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Sand Prawns Mitigate the Impact of Prolonged Drought on the Biology of a Temporary Open/Closed Estuary

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Abstract: The role of the sand prawn, *Callichirus kraussi* (Stebbing, 1900), as an ecosystem engineer was evaluated using a three-month-long caging experiment during a prolonged drought in the lower reaches of the temporarily open/closed Kasouga Estuary along the eastern seaboard of South Africa. The current study indicates that at intermediate densities, the burrowing activities of the sand prawn contributed to a significant increase in the microphytobenthic algal concentrations and a concurrent increase in the abundance and biomass of the macrofauna ($P < 0.05$ in all cases). The increase in macrofauna abundance and biomass could largely be ascribed to the elevated densities of the gastropod, *Nassarius kraussianus* which were sustained by the elevated microphytobenthic biomass. As such, the sand prawn *Callichirus kraussi* was established to be an important ecosystem engineer as the results indicate that intermediate densities of the sand prawn may locally contribute to increases in the biology even during those periods when the system is stressed, in this case, the prolonged drought.

Keywords: Ecosystem engineers; bioturbation; sand prawn; drought

1. Introduction

Ecosystem engineers are organisms that change the state of matter, both biotic and abiotic, by altering their environments through bioturbation [1–4]. The mixing and alteration of sediment structure in coastal habitats is thought to be the primary drivers of biodiversity as they have a fundamental effect on the environment [5]. Bioturbation facilitates the dispersal of particles in sediments, modifies geochemical cycling alters food sources, and alleviates the transport of water and gaseous exchange in soils [6]. Because bioturbators modify the availability of resources to other species, they are viewed as ecosystem engineers [5]. Bioturbation, therefore, affects the physical (by constructing burrows, mound construction, ploughing of the surface, and trampling) and chemical (the mixing of water and solutes) characteristics of soft-sediment habitats [7,8] which promotes food availability, species recruitment, increases oxygenation and mineralization and modifies the distribution of microalgae and species composition of macrofaunal species [2,4,9–12].

The South African coastline is numerically dominated by temporarily open/closed estuaries (TOCEs) that under natural conditions, are periodically separated from the marine environment by a sandbar at the mouth [13–16]. The duration of this separation is largely a function of rainfall within the catchment area and the extent of the sandbar [17]. During periods of drought, TOCEs may be separated from the marine environment for periods exceeding 12 months [13,16]. Mouth status plays an important role in determining the physical properties of the water column and consequently, the biology within these systems [18]. Temporarily open/closed estuaries are generally characterized by low species richness [19] due to the lack of recruitment opportunities for marine breeding species into these systems and the fact that many marine species are incapable of completing their life cycles in these systems [12]. Moreover, extreme variability in physico-chemical factors such as temperature

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and salinity, typically recorded within these systems can pose physiological constraints on many species, particularly freshwater and marine representatives [20,21].

The sand prawn, *Callichirus kraussi* (Stebbing, 1900), has been identified as a key component of the macrobenthic fauna in soft sediment nearshore marine environments and estuaries, including TOCEs along the southern African coastline. [1,22]. Densities of sand prawn are highly variable and may attain levels of up to 100 ind m^{-2}. Sand prawns create burrows extending over 1m into the sediment, bringing the sediment to the surface where it is deposited in volcano-like mounds [23, 2]. The burrowing activity of the sand prawn modifies the sediment's biogeochemical properties, particularly pore-water, nutrients, and gaseous exchange between the sediment and water column and sediment granulometry and erodability [2,4,12]. Sand prawns modify nutrient cycles in the sediments and water column [24] and also contribute to the alteration of sediment texture (digenesis), mixing of water and solutes (bio-irrigation), and the displacement of non-living organisms [25]. Bioturbation fuels plankton primary production by releasing nutrients from sediments into the water column [9]. The direct release of nutrients, as well as nutrient cycling, are both enhanced by bioturbation through sediment oxygenation and an increase in the surface area available for microbial production and activity [7]. Therefore, bioturbation changes the dispersion deepness of organic matter and can raise the food stock and quality in sediments for deposit feeders. In addition to having a noticeable impact on bacteria, microalgae, meiofauna, macrofauna, and seagrasses in estuarine environments, sand prawns play a significant role in the structuring of soft-bottom communities through their sediment reworking activities [10,24,26,27]. Studies have shown that the presence of sand prawns can lead to a decrease in the abundance of macrofauna due to direct physical disturbances or competition for space and resources [28]. However, in other cases, they can promote biodiversity by creating habitats that are more favorable to certain species [29]. For instance, the presence of sandprawn burrows can provide shelter for small invertebrates or offer an oxygenated refuge in otherwise anoxic sediments [10].

