, during the study. Quadrat 50 was identified as an outlier in the analysis. ANOSIM procedure of PRIMER indicated that the differences between the groupings were not significantly different from one another (Global R value 0.78; $P > 0.05$). Densities of the sandprawn in the four groupings identified with the hierarchical cluster analysis ranged between 0 and 44 ind m^{-2} in Group 1, between 0 and 86 ind m^{-2} in Group 2, between 0 and 156 ind m^{-2} in Group 3 and between 0 and 132 ind m^{-2} in Group 4. The groupings appeared therefore, to be independent of the density of the sandprawn within the region of investigation.

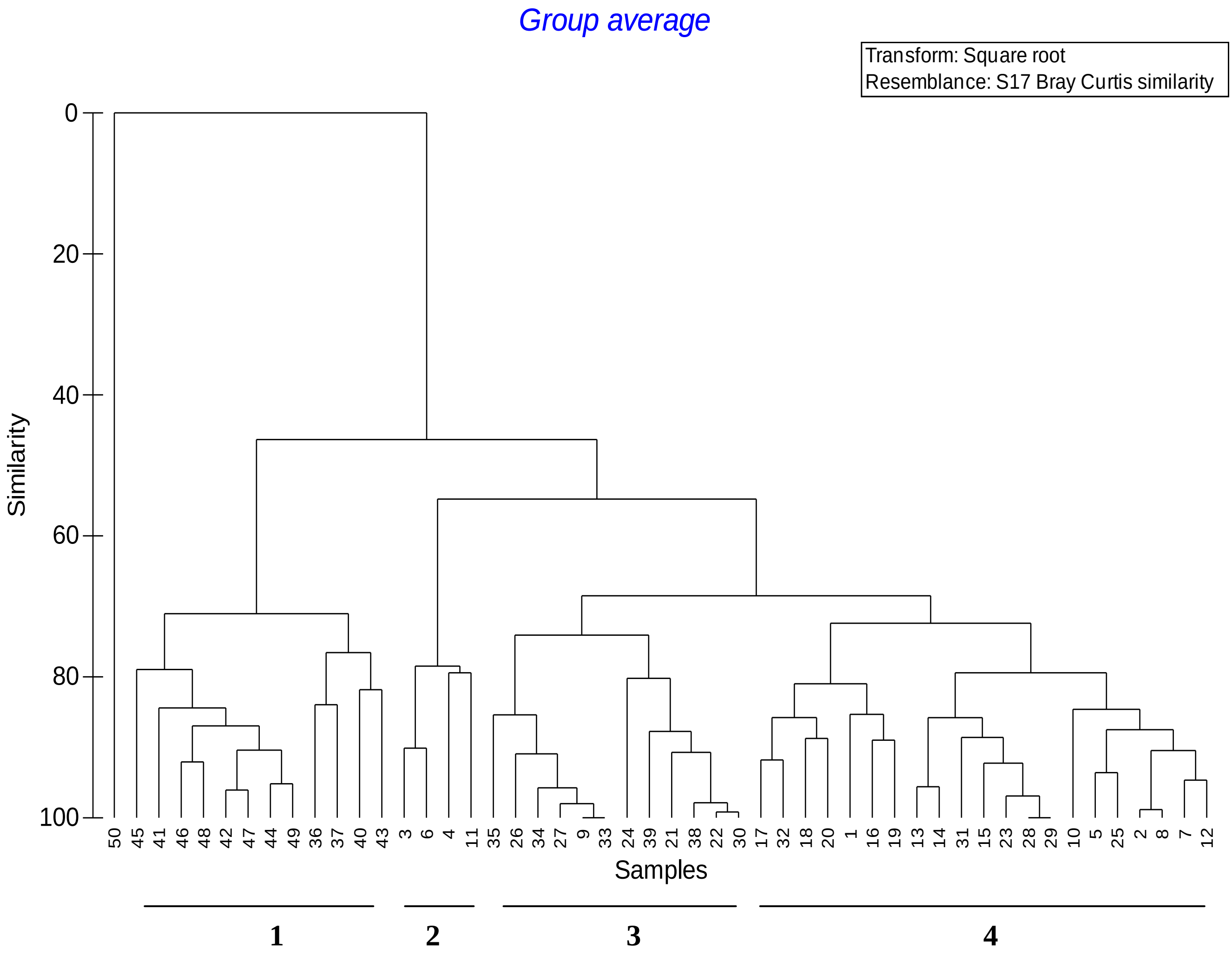


Figure3.5. Dendrogram showing the associations in macrobenthic community structure between the different quadrats occupied in the temporarily open/closed Kasouga Estuary located on the Eastern Cape coat of South Africa.

3.4. Discussion

This field study was conducted with the aim of assessing the role of the sandprawn, *Callichirus kraussi*, as an ecosystem engineer in the lower reach of the temporarily open/closed Kasouga Estuary located on the Eastern Cape coastline of South Africa. The estimates of the percentage organic content of the sediment, the concentration of the microphytobenthic chl-a concentrations alga and the abundance and biomass of the macrofauna recorded in the different quadrats during this study are in the range reported for other temporarily open/ closed estuaries (TOCEs) within the warm temperate biogeographic region of the southern African coastline (see for example Froneman 2003; Teske and Wooldridge 2001; Whitfield *et al.*, 2008**).** The estimated values are, however, lower than those reported for permanently open estuaries within the same region (Adams *et al*. 1999; de Villiers and Hodgson 1999; Heyns and Froneman 2010.) The reduced values recorded for in the smaller temporarily open/closed systems can be linked to presence of a sand bar at the mouth which restricts the recruitment of marine breeding invertebrates into these systems (Whitfield *et al*., 2010). Alternatively, the reduced biological estimates within TOCEs can be ascribed to the general low productivity of these systems due to the low macronutrient availability in these systems as a result of the low freshwater inflow (Whitfield *et al*., 2008).

During this study, there was no significant correlation between the sandprawn densities and the percentage organic content of the sediments ($P > 0.05$; Figure 3.2). This finding is in stark contrast to the findings of Pillay *et al*. (2011) which demonstrated that presence of the sandprawn contributed to increased organic content of the sediments in Durban Bay, KwaZulu-Natal. *C. kraussi* modifies the organic content of the sediment by accumulating organic material in the lining of their burrows. In some cases they collect this material from the surface and store it in the walls or chambers of their burrows (Ott *et al*., 1976; Suchanek, 1983, 1985). In this sense *C.kraussi* "gardens" microorganisms by providing an organically rich oxygenated medium and, perhaps, reducing inhibitory metabolites (Hyllenberg, 1975; Aller and Yingst, 1985). Alternatively, the increase in the organic content of the sediments in the presence of the sandprawn may also be attributed to their feeding activities. Callianassids are primarily deposit feeders and remove organic material from sand grains from sediments in the burrows and then deposit the residue outside the burrow opening (Zeibis *et al*., 1996. Pillay *et al* (2011) suggested that the enhancement of organic content recorded in the *Callichirus* beds may have been due to faecal production by *C.kraussi*. It has been estimated that 1.4g of faeces is produced by *C.kraussi* per burrow per tidal cycle in the Palmiet River Estuary, South Africa, with a total production of 3154 kg organic material.$yr^{-1}.km^{-2}$ from this source (Branch and Day, 1984). It is important to note, however that there are several potential sources of organic carbon recorded in the sediments including the sinking of dead organisms and detritus derived from the overlying waters (Paulo *et al*., 2011). Additionally, faecal material derived from the infauna may also contribute to the organic pools within the sediment. The absence of any distinct pattern in the percentage content of the organic matter therefore, likely reflects the variety of carbon sources in the Kasouga Estuary.

During this study, the concentrations of microphytobenthic algae were negatively correlated to the abundances of the sandprawn ($P < 0.05$; Figure 3.3). Results of studies conducted in a variety of southern African TOCEs indicate that maximum microphytobenthic algal biomass is attained during the closed phase of these systems (Nozais *et al*. 2001; Perissinotto *et al*. 2002; Perissinotto *et al*. 2006). Variations in the microphytobenthic algal concentrations in TOCEs can be linked to re-suspension of sediments, particularly following the inflow of freshwater into the system (Nozais *et al*. 2001; Whitfield *et al*. 2008). The role of bioturbation by *C.kraussi* in reducing surface microalgae biomass is now well established in shallow water coastal ecosystems both locally (Branch and Pringle, 1987; Pillay and Branch 2011) and worldwide (Rowden and Jones, 1993). It is thus likely that the reduced concentrations of the microphytobenthic algae observed with an increase in the abundances of sandprawn reflects the influence of the sandprawn in the re-suspension of the sediments during their burrowing and feeding activities.. Indeed, the rates of bioturbation were significantly correlated to the sandprawn densities ($P < 0.05$; Figure 3.3.). Sediment turnover by sandprawns likely buries microalgae, thus starving them of light and nutrients that are required for photosynthesis (Branch and Pringle, 1987; Pillay *et al*., 2007a).

During the field study, the increase in sandprawn densities did not appear to contribute to a decline in the macrofaunal abundance or biomass (Figure 3.4). This result is in contrast to several studies conducted in other regions of the world where callianassids have been shown to play an important role in structuring the benthic communities in shallow water ecosystems (Peterson, 1977; Murphy, 1985). Most of the effects of callianassids on macrofauna arise due to the deposition of residual sediment from burrows at the sediment surface (Pillay *et al*., 2007b). *Callichirus.kraussi* burrows can reach depths of 1m and a sediment turnover rate of $12\text{kg.m}^{-2}.\text{d}^{-1}$ has been measured (Branch and Pringle, 1987). These turnover rates of the sediment may bury surface and sub-surface fauna, leading to either mortality or metabolic losses due to loss of feeding time or investment of energy to overcome burial (Pillay *et al*. 2007a; 2007b). Tube-dwelling species may also suffer mortalities due to destruction of tubes or smothering, or experience greater energetic demands to maintain their tubes open (Branch and Pringle, 1987). It is also possible that surface organisms may become susceptible to predation if forced to emigrate from habitats occupied by bioturbators (Flach, 1993; Pillay *et al.*, 2007b). The role of sand prawns as ecosystem engineers is, however, strongly density dependant (Pillay *et al.*, 2007a). During this investigation, the mean sand prawn density in the different quadrats in the lower reaches of the Kasouga Estuary was 36 ind m^{-2} (range 0 to 156 ind m^{-2}), well below the density values of Pillay *et al*. (2007b) (range 0-264 ind m^{-2}), where the sand prawn was demonstrated to play an important role in structuring the macrofaunal community structure in Durban Bay. The absence of any notable effect of *C.kraussi* on the macrofaunal community structure, in the lower reaches of the Kasouga Estuary is therefore, not unexpected (Figure 3.5). Several factors have been shown to structure the macrofaunal assemblages within TOCEs within the warm temperate biogeographic region of the southern African coastline including salinity, sediment type, mouth phase (open vs. closed) and food availability (Teske and Wooldridge 2001; 2003). The groupings of macrofauna indentified with the numerical analyses thus, likely reflect the complex interaction between physico-chemical and biological factors. The low abundances of the *C.kraussi* in the Kasouga Estuary can likely be linked to the intense exploitation of these organisms by line-fisherman who use the sand prawn as bait species for recreational fishing (per obs, T Henninger). Additionally, the harvesting activities of the fisherman may further contribute to the decline in recruitment through habitat destruction (Wynberg and Branch 1994).

