Endobenthic Ecosystem Engineering: influence of sandprawns (*Callichirus kraussi)* on zooplankton assemblages

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Dissertation

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ABSTRACT

Ecosystem engineering activities of the burrowing Southern Africa sandprawn (*Callichirus kraussi*), were shown in recent research to influence bentho-pelagic coupling in soft sediment estuarine ecosystems through reducing phytoplankton biomass in the overlaying water. The phytoplankton reduction mechanism was hypothesized to be driven by their adsorption along sandprawn burrow walls during irrigation. However, given that phytoplankton is a major trophic resource for filter feeders, any effect of sandprawns in reducing phytoplankton biomass may generate possible indirect effects on filter feeders such as zooplankton assemblages. To date, there has been no known research addressing questions on density of sandprawns and associated effects on zooplankton assemblages. This study therefore aimed to address this knowledge gap and quantify the influence of ecosystem engineering by *C. kraussi* on two size categories of zooplankton assemblages; mesozooplankton and microzooplankton, based on the premise that water pumping activities would lead to a decline in abundance of phytoplankton (adsorption onto burrow walls), thereby, resulting in negative bottom-up effects on zooplankton assemblages. This aim was accomplished using an 18-days mesocosms laboratory experiment, with each experimental mesocosm being each half-filled with sediment and water collected from the Zandvlei Estuary and divided into 3 treatments of varying *C. kraussi* densities (0% (control), 50% and 100% natural sandprawn density, n = 3). At the end of the experiment, increases in *C. kraussi* densities from controls to 100% treatments resulted in declines in abundance of total phytoplankton cells, nanophytoplankton, and picophytoplankton. However, sandprawn density had no significant effect on zooplankton assemblages, which were dominated by hyperbenthic taxa. There were discernible trends in dominance at the taxon level in microzooplankton and mesozooplankton assemblages. The copepod order Hapacticoida became increasingly dominant in both assemblages from control to 100% treatment with percentage contributions increasing from

79.23% to 95.93% in the microzooplankton assemblage and 43.07% to 92.28% in the mesozooplankton assemblage. Increasing dominance in both microzooplankton and mesozooplankton assemblages with increasing sandprawn density were confirmed using dominance plots. In conclusion, the main findings in this experiment suggest that endobenthic ecosystem engineering effects may not be confined to the sedimentary components of estuarine ecosystems but may extend to generate subtle effects on zooplankton taxa, mainly by way of increasing dominance. This study is the first direct evidence of the bentho-pelagic coupling effects of endobenthic ecosystem engineers on pelagic zooplankton assemblages that are dominated by hyperbenthic taxa and lays the foundation for subsequent research into understanding consequences of endobenthic ecosystem engineering on pelagic ecosystems.

INTRODUCTION AND LITERATURE REVIEW

1.1 Ecosystem engineers

Although ecologists over the years have used food availability, predators, competition and abiotic variability to predict the abundance and distribution of organisms (Haemig, 2012), it is clear that other factors are also influential. Ecosystem engineering is one of these other factors, which involves organisms called "ecosystem engineers" that create, modify and maintain habitats. Haemig (2012), Lill & Marquis (2003) and Wright *et al*., (2002) state that ecosystem engineers significantly modify biodiversity, and abundance and distribution of plants and animals. Aside from the fact that the phrase "system engineer" was earlier recognized in 1881 by Darwin, the concept of ecosystem engineers was later proposed by Lawton & Jones (1993). The phrase "system engineer" was first recognized in 1881 by Darwin and later proposed as "ecosystem engineers" by Lawton & Jones (1993). This concept was initially used to link organisms and ecosystems with emphasis on the physical repercussion of biological activity. Subsequently, the activities of ecosystem engineers were formally recognized as processes that were not directly trophic or competitive but rather that involved environmental modification by organisms (Jones et al., 1994).

Jones *et al*. (1994), in their formal classification of organisms as ecosystem engineers, categorized engineers into two types: autogenic and allogenic. Autogenic ecosystem engineers alter ecosystems through their own physical structures. Examples of autogenic engineers would be oysters, which are the primary habitat modifiers in intertidal environments where they play a significant role in retention of moisture and creation of shade at low tide that protects sympatric organisms from desiccation and extreme stress (Helmuth *et al*., 2006; McAfee *et al*., 2017; Silliman *et al*., 2011; Somero, 2002). On the other hand, allogenic ecosystem engineers transform resources from one physical state to another through their behavior and activities (Jones *et al*., 1994). A well-researched allogenic ecosystem engineer is the beaver, which constructs dams across flowing water bodies that trap sediments and organic matters and leads to the creation of wetlands. Invariably, these changes inadvertently alter nutrient cycles and ultimately impact the communities of plant and animal in that ecosystem (Jones *et al*., 1994).

In general, the modifications induced by ecosystem engineers are a result of the abiotic conditions they cause, which extends to interspecific trophic relationships within the food-web such as predation and competition (Jones *et al*., 1994, 1997; McAfee *et al*., 2016). According to Crain and Bertness (2006), the influence of ecosystem engineers on sympatric communities increases simultaneously in relation to the degree to which they alter the physical and biological conditions of the ecosystem. Likewise, Bertness and Callaway (1994) postulated that the shift from negative to positive effects of ecosystem engineering will increase with increasing levels of biotic and abiotic stress. Examples of the positive effects of ecosystem engineering are buffering of harsh edaphic conditions as shown by plant engineers in saltmarshes, and/or habitat-amelioration, which positively influences recruitment and protects against desiccation. Other examples of harsh physical conditions that ecosystem engineering could ameliorate are heat/desiccation stress, osmotic stress, soil hypoxia and disturbance (Bertness & Callaway, 1994).

Marine sedimentary ecosystem engineers can be divided into epibenthic and endobenthic engineers, based on the duration of time spent below or above the sediments. However, both autogenic and allogenic ecosystem engineers occur ubiquitously in many coastal ecosystems, though often separately at patch-scales and with different functional effects on sympatric biota (Pillay & Branch, 2011). Endobenthic macroinvertebrate species may modify the soft-bottom sedimentary ecosystem through their feeding and burrowing activities (Bouma et al. 2005, Henninger & Froneman 2013, Gacia et al. 2003). Also, through bioturbation and bio-irrigation activities of endobenthic organisms, many resource flows (e.g resource availability) can be influenced. In contrast, epibenthic ecosystem engineers mainly influence benthic ecosystems through effects on local hydrodynamics, therefore altering local sediment dynamics and particle trapping (Bouma *et al*., 2005; Gacia *et al*., 2003).

1.1.1 South African sandprawn, *Callichirus kraussi*

The South African sandprawn, *Callichirus kraussi* (formerly *Callianassa kraussi*) is a benthic crustacean that is a dominant ecosystem engineer locally. Sandprawns influence sedimentary biogeochemical processes, species composition and diversity, and community structure mainly through bioturbation (Moyo *et al*., 2017; Pillay & Branch, 2011; Venter *et al*., 2020). According to Branch *et al*. (2017), *C. kraussi* is found to be predominant from Luderitz Bay in Namibia to Inhambane region in Mozambique along the southern African coast. Also, sandprawns are an integral part the macrofauna of South African temporarily open/closed (TOCEs) and permanently open estuaries (POEs) and marine embayments (Whitfield, 1992). They occur in densities of 150-200 individuals.m^{-2} (Branch & Pringle, 1987; Siebert & Branch, 2005) and live in self-created intricate networks of burrows that sometimes span 2-3 meters deep (Forbes, 1973; Venter *et al*., 2020).

The life cycle of sandprawns is abbreviated as it has no planktonic larval stages (Forbes, 1973) and it is completed within estuaries (Hanekom & Russell, 2015). The larvae of *C. kraussi* may occasionally be recorded in the water column but the vast majority remain protected within the parent burrows (Forbes, 1973). Although adult sandprawns can tolerate a salinity as low as 1 (Practical Salinity Units – PSU), they require salinity >20 for successful development of eggs and the megalopa stage (Forbes, 1977).