Global climate change along the southern African coastline has been implicated in the increased incidence of extreme weather events including storm activity, increased wave height, and prolonged droughts [32,33]. These events are likely to have a far-reaching effects on the ecosystem functioning of TOCEs within the subregion [32,34] Much of the Eastern Cape province of South Africa experienced a severe drought from 2015 to 2019 which contributed to the prolonged mouth closure of TOCEs within the region [33]. The current investigation was conducted to assess the role of the sand prawn, *C. kraussi*, as an ecosystem engineer under conditions of prolonged mouth closure in a temperate TOCE located along the southeastern coastline of South Africa. The study was conducted employing a 16-week-long caging experiment set up in the lower reach of a temperate temporarily/open closed estuary in the Eastern Cape province of South Africa

2.Study Site

This study was conducted in the lower reach of the medium-sized warm-temperate Kasouga Estuary located on the south-eastern coastline of South Africa which enters the Indian Ocean at 33^{0} 39′ 17′′ S 26^{0} 44′ 08′′ E [35,36]. Its surface area and width are estimated at 22 hectares and 150m, respectively and the estuary is navigable for about 2.5 km with its main channel depth varying between 0.5 m and 2 m [37]. This system is considered to be pristine and in good ecological condition due to limited agricultural activities within its 39 km^2 catchment area [38,39]. Due to limited freshwater inflow because of a small catchment area, the Kasouga Estuary receives limited freshwater which consequently results in low levels of macronutrients entering the system [40]. Compared to permanently open estuaries in the region, Kasouga Estuary supports low levels of phytoplankton (< 2.0mg Chl-a m-3) and zooplankton biomass (< 15 mg dwt m-3) [39]. The zooplankton community is numerically and dominated by copepods such as the *Pseudodiaptomus hessei* and *Paracartia longipatella* [41,42]. Additionally, benthic communities in TOCEs typically include diverse macrofaunal and meiofaunal assemblages such as polychaetes, amphipods, mollusks (e.g., gastropods like *Nassarius kraussianus*), and crustaceans, including the burrowing sand prawn (*Callichirus kraussi*) [10,11].

Microphytobenthic communities, such as benthic diatoms, also play a significant role in primary production nutrient cycling through bioturbation and organic matter decomposition [12].