Summary

Results of the field study indicated that increased densities of sandprawn contributed to a decline in the microphytobenthic algal biomass, most likely the result of bioturbation generated by the burrowing activities of the prawn. In contrast, there were no significant correlations between the densities of the sandprawn and the estimates of the organic content of the sediments or the macrofaunal abundance and biomass (P >. 0.05 in all cases). This result is inconsistent with the published literature (see for example Berkenbusch *et al.*, 2000; Hughes *et al*., 2000; Cadée, 2001; Pillay *et al*. 2007; Pillay and Branch 2011) and can likely be attributed to the generally low densities of the sandprawn recorded in the lower reach of the Kasouga Estuary during the study.

CHAPTER 4

Experimental evidence of the role of *C.kraussi* as a system engineer in the temporarily open/closed Kasouga Estuary, Eastern Cape.

4.1 Introduction

Southern African TOCEs are characterised by low species richness, although some species can attain very high densities (Forbes, 1973a; Schlacher and Wooldridge, 1996; Whitfield, 1998). The sand prawn, *Callchirus kraussi*, which can attain levels of up to 350 ind.m^{-2}, is one species that is extremely common in lower reaches of TOCEs (Siebert and Branch, 2005a, b). *C.kraussi* is able to complete it life cycle within estuaries (Forbes, 1973). Protected within the parent burrows and barely recorded in the water column, the larvae of *C.kraussi* burrow laterally from the parent burrow, eventually forming surface openings to their own burrows, two to three months after hatching (Forbes, 1973b). The peak in breeding occurs in austral winter or spring (May-August), with a secondary minor breeding occurring in summer (November – January) (Forbes, 1977). Both sexes live for approximately two years, with females attaining a carapace length of 8-9 mm, while males reach a maximum carapace length of 11-13mm (Forbes, 1977).

Previous studies indicate that the burrowing activities of the sandprawn in large permanently open systems or intertidal sand flats affect the composition of the benthic flora and fauna on and in sediments, as well as the redox potential and composition of sediments (Berkenbusch *et al.*, 2000; Hughes *et al.*, 2000; Cadée, 2001; Flach and Tamaki, 2001; Siebert and Branch, 2005a, b; Meysman *et al.*, 2006; Pillay *et al.*, 2007a; b; Pillay and Branch

2011). As a consequence, sandprawns can be considered as important ecosystem engineers within these ecosystems (Jones *et al*., 1994). Since the densities of sandprawn within southern African TOCEs can attain levels comparable to those in permanently open estuaries within the same geographic region (Teske *et al*. 2006), it is likely that these organisms also play an important role in structuring the benthic community within these systems. In the previous chapter, evidence of the role of the sandprawn as an ecosystem engineer in the temporarily open/closed Kasouga estuary was not conclusive; largely it is suggested as a result of their low densities within the estuary. This study aimed to experimentally assess the effect of the sandprawn, *Callichirus kraussi*, as an ecosystem engineer in the lower reach of the temporarily open/closed Kasouga Estuary situated on the Eastern Cape coastline of southern Africa.

4.2 Materials and methods

The experimental manipulation was restricted to the lower reach of the temporarily open/closed Kasouga Estuary (33°39′11″S, 26°44′01″E), located along the Eastern Cape coast of the Eastern Cape Province, South Africa. A detailed description of the estuary is presented in Chapter 2. The experimental manipulations were conducted over a period of eighteen weeks in summer (October 2011- January 2012) using caging experiments. The estuary remained closed throughout the duration of the study. Ten cages (50 x 50 x 30 cm lined with 1 mm mosquito netting on the bottom and sides) were buried in the sediment of the lower reaches of the estuary according to the method described in Pillay *et al*. (2007) (Figure 4.1). Thereafter, the cages were filled with estuarine sand which had been sundried for two weeks prior to the experiment to ensure faunal absence. The edges of the cages protruded approximately 5cm above the sediment.

Figure 4.1 Experimental cages employed to assess the role of the sandprawn, *Callichirus kraussi*, as an ecosystem engineer in the lower reach of the temporarily open/closed Kasouga Estuary on the Eastern Cape coastline of South Africa.

The cages were not roofed to ensure that water column recruitment of the macrofauna could take place (Figure 4.1).

After a period of two weeks, 20 adult sandprawn of between 31 to 55 mm (standard length (SL); with mean of 40.1 ± 4.35 mm) were collected with the aid of a prawn pump and added to five of the cages, now known as inclusion cages. Densities of the sandprawns within the inclusion cages were thus 80 ind. per m^{-2}. The remaining five cages were left free of sandprawns to act as exclusion cages. Five 50 x 50 cm quadrants in the immediate vicinity of the cages acted as procedural controls. Densities of the sandprawn within the procedural controls ranged from 48 to 96 ind m^{-2} (mean = 78 ind m^{-2}).

After a period of 18 weeks, the rates of bioturbation, the microphytobenthic alga concentration and the abundance and biomass of the epi- and infana in the different treatments were determined as described below.

4.2.1 Bioturbation

Centrifuge tubes (aperture area = 0.78 cm^2, length = 10 cm, with bottom 2 cm tapered) were employed as sediment traps to estimate the bioturbation created by *C. kraussi.* The aspect ratio (length/diameter) of each centrifuge tube was 10:1, considered as the optimum value to prevent re-suspension of trapped sediments (Ellis *et al*. 2002). Three tubes were deployed per cage. The tubes were buried in sediment with ~ 2 cm of the tube protruding above the sediment surface. After 1 hr, the tubes were sealed with plastic caps and transported to the laboratory. In the laboratory, the sediment in each tube was extracted and dried at 60 °C for 24 hr before being weighed. The amount of sediment within each trap was used as an index of sediment erodability, and expressed as $g.cm^{-2}.hr^{-1}$.

4.2.2 Microphytobenthic chl-a concentrations and Sediment Organic matter (SOM)

Microphytobenthic chl-a concentrations were determined by collecting a surface sample of the sediment in a test tube (10 cm long and one cm diameter) from each of the cages and the procedural controls. The tubes were kept in the dark inside a cooler box until their return to the laboratory and then maintained in the freezer together with 30 ml 90 % acetone per sample until processing. Chlorophyll-*a* concentrations were determined fluorometrically employing a Turner 10AU fluorometer before and after acidification (Holm-Hansen and Riemann 1978). Chl-*a* concentrations were expressed as µg chl-*a* cm^{-2}. Sediment organic matter (SOM) was determined from sediment samples collected in a similar manner to that described above. The sediment was dried within a 60 °C oven for 48 hours, after which it was weighed and organic matter combusted at 450 °C for five hours. SOM concentrations were then calculated as the difference between the pre-combusted and combusted weights and expressed as percent organic matter present. Results were expressed as percentage of the total sediment weighed.

4.2.3 Epi- and infaunal abundances and biomass

To compare the community structure of the epi- and infauna within the different treatments, the sediment within the cages and procedural controls were collected and sifted through a 1 mm mesh filter. A Van Veen Grab was used to collect the macrofauna within the procedural controls. The organisms collected in the different treatments were identified to the species level using the keys of Day (1969) and Branch *et al*. (1994). Total abundances were expressed as ind m^{-2}. The wet biomass per cage was determined by weighing the samples on a Sartorius Electronic Microbalance after removing the excess water with blotting paper. Values were expressed as g wwt. m^{-2}. Values for the different treatments were pooled.

4.2.4 Community analyses

The macrobenthic community structure (epi- and infauna) in the different treatments were analysed using the statistical package, PRIMER (Plymouth Routines in Multivariate Ecological Research) (Clarke and Warwick 1994). To evaluate potential groupings in community structure between the different sites, a hierarchical cluster analysis was employed. Species abundance data were log transformed in order to reduce the bias due to highly abundant species (Legendre and Legendre 1983) and the Bray-Curtis similarity measure applied after which a dendrogram was plotted using complete linkage. To test for differences between the observed groupings, the one-way ANOSIM procedure (a program of PRIMER) was employed, after Field *et al*. (1982). To identify which species were responsible for the observed groupings, the SIMPER analysis was used and species, which contributed 5% or more to the observed groups, were listed.

4.2.4 Statistical analyses

Differences in the measurements between the various treatments were tested using one-way ANOVAs, followed by Tukey HSD post-hoc tests to display significant differences and homogenous groups, using the computer package, Statistica 10 (StatSoft). The data met all requirements for the analyses and were thus not log-transformed. Species diversity within the different treatments was estimated using the Margaleff Diversity Index using *Microsoft EXCEL* .

4.3 Results

4.3.1 Sediment bioturbation

The estimates of the bioturbation in the exclusion cages ranged from 0.05 g.cm^{-3}.h^{-1} to 0.33 g.cm^{-3}.h^{-1} (Figure 4.1). In inclusion cages the estimated bioturbation ranged from 0.27 g.m^{-3}.h^{-1} to 0.53 g.m^{-3}.h^{-1} and from 0.34 g.m^{-3}.h^{-1} to 0.58 gm^{-3}h^{-1} in the procedural controls (Figure 4.1). ANOVA indicated that the bioturbation in exclusion treatments were significantly different from the other two treatments ($F = 6.72$; $P = 0.01$). There was no significant difference in the bioturbation rates between inclusion treatments and procedural controls ($P > 0.05$).

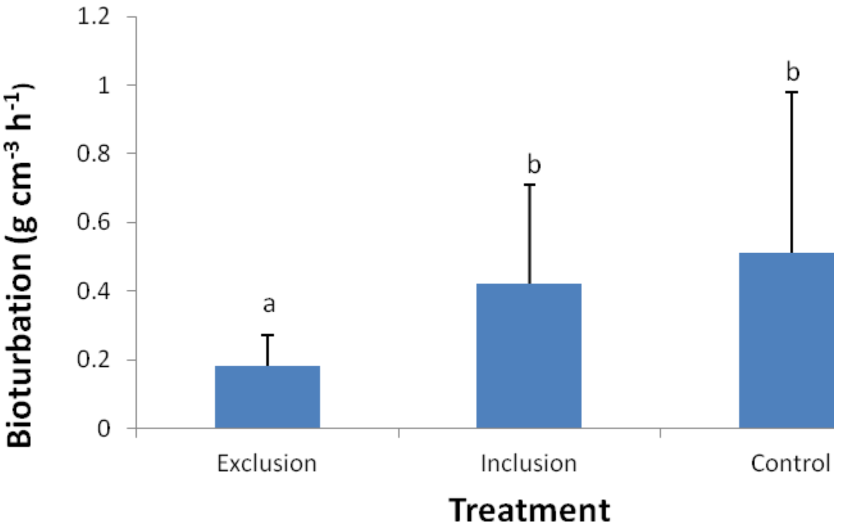


Figure 4.1 Mean bioturbation in the three treatments in the lower reach of the temporarily open/closed Kasouga Estuary. Error bards are standard deviation. Different letters indicate a significant difference (ANOVA).