1.1.2 Bentho-pelagic coupling and ecosystem engineering by *Callichirus kraussi*

Bentho-pelagic coupling is described as the interaction between the bottom substrata and water column habitats of an aquatic environment through energy, mass or nutrient exchange (Griffiths *et al*., 2017; Venter *et al*., 2020b). However, these interactions are strongly influenced by the activities of benthic organisms, especially thalassinidean crustacean species in marine and estuarine soft sediments (Holthuis, 1980; Moyo *et al*., 2017). Earlier, the views of researchers on bentho-pelagic coupling focused on the top-down interactions, deposition of detritus to the benthic habitat (Graf, 1992; Hargrave, 1973; Smetacek, 1985; Suess, 1980), bio-resuspension (Graf & Rosenberg, 1997) and the release of inorganic nutrients from the sediments (Raffaelli *et al*., 2003). Recently, there has been growing interest and appreciation of the intricacy of these interactions, which has led to a significant increase in research on processes that couple benthic and pelagic habitats, with emphasis on those mediated by living organisms (Baustian *et al*., 2014; Griffiths *et al*., 2017; Marcus & Boero, 1998; Raffaelli *et al*., 2003; Schindler & Scheuerell, 2002). The influence of sandprawns and similar endobenthic crustaceans on estuarine ecosystem structure and function is attributed to their burrowing/bioturbating activities (Henninger & Froneman, 2013; Rowden & Jones, 1993). Specifically, they transfer reworked sediment to the sediment-water interface, which is deposited in volcano-like mounds around the openings to the burrows (Forbes, 1977; Pillay *et al*., 2007; Rowden & Jones, 1993). In reference to the amount and the depth of sediment reworked by callianassid crustaceans, they are ranked among the most influential bioturbators in coastal soft sediment ecosystems (Cadée, 2001; Venter *et al*., 2020). Generally, though, except for their effects on nutrient fluxes from sediments to overlying waters, little else is understood of their role in bentho-pelagic coupling processes. The focus of this research study is therefore on the bentho-pelagic coupling effect of sandprawn (*C. kraussi*) ecosystem engineering on zooplankton assemblages in soft-bottom estuarine ecosystem. This interest stems from the prior work demonstrating that sandprawns can reduce phytoplankton biomass by roughly 50% relative to controls lacking them (Venter *et al*. 2020). Given that phytoplankton are important food sources for estuarine zooplankton (Kibirige *et al*., 2002; Perissinotto *et al*., 2000, 2003), it is plausible for sandprawn presence and increasing density to alter zooplankton assemblages *via* effects on trophic resource availability (reduction in phytoplankton biomass). This premise will be expanded on later in the Introduction.

1.2 Biology and ecology of zooplankton

Zooplankton are unicellular and multicellular microscopic pelagic organisms that inhabit both marine and freshwater ecosystems. Zooplankton are typically diverse, but abundance is low (Santhanam *et al*., 2019) and their sizes vary between a few microns to a millimeter (Goswami, 2004). According to Santhanam *et al*. (2019), in 1887, Victor Hensen started the use of the term "plankton", which is derived from the Greek word meaning "wandering" or "drifting" while "zoo" refers to animals. This name "plankton" was adapted by Victor Hensen to designate a group of organisms constituting all free and involuntary floating organic particles in open water, in which orientation is dictated by the direction of water movement. Zooplankton are important organisms in aquatic ecosystems because of their functions in aquatic productivity, primarily due to their link between phytoplankton and higher trophic levels (Gajbhiye, 2002; Perumal *et al*., 1998; Santhanam *et al*., 2019). Moreso, they can rapidly colonize and recolonize both new and old habitats depending on prevailing environmental factors, and this is due to their small sizes and short generation time (Ger et al., 2014; Szűcs et al., 2017). They are rich in minerals, lipids and fatty acids which make them an important source of food for fish (Gul *et al*., 2015). Due to their different ways of responding to stresses, zooplankton usage as biological indicators in aquatic ecosystems is gaining momentum (Okorafor *et al*., 2013; Sousa *et al*., 2008).

Zooplankton can be classified based on planktonic stages and sizes. In terms of planktonic stages, they grouped into holoplankton and meroplankton; the former refers to organisms that remain in planktonic form throughout their life cycles, being unattached to any substrate. The latter group remains planktonic for a part of their life. Rotifers, cladocerans, copepods and ostracods are the major zooplankton groups predominant in most tropical freshwater ecosystems (Witty, 2004), while meroplankton dominate in the ocean and are comparatively scarce in freshwater (Rogers & Thorp, 2015). Also, meroplankton consists of a few insects (freshwater), veligers of some bivalve molluscs and mites. Based on their sizes, zooplankton are classified into macroplankton (2 - 200 cm); mesoplankton (200 – 2000 µm), microplankton (20 – 200 µm), nanoplankton (2 – 20 µm) and picoplankton (0.2 – 2 µm; Soares et al., 2011).

The adaptability of copepods to variable conditions distinguishes them from other zooplankton (Reid & Williamson, 2010) and is probably the reason they are reported as the most abundant group of zooplankton. There is differentiation reported in the feeding habits of copepods; the smaller copepods feeds on heterotrophic protists while the larger ones feed on both autotrophic and heterotrophic food sources (protozoan and metazoan) and detritus (Turner, 2004). Sharma *et al*. (2013) reported that abundance of copepods and cladocerans are food-dependent (i.e the availability of variety of foods) and temperature dependent.

Ostracods are ubiquitous, as they are found in all aquatic environments – freshwater, brackish waters and marine (Martens *et al*., 2007). They have streamlined body shapes with a hinged bivalved chitinous shell presenting a smooth, thin calcified bean shaped carapace. Their bodies are not obviously segmented like the other crustaceans (Karanovic, 2012). According to Pieri *et al*.

(2009), whilst they are mostly benthic, they also occur in semiterrestrial environments. Some taxa of ostracods exhibit both sexual and asexual modes of reproduction (which is dependent on environmental conditions) and metamorphose through different growth stages to the final adult stage. They have a wide feeding range as they ingest bacteria, detritus and diatoms (Pieri *et al*., 2009). Compared to other crustaceans, the outer shell of ostracods is hard, and it easily forms fossils. McCormack *et al*., (2019) reported that they are increasingly been used as paleo-environmental indicators because they have the most known complete fossil records.

1.2.1 Species composition, diversity, and abundance of zooplankton

South African estuaries are populated by highly diverse zooplankton (Grindley, 1981; Wooldridge, 1999). In past studies carried out on South African estuarine systems, few genera of copepods and mysids dominated the endemic holozooplankton components of the systems (Grindley, 1981; Wooldridge, 1999). On the south and the east coast of South Africa, mysids are predominantly represented by *Mesopodopsis africana, M. wooldridgei*, *Gastrosaccus brevifissura, G. gordonae* and *Rhopalophthalmus terranatalis* (Grindley, 1981; Wooldridge, 1999; Wooldridge & Bailey, 1982). According to the findings of Grindley (1981) on regional composition of zooplankton, the west coast of South Africa estuarine systems is dominated by *Acartia longipatella* and *A. africana,* whilst *Pseudodiaptomus hessei* and *Oithona plumifera* are often abundant. Calanoid copepods *Acartiella natalensis* and *Pseudodiaptomus hessei* numerically dominated zooplankton in the Kariega Estuary in the eastern cape with peak abundance occurring during autumn as reported by Froneman (2001) who inferred that this abundance can be related to seasonal phytoplankton production, absence of river flooding (Perissinotto *et al*., 2000) and a relatively stable euhaline estuarine environment as observe by Lawrence *et al*. (2004). Conversely, abundance decreases as some zooplankton are displaced to the sea due to flooding during winter (Mbandzi *et al*., 2018), which is similar to the results of Wooldridge and Melville-Smith (1979) in South African estuaries under flooding conditions. Other common taxa that are found in South African estuarine systems are chaetognaths, ctenophores, amphipods and ciliates, while the rare taxa are euphausids, foraminiferans, salps and hydroids (Grindley 1981). However, large numbers of polychaetes, bivalves (Blaber *et al*., 1984), cladocerans and ceriodaphnians (Connell *et al*., 1981) are generally found in highly perched river-dominated estuaries. Whilst copepods are typically numerically dominant, mysids are often more important in terms of biomass. The abundance of mysids is also often underestimated as a result of inadequate sampling procedures (Wooldridge, 1999).

Whilst the trends in zooplankton temporal abundance are generally determined by temperature, seasonal rainfall is also important (Wooldridge, 1999). In addition, Zhao *et al*. (2018) reported the influence of other factors such as local physiochemical (e.g., nutrient level, turbidity, salinity) and biological conditions (e.g., phytoplankton abundance and fish predation) playing a pivotal role in determining zooplankton community structure. Generally, zooplankton peak abundance and biomass is recorded during the months of December - February in TOCEs, with the exception of a few estuaries (Grindley, 1981; Wooldridge, 1999). For example, the Klein Estuary exhibited peak abundance during the months of June – August, and in the Lourens Estuary, peak abundance is recorded in the months of March – May (Grindley, 1981; Montoya-Maya & Strydom, 2009). In TOCEs, the opening and closure of the mouth of the estuaries often overrides these trends (Montoya-Maya & Strydom, 2009).

Salinity also plays an important role in the abundance of zooplankton in most estuaries in reference to their axial and vertical salinity gradients. Wooldridge (1999) reported the dominance of stenohaline assemblages in the lower reaches, which are more adapted to high salinity with low plasticity for wide variations in salinity, resulting in a strong affinity for open sea conditions.