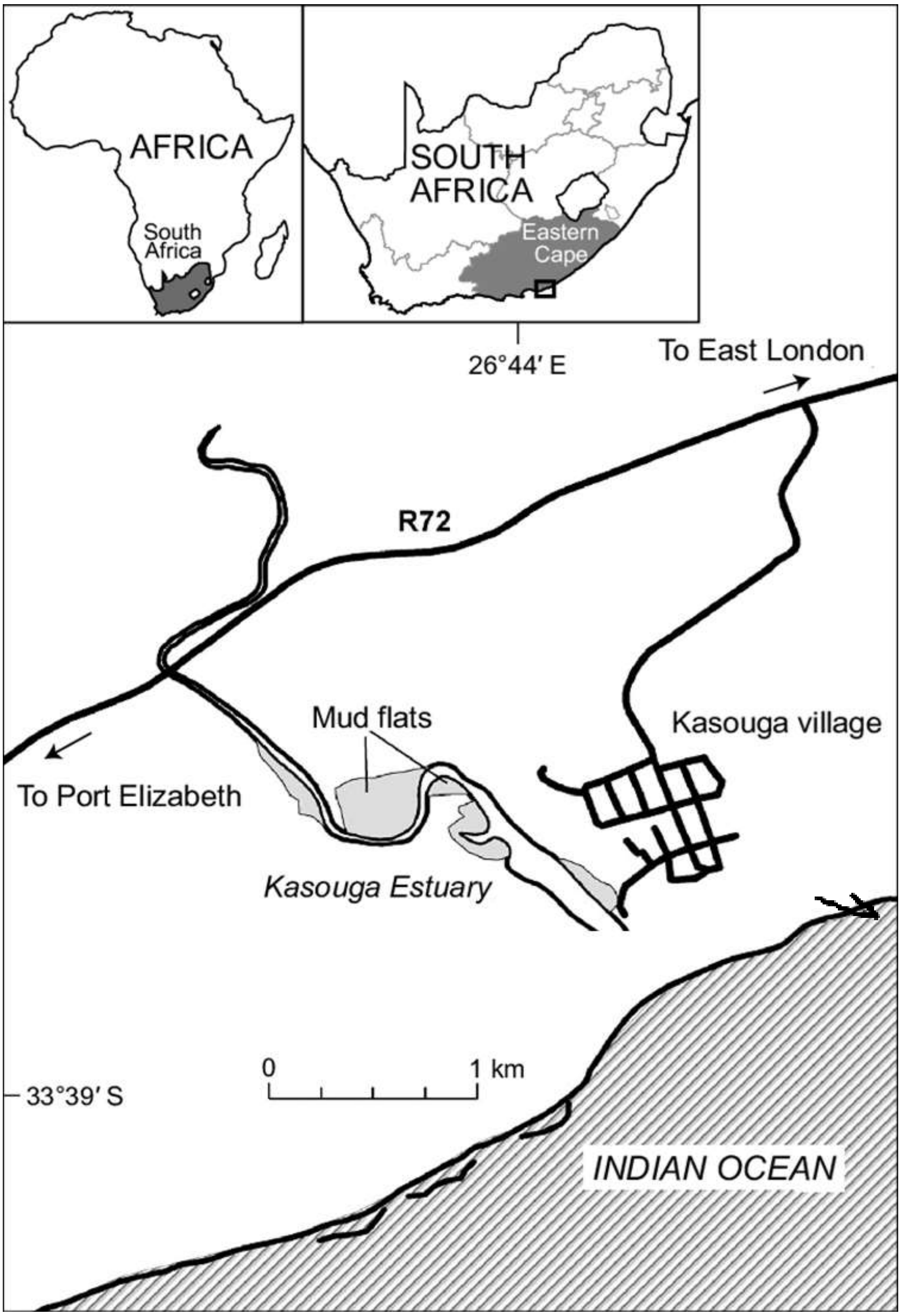

Figure 1. Geographic location of Kasouga Estuary along the southern African coast (after Froneman, 2013). The caging experiment was conducted in the lower reach of the system.

3. Materials and Methods

Caging experiments were conducted in the lower reach of the temporarily open/closed Kasouga Estuary. Manipulations were conducted over a period of three months from 1 January to 15 March 2020. The densities of the sand prawn in the lower reach of the system where the experiment was conducted ranged from 5 to 36 and m^{-2} (determined by counting the number of active burrows- data not shown). Stainless steel open-topped cages with dimensions of 50 cm × 50 cm × 30 cm, with 1 mm mosquito netting on the bottom and sides, were buried in the sediment, leaving ≈10 cm protruding

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above the sediment, in the lower reaches of the estuary and were filled with sun-dried sand collected from the edge of the estuary 48 hours before the study to ensure faunal absence at the onset of the study. The cages were not roofed, since this would affect their colonization from the water column and would alter the light environment. Three weeks after installing the cages, sand prawns of between 43 to 54 mm standard length (mean = 44.3 ± 5.35 mm), were collected from the lower reach of the estuary using a prawn pump. Four treatments were prepared. For the control, prawns were absent from the cages. For Treatment 1, 5 prawns were added, Treatment 2, 10 prawns, and for Treatment 3, 20 prawns were added to each of the cages. Three replicates were prepared for each treatment. Cages were monitored weekly to ensure that prawn densities in the various treatments remained constant. Densities of the prawn within the cages were assumed to correspond to the number of burrows [9]. At the end of the experiment, bioturbation by the sand prawn, microphytobenthic algal concentrations, and the abundance, biomass and community composition of the macrobenthos (epifauna and infauna) were determined as described below.