4.3.2 Sediment Organic Matter

The percentage organic matter in the sediments in the exclusion cages ranged from 0.81 % to 1.37 % and between 1.98 % and 2.87 % in the inclusion cages (Figure 4.2). The percentage organic matter in the sediments of the procedural controls ranged from 1.78 % to 2.56 % (Figure 4.2). The percentage organic matter in the sediments of exclusion treatment was significantly higher than the other two treatments ($F = 26.39$; $P < 0.001$). There was no significant difference in the percentage organic matter of the sediments between the inclusion treatments and the procedural controls (Figure 4.2; $P > 0.05$).

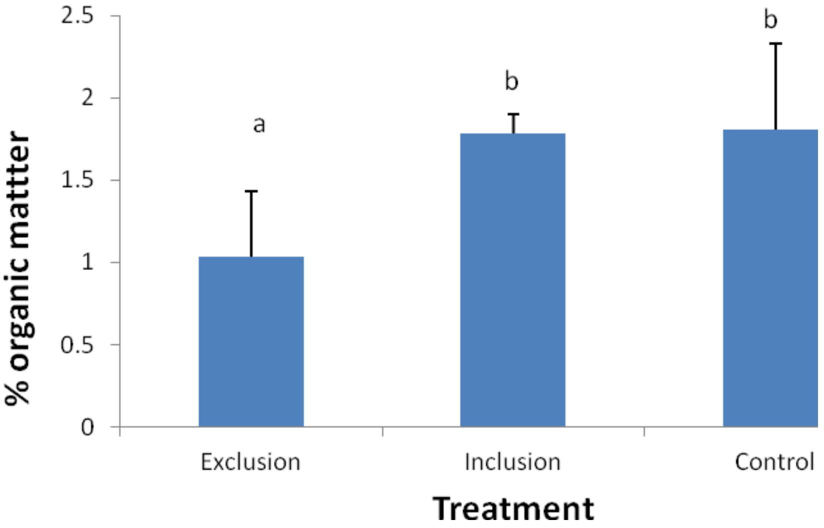


Figure 4.2 Mean percentage organic matter of the sediments in the three treatments in the lower reach of the temporarily open/closed Kasouga Estuary. Error bards are standard deviation. Different letters indicate a significant difference (ANOVA).

4.3.3. Microphytobenthic chl-a concentrations

The microphytobenthic chl-a concentrations in the different treatment ranged from 0.298 µg chl-a.cm^{-2} to 0.53 µg chl-a cm^{-2} in the exclusion cages, from 0.107 µg chl-a.cm^{-2} to 0.216 µg chl-a.cm^{-2} in the inclusion cages and from 0.153µg chl-a.cm^{-2} to 0.206 µg chl-a.cm^{-2} in the procedural controls (Figure 4.30). ANOVA indicated that the microphytobenthic algal concentrations in exclusion treatments were significantly higher than in the other two treatments ($F = 18.65$; $P < 0.001$). There was no significant difference in the microphytobenthic chl-a concentrations between the inclusion treatments and the procedural controls ($P > 0.05$).

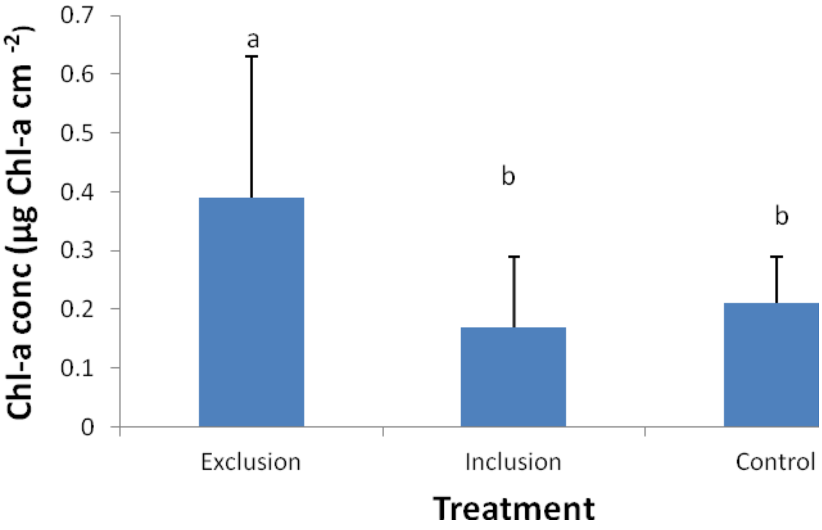
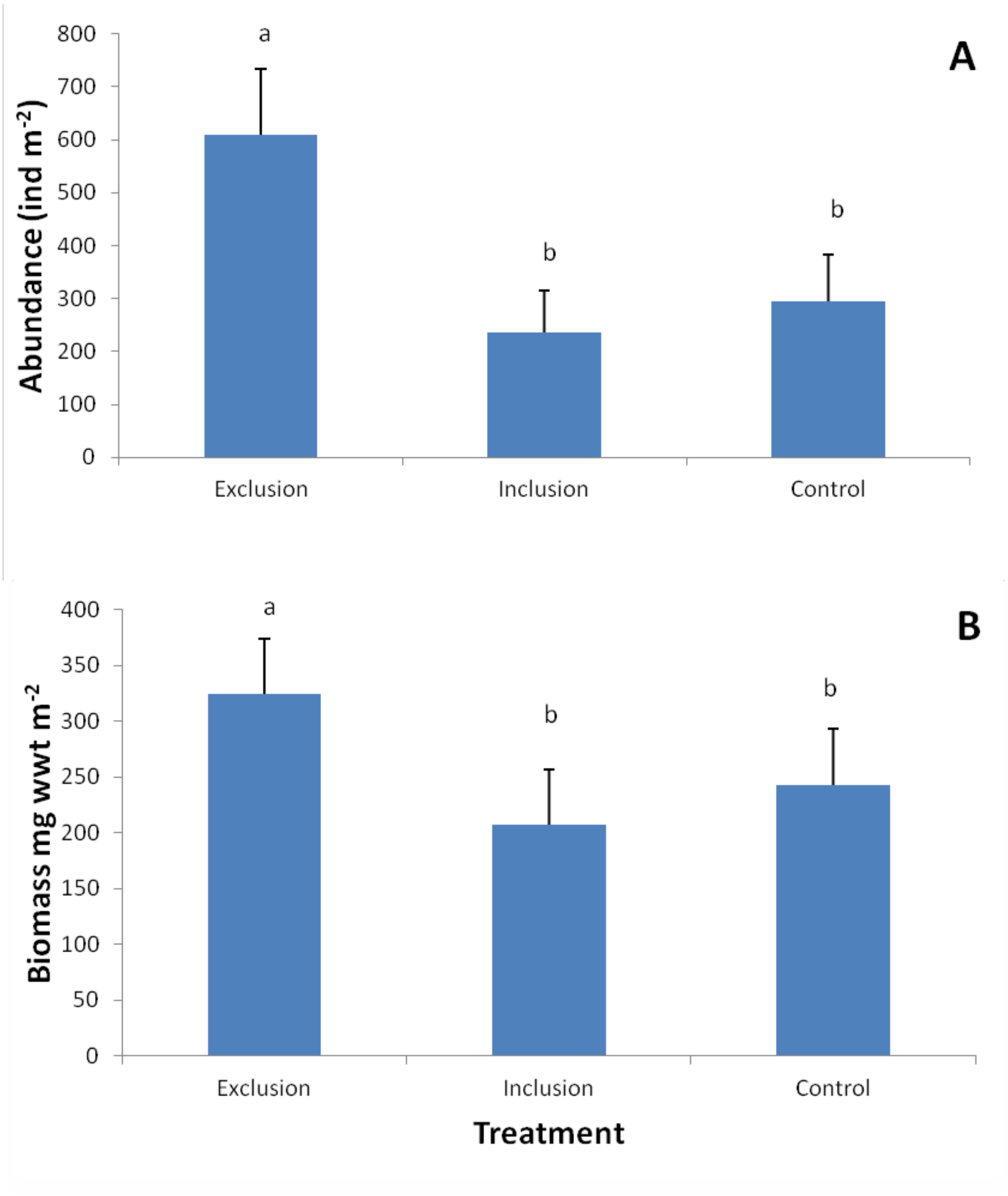


Figure 4.3 Mean microphytobenthic chl-a concentration in the three treatments occupied in the lower reach of the temporarily open/closed Kasouga Estuary. Error bars are standard deviation. Different letters indicate a significant difference (ANOVA).

4.3.4 Epifaunal abundances and biomass

The epifaunal community within the different treatments was represented by a single species, the tick shell, *Nassarius kraussianus*. The abundances of the epifauna in the exclusion cages ranged from 464 ind.m^{-2} to 784 ind.m^{-2}. In inclusion cages the epifaunal abundances ranged from 164 ind.m^{-2} to 360 ind.m^{-2} and from 176 ind.m^{-2} to 384 ind.m^{-2} in the procedural control cages (Figure 4.4A). ANOVA indicated that the total abundances in epifauna in the exclusion treatments were significantly higher than those recorded in the inclusion treatment and procedural controls (F = 20.77; $P < 0.05$). There was no significant difference between inclusion treatment and procedural controls ($P > 0.05$). The epifaunal biomass ranged from 252.4 gwwt.m^{-2} to 406.5 gwwt.m^{-2} in the exclusion cages from 158.2

gwwt.m^{-2} to 290.1 gwwt.m^{-2} in the exclusion treatments and from 203.5 gwwt.m^{-2} to 307 gwwt.m^{-2} in the procedural control cages (Figure 4.4B). There was no significant difference exclusion treatment and procedural control. There was significant difference between the exclusion treatment and inclusion treatments (F = 7.48; P = 0.008).



.

Figure 4.4 Mean epifaunal abundances (**A**) and biomass (**B**) in the three treatments occupied in the lower reaches of the temporarily open/closed Kasouga Estuary. Error bars are standard deviation. Different letters indicate a significant difference (ANOVA).

.5.3.5 Infaunal abundances and biomass

The infauna in the different treatments comprised three species of isopod (*Pontogeloides latipes*, *Apanthura sandalensis*, and *Exosphaeroma estuarium*), one amphipod species (*Grandiedirella lignorum*), two bivalves (*Solen capensis* and *Donax serra*), and two polychaetes (*Lumbrineris tetraura* and *Marphysa sanguinea* and an unidentified sp).