Stenohaline zooplankton species have been recorded up to a point where the salinity falls below 28‰ (Grindley, 1981). Invariably, this assemblage exhibits high species diversity (Wooldridge, 1999). The upper reaches of estuaries, where the salinity drops below 4‰, are typically dominated by oligohaline or freshwater communities (Grindley, 1981; Wooldridge, 1999). However, these communities are sparsely represented in South African estuaries in terms of biomass (Wooldridge, 1999). On the other hand, euryhaline estuarine zooplankton is well-represented in terms of abundance and biomass in most South African estuaries (Wooldridge & Deyzel, 2009). In their study on the zooplankton assemblage of Great Berg Estuary in western cape, South Africa, Wooldridge and Deyzel (2009) showed that the dominating euryhaline forms in the zooplankton found were *Pseudodiaptomus hessei* (copepods), the mysid shrimps *Mesopodopsis wooldridgei* and *Rhopalophthalmus terranatalis*, and fish larvae (particularly of *Gilchristella aestuaria*).

1.2.2 Bentho-pelagic coupling between sandprawns and zooplankton assemblages

There is no known research on the influence of the bioturbation activities of sandprawns or similar endobenthic crustaceans on zooplankton assemblages. However, considering the recent research by Venter *et al.* (2020) on the effects of burrowing activities of sandprawns in reducing phytoplankton biomass by roughly 50% in experimental mesocosms, it can be extrapolated that they may indirectly influence zooplankton assemblages because of their dependence on phytoplankton as source of food (Carpenter *et al*., 1985; Chang *et al*., 2014; Elser & Goldman, 1991; Kibirige *et al*., 2002; Perissinotto *et al*., 2000, 2003). As reported by (Gołdyn & Kowalczewska-Madura, 2008a), zooplankton selectively graze on phytoplankton communities, but there is also a bottom-up effect of phytoplankton on zooplankton. This therefore indicates that changes in abundance of phytoplankton biomass will potentially induce changes in the assemblage of zooplankton. In the context of the current study, the recent work detailing how phytoplankton biomass declines in the presence of sandprawns, likely due to phytoplankton cells being adsorbed onto the wall of their burrows during bi-directional water pumping (Venter *et al*., 2020), forms the basis for the expectation that sandprawn-induced declines in phytoplankton biomass may alter zooplankton assemblages. Sandprawns and other endobenthic crustaceans have been described as "gardeners" because they adsorb and accumulate microalgae, including phytoplankton and other particulate organic matter onto the mucous-lined walls of their burrow during irrigation (Griffen *et al*., 2004; Pillay & Branch, 2011), thereby increasing their food supply (Coelho, 2004; Frey & Howard, 1975). It is valid therefore to infer from these studies the possibility of sandprawns mediating bentho-pelagic coupling through indirect effects on zooplankton via direct effects on phytoplankton biomass.

1.3 The Problem Statement and Justification of the Study

Based on the most recent review on ecosystem engineering by thalassinidean crustaceans, to date, all studies on this subject have focused on advancing knowledge of the ecological significance of the engineering activities of particular species in coastal ecosystems within a narrow context of ecological conditions (Pillay, 2019). This has limited understanding of the functional relevance of thalassinideans as ecosystem engineers, thereby, leaving ecologist with several unanswered questions. Moreso, little is known on the extent of the mediating effect imposed by other biotic and abiotic factors on the influence of engineering activities of thalassinidean ecosystem engineers (as *Callichirus kraussi* in this study) on sympatric organism assemblages, both benthic and pelagic. As such, there are knowledge gaps regarding contextual processes and subsequent effects on assemblages, particularly in pelagic environments (Pillay, 2019; Venter *et al*., 2020).

Presently, no study has been conducted on the ecosystem engineering effects of sandprawns such as *C. kraussi* on zooplankton assemblages, considering phytoplankton biomass as a mediating factor, in response to sandprawn bioturbation and/or irrigation activities. Additionally, there is limited understanding of the implications of the novel water filtration significance of the ecosystem engineering of *C. kraussi* as reported by Venter *et al.* (2020) on pelagic assemblages broadly, including zooplankton, with the above-mentioned study emphasizing a decrease in phytoplankton biomass due to their adsorption on sandprawn burrow walls during bi-directional water pumping by *C. kraussi*. While decreasing phytoplankton biomass by sandprawns has the potential to improve water quality, especially in urban eutrophic ecosystems, indirect effects on pelagic consumers such as zooplankton are unknown, yet this assemblage can be affected by the shift in the biomass of phytoplankton, since this is their major trophic resource (Jose & Furio, 2015; Chen *et al*., 2012). Understanding of the indirect effects of sandprawns on zooplankton also sheds light on broader implications of sandprawn ecosystem engineering, since zooplankton are themselves key components of pelagic food webs, with several secondary and tertiary consumers reliant on them as trophic resources.

More broadly, this research will expand understanding of the role of endobenthic crustaceans in bentho-pelagic coupling processes in coastal ecosystems. By understanding their effect on zooplankton abundance and community composition, a broader understanding of the intrinsic relationship that exist between endobenthic ecosystem engineering, pelagic ecosystems, and bentho-pelagic coupling processes will be gained.

1.4 The study hypothesis

The hypothesis tested in this study is that ecosystem engineering by *C. kraussi* would elicit changes in zooplankton assemblages. This is based on the premise that water pumping by sandprawns would lead to declines in abundance of phytoplankton (due to adsorption onto burrow walls (Venter *et al*., 2020), thus initiating negative bottom-up effects on zooplankton assemblages. The hypothesis will be evaluated for two size classes of zooplankton viz. microzooplankton and mesozooplankton.

METHODOLOGY

2.1 Sample collection site

The aim of this study was carried out using an *ex situ* mesocosm experiment. The materials (sandprawns; *Callichirus kraussi*, sediment and water samples) for this experiment were collected from the Zandvlei Estuary (34°05'S; 18°28'E), located in southern Cape Town adjacent to Muizenberg within False Bay (Figure 1). This estuary is 2.6 km long with an approximate maximum depth of 2 m and a maximum width of 0.5 km (Harding, 1994; Whitfield & Baliwe, 2013). Zandvlei is the only functional estuary on Cape Town's False Bay coast and it is among 75% of South Africa's 290 functional open/closed estuaries, which are likened to intermittently closed and opened lakes and lagoons (ICOLLs) (Lemley *et al.*, 2019; Skowno *et al.*, 2019).

Over the years, significant anthropogenic manipulations have occurred in and around the Zandvlei Estuary including general infrastructure building, drainage channel construction, dredging, construction of bridges and artificial mouth opening and closure (Harding, 1994; Quick & Harding, 1994). Consequently, extensive urbanisation has increased run-off and nutrient loading *via* river inputs, which has caused significant changes in water quality (Harding, 1993; 1994), ecological functioning (Davies *et al.*, 1989; Dick, 1992; Harding, 1994; Stewart & Davies, 1986) and recreational use (Harding, 1993; Thornton *et al.*, 1989) of this estuary.

2.2 Sample collection

The sandprawns, water and sediment were collected from the sandprawn biotope in the lower reach of the estuary (Figure1) which is intertidal under open-mouth conditions. Sediment was collected