3.1. Bioturbation

Centrifuge tubes, 10 cm long with a mouth of 0.78 cm^2, were employed as sediment traps to estimate bioturbation by *C. kraussi*. The aspect ratio (length: diameter) of each tube was 10:1, considered the optimum value to prevent re-suspension of trapped sediments [44]. Tubes were buried vertically, leaving ~2 cm protruding above the sediment surface. Tubes were sealed after 1 h and the sediment in each was extracted and dried at 60 °C for 24 h and weighed using a Sartorius microbalance. The amount of sediment within each tube was employed as an index of sediment erodability and expressed as g cm^{-2} h^{-1} [44]

3.1.1. Microphytobenthic Algal Concentrations

Microphytobenthic algal concentrations were determined by collecting a sediment surface sample in the upper 1 cm of the sediment from each cage using a polycarbonate tube. The tubes were sealed and kept in the dark in a cooler box until their return to the laboratory and were stored at −40 °C freezer in the dark with 30 ml 90% acetone until processing. Total microphytobenthics chlorophyll a (Chl-a) concentrations were then determined fluorometrically using a Turner 10-AU fluorometer before and after acidification [45]. Microphytobenthic Chl-a concentrations were expressed as µg Chl a cm^{-2}.

3.1.2. Epifauna and Infauna Community Structure

To compare the macrobenthic community structure of the epifauna and infauna in the different treatments, the sediment in the cages was collected at the end of the experiment and sifted through a 1 mm mesh on site. The organisms collected were preserved in 70% alcohol and transported to the laboratory. Species composition was identified to the lowest taxon using identification keys [46]. Epifaunal and infaunal abundances were expressed as ind. m^{-2} (epifauna) or ind. m^{-3} (infauna), wet biomass per cage, expressed as g wwt m^{-2} (epifauna) or g wwt m^{-3} (infauna). Wet weight was determined by removing excess water from the animals using blotting paper and weighing to the nearest 0.1g using an Sartorius electronic balance. .

4. Statistical Analysis

To test for significant differences between the various treatments, a one-way ANOVA was employed. *Post hoc* Tukey test was then used to determine the sources of variation. Species diversity was calculated using Simpson`s diversity index (1-D). Non-metric Multi-Dimensional Scaling (MDS) was then employed to compare the macrofaunal community structure in the various treatments. Finally, Analysis of Similarity (ANOSIM) test was employed to detect the degree of similarity between the various treatments and to identify which species accounted for the differences between

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the various groupings identified in the MDS. Data analysis was conducted using the statistical packages, Statistica version 8, Past version 4, Minitab, and Microsoft Excel.

5. Results

The estuary remained closed throughout the duration of the caging experiment because of the protracted drought within the region. Due to the presence of an extensive sandbank at the mouth of the system, no overtopping events were recorded over the duration of the caging experiment.

5.1. Bioturbation

Bioturbation rates in the control cages (prawns excluded) ranged between 0.018 and 0.031 g cm^2 h^{-1} (mean = 0,025 g cm^2 h^{-1}, SD=0.006). By contrast, the bioturbation rates in Treatment 1 ranged from 0.018 to 0.039 g cm^2 h^{-1} (mean = 0,030 g cm^2 h^{-1}, SD= 0.009) and between 0.047 and 0.058 g cm^2 h^{-1} (mean = 0,053 g cm^2 h^{-1}, SD= 0.005) in Treatment 2. The mean bioturbation rate in Treatment 3 was 0.076 g cm^2 h^{-1} (range 0.065- 0.093 g cm^2 h^{-1} , SD = 0.013, Figure 2(a)). ANOVA indicated that the bioturbation rates in Treatments 2 and 3 were significantly higher than those recorded in the Control and Treatment 1 ($F= 29.78$, $P < 0.001$). There were no significant differences in the bioturbation rates between Treatment 2 and Treatment 3 ($P> 0.05$). Similarly, the bioturbation rates in the Control and Treatment 1 were not significantly different from one another ($P > 0.05$).

5.1.1. Microphytobenthic Algal Concentrations

Total microphytobenthic algal concentrations in the control cages ranged from 0.06 to 0.104 µg chl-a cm^{-2} (mean = 0,089 µg chl-a cm^{-2} , SD = 0.016) (Figure 2b). Microphytobenthic algal concentrations in Treatment 1, ranged from 0.094 - 1.203 µg chl-a cm^{-2} (mean = 0,627 µg chl-a cm^{-2} , SD= 0.61) from 0.047 to 0.058 µg chl-a cm^{-2} (mean = 0,058 µg chl-a cm^{-2} , SD= 0.018) in Treatment 2 and from 0.065 to 0.093 µg chl-a cm^{-2} (mean = 0,032 µg chl-a cm^{-2} , SD= 0.007) in Treatment 3, (Figure 2(b)). ANOVA revealed that there was a significant difference between all treatment groups (F= 3,48, P< 0.05,).