Infaunal abundances in exclusion cages ranged from 412 ind.m^{-2} to 984 ind.m^{-2}. In inclusion cages the infaunal abundances ranged from 96 ind.m^{-2} to 272 ind.m^{-2} and from 176 ind.m^{-2} to 304 ind.m^{-2} in the procedural control cages (Figure 4.5A; Table 4.1). Abundances of the infauna in the exclusion treatment were significantly higher than the other two treatments ($F = 20.06$; $P < 0.001$). There was no significant difference between the inclusion treatment and procedural control. The biomass of infauna in the exclusion cages ranged from 5.81 gwwt.m^{-2} to 9.85 gwwt.m^{-2}. In inclusion cages, the infaunal biomass ranged from 1.03 gwwt.m^{-2} to 4.19 gwwt.m^{-2} and from 3.61 gwwt.m^{-2} in the procedural control cages (Figure 4B; .Table 4.1). Biomass of infauna in exclusion treatment significantly higher than the other two treatments ($F = 19.11$; $P < 0.05$). There was no significant difference between the inclusion treatment and procedural control ($P > 0.05$).

Table 4.1 Mean macrofaunal abundance, biomass and species diversity in the different treatments during the caging experiment conducted in the lower reach of the temporarily open/closed Kasouga Estuary. Values in brackets are standard deviation

	Exclusion	**Inclusion**	**Procedural**
Epifauna			
Abundance (ind m^{-2})	609 (±124)*	236 (±78)	294 (±88)
Biomass (mg wwt m^{-2})	324.7 (±57.2)*	207.1 (±50.3)	243.0(±38.6)
Infauna			
Abundance (ind m^{-2})	691 (±224)**	196 (±66)	236 (±46)
Biomass (mg wwt m^{-2})	7.85(±1.71)*	2.82(±1.14)	4.63(±0.95)*
Margaleff Diversity index	1.17 (±0.13)	1.19 (±0.15)	1.21 ±0.08)

* Indicates a significant difference (ANOVA; $P < 0.05$)

** Indicates a significant difference (ANOVA; $P < 0.001$)

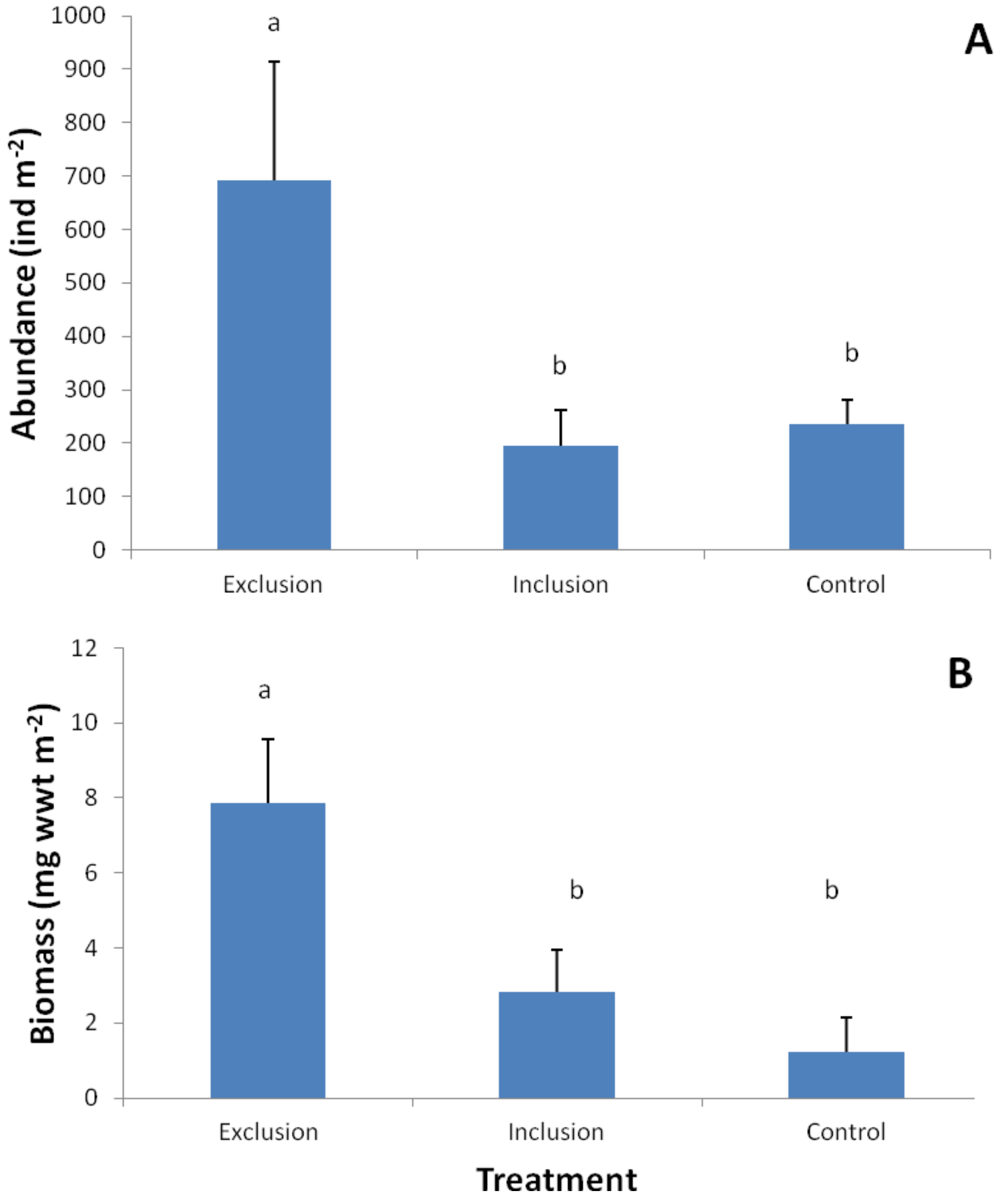


Figure. 4.5 Mean infaunal abundance (**A**) and biomass (**B**) in the three treatments occupied in the lower reach of the temporarily open/closed Kasouga Estuary. Error bars are standard deviation. Different letters indicate a significant difference (ANOVA).

5.3.6 Numerical analyses

Numerical analyses identified two groups of samples, designated Groups 1 and 2 (Figure 5.6). Group 1 comprised the all exclusion treatments while Group 2, was made up of a combination of inclusion and procedural control treatments. ANOSIM procedure of PRIMER indicated that the differences between the groupings were significantly different from one another (Global R value 0.98; $P < 0.05$). SIMPER routine of the PRIMER package indicated that the differences between the two groups could be related to the numerical abundances of individual taxa rather than the presence or absence of species. The six most numerically abundant species within each of the groups identified with the hierarchical cluster analyses are listed in Table 5.1. Collectively, these species accounted for > 85% of the similarity within each group identified with the hierarchical cluster analysis.

5.3.7. Species diversity

Margaleff diversity index values ranged from 1.02 to 1.38 in the inclusion treatments, from 1.14 to 1.38 in the procedural controls and from 0.98 to 1.30 in the exclusion treatments (Table 4.1). ANOVA indicated that there were no significant differences in the diversity index values between the different treatments during the caging experiment ($P > 0.05$).

Table 4.2. The results of similarity percentage (SIMPER) routine that determined the relative contribution of individual species to community structure between the different groups identified with the hierarchical cluster analyses. Values in brackets are mean abundance within each group

Group	Species
1	*Nassarius kraussianus* (646); *Exosphaeroma hylocoetes* (252); *Apanthura sandalensis* (152) *Grandiedirella lignorum* (60) *Lumbrineris tetraura* (26) *Marphysa sanguine* (16)
2	*N.kraussianus* (286); *E.hylocoetes* (98) *L. tetraura* (52); *M sanguine* (12) *G. lignorum* (8); Unidentified polychaete (8)

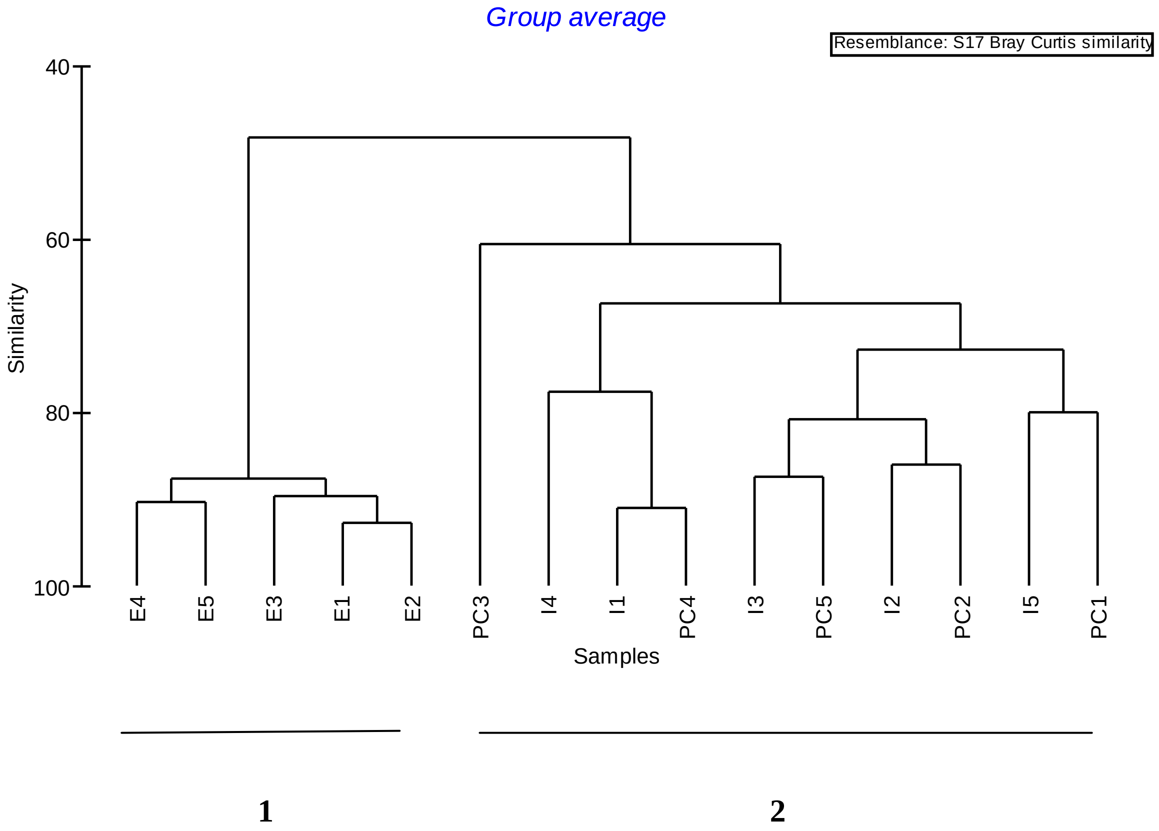


Figure 4.6. Results of the numerical analyses conducted on the macrofaunal abundances in the different treatements during the caging experiments. E = Exclusion treatment; PC = Procedural control; I = Inclusion treatment

4.4. Discussion

Results of the field experiment conducted in the lower reach of the temporarily open/closed Kasouga Estuary indicated that the role of the sandprawn, *Callichirus kraussi*, as an ecosystem engineer was limited to reducing the microphytobenthic algal concentrations, largely mediated by the bioturbation activities of the sandprawn (Chapter 3). This result was in contrast to several previous studies conducted elsewhere in the world (Pillay and Branch 2011) and indeed South Africa, where callianassids have been demonstrated to play a significant role in structuring the macrofaunal communities within shallow water marine ecosystems (Siebert and Branch, 2005; Pillay *et al.* 2007a). It was suggested that the absence of any effect of *C.kraussi* on the macrobenthic community structure of the Kasouga Estuary could be related to their low densities during the time of the field study. The current study was undertaken with the aim of experimentally assessing the potential role of *C.kraussi* as an ecosystem engineer. This was achieved by artificially increasing the densities of the sandprawn within the experimental treatments and assessing the response of the macrofaunal community over time to the presence/absence of the prawn.