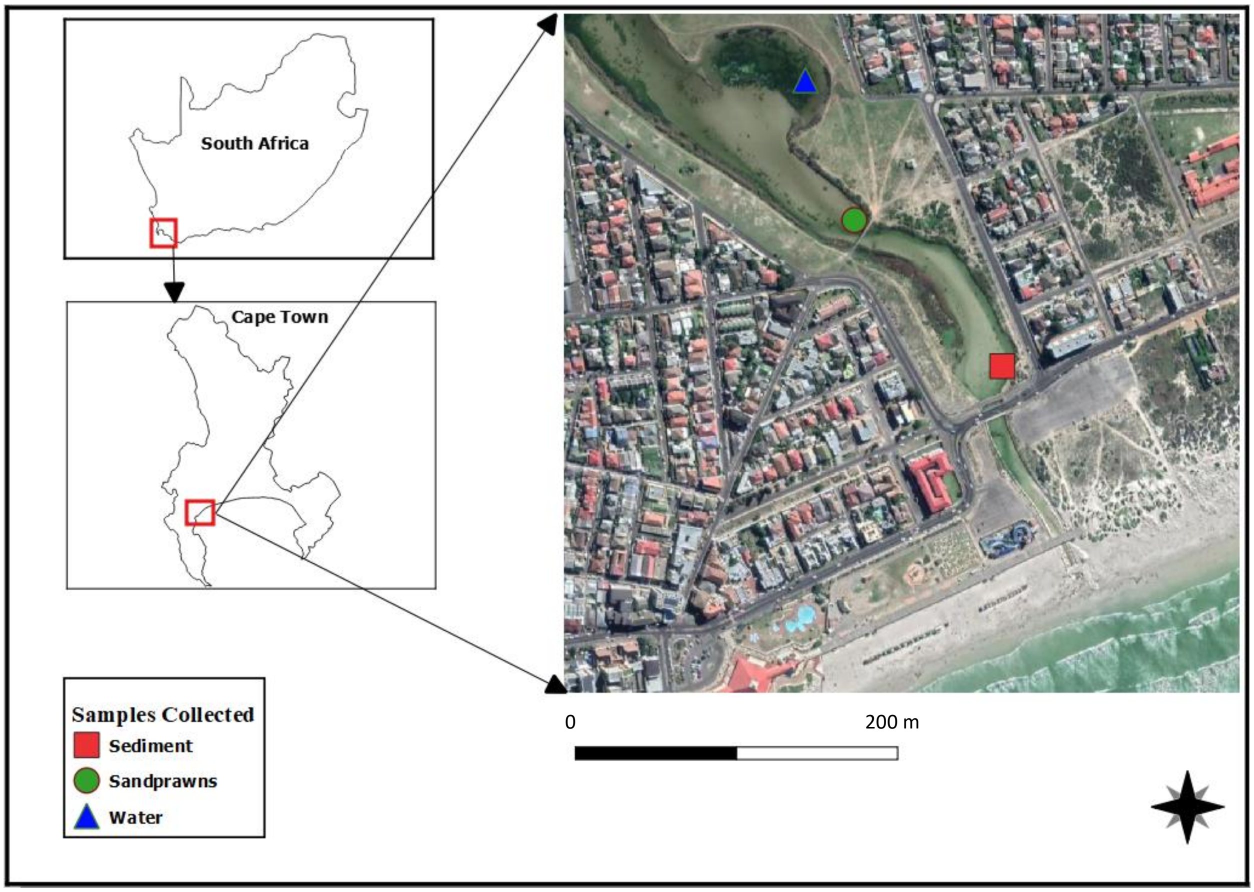


Figure 1: Location of the sample collection site, Zandvlei Estuary

Figure 2: Experimental set-up showing layout of experimental mesocosms in the aquarium facility in the John Day building, University of Cape Town

using a shovel to gently scrape the topmost layer (± 20 cm) of the sediment and sieved through a 2mm mesh into buckets to remove larger organisms and debris. Subsequently, water (± 150 L; temperature = 15°C; salinity = 35‰) for the experiment was collected with buckets, followed by the removal of visible materials such as macroscopic algae or plastic by hand. For the sandprawns, non-gravid individuals longer than 4cm sandprawns (rostrum to telson) were collected with stainless steel prawn pumps (length = 90 cm, diameter = 5 cm) and packed on damp layered sheets of newspaper for transportation.

2.3 Experimental design

An 18-day mesocosm experiment, adapted from Pillay *et al*. (2012) and Venter *et al*. (2020), was used to determine the influence of sandprawns (*Callichirus kraussi*) on zooplankton assemblages (Figure 2). The experiment was carried out in the aquarium facility of the Department of Biological Sciences, University of Cape Town. The experiment comprised nine (9) 25 L black buckets (30 cm deep), each half-filled sediment and then filled with water collected from the Zandvlei Estuary, which acted as experimental mesocosms. All mesocosms were individually aerated and allowed to settle for 1 day before the introduction of sandprawns. Three treatments were employed: 0% (hereafter referred to as control), 50% and 100% of natural sandprawn density, based on a maximum of 200 individuals$\cdot$m^{-2} reported by Branch and Pringle (1987).

Treatments were replicated three times. Sandprawn number per treatment (50% treatment: 6 individuals/mesocosm; 100% treatment: 12 individuals/mesocosm) was determined by scaling down natural maximum sandprawn density (200 individuals$\cdot$m^{-2}) to the mesocosm surface area (Branch & Pringle, 1987; Venter *et al*., 2020b). The aquarium's temperature and daylight duration were set to 15°C and 12 hours day/night light cycle to mimic natural conditions.

2.4 Sample preparation

2.4.1 Environmental variables

Water quality variables (oxygen concentration, temperature, pH, and conductivity) were measured every 3 days for the duration of the experiment (18 days). Dissolved oxygen concentration was measured qualitatively using a Sera Oxygen (O_2) Aquarium Test kit. Temperature and pH were measured using a Crison PH25 pH meter while a YSI Ecosense EC300 probe was used to measure conductivity.

2.4.2 Nutrients

Water column nutrient levels (40 ml from surface layer of the water) were measured every three days throughout the experimental period (18 days). Nitrite (NO^{2-}) and ammonia (NH_3) were the nitrogen (N) compounds measured, while phosphorous (P) was measured as orthophosphate (PO_3^{4-}).

PO_3^{4-}, NO^{2-} and NH_3 were analysed using a photometer (Hanna Instruments Multiparameter Bench Photometer for Aquaculture: HI 83203) using the designated reagents for each nutrient as shown in Table 1.

Table 1: Reagents and methods used to measure the nutrients concentrations

Response Variable	Reagent code	Range	Method
Phosphate ($PO_3^{4-)}$	HI 93715-01 0.00	0.00-10.00	Nessler
Nitrite (NO_2-)	HI 93707-01	0.00-1.15	Diazotization
Ammonia (NH_3)	HI 93713-01 0.00	0.00-2.50	Ascorbic Acid

2.4.3 Phytoplankton and bacteria biomass

Changes in phytoplankton and bacterial assemblages were analysed in detail by De Cerff (2021) as part of her MSc degree, using the exact experiment as described above. Essentially, De Cerff (2021) analysed the water column variables from this mesocosm experiment over an 18-day period to quantify the effects of burrowing sandprawns on phytoplankton and pelagic bacterial assemblages. Flow cytometry, a powerful tool for quantifying aquatic micro-organisms, was used to measure responses of phytoplankton and bacterial assemblages. I make use of the final day's results from De Cerff's (2021) data to explain trends recorded for zooplankton assemblages, which is the focus on my dissertation.

2.4.4 Zooplankton assemblages

Water samples for analysis of zooplankton were collected at the end of the experiment (18 days). Specifically, 5 L of water were collected each from each of the mesocosms and filtered sequentially through 200 µm and 10 µm nylon meshes to separate zooplankton into micro and meso size classes. Samples were then fixed in 90% ethanol for 15 seconds, followed by preservation in 5 ml 70% ethanol. Zooplankton were counted and identified on Sedgewick Rafter counting chamber under a microscope with a digital camera (Leica DM500 Binocular Microscope). The zooplankton were identified using an appropriate zooplankton guide (Gibbons, 1997).

2.5 Statistical Analysis

Nonparametric statistical methods were used for data analysis, given that they make no explicit assumptions regarding the distributions of original variables (Clarke & Ainsworth, 1993; Clarke & Green, 1988). Data were tested for normality with and without transformation, but normality could not be achieved. Data for nutrients (PO_3^{4-}, NO^{2-} and NH_3), phytoplankton biomass, and bacteria biomass were expressed as percentage changes (relative quantities) from the start of the experiment to the end (Day 1 vs Day 18). However, for zooplankton assemblages, data were collected from Day 18 only and were expressed as density (absolute quantities). It was not possible to obtain Day 1 and Day 18 zooplankton samples given the small sizes of mesocosms. Sandprawn densities were the explanatory variable in this research experiment.

PRIMER (Plymouth Routines in Multivariate Ecological Research) v 6.1.1.8 with PERMANOVA+ (Permutational Multivariate Analysis of Variance) v 1.0.8 add-on was used to carry out multivariate analyses. Non-metric multidimensional scaling (nMDS) was used to visually assess the differences in the micro-zooplankton and meso-zooplankton assemblages among the sandprawn treatments. nMDS ordinations were constructed from resemblance matrices generated from Bray-Curtis similarities based on untransformed and unstandardised abundance data. Similarity percentages from the cluster analysis were projected on the nMDS ordinations to understand the similarity of the groupings. PERMANOVA was employed to test the effects of different sandprawn densities on micro- and mesozooplankton assemblages. For the micro- and microzooplankton assemblages, the DIVERSE procedure was used to calculate species richness (S) expressed as total species, evenness (J') expressed as Pielou's evenness, and total abundance of zooplankton (N) expressed as total individuals. The DOMINANCE procedure was used to assess the change in relative contribution of taxa within the zooplankton assemblages across sandprawn treatments using the mean taxon ranks. SIMPER identified each taxon's contribution to the zooplankton assemblages in each of the different sandprawn treatments.

SPSS v19 (Statistical Package for the Social Sciences) was used to carry out the univariate analyses. Boxplots were used to show trends visually. Kruskal-Wallis Rank tests were used to assess the significance of the different sandprawn treatments on the biotic and abiotic variables.

Pairwise *post hoc* Dunn tests with Bonferroni adjustments were applied to detect significant differences in cases where significant sandprawn effects were detected.