5.1.2. Macrobenthic Abundances

Total macrobenthic abundances in the control cages varied from 68 to 203 ind m^{-3} (mean = 127 ind m^{-3} ,SD=67.8), while in Treatment 1 the values ranged between 98 and 254 ind m^{-3} (mean = 18 ind m^{-3} 1, SD=68.8). In Treatment 2, the total macrobenthic abundances ranged between 38 to 72 ind m^{-3} with (mean =56.7 ind m^{-3} ,SD=14.7) and between 38 and 53 ind m^{-3} (mean = 46.5 ind m^{-3}, SD=6.7) in Treatment 3 (Figure 2c). One-way ANOVA indicated that the total macrobenthic abundances did not differ significantly between the Control and the various treatments (F=6.7, P=0.006, figure 2(c).

5.1.3. Macrobenthic Biomass

Macrobenthic biomass in the Controls and Treatment 1 ranged from 4.92 to 8.14 mg wwt m^{-3} (mean =6.20 mg wwt m^{-}, SD = 1.48) and between 9.18 and 18.5 mg wwt m^{-3}, (mean = 13.2 mg wwt m^{-}, SD = 3.88), respectively. In Treatment 2 the macrobenthic biomass ranged from 3.06 to 4.18 mg wwt m^{-3} (mean = 3.80 mg wwt m^{-}, SD = 0.508) while in Treatment 3 it ranged between 1.95 and 3.18 mg wwt m^{-3} (mean =2.56 mg wwt m^{-}, SD = 0.642) (Figure 2(d)). ANOVA indicated that the total macrobenthic biomass in Treatment 1 was significantly higher than that recorded in Treatments 2 and 3 (F=21.4, P< 0.001).

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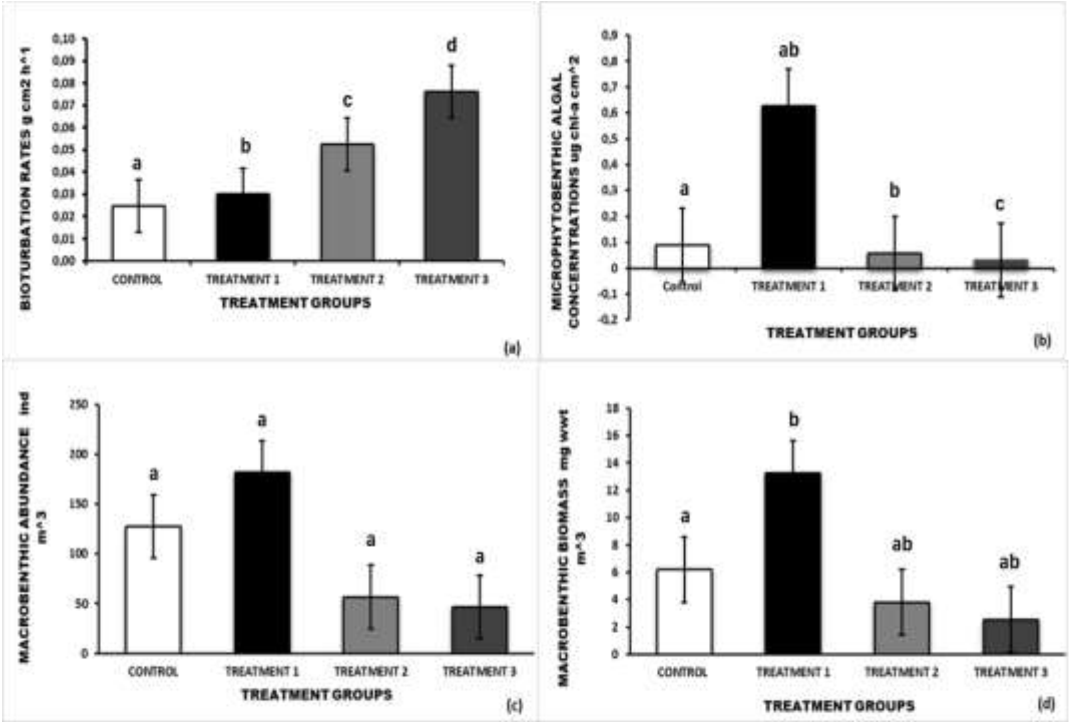

Figure 2. (a) Sediment bioturbation rate, (b) macrophytobenthic algal concentrations, (c) macrobenthic abundance, (d) macrobenthic biomass in various treatments in Kasouga estuary. Error bars denote SD. Different letters indicate a significant difference (ANOVA, $P < 0.05$).