In agreement with a study by Pillay *et al.* (2007a), the presence of the sandprawn contributed to a significant increase in the organic content of the sediment ($P < 0.05$; Figure 4.2) Sandprawns modify the organic content of the sediment by accumulating organic material in the lining of their burrows (Ott *et al*., 1976; Suchanek, 1983, 1985). In some cases they collect this material from the surface and store it in the walls or chambers of their burrows (Ott *et al*., 1976; Suchanek, 1983, 1985). In this sense *C.kraussi* “gardens” microorganisms by providing an organically rich oxygenated medium and, perhaps, reducing inhibitory metabolites (Hyllenberg, 1975; Aller and Yingst, 1985). Alternatively, the increase in the organic content of the sediments in the presence of the sandprawn may also be attributed to their feeding activities. Callianassids are primarily deposit feeders and remove organic material from sand grains from sediments in the burrows and then deposit the residue outside the burrow opening thereby increasing the sediment organic levels (Zeibis *et al.*, 1996),

The results of this caging experiment indicated that the total macrobenthic abundance and biomass in the exclusion treatments were significantly higher than those in both the inclusion and procedural control treatments (Figures 4.4 and 4.5; $P < 0.05$ in all cases). Pillay *et al.* (2007) in Durban Bay, South Africa, demonstrated that the abundance of macrofauna, species richness and in most cases diversity, were strongly influenced by the bioturbative activities of *C.kraussi. Callichirus kraussi* pump large volumes of water through their burrows (up to 3 450 ml.day^{-1}), thereby bringing elevated suspended sediment to the overlying water (Colin *et al.*, 1986; Branch and Pringle, 1987). The deposition of the sediment at the surface may bury the subsurface fauna, leading to their deaths or causing metabolic losses due to the feeding time that these organisms loose, and the energy that use overcoming burial (Ellis *et al.*, 2002). In addition, the infauna may incur increased predation rates as they migrate from areas that are heavily bioturbated. Flach (1993) demonstrated that although the lugworm *Arenicola marina,* had no direct effect on the survival rates of the amphipods *Corophium volutator* and *C.arenarium* in aquaria, it did interfere with their tubes, leading to emigration of the amphipods to lugworm-free sections of the tanks. In the process of their escape they experienced significantly greater predation from the crab *Carcinus maenans* and the shrimp *Crangon crangon*.

The bioturbative activities of the sandprawn may further reduce the abundance and biomass of the macrofauna through the enhanced erodability of sediment deposited at the water-sediment interface (Pillay and Branch 2011). A study by Paterson and Hagerthy (2000) showed that biofilms on sediments serve to bind the topmost sediment layer, promoting smooth laminar flow of water over the sediment and water. In sediments that are bioturbated, natural sediment stabilizers like bacteria (Dade *et al*., 1990), diatoms (Madsen *et al*., 1993) and EPSs (Paterson, 1997) are reduced, the sediment bed resists water flow over it, and flow becomes turbulent, increasing the erodability of the beds. Under these conditions, the filtration apparatus of filter feeders become clogged by the sediment that is being expelled (Rhoads and Young, 1970). Additionally small organisms or early developmental stages of macrofauna can be become washed away into the water column because of increment in sediment erodability. The organisms that are swept into the water column and suffer increasing exposure to predators such as fish, shrimps or crabs (Flach, 1993).

In agreement with the study of Pillay *et al*. (2007a), the presence of the sandprawn contributed to a significant decrease in the abundances and biomass of the epifauna, represented by the gastropod, *Nassarius kraussianus* ($P < 0.05$ in both cases; Figure 4.4). Pillay *et al*. (2007a) demonstrated that the gut pigment concentrations of *N. kraussianus*, were strongly linked to the presence or absence of *C.kraussi*. It was proposed that the lowered gut pigmentation concentrations in areas with high densities of *C.kraussi* may be a result of two mechanisms. Firstly, the high sediment bioturbation by *C.kraussi* may reduce the feeding time by the gastropod as it spends more time overcoming burial. Alternatively, the bioturbation generated by the *C.kraussi* may reduce the levels of microalgae on the sediment surface, thus depriving the gastropod of this food source (Pillay *et al*., 2007a). Indeed, this study found that the microphytobenthic algal concentrations were significantly lower in the treatments with *C.kraussi* (P< 0.05; Figure 4.2). This result is in agreement with the published literature which has demonstrated that the bioturbation of the sand prawn may retard the growth of microalgae, bacteria, and the diminishing levels of extracellular polymeric substances produced by microbiota (EPSs) (Branch and Pringle, 1987; Pillay and Branch 2011). The reduced epifaunal abundances and biomass in the presence of *C.kraussi* during this study thus probably reflects the reduced food availability (Figure 4.4).

Results of the numerical analyses indicated that the presence of the sand prawn contributed to decreased abundances of both the epi- and infauna but not to changes in the species composition (Figure 4.5). The separation between the different treatments could be ascribed to changes in the relative abundances of the numerically dominant species as appose to the presence or absence of individual taxa (Figure 4.5; Table 5.1). Indeed, it is worth noting that there was no significant difference in the Margaleff diversity indices values between the different treatments (P > 0.05).

Summary

Results of caging experiment indicated that the presence of the sandprawn *Callichirus krausii* contributed to a significant decrease in the microphytobenthic algal concentrations and the abundances and biomass of both the epifauna and infauna (Figures 4.2 to 4.4). The decrease in the microphytobenthic algal concentrations in the presence of the sandprawn appears to be related to the bioturbation generated by their burrowing and feeding activities

(Branch and Pringle, 1987; Pillay and Branch 2011). The decrease in the epi- and infaunal abundances and biomass appears to be related to decreased food availability and disturbance. Numerical analyses indicated that the sandprawn did not contribute to a change in the species composition within the epi- and infauna within the lower reach of the temporarily open/closed Kasouga Estuary.

CHAPTER 5

FINAL DISCUSSION

Over the past decade, numerous studies have been conducted on the biology of temporarily open/closed estuaries (TOCEs) in both the subtropical (Perissinotto et al. 2003; 2004; 2010) and warm temperate (Allan *et al.* 2008; Froneman 2003; 2006; Whitfield *et al.* 2008; 2012) biogeographic zones along the southern African coastline. The results of these studies have highlighted the importance of both freshwater inflow (salinity regimes) and mouth phase (open and closed) in determining the productivity and species composition of both the invertebrates (zooplankton) and vertebrates (fish and birds) community structure within these systems (Whitfield *et al*. 2008; Perissinotto *et al*. 2010). To date, few studies have attempted to investigate the importance of biological interactions in structuring the biological communities within these estuaries.

The current study was undertaken with the aim of assessing the role of the sand prawn, *Callichirus krausii* (Stebbing) as an ecosystem engineer in the lower reach of the temporarily open/closed Kasouga Estuary situated on the Eastern Cape coastline of South Africa. The study comprised two components. The first component was based on field observations and correlations between the physico-chemical (sediment bioturbation and sediment organic matter) and biological (microphytobenthic algal concentrations and macrobenthos abundances and biomass) variables and the abundances of the sandprawn, were assessed. This approach was consistent with the published literature as the majority of studies examining the effects of sandprawn bioturbation on macrofauna community structure in a variety of shallow aquatic systems have been based on field correlations (e.g. Posey, 1986; Berkenbusch *et al.*, 2000). The second component of the study incorporated experimental manipulations to better assess the role of the sandprawn, *C.kraussi* as an ecosystem engineer.

In agreement with the published literature for both the northern and southern hemisphere (Posey, 1986; Berkenbusch *et al.*, 2000; Pillay *et al*. 2007), the bioturbative activities of the sandprawn contributed to a decrease in the microphytobenthic algal concentrations in the temporarily open/ closed Kasouga Estuary (Figures 3.4 and 4.5). *Callichirus kraussi* pump large volumes of water through their burrows (up to 3 450ml.day^{-1}), thereby bringing elevated suspended sediment to the overlying water (Colin *et al*., 1986; Branch and Pringle, 1987). The re-suspension and subsequent deposition of the sediment on the surface likely buries the microphytobenthic chl-a concentrations and contributes to a changing light environment with the subsequent decrease in their growth. Stable isotope studies suggest that the microphytobenthic chl-a concentrations represent the most important carbon source for the plankton and selected fish species during the closed phase of these systems (Froneman 2002). The bioturbative activities of the sandprawn therefore, likely have important implications for energy flow and cycling within temporarily open/closed estuaries. It is worth noting that a recent mesocosm study by Pillay *et al.* (2012) demonstrated that the bioturbative activities of *C. kraussi* can play an important role in modulating energy flow to estuarine nektonic species.

Results of the caging experiments indicate that the presence of the sandprawn contributed to decreased abundances and biomass of the macrofauna in the lower reach of the

Kasouga Estuary (Figure 4.5). This finding is in agreement with a similar study conducted in Durban Bay, KwaZulu-Natal (Pillay *et al*. 2007a) and indeed, in other shallow water ecosystems in the northern hemisphere (Berkenbusch *et al*. 2000; Berkenbusch and Rowden, 2003; Pillay and Branch 2011). Benchley (1981) hypothesized that the susceptibility of organisms to bioturbation are strongly dependent on their mobility. In her study, she demonstrated that the densities of the sedentary tube builders, like the spionid polycheate *Rhynchospio arenicola* and the tanaid *Leptochelia dubia*, were significantly reduced by the bioturbative activities of the mud shrimp *Upogebia pugettensis*, and the lugworm *Arenicola marina* and the sand dollar *Dendraster exentricus*, but mobile organisms including surface suspension-feeding and burrowing bivalves and polychaetes were unaffected by bioturbation. This mobility hypothesis is frequently used to explain the relative effects of sandprawns on macrofauna with different mobility capabilities (Posey, 1986; Siebert and Branch, 2005b, 2007). Though mobile organisms are likely to evade disturbances by bioturbation these organisms will carry a metabolic cost. The gastropod, *N.kraussianus*, does survive the bioturbative effects of *C.kraussi*, but the uptake of microalgal food is reduced (Pillay *et al*., 2007). If the reduction in microalgal food uptake is sustained, growth, reproduction and survival are diminished, leading to emigration to avoid areas that are not bioturbated by *C.kraussi*. The decrease in the abundance and biomass of the epi- and infauna in the presence of the sandprawn during the caging experiments is therefore, not unexpected. It is worth noting, however, that the impact of the sandprawn in structuring the macrofaunal community appears to be strongly density dependant. During the field experiments, there was no significant correlation between the macrofaunal abundance and biomass and the densities of the sand prawn ($P > 0.05$ Figure 3.5). The absence of any direct effect was suggested to be the result of the generally low densities of the sandprawn that were recorded during the study