RESULTS

3.1 Environmental variables

3.1.1 Abiotic variables

Variation in temperature, pH, conductivity, and concentrations of phosphate and ammonia was not significantly influenced by the different sandprawn densities. However, nitrite concentration did vary among sandprawn treatments (Kruskal-Wallis Rank Test, $H_{(2,6)} = 6.252$, $p = 0.044$, Table 2). The pairwise *post hoc* Dunn test with Bonferroni adjustments detected statistically significant nitrite variation between the 100% and control treatments (p = 0.041), with no statistically significant variation between 100% and 50% (p = 1.00), and 50% and control treatments (p = 0.348). Nitrite concentration was greatest (0.71±0.29SE), and lowest (0.04±0.02SE) in 0% and 100% sandprawn treatments, respectively. Also noteworthy was the high SE value in the 100% sandprawn treatment (Table 2).

3.1.2 Biotic variables

Total heterotrophic bacteria (THB), *Prochlorococcus* and *Escherichia coli,* dominated all treatments, cumulatively accounting for 84.14%, 74.40% and 80.25% of community structure in the control, 50% and 100% sandprawn density treatment (Table 3). However, there was decline in their percentage contributions from control to 100% sandprawn treatment. Nanophytoplankton, total phytoplankton cells and picophytoplankton showed regular decline trends from control to 100% treatment. Generally, average similarity in the biotic variables declined with increase in sandprawn density (Table 3).

Table 2: Summary of variation in the environmental variables (mean ± SE) measured at the end of the laboratory experiment testing effects of sandprawns on zooplankton assemblages. Outputs of Kruskal-Wallis rank tests are also shown on the right. Statistical descriptions: H = Kruskal-Wallis rank test statistic, df = degrees of freedom (internal; external), and p–values. Values in bold indicate statistical significance, and different superscripts denote within-treatment differences (post hoc Dunn).

	Density			**Kruskal-Wallis rank test**		
	0%	**50%**	**100%**	***H***	**df**	***p*-value**
Abiotic variables						
Temperature (°C)	14.93±0.17	14.40±0.30	14.50±0.50	1.948	2;6	0.378
pH	8.09±0.03	8.08±0.07	8.01±0.09	0.560	2;6	0.756
Conductivity (mS·cm^{-1})	41.05±0.39	43.24±1.89	41.92±0.48	1.067	2;6	0.587
Nutrient variables						
Phosphate PO_4^{3-} (mg·L^{-1})	3.13±1.32	2.05±0.90	2.98±1.32	1.156	2;6	0.561
Nitrite NO_2^{-} (mg·L^{-1})	$0.71\pm0.29^{\mathbf{a}}$	$0.09\pm0.03^{\mathbf{ab}}$	$0.04\pm0.02^{\mathbf{b}}$	6.252	2;6	**0.041**
Ammonia NH_3 (mg·L^{-1})	10.15±0.12	10.64±0.56	9.69±0.69	1.142	2;6	0.491

Table 3: *SIMPER results of the percentage change in relative abundance of biotic variables in experimental sandprawns treatments (control, 50% and 100%)*

Control
Average similarity: 75.92

Biotic variables	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
THB	101.77	27.37	4.53	36.05	36.05
Prochloroccocus	73.48	23.02	8.11	30.32	66.37
Escherichia coli	53.15	13.49	4.38	17.77	84.14
Nanophytoplankton	16.33	4.66	6.61	6.13	90.27
Cryptophyte	11.78	3.66	4.47	4.82	95.09
Total phytoplankton cells	8.07	2.23	6.03	2.94	98.02
Picophytoplankton	5.57	1.50	5.63	1.98	100.00

50%
Average similarity: 69.03

Biotic variables	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
THB	82.16	22.11	6.27	32.04	32.04
Prochloroccocus	47.72	17.29	5.72	25.05	57.09
Escherichia coli	48.35	11.95	1.11	17.31	74.40
Cryptophyte	21.60	7.86	1.30	11.39	85.79
Nanophytoplankton	15.65	6.36	3.52	9.21	95.00
Total phytoplankton cells	5.79	2.28	2.36	3.30	98.30
Picophytoplankton	3.01	1.17	1.87	1.70	100.00

100%
Average similarity: 58.26

Biotic variables	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
THB	86.30	16.77	1.75	28.79	28.79
Prochloroccocus	79.69	15.66	2.05	26.88	55.67
Escherichia coli	79.72	14.32	2.16	24.58	80.25
Cryptophyte	15.42	5.21	3.94	8.93	89.18
Nanophytoplankton	13.59	4.31	6.88	7.39	96.58
Total phytoplankton cells	4.31	1.34	13.67	2.31	98.89
Picophytoplankton	2.13	0.65	12.88	1.11	100.00

Note: Av.Abundance = Average Abundance; Av.Sim = Average Similarity; Sim/SD = Similarity/Standard Deviation; Contrib% = Percentage Contribution; Cum% = Cumulative Percentage

3.2 Zooplankton assemblages

The nMDS ordination showed no distinctive grouping of the nine mesocosms according to the sandprawn densities based on microzooplankton (Figure 3A) and mesozooplankton assemblages (Figure 3B). These were statistically validated by PERMANOVA, which showed no significant sandprawn effects on microzooplankton ($P_{(perm)} = 0.616$) and mesozooplankton ($P_{(perm)} = 0.211$). In both micro- and mesozooplankton assemblages, the majority of the mesocosms were 80% similar in terms of species composition and abundance.

In the microzooplankton assemblages across the different sandprawn treatments, Hapacticoida (79.23%, av.abun = 415.67 individuals/5L) and Ostracoda (11.47%, av.abun = 65 individuals/5L) dominated assemblages and cumulatively contributed between 90% and 99% to assemblage structure. However, Nematoda, Foraminifera, and Polychaeta contributed less than 4% to community structure across the sandprawn treatments. The 50% sandprawn treatment had the highest average similarity (87.89%; Table 4) within treatments.

For mesozooplankton, abundance across all treatments was low relative to microzooplankton. Generally, average abundance and percentage contribution of Hapacticoida increased with an increase in sandprawn densities from control (av.abun = 35.33 individuals/5L, contribution = 43.07%) to 100% sandprawn treatment (av.abun = 119.67 individuals/5L, contribution = 92.28%). In contrast, Nematoda and Ostracoda decreased with an increase in sandprawn densities across the treatments. However, Calanoida and Polychaeta were only present in control and 100% treatment, respectively. Similarity of mesozooplankton assemblages varied from 44.33% in control to 59.72% in the 100% sandprawn treatment (Table 5).