5.1.4. Epifaunal and Infaunal Community Structure

The epifaunal species recorded in the cages included three species of isopods: *Pontogeloides latipes*, *Apanthura sandalensis*, and *Exosphaeroma estuarium*, one species of amphipod, *Grandidierella lignorum*, two bivalve species, *Solen capensis* and *Donax serra*, and two polychaete species, *Lumbreneus tetaura* and *Marphysa sanguinea*. The epifaunal species included *Nassarius kraussianus*, *Ceratonereis* species, *Cirolana* species, and *Nephtys* species. The most common infaunal species were the isopods *E. estuarium* and *P. latipes*, and the amphipod *G. lignorum*, while the most common epifaunal species was *N. kraussianus*. The least common species were the bivalves *Donax serra* and *Solen capensis*. There were no significant differences in the community structure of epifaunal and infaunal species between the control and treatment groups ($F = 16.29$, $P = 1.13E\text{-}23$).

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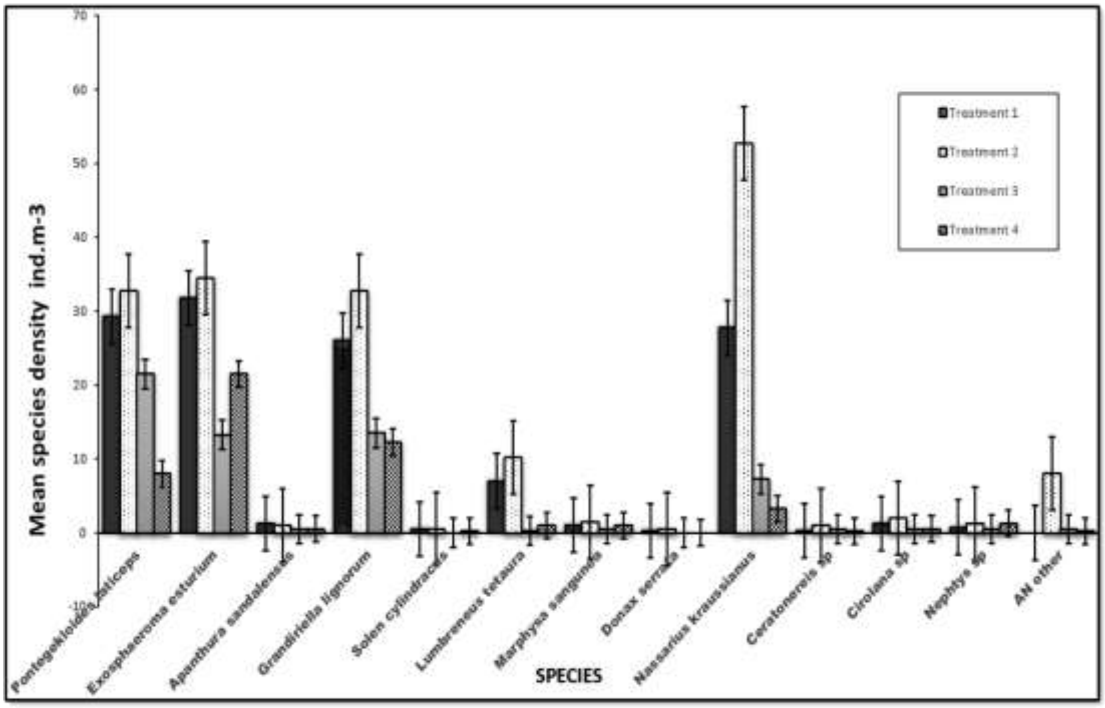

Figure 3: Mean species density in four treatments ((T1- Control- 0 ind/m², T2- 5 ind/m², T3- 10 ind/m², T4- 20 ind/m²) in the Kasouga Estuary. Error bars denote SD.

5.1.5. Bray Curtis Cluster Analysis

At the 70% similarity level, hierarchical cluster analysis identified two distinct groupings, designated Groups 1 and 2. Group 1 largely comprised the Control and Treatment 1 samples, while Group 2 comprised samples from Treatments 2 and 3 (Figure 5). One of the replicates for Treatment 2 was identified as an outlier. ANOSIM indicated that the differences between the two groups was significant (R=0.37, P= 0.008). The most prevalent epifaunal species was *Nassarius. kraussianus*, whereas the most prevalent infaunal species were the isopods Exosphaeroma *estuarium* and *Pontegekloides latipes,* as well as the amphipod *Grandiriella. lignorum*. The two bivalves, *Donax serra* and *Solen capensis,* were the least common species among the infauna.