Results of the caging experiments indicated that bioturbative activities of *C.kraussi* did not contribute to a change in the macroinvertebrate species composition in the lower reach of the Kasouga Estuary (Figure 4.5). The potential for burrowing species to indirectly affect other nektonic or pelagic species by restricting the energy flow has been raised in previous work on callianassid sand prawns from Durban Bay, South Africa (Pillay, 2006; Pillay *et al*., 20087. That research utilized a long-term data set to track changes in the benthic invertebrates and ichthyofauna of the littoral sand flat for a period of over 8 years. When *C.kraussi* was initially rare, burrowing infauna, dominated by *Eumarcia paupercula,* dominated the benthos, with bottom feeding fish dominating the ichthyofauna and the bivalve siphons being the main food item found in fish stomachs, which were contributing up to 60% of the fish diets. When *C.kraussi* became more established the fish shifted to the dominance of zooplanktivorous species, and the bivalve siphons were no longer recorded in stomachs of the previously numerically dominant demersal fish species (Pillay *et al*, 2008). Unfortunately due to a reduction in the water level of the estuary, the caging experiment was terminated 18 weeks after the commencement of the study. It is possible that the absence of any measurable effect of the sandprawn on the macrofaunal community structure observed during the caging experiments reflects the short duration of the study. It is worth noting, however, that there were no significant differences in the estimates of macrobenthic abundance, biomass and species diversity between the procedural controls and inclusion treatments ($P > 0.05$ in all cases).

Sediment turnover by burrowing shrimps and prawns have been implicated in population crashes of benthic invertebrates (Tamaki, 1994; Flach and Tamaki, 2001; Amaro *et al*., 2007, van Nes *et al*., 2007). For example in Ariake Sound, Japan, a 10-fold increase in the density of the ghost shrimp *Nihonotrypaea harmandi* between 1979 and 1998 was linked to the local extinction of the grazing gastropod, *Umbonium moniliferum* (Tamaki, 1994). Following this, in the North Sea, a 5-fold increase in the density of the burrowing shrimp *Callianassa subterranean* between 1982 and 1992 led to a 90% decline in the abundance of the brittle star *Amphiura filiformis* (van Nes *et al*., 2007). More recently, Pillay *et al*. (2012) demonstrated that changes in the numerical abundance of *C.kraussi* in Durban Bay, South Africa, were associated with shifts in the macrofaunal community structure and dietary switch in fish. These data would suggest that under very high densities, *C.kraussi* may contribute to the decline and possible local extinction of macrobenthic fauna in lower reaches of temporarily open/closed estuaries. Temporarily open/closed estuaries are highly dynamic ecosystems reflecting amongst others the influence of freshwater inflow and mouth phase (Perissinotto *et al.,* 2010; Whitfield *et al.*, 2008; 2012). The outflow of estuarine water following a breaching event coincides with a decline in the abundances and biomass of fauna within the estuary presumably as the biomass-rich waters are exported to the marine environment (Froneman, 2004; Allan and Froneman, 2008; Whitfield *et al*., 2008). The observed decrease can also likely be attributed to the loss of habitats by removal of submerged macrophytes within the littoral zone that acts as a refuge (Henninger *et al*., 2008). In addition to changes in water levels, temporarily open closed estuaries are characterized by dramatic shifts in salinity regimes with salinities ranging between freshwater and hypersaline (Whitfield *et al*., 2008). Although adult sandprawns are able to tolerate salinity values as low as 1 (PSU), the successful development of eggs and larval stages require salinity values > 20 (Forbes, 1978). Indeed, populations occurring in waters where salinity values are permanently < 17 are not self-maintaining and must be recruited from elsewhere (Forbes, 1978). These data would suggest that due to the dynamic nature of these systems, densities of sandprawn within southern African temporarily open/closed estuaries are unlikely to attain those levels which may ultimately contribute to population crashes of macrofauna within the lower reaches of these systems. It is worth noting that the analysis of the published literature would suggest that densities of sand prawn within TOCEs are substantially lower than those recorded in larger permanently open systems or marine bays (Table 1.1).

In conclusion results of the current study indicate that the sandprawn *Callichirus kraussi*, can be regarded as an important ecosystem engineer within the lower reach of the temporarily open/ closed Kasouga Estuary along the Eastern Cape coastline (Chapter 4). The bioturbative activities of the prawn contributed to a decrease in microphytobenthic algal concentrations and the abundance and biomass of both the epi- and infauna. These findings are in agreement with several studies conducted both locally (Branch and Pringle, 1987; Siebert and Branch, 2005; Pillay *et al.* 2007) and in the northern hemisphere (Berkenbusch *et al*., 2000; Pillay and Branch, 2011). The role of the sandprawn in structuring the invertebrate community structure is, however, strongly density dependant.

5.2. Future research

1. Due to receding water levels in the estuary, the caging experiments were conducted only for a period of 18 weeks. Studies conducted elsewhere in the world have highlighted the importance of long-term studies in assessing the role of ecosystem engineers on shallow marine ecosystems functioning (Pillay *et al*., 2007). A long-term caging experiment will better allow us to assess the role of the sandprawn in structuring the macrofaunal community structure within TOCEs.
2. The majority of previous studies have focused on the response of the macrofauna community to the bioturbative activities of callianassids (Tamaki,1994; Flach and Tamaki, 2001; Amaro *et al*., 2007, van Nes *et al*., 2007) Pillay et al. 2007a; b; c;

2012). Virtually nothing is known of the response of the meiofauna to the activities of the sand prawn (Pillay and Branch 2011). Future studies should attempt to assess the role of sandprawns as ecosystem engineers on the meiofuana of TOCEs. Also the macrozoobenthos <1mm and > 63µm may be an important component to investigate in the future.

3. Aquatic ecosystems are composed of the benthic and pelagic compartments which are linked by the flow of inorganic and organic materials, which is often called benthic-pelagic coupling (Raffaelli *et al*., 2003). Such connectivity is crucial to the functioning of aquatic systems and is governed by a number of biotic and abiotic processes. Of the biotic processes, bioturbation is known to be important in the coupling of benthic and pelagic compartments, but most studies have focused on the ability of bioturbators to alter fluxes of nutrients from the benthos into the water column (Ziebis *et al*., 1996; Lohrer *et al*., 2004, D'Andrea and DeWitt, 2009). The results of this and previous studies (see for example Pillay et al. 2007a; 2012) indicate that the bioturbative activities of the sandprawn contributed to a decline in the microphytobnethic algal stocks in the lower reach of the Kasouga Estuary. The decline in microphytobenthic algal stock within the estuary is likely to contribute to alterations in benthic-pelagic coupling. Future studies should attempt to assess the impact of the decline of the microphytobnethic algal concentrations of the food web structure and energy flow in TOCEs.
4. Although several commercially exploited marine fauna species are well recognized as ecosystem engineers, the consequences of their removal from ecosystems remain largely unknown beyond the single species or population level (Coleman and Williams, 2002). The over-exploitation of engineering species is likely to have consequences that extend beyond their own decline and strongly affect the rest of the

ecosystem (Reise, 1982). An example was the harvesting of oysters and the consequence destruction of oyster reefs which resulted in multiple ecosystem effects (Reise, 1982; Lenihan and Peterson, 1998). Cretchley (1996) demonstrated that the digging activities of bait collectors had a far greater effect on sand- and mud prawn populations than the removal of the animals alone. The compaction of the sediments following the collection of bait results in loss of habitat limiting the recovery of the invertebrate populations (Wynberg and Branch, 1994; Jooste, 2003). The intense exploitation/harvesting of sand prawns for recreational fishers that typically occurs in TOCEs (pers. Obs) may have long term-effects on the macrofaunal community structure within these systems particularly under conditions where the populations of these organisms are not self sustaining. The short and long- term impact of the exploitation of the sandprawn on the ecosystem functioning of TOCEs should be investigated.

CHAPTER 6

References

Adams J, Bate G, O'Callagan M (1999). Estuarine microalgae. In: Allanson BR Baird D (eds), Estuaries of South Africa. Cambridge University Press, Cambridge, United Kingdom, pp 91-100

Allan EL, Froneman PW (2008). Spatial and temporal patterns in bacterial abundance, production and viral infection in a temporarily open/closed southern African estuary. *Estuarine, Coastal and Shelf Science* 77: -731-742.

Aller RC, Dodge RE (1974). Animal-sediment relations in a tropical lagoon, Discovery Bay, Jamaica. J Mar res 32: 209-232

Aller RC and Yingst (1985). Effects of the marine deposit-feeders *Heteromastus filiformis* (Polycheata), *Macoma baltica* (Bivalvia) and *Tellina texana* (Bivalvia) on averaged sedimentary solute transport, reaction rates, and microbial distributions. *J. Mar. Res.* 43: 615-645.

Aller RC Yingst JY, Ulman WJ (1993).Comparative biogeochemistry of water in intertidal *Onuphis* (Polychaete) and *Upogebia* (Crustacea) burrows: temporal patterns and causes. J Mar 41: 571-602

Amaro TPF, Duineveld GCA, Bergman MJN, Witbaard R, Scheffer M (2007). The consequences of changes in abundance of *Callianassa subterranean* and *Amphiura filiformis* on sediment erosion at the Frisian Front (south-eastern North Sea). *Hydrobiologia* 589: 273-285

Berkenbusch K, Rowden AA, Probe*rt, P.K.* (2000). Temporal and Spatial variations in macrofauna community composition imposed by the ghost shrimp *Callianassa filholi* bioturbation. J Mar Biol Ecol 60: 17-33

Berkenbusch, K; Rowden, A.A. (2003). Ecosystem engineering – moving away from the "just-so" stories. New Zealand Journal of Ecology 27(1): 67-73

Bertness MD (2007) Atlantic shorelines: natural history and ecology. Princeton University Press, Princeton, 433 pp

Bouma TJ, De Vries MB, Low E, Peralta, Tánczos IC, van de Koppel J, Herman PMJ (2005). Trade offs related to ecosystem-engineering: a case study on stiffness of emrging macrophytes. Ecology 86: 2187-2199

Bouma T.J.; Friedrichs, M.; van Wesenbeeck, B.K.; Temmerman, S.; Graf, G.; Herman, P.M.J. (2009). Density-dependent linkage of scale dependent feedbacks: a flume study on the intertidal macrophytes *Spartina anglica*.OIKOS (in press)

Branch, G.M.; Pringle, A. (1987). The impact of *Callianassa kraussi* Stebbing on sediment turnover and on bacteria, meiofauna and benthic microflora. J Mar Biol Ecol 107: 219-235

Branch, G.M., Griffiths, C.L., Branch, M.L. and Beckley, L.E. (1994). Two Oceans. A guide to the marine life of southern Africa.David Philip, Cape Town and Johannesburg.