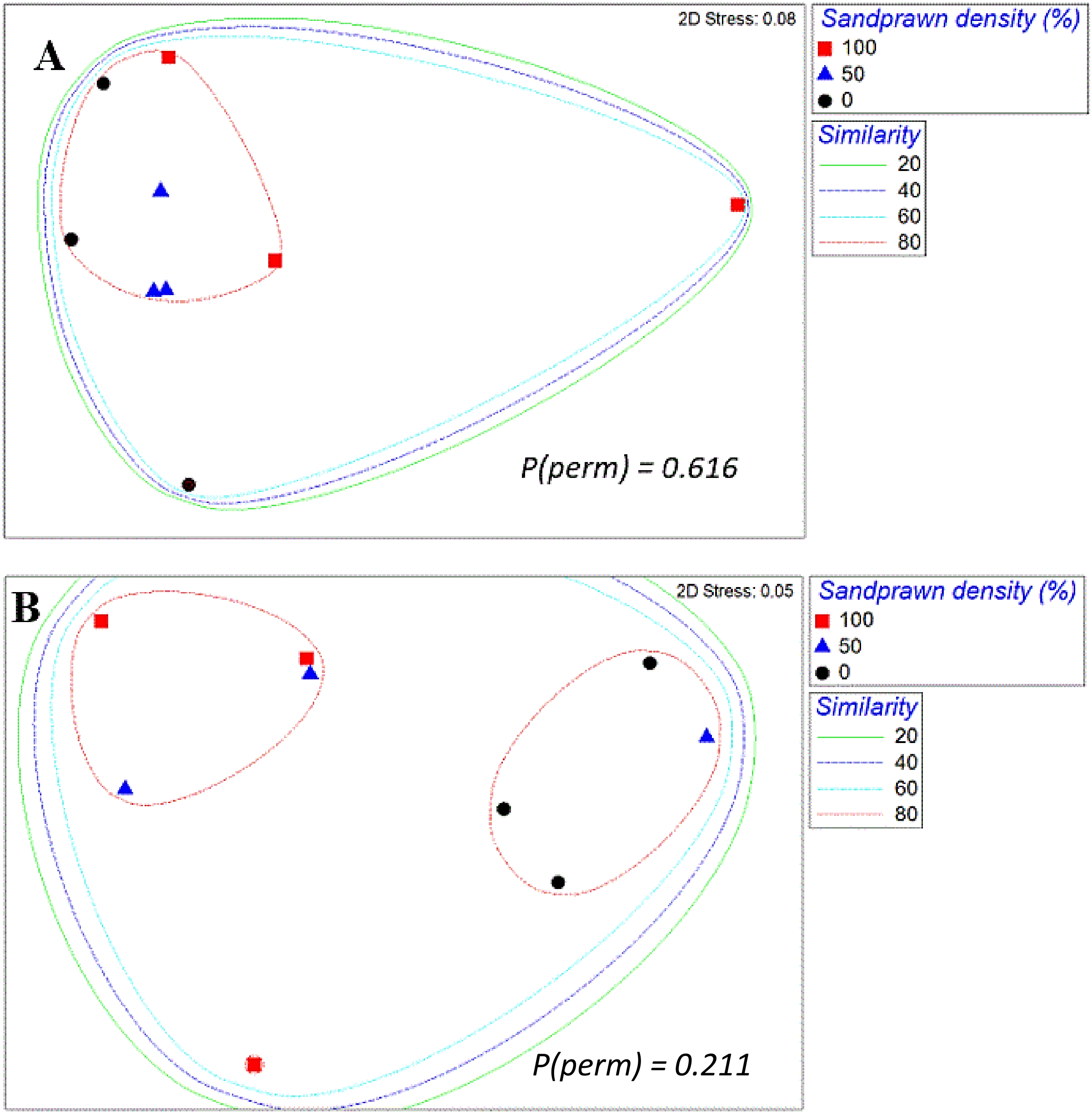


Figure 3: Non-metric multidimensional scaling (nMDS) ordination, including percentage similarity, showing spatial variation in the nine mesocosms with three different sandprawn treatments (0%, 50% and 100% of maximum natural density). Results for microzooplankton **(A)** *and mesozooplankton* **(B)** *at the end of the laboratory experiment are shown. Similarity percentages from the cluster analysis are projected on the nMDS plot to aid the visualisation of the grouping, P(perm) = significance level determined from PERMANOVA.*

Table 4: *Results of SIMPER showing percentage contribution and average abundance of Microzooplankton taxa to assemblage variance in experimental sandprawns treatments (control, 50% and 100%)*

Microzooplankton					
Control **Average similarity: 39.16**					
Taxon	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Harpacticoida	415.67	31.03	2.05	79.23	79.23
Ostracoda	65.00	4.49	0.67	11.47	90.70
Nematoda	22.67	3.35	1.92	8.54	99.25
Foraminifera	7.00	0.25	1.53	0.63	99.88
Polychaeta	1.00	0.05	0.58	0.12	100.00
50% **Average similarity: 87.89**					
Taxon	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Harpacticoida	310.67	69.71	18.71	79.32	79.32
Ostracoda	102.33	14.94	1.21	17.00	96.32
Nematoda	19.33	3.24	1.58	3.68	100.00
100% **Average similarity: 62.14**					
Taxon	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Harpacticoida	736.00	59.61	3.08	95.93	95.93
Ostracoda	54.67	2.16	0.73	3.48	99.41
Nematoda	19.00	0.37	0.58	0.59	100.00

Note: Av.Abundance = Average Abundance; Av.Sim = Average Similarity; Sim/SD = Similarity/Standard Deviation; Contrib% = Percentage Contribution; Cum% = Cumulative Percentage

Table 5: *Results of SIMPER showing percentage contribution and average abundance of mesozooplankton taxa to assemblage variance in experimental sandprawns treatments (control, 50% and 100%)*

Mesozooplankton

Control

Average similarity: 44.33

Taxon	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Harpacticoida	35.33	19.09	2.12	43.07	43.07
Calanoida	39.00	12.91	0.91	29.12	72.19
Nematoda	13.33	12.04	2.20	27.17	99.35
Ostracoda	1.00	0.29	0.58	0.65	100.00

50%

Average similarity: 58.96

Taxon	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Harpacticoida	39.33	40.24	4.88	68.25	68.25
Nematoda	18.67	16.78	18.85	28.45	96.70
Ostracoda	5.33	1.95	0.58	3.30	100.00

100%

Average similarity: 59.72

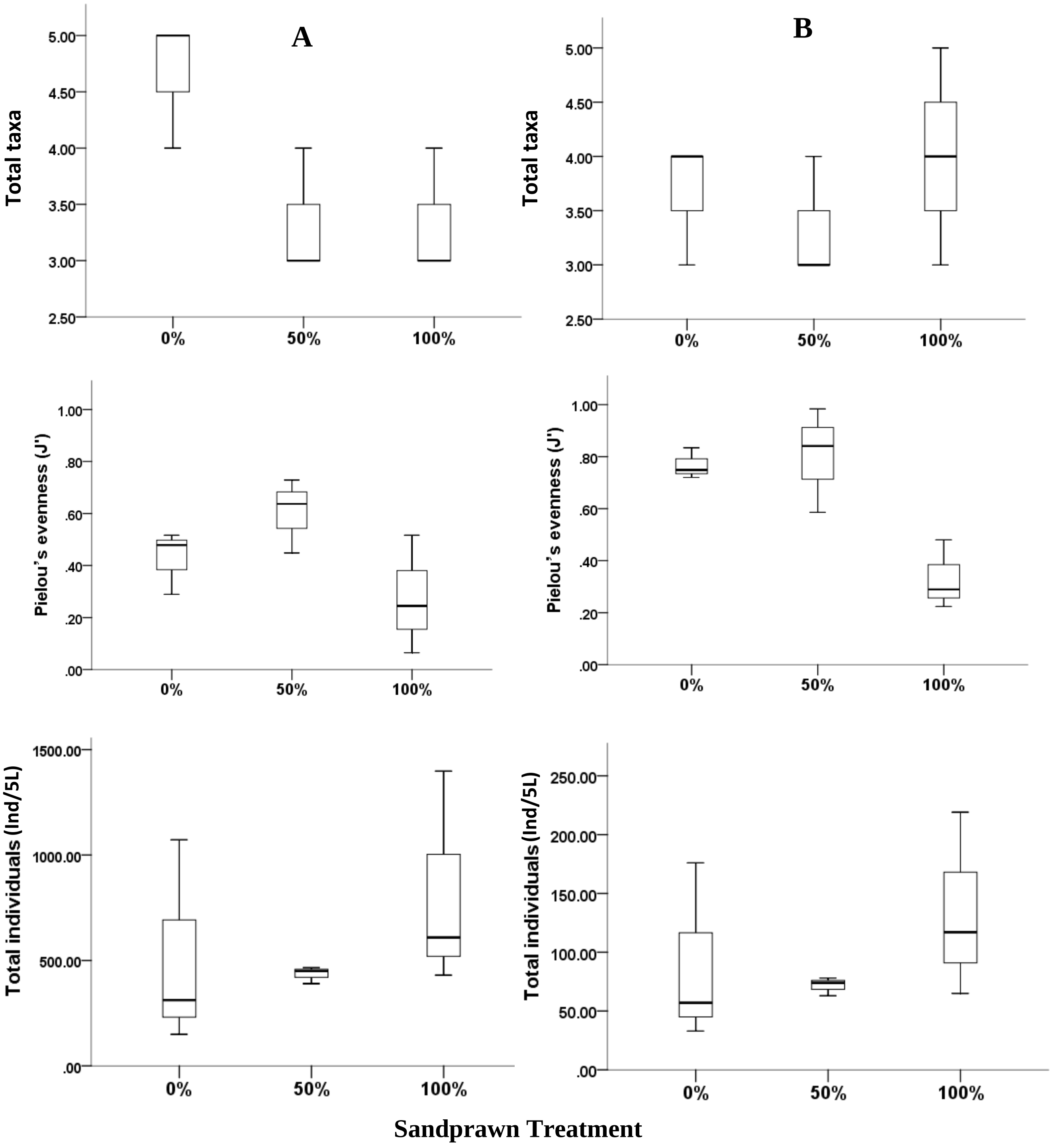
Taxon	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Harpacticoida	119.67	55.10	4.55	92.28	92.28
Nematoda	8.00	2.38	0.58	3.99	96.26
Ostracoda	4.00	2.00	3.86	3.34	99.61
Polychaeta	0.67	0.23	0.58	0.39	100.00

Note: Av.Abundance = Average Abundance; Av.Sim = Average Similarity; Sim/SD = Similarity/Standard Deviation; Contrib% = Percentage Contribution; Cum% = Cumulative Percentage

3.2.1 Diversity

Generally, variance in zooplankton community metrics was negligible in the study. Specifically, indices of the microzooplankton (Figure 4A) were statistically consistent across sandprawn treatments (Kruskal-Wallis Rank Test; taxa richness (H = 4.876, df = 2, p = 0.087, evenness (H = 3.200, df = 2, p = 0.202 and total abundance (H = 1.867, df = 2, p = 0.393)). A similar trend was apparent for mesozooplankton (Figure 4B), with taxa richness (H = 1.147, df = 2, p = 0.564), evenness (H = 5.600, df = 2, p = 0.061) and total abundance (H = 1.867, df = 2, p = 0.393) being statistically similar across sandprawn treatments.

It is noteworthy that the taxa richness for microzooplankton and evenness for mesozooplankton were marginally non-significant. Visually, mean taxa richness in microzooplankton was greater in controls relative to +sandprawn treatments (Figure 4). Evenness was lowest in 100% treatment for both microzooplankton and mesozooplankton assemblages. In terms of dominance curves, taxon dominance was greatest in 100% treatments, but declined in control and 50% sandprawn treatments in both microzooplankton (Figure 5A) and microzooplankton (Figure 5B) assemblages. From Figure 5, it is evident that for both micro- and mesozooplankton, the most numerically abundant taxa in the 100% sandprawn treatments were also more numerically dominant, based on their contribution to zooplankton community structure. In the 50% sandprawn treatments and controls, the most numerically abundant taxa decreased in their contribution to zooplankton community structure (i.e. dominance declined).


A
B
Total taxa
5.00
4.50
4.00
3.50
3.00
2.50
Pielou’s evenness (J')
1.00
.80
.60
.40
.20
.00
Total individuals (Ind/5L)
1500.00
1000.00
500.00
.00
250.00
200.00
150.00
100.00
50.00
0%
50%
100%
Sandprawn Treatment

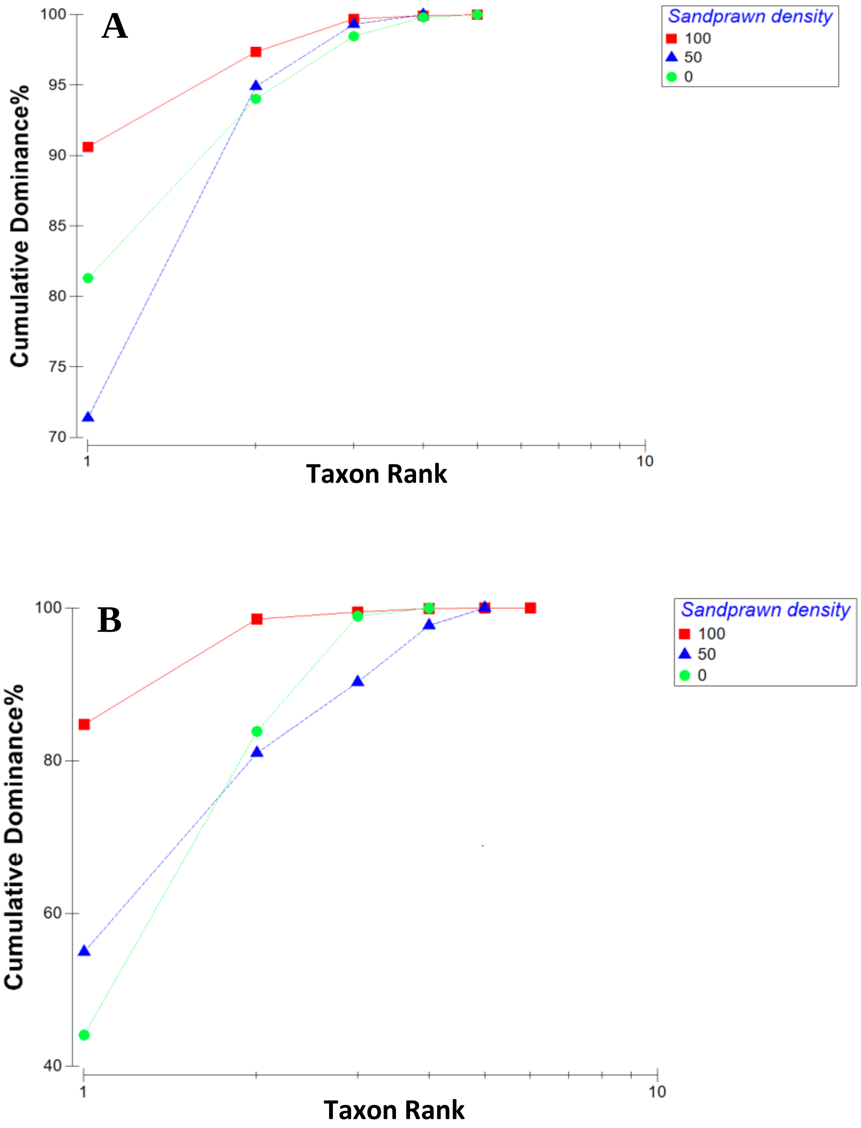


Figure 5: Dominance curves for microzooplankton (Figure 5A) and mesozooplankton (Figure 5B) assemblages based on total abundance from the nine mesocosms.

Discussion

4.1 General Discussion

This research examined the ecosystem engineering effects of sandprawns (*Callichirus kraussi*) on zooplankton assemblages (microzooplankton and mesozooplankton assemblages) to expand understanding of their role in benthopelagic linkages in estuarine ecosystems using laboratory mesocosm experiments. I hypothesized that *C. kraussi* bioturbation of the sediment would reduce phytoplankton abundance available to zooplankton assemblages (based on the findings of Venter *et al*. (2020) and therefore, expected negative bottom-up alteration of zooplankton assemblages in terms of taxa richness, evenness total abundance and overall taxonomic composition, given that phytoplankton is a key trophic resource for zooplankton (Carpenter *et al*., 1985; Chang *et al*., 2014; Elser & Goldman, 1991; Kibirige *et al*., 2002; Perissinotto *et al*., 2000, 2003). Overall, the experiment provided important insights on how sandprawns may affect zooplankton assemblages, but there were also methodological limitations that can affect interpretation of results. The first limitation is that the zooplankton assemblage at the start of the experiment was not known. Due to the limited sizes of mesocosms, sufficient water volumes could not be collected to assess start and end zooplankton assemblages in response to sandprawns. In hindsight, it would have been useful to use zooplankton samples from the estuary as an approximation of starting assemblages in experimental mesocosms. This is an aspect that should be considered in similar experiments in the future; alternatively, larger mesocosms need to be used, though this imposes additional practical challenges. The second logistical consideration is that while my initial aim was to assess effects of sandprawns on zooplankton assemblages, the assemblage used in the experiment was dominated by hyperbenthic organisms, likely due to the shallow, well-mixed nature of the Zandvlei Estuary at the time of collecting samples. At the onset of the experiment, there was no way of knowing that the zooplankton would be dominated mainly by hyperbenthic individuals, however, findings are still relevant in shedding light on responses of hyperbenthic-dominated zooplankton to sandprawns.

Findings from my experiment indicate that sandprawn densities had no significant effect on zooplankton assemblages as a whole, but there were discernible trends at the taxon level in microzooplankton and mesozooplankton assemblages. Specifically, the increase in *C. kraussi* density had a marginally non-significant effect on taxa richness (for microzooplankton) with an observable decline in this metric. Similarly, evenness (for microzooplankton) was marginally non-significantly affected by increasing sandprawn density, with values decreasing from the control to 100% sandprawn treatment. Cumulative dominance curves were consistently less steep (indicating high dominance) in the 100% sandprawn treatment for both the microzooplankton and mesozooplankton assemblages. For the nutrients, nitrite (NO_2^-) concentrations increased in the presence of *C. kraussi* **(Table 1).** In this study, 74-84% of the relative abundance of biotic responses variables was accounted for by total heterotrophic Bacteria (THB), *Prochlorococcus* (Cyanobacteria) and *E. coli* while 16-26% was accounted for by nanophytoplankton, picophytoplankton, cryptophytes and total phytoplankton cells. Nanophytoplankton, picophytoplankton and total phytoplankton declined with increasing sandprawn density and coincided with an increase in Harpacticoida in both microzooplankton and mesozooplankton assemblages. From control to +*C. kraussi* treatments the abundance of THB declined, the highest and lowest abundance of *Prochlorococcus,* and *E. coli* were recorded in 100% and 50% +*C. kraussi* treatments respectively.

The reduced rate of decline of total heterotrophic Bacteria (THB) in the +sandprawn treatments and the increasing abundance trend from 50% to 100% +sandprawn treatment for both *Prochlorococcus* and *E. coli,* and cryptophytes in the 50% sandprawn treatment suggests that these groups are resilient to filtration and bio-adsorption effects of sandprawn burrow walls, which could be attributed to faster turnover rate typically displayed by bacterial groups (Song *et al*., 2017). Bacteria are typically suited to temporarily fluctuating nutrient-rich environments (MacArthur & Wilson, 1967; Song *et al*., 2017) such as estuaries, which act as transitional zones between freshwater and marine environments, where variability in tides, waves, and changing salinity and sediment are significant (Potter *et al*., 2010; Thrush *et al*., 2013; Zapata *et al*., 2018). Thus, it is likely that the bacterial dominance in the water samples reflected their *in situ* abundance before the onset of the experiment in the laboratory. Also, it is possible that water filtration by *C. kraussi* was advantageous to bacteria. Specifically, phytoplankton reductions recorded previously (Venter *et al*., 2020) and in this study may have had promotive effects on bacteria. Similarly, declines in NO_2^- could also have indirectly benefitted bacteria. Overall, in my study, THB, *Prochlorococcus*, and *E. coli* appear least affected by increasing sandprawn abundance, with evidence of their resilience implied by increases in their abundance in some cases.