Brenchley GA (1981) Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. *J Mar Res* 39: 767-790

Cadée, G.C. (2001). Sediment dynamics by bioturbation organisms. In: Reise, K. (Ed) Ecological comparisons of sedimentary shores, ecological studies, vol 151. Springer, Berlin.pp 149-171

Clarke, K.R. and Warwick, R.M. (2001). Changes in marine communities: an approach to statistical analysis and interpretation. Primer-E: 2nd Edition. Plymouth, UK. 172 pp.

Coleman FC, Williams SL (2002). Overexploitating marine ecosystem engineers: potential consequences for biodiversity. *Trends in Ecology and Evolution* 17(1): 40-44

Colin PL, Suchanek TH, McMurty G (1986). Water pumping and particulate resuspension by callianasids (Crustecea: Thalassinidae) at Enewetak and Bikini Atolls, Marshall Islands. *Bulletin of Marine Science* 38: 19-24

Cuddington K, Hastings A (2004). Invasive engineers. *Ecol Model* 178: 335-347

Dade WB, Davies JD, Nichols PD, Nowell ARM, Thistle D, Trexler MB, White DC (1990). Effects of bacterial exopolymer adhesion on the entrainment of sand. *Geomicrobial J* 8:1-16

D'Andrea AF, DeWitt TH (2009). Geochemical ecosystem engineering by the mud shrimp *Upogebia pugettensis* (Crustecea: Thalassinidae) in Yaquina Bay, Oregon: density-dependent effects on organic matter remineralization and nutrient cycling. *Limnol Oceanogr* 54: 1911-1932

Day JH (1969). A guide to marine life on South African shores. AA Bakema, Cape Town. South Africa.

De Villiers, C.J. and Hodgson, A.N. (1999). Studies on estuarine macroinvertebrates: The macrobenthos. In: *Estuaries of South Africa*, (eds) B.R. Allanson and D. Baird, 1st edn, pp167 – 191. Cambridge University Press, Cambridge.

DWAF (DEPARTMENT OF WATER AFFAIRS AND FORRESTRY, SOUTH AFRICA) Benthic Macrofauna of the Grat Brak Estuary, Monitoring Results 2001. URL: www.dwaf.gov.za/wma/wcpe/gouritz/greatbrak. Accesed June 2012.

Ellis J, Cumming V, Hewitt J, Thrush S and Norkko A (2002). Determining effects of suspended sediment on condition of suspension bivalve (*Atrina zelanica)*: results from a survey, a laboratory experiment and field transplant experiment. *Journal of Experimental Marine Biology and Ecology* 267: 147-174.

Flach EC (1993). The distribution of the amphipod *Corophium arenarium* in the Dutch Wadden Sea: relationships with the sediment composition and presence of cockles and lugworms. *Neth J Sea Res* 31: 281-290

Flach E and Tamaki A (2001) Competitive bioturbators on intertidal sand flats in the European Wadden Sea and Riaka Sound in Japan. In: Reise K(ed) Ecological Comparisons of Sedimentary Shores, Ecological Studies, vol.151. Springer-Verlag, Berlin, Heidelberg, pp 276-293

Forbes AT (1973a). A study of the burrowing sandprawn *Callianassa kraussi* Stebbing (Crustecea: Decapoda: Thalassinidae). PhD thesis, Rhodes University, Grahamstown, South Africa

Forbes, A.T. (1973b). An unusual abbreviated larval life in estuarine burrowing prawn *Callianassa kraussi* (Crustacea: Decapoda: Thalassunidae). Mar Biol 22: 361-365.

Forbes AT (1977). Breeding and growth of the burrowing prawn *Callianassa kraussi* Stebbing (Crustecea: Decapoda: Thalassinidae). *Zoologica Africana* 12: 149-161.

Field JG, Clarke KR, Warwick RM (1982). A practical strategy for analyzing multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37-52

Forbes, A.T. 1(978). Maintenance of non-breeding populations of the estuarine prawn *Callianassa kraussi* (Crustacea, Anomura, Thalassinidea). *Zoologica Africana* **13**: 33 – 40.

Froneman PW (2002a). Food web structure in three contrasting estuaries determined by stable carbon isotope analysis. *African Journal of Aquatic Sciences* 27: 107-115

Froneman PW (2002b). Seasonal variations in selected physico-chemical and biological variables in the temporarily open/closed estuary (South Africa). *African Journal of Aquatic Science* 27: 117-123

Froneman PW (2003). Food web dynamics in a temperate temporarily open/closed estuary (South Africa). *Estuarine, Coastal and Shelf Science* 55: 87-95

Froneman PW (2004). *In situ* grazing rates of the copepods, *Pseudodiaptomus hessei* and *Acartia longipatella* in a temperate, temporarily open/closed estuary. *South African Journal of Science* 100: 577-583.

Froneman PW (2006) The population dynamics of the caridean shrimp, *Palameon peringueyi*, in a small intermittently open Eastern Cape estuary. *African Journal of Aquatic Science* 31(2); 197-203.

Gacia, E.; Duarte, C.M.; Marba, N.; Terrados, J.; Kennedy, H.; Fortes, M.D.; Tri, N.M. (2003). Sediment deposition and production in SE-Asia seagrass meadows. Estuar Coast Mar Sci 56: 909-919

Grange, N. and Allanson, B.R. (1995). The influence of freshwater inflow on the nature, amount and distribution of seston in estuaries of the Eastern Cape, South Africa. *Estuarine, Coastal and Shelf Science* **40**: 403 – 420.

Hanekom N (1980). A study of two thalassinid prawns in the non-Spartima regions of the Swartkops Estuary, Phd thesis, University of Port Elizabeth, Port Elizabeth.

Henninger T, Froneman PW, Hodgson AH (2008). Population dynamics of the estuarine isopod, *Exosphaeroma hylocoetes* in three temporarily open/closed southern African estuaries. *African Journal of Zoology* 43: 202-217.

Heyns, E., Froneman, P.W. (2010). Spatial and temporal patterns in the hyperbenthic community structure in southern African permanently open estuary. *Estuarine, Coastal and Shelf Science.* 88: 105-115.

Holm-Hansen, O. and Rieman, B. (1978). Chlorophyll a determination: improvements in methodology. *Oikos* **30**: 438 – 447.

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: s consensus of current knowledge. *Ecol Monogr* 75: 3-35.

Hughs DJ, Atkinson RJA, Ansell AD (2000). A field test of the effects of megafaunal burrows on benthic chamber measurements of sediment-water solute fluxes. *Marine Ecology Progress Series* 195: 189- 199

Hyllenberg J (1975). Selective feeding by *Aberenicola pacifica* with notes on *Aberenicola vagabunda* and a concept of gardening in lugworms. *Ophelia.* Vol 14, pp 729-742

Jones, C.J., Lawton, J.H. and Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos* **69**: 373 – 386.

Jones, C.G.; Lawton, J.H.; Shackak, M. (1997a) Ecosystem engineering by organisms: Why semantics matter. Trends in Ecology and Evolution 12: 275

Jones, C.G.; Lawton, J.H.; Shackak, M. (1997b). Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78: 1946-1957

.

Jooste, J.G. (2003). An assessment of bait availability, utilization and management guidelines in Eastern Cape estuaries. MSc. Thesis, University of Port Elizabeth.

Koike, R.C.; Mukai,H. (1983). Oxygen and nitrogen contents and fluxes in burrows of the shrimps *Callianassa japonica* and *Upogebia major*. Mar Ecol Prog Ser 12: 185-190

Lach, E.; Tamaki, A. (2001). Competitive bioturbators on intertidal sand flats in European Wadden Sea and Ariake Sands in Japan. In. Reise, K (Ed). Ecological comparisons of sedimentary shores, ecological studies, vol 151. Springer, Berlin. Pp 149-171

Lawton, J.H.; Jones, C.G. (1993). Linking species and ecosystem perspectives. Trends in ecology and Evolution 8: 311-313

Lach, E.; Tamaki, A. (2001). Competitive bioturbators on intertidal sand flats in European Wadden Sea and Ariake Sands in Japan. In. Reise, K (Ed). Ecological comparisons of sedimentary shores, ecological studies, vol 151. Springer, Berlin. Pp 149-171

Lawton, J.H.; Jones, C.G. (1993). Linking species and ecosystem perspectives. Trends in ecology and Evolution 8: 311-313

Legendre P and Legendre L (1983). Numerical Ecology. First English Edition. Elsevier Scientific publishing Company, Amsterdam.

Lenihan HS, Paterson CH (1998). How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyter reefs. *Ecol Appl* 8: 128-140

Lohrer AM, Thrush SF, Gibbs MM (2004). Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* 431: 1092-1095

Lubke RA (1998). The coastal environment. In: Field guide to the eastern and southern cape coasts, (eds) RA Lubke and I de Moor, pp 3-9. University of Cape Town Press, South Africa.

Lutjeharms JRE (1998) Coastal hydrgraphy. In: Field Guide to the Eastern and Southern Cape Coasts (eds) RA Lubke and I de Moor, pp 50-61, University of Cape Town Press, South Africa

Lutjeharms JRE, Cooper J, Roberts M (2000). Upwelling at the inshore edge of the Agulhas Current. *Continental Shelf Research* 20: 737-761

MadsenNP, Nillson P, Soundback K (1993). The influence of benthic microalgae on the stabilization of subtidal sediment. *J Exp Mar Biol Ecol* 170: 159-178

Meysman FJR, Middelburg JJ, Hiep CHR (2006). Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology and Evolution* 21: 688-695

Murphy RC (1985). Factors affecting the distribution of the introduced bivalve, *Mercenaria mercenaria*, in a California lagoon – the importance of bioturbation. *J. Mar. Res.*43: 673-692

Murphy, R.C.; Kremer, J.N. (1992). Benthic community metabolism and the role of deposit-feeding callianasid shrimp. J Mar Res 50: 321-340

Nel PL (2006). Exploitation and Biology of the bait organism *Callianassa kraussi* Stebbing (Crustecea: Decapoda: Thalassinidae) in Langebaan Lagoon, M.Sc thesis, University of Cape Town, Cape Town.

Nozais C, Perrisinotto R, Mundree S (2001). Annual cycle of microalgal biomass in a South African teomporarily-open estuary: nutrients versus light limitation. *Marine Ecology Progress Series* 223: 39-48.

Orr KK (2008). Spatial and temporal variations in metals in the sediment and water of selected Eastern Cape estuaries, Soouth Africa, MSc thesis, Rhodes University, Grahamstown, South Africa.

Ott JA, Fuchs B, Fuchs R and Malasek A (1976). Observations on biology of *Callianassa stebbingi* Borradaille and *Uppogebia litoralis* Risso and their effect upon the sediment. *Senckenbergiana Marit* Vol 8, pp 61-79

Paterson DM (1997). Biological mediation of sediment erodability: ecology and physical dynamics. In: Burt N, Parker R, Watts J (eds) Cohesive sediments. Wiley, Chichester, pp215-229

Paterson DM, Hagerthy SE (2000). Microphytobenthos in contrasting coastal ecosystems: biology and dynamics. In: Reise K (ed) Ecological comparisons of sedimentary shores, ecological studies, vol 151. Springer, Berlin, pp 105-125

Paulo JG, Flores Montes M, Santos Junior AC, Batista TNF, Travassos RK, do Nacimento Filho GA, Gaspar FL, Pitanga ME (2011). Allochthonous and auchthous organic matter in an urban tropical estuarine area of northeastern Brazil. Journal of Coastal research 64, 1978-1801.

Perissinotto R, Walker DR, Webb P, Wooldridge TH, Bally R (2000). Relationships between zoo- and phytoplankton in a warm temperate, semi-permanently closed estuary, South Africa. *Estuarine, Coastal and Shelf Science* 51: 1-11

Perissinotto R, Nozais C, Kiberige I (2002). Spatio-temporal dynamic of phytoplankton and microphytobenthos in a South African temporarily-open estuary. *Estuarine, Coastal and Shelf Science* 55: 47-58

Perissinoto R, Iyer K, Nozais C (2006). Response of microphytobenthos to flow and trophic variation in two South African temporarily open/closed estuaries. *Botanica Marina* 49: 10-22

Peterson CH (1977). Competitive organization of the soft-bottom macrobenthic communities of the southern Calirfonia lagoons. *Mar. Biol.43*: 343-359

Pillay, D. (2006). The influence of bioturbation by sandprawn *Callianassa kraussi* Stebbing on macrobenthic assemblages of the Little Lagoon. PhD Thesis, University of KwaZulu-Natal, Durban, South Africa.

Pillay D, Branch GM, Forbes AT (2007a). The influence of bioturbation by the sandprawn *Callianassa kraussi* on feeding and survival of the bivalve *Eumarcia paupercula* and the gastropod *Nassarius kraussianus*. *Journal of Experimental Marne Biology and Ecology* 344: 1-9

Pillay, D.; Branch, G.M.; Forbes, A.T. (2007b). Experimental evidence for the effects of the thalassinidean sandprawn *Callianassa kraussi* on macrobenthic communities. Mar Biol 152: 611-618

Pillay D, Branch GM, Forbes AT (2007c). Effects of *Callianassa kraussi* on microbial biofilms and the recruitment of macrofauna: a novel hypothesis or adult-juvenile interactions. *Marine Ecology Progress Series* 347: 1-14

Pillay D, Branch GM, Forbes AT (2008). Habitat change in an estuarine embayment: anthropogenic influences and a regime shift in biotic interactions. *Marine Ecology Progress Series* 370: 19-31

Pillay D (2010). Expanding the envelope: linking invertebrate bioturbators with micro-evolutionary change. *Marine Ecology Progress Series* 409: 301-303.

Pillay D and Branch (2011). Bioengineering effects of burrowing Thalassinidean shrimps on marine soft-bottom ecosystems. Oceanographyand Marine Biology 49:137-292

Pillay, D., Branch, G.M., Dawson, J., Henry, D. (2011). Contrasting effects of ecosystem engineering by cordgrass *Spartima maritima* and the sandprawn *Callianassa kraussi* in a marine-dominated lagoon. Estuarine, Coastal and Shelf Science 91: 169-176

Pillay D, Williams C, Whitfield AK (2012). Indirect effects of bioturbation by burrowing sandprawn *Callichirus kraussi* on a benthic foraging fish, *Liza Rhichardsonii. Marine Ecology Progress Series* 453: 151-158

Posey MH (1986). Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis. Marinr Ecological Progress Series* 31:15-22

Posey MH, Dumbauld BR, Armstrong DA (1991). Effects of a burrowing mud shrimp, *Upogebia pugettensis* (Dana), on abundance s of macro-infauna. *J Exp Mar Biol Ecol* 148: 283-294.

Raffaelli D, Bell E, Weithof G, Matsumoto A and others (2003). The up and downs of benthic ecology: consideration of scale, heterogeiny and surveillance for benthic-pelagic coupling. *J Exp Mar Biol Ecol* 285-286: 191-20

Rhoads DC, Young DK (1970). The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J Mar Res* 28: 150-178.

Ross GJB (1988). Coastal Hydrography. In: “A field guide to the Eastern Cape Coast”. Lubke RA, Gess FW and Bruton MN (Eds). The Grahamstown centre of the wildlife society of Southern Africa, Grahamstown, Grahamstown, pp19-30

Rowden AA, Jones MB (1993) Critical evaluation of sediment turnover estimates for Callianassidae (Decapoda: Thalassinidae). *J Exo Mar Biol Ecol* 173: 265-272

Schlacher TA and Wooldridge TH (1996). Axial zonation patterns of subtidal macrozoobenthos in the Gamtoos Estuary, South Africa. *Estuaries* 19: 680-696

Siebert T, Branch GM (2005a). Interactions between *Zostera capensis, Callianassa kraussi* and *Upegebia Africana*: deductions from field surveys in Langebaan Lagoon, South Africa. *African Journal of Marine Science* 27: 345-356

Siebert T, Branch GM (2005b) Interactions between *Zostera capensis* and *Callianassa kraussi*: influences on community composition of eelgrass beds and sandflats. *African Journal of Marine Science* 27: 357-373

Siebert T, Branch GM (2006) Ecosystem engineers: interactions between eelgrass *Zostera capensis* and the sandprawn *Callianassa kraussi* and their indirect effects on the mudprwan *Upogebia Africana*. *J Exp Mar Biol Ecol* 338: 253-270

Siebert T, Branch GM (2007) Ecosystem engineers: Interactions between eelgrass *Zostera capensis* and the sandprawn *Callianassa kraussi* and their indirect effect on the mudprawn *Upogebia afrcana*. *J Exp Mar Biol Ecol* 340: 11-24

Stone AW (1988). Climate and weather. In: “A field guide to the Eastern Cape Coast”. Lubke RA, Gess FW, Bruton MN (Eds). The Grahamstown centre of the wildlife society of Southern Africa, Grahamstown, Grahamstown, pp 19-30

Stone AW, Weaver AvB and West WO (1998). Climate and Weather. In: Field Guide to the Eastern and Southern Cape Coasts (eds) RA Lubke and I de Moor, pp 41-49, University of Cape Town Press, South Africa.

Suchanek TH (1983). Control of seagrass communities and sediment distribution by *Callianassa* (Crustecea, Thalassinidae) bioturbation. *J. Mar. Res. Vol 41, pp. 281-298*

Suchanek TH (1985), Thalassinid shrimp burrows: ecological significance of species-specific architecture. *Proc. 5th Int. Coral Reef Conf.* Vol. 5, pp 205-210

Tamaki A, (1988). Effects of the bioturbating activity of the ghost shrimp *Callianassa japonica* Ortmann on migration of a mobile polychaete. *J Exp Mar Biol Ecol* 120: 81-95

Tamaki A (1994). Extinction of the trochid gastropod, *Umbonium (Suchium) moniliferum* (Lamarck), and associated species on an intertidal sand flat. *Res Popul Ecol* 36: 225-236

Teske, P.R. and Wooldridge, T. (2001). A comparison of the macrobenthic faunas of permanently open and temporarily open/closed South African estuaries. *Hydrobiologia* 464: 227 – 243.

Teske, P.R. and Wooldridge, T. (2003). What limits the distribution of subtidal macrobenthos in permanently open and temporarily open/closed South African estuaries? Salinity vs. sediment particle size. *Estuarine, Coastal and Shelf Science* **57**: 225 – 238.

Teske, P.R. and Wooldridge, T. (2004). Affinities of some common estuarine macroinvertebrates to salinity and sediment type: empirical data from Eastern Cape estuaries, South Africa. *African Zoology* **39**: 183 – 192.

Van der Heide T, van Nes EH, Geerling GW, Smoldres AJP, Bouma TJ, van Katwijk MM (2007) Positive feedbacks in seagrass ecosystems-theoretical and management implications. *Ecosystems* 10:1311-1322.

Van Wesenbeeck BK, van de Koppel J, Herman PMJ, Bertness MD, van der Wal D, Bakker JP, Bouma TJ (2008). Potential for sudden shifts in transient systems: distinguishing between local and landscape-scale processes. *Ecosystems* 11: 1133-1141.

Volkenborn N, Hedtkamp SIC, van Beusekokm JEE, Reise K (2007). Effects of bioturbation and bioirrigation by lugworms (*Arenicola marina)* on physical and chemical sediment properties and implications for intertidal habitat succession. *Estuarine Coastal Shelf Science* 74: 331-343.

Volkenborn N, Reise K (2006). Lugworm exclusion experiment: responses by deposit feeding worms to biogenic habitat transformation. *J Exp Mar Biol Ecol* 330: 169-179.

Vorsatz J (1999) Life history strategies in the estuarine sandprawn *Callianassa kraussi*, MSc dissertation University of Port Elizabeth, Port Elizabeth.

Wooldridge TH, McGwynne L (1996) The estuarine environment. Report No. C31. Institute of Coastal Research, Port Elizabeth, South Africa. 91pp

Waslechuck DG, Matson EA, Zajak RN, Dobbs FC, Tramontano JM (1983). Geochemistry of burrow waters vented by a bioturbating shrimp in Bermudian sediments. *Mar Biol*72: 219-225

Whitfield AK (1992). A characterization of southern African estuarine systems. *South African Journal of Science* 18:89-103

Whitfield AK (1998) Biology and ecology of of fishes in southern African estuaries. Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology, No.2, 223pp

Whitfield AK, Adams JB, Bate GC, Bezuidenhout K, Bornman TG, Cowley PD, Froneman PW, Gama PT, James NC, MaKenzie B, Riddin T, Snow GC, Strydom NA, Taljaard SS, Terode AI, Theron AK, Turpie JK, van Niekerk L, Vorwerk PD, Wooldridge TH (2008). A multidisciplinary study of s small intermittently open South African estuary with particular emphasis on the influence of mouth state on the ecology of the system. *African Journal of Marine Science.* 30(3): 453-473.

Whitfield AK, Bate GC, Adams JB, Cowley PD, Froneman PW, Gama PT, Strydom NA, Taljaard S, Theron AK, Turpie JK, Van Niekerk L, Wooldridge TH (2012). A review of the ecology and management of temporarily open/closed estuaries in South Africa, with particular emphasis on river flow and mouth state as primary drivers of these systems. *African Journal of Marine Science* 34.1: 178-191

Wynberg, R.P. and Branch, G.M. (1994). Disturbance associated with bait collection for sandprawns (*Callianassa kraussi*) and mudprawns (*Upogebia africana*): long-term effects on the biota of intertidal mudflats. *Journal of Marine Research* **52**: 532 – 558.

Ziebis W, Forster S, Huettel M, Jorgensen BB (1996). Complex burrows of the mud shrimp *Callianassa truncuta* and their geochemical impact in the sea bed. *Nature* 382: 612-622