The reduction in picophytoplankton, nanophytoplankton and total phytoplankton cells in this study is similar to the results of Venter *et al*. (2020), who demonstrated the ability of sandprawns to filter phytoplankton from water with evidence supporting adsorption of phytoplankton onto the burrow walls. Because *C. kraussi* are deposit-feeders, the decline in the picophytoplankton and total phytoplankton cells in my study are likely to similarly be driven by phytoplankton adsorption onto burrow walls during irrigation/ventilation through bi-directional pumping (Venter *et al*., 2020). According to Venter *et al*. (2020), concentration of Chlorophyl *a* (Chl-a) along burrow walls of sandprawns were greater relative to surface sediments and controls. Similar findings have been reported by (Branch & Pringle, 1987; Moyo *et al*., 2017; Papaspyrou *et al*., 2005). The steady decline in abundance of pico-, nano- and total phytoplankton cells but positive effect on cryptophytes, suggests that adsorption of pelagic particles along sandprawn burrow walls may be selective, perhaps due to differences in sizes or other biological traits. The lack of a declining trend in cryptophytes and their increase in the 50% treatment may be attributed to their 10-50 µm size range, which is higher than the size range of picophytoplankton (0.2 – 2.0 µm) and nanophytoplankton (2.0 – 20 µm) (Hoef-Emden & Archibald, 2016; Lévêque, 2000; Smyth *et al*., 2019). The locomotion ability of cryptophytes may also explain the lack of declines in their abundance with increasing sandprawn density. Locomotion by means of flagella (Gołdyn & Kowalczewska-Madura, 2008b; Hibberd *et al*., 1971; Sleigh, 1991) may allow individuals to escape the water pumping activities of sandprawns and hence adsorption onto burrow walls.

My findings for the zooplankton component of the experiment contradicted my hypothesis of *C. kraussi* altering assemblages, primarily through negative bottom-up effects on phytoplankton. While the result deviated from the hypothesis at a community level, there were patterns at taxon levels indicating a sandprawn effect. It is important to note that the recorded zooplankton in this experiment all fall within the component of plankton referred to as the hyperbenthos (Dinning & Metaxas, 2013); these are organism that reside above the sediment surface (Mees & Jones, 1997; Snelgrove, 2013). The prominence of hyperbenthic organisms in the zooplankton assemblage in my study is likely explained by the open-mouth state of Zandvlei during the period when samples were collected, which resulted in significant declines in water levels. Shallow water depth in the sandprawn-dominated zone (less than 1 m) where water was collected for my experiment, likely explain the predominance of hyperbenthic taxa in the zooplankton assemblages in my experiment. Because the samples were collected at the lower reaches of the estuary (closer to the mouth), wave action and tidal influence likely lead to a strong coupling between the benthic and the pelagic zones. In the research study of Ubertini *et al*. (2012) on the spatial variability of bentho-pelagic coupling in an estuarine ecosystem, they agreed that strong physical factors and benthic macrofauna bioturbation control the pelagic components via resuspension in shallow water estuaries. Similar inferences were drawn in the review of the zooplankton and hyperbenthos of temporarily open and closed estuaries (TOCEs) in South Africa, with freshwater inflow and mouth phase being dominant ecological determinants (Froneman, 2002, 2006; Kibirige & Perissinotto, 2003; Schlacher & Wooldridge, 1995; A. Whitfield *et al*., 2012).

Microzooplankton and mesozooplankton assemblages in my experiment were numerically dominated by Harpacticoida, which generally showed positive responses to increases in *C. kraussi* density. This can mechanistically be explained by the change in plankton communities in the water column with increasing *C. kraussi* densities, which would influence the composition of zooplankton, based on other studies (Gołdyn & Kowalczewska-Madura, 2008b). In addition, distinct benthic conditions created by sandprawn burrowing may additionally explain the dominance of Harpacticoida with increasing sandprawn abundance. The greater Chlorophyl *a* (Chl-*a*) levels along burrow walls reported for sandprawn relative to surface sediments (Venter *et al*. 2020) may favour Harpacticoids. Greater Chl-a levels in burrow walls have also been reported in several other studies (Branch & Pringle, 1987; Moyo *et al*., 2017; Papaspyrou *et al*., 2005). Furthermore, macrofaunal burrows in marine sediment has been shown to have stimulatory effect on microbial metabolic activities (Reichardt, 1988), with other studies reporting higher abundance of bacteria along the burrow walls compared to the surrounding sediments (Kinoshita *et al*., 2008). Given that Harpacticoida are predominantly benthic, the increase in abundance of this group in the plankton could be due to greater phytoplankton and bacterial material along burrow walls in the presence of sandprawns. Apart from increases in benthic burrow trophic resources, it is possible that Harpacticoida benefitted from other pelagic trophic resources that increased with increasing density of *C. kraussi*. Within the water column, *E. coli*, *Prochlorococcus* and cryptophytes (to a smaller extent) increased in abundance with increasing sandprawn density. It is possible therefore that the increase in Harpaticoida could be due to the increases in the above-mentioned pelagic resources. These pelagic resources fall within the wide range of food resources of harpacticoids, which are known to have complex feeding habits and sometimes referred to as "indiscriminate feeder" (Buffan-Dubau & Carman, 2000; Hicks & Coull, 1983; Montagna *et al.*, 1995). This is suggestive of Harpacticoida displaying high trophic plasticity which potentially offers an advantage over the other zooplankton taxa present in my experiment.

Ostracoda and Nematoda were generally the second-most abundant taxa in both the micro- and mesozooplankton samples but were more abundant in the microzooplankton assemblage. From the result of this experiment, intermediate sandprawn density resulted in increased Ostracoda abundance and that of Nematoda in microzooplankton and mesozooplankton assemblage respectively. Like Harpacticoida, Ostracoda and Nematoda are predominantly benthic dwellers with wide trophic plasticity (Arashkevich, 1977; Cannon, 1934; Kornicker *et al*., 1976; Liperovskaya, 1948; Modig *et al*., 2000; Smith *et al*., 2015) and could positively benefit from the activities of increasing sandprawn density, as discussed to explain the increasing dominance of Harpacticoida with greater sandprawn density.

The diversity metrices for both microzooplankton and mesozooplankton were expected to be influenced negatively by the influence of increasing density of *C. kraussi* on phytoplankton abundance. This is similar to ideas on deposit-feeder effects on benthic organism, where a combination of habitat alteration and declines in trophic resources can alter assemblages (Bouma *et al*., 2009; Jones *et al*., 1997; Lohrer *et al*., 2004; Pillay, 2019; Pillay & Branch, 2011; Reise, 2002; Rhoads, 1970). However, such ideas can be extended for hyperbenthic zooplankton considering their dependence on benthic environments and processes occurring therein. However, in my experiment, there were no clear indications of sandprawn effects on zooplankton diversity metrics. Changes in dominance of taxa were observed in my study; in the microzooplankton, some taxa (Foraminifera and Polychaeta) disappeared with increases in sandprawn density relative to control levels. This is indicative of their sensitivity to sandprawn presence. Evenness declines in this study, though marginally non-significant statistically, is reflective of the increase in dominance of Harpacticoida.

4.2 Conclusion

Findings of this study have shown that *C. kraussi* had no significant effects on microzooplankton and mesozooplankton at the community level but effects on the dominance of individual taxa in both assemblages were apparent. Only three taxa; Harpacticoida, Ostracoda and Nematoda were found consistently present in both microzooplankton and mesozooplankton assemblages. Taxa dominance was highest at maximum (100%) density of *C. kraussi*, with assemblages being increasingly dominated by one taxon viz. the Harpacticoida. This may be due to (1) an overall decline in phytoplankton and picoplankton cells with increasing sandprawn density, and (2) a general similarity in the pelagic bacterial components, with some trophic components increasing idiosyncratically with sandprawn density (eg. *E. coli*).

This research suggests a need to further investigate the influence of ecosystem engineering by sandprawns on zooplankton assemblages, particularly in the context of shifts in dominance in zooplankton assemblages. Understanding such effects as well as the underlying driving mechanism, will shed light on the consequences of sandprawn ecosystem engineering on marine ecosystems (particularly shallow estuarine and lagoonal systems). In general, the findings in this experiment suggests that benthic ecosystem engineering is not limited to sedimentary components of ecosystems but may extend to generate subtle effects on zooplankton taxa. To my knowledge, this is the first direct evidence indicating that bioturbating sandprawns can influence zooplankton assemblages (albeit subtly), possibly through impacts on food resource availability, resulting in shifts in taxon dominance.

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