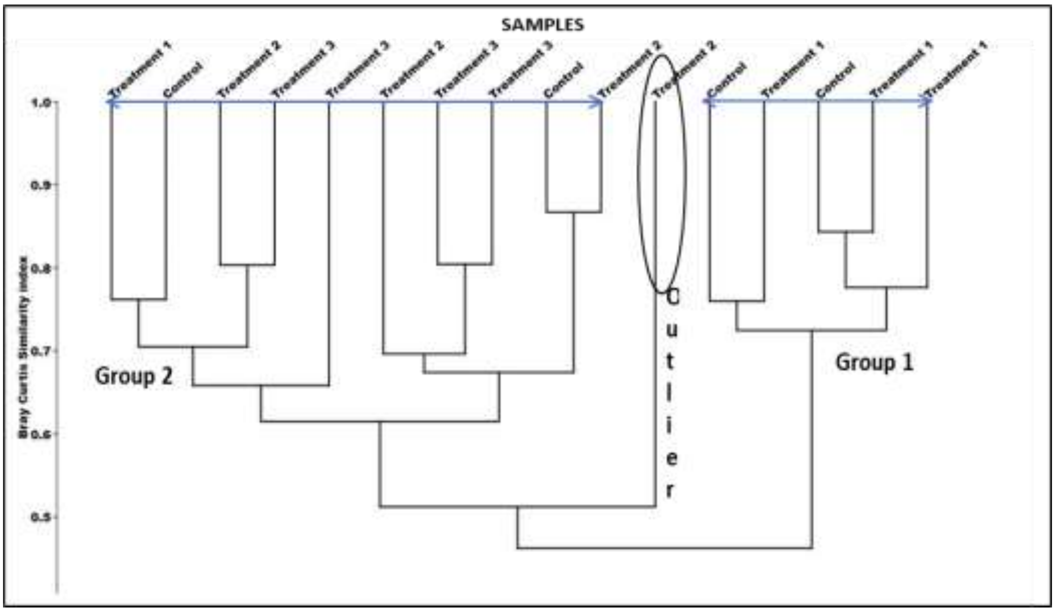

Figure 4. Multi-dimensional scaling (MDS) hierarchical cluster plot, showing Bray-Curtis similarity for the different treatments. Blue lines on the dendrogram indicate different groups and the outlier is circled.

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Table 1. Showing SIMPER analysis for the most abundant infauna and Epifaunal species with their contributions to the Bray Curtis cluster groupings.

Species	Mean Abundance (Group 1)	Mean Abundance (Group 2)	Average Dissimilarity	% Contribution	Cumulative %
Nassarius kraussianus	35	13.67	12.6	27.7	27.7
Pontegekloides laticeps	45.5	25.33	9.069	19.94	47.64
Exosphaeroma esturium	28	20.67	8.475	18.63	66.27
Grandiriella lignorum	30.67	19.67	7.876	17.32	83.59

SIMPER analysis indicated that *Nassarius kraussianus* was the most influential species, contributing 27.7% to the dissimilarity between the groups, with *Pontegekloides laticeps* having a higher mean abundance in Group 1. *Exosphaeroma esturium* and *Grandiriella lignorum* also contribute significantly to the differences between the groups, with contributions of 19.9%, 18.6%, and 17,3 %. respectively.

6. Discussion

Historically, studies on estuarine ecosystem functioning of temporarily open/closed South African estuaries have largely focused on the importance of freshwater inflow, sediment characteristics, and mouth status in determining biological community structure within these systems [16,43–45]. There is now, however, a growing appreciation of the importance of non-trophic interactions in driving community dynamics within these systems [47]. Ecosystem engineers have emerged as one of the forms of non-trophic interactions responsible for shaping communities and ecosystems within shallow water marine ecosystems [26,48–51]. The current study was conducted to assess the role of the sand prawn, *Calianassa kraussi* as an ecosystem engineer in a TOCE during a prolonged drought which contributed to the Kasouga Estuary along the south-east coastline of South Africa being separated from the marine environment for a period exceeding 12 months.

Studies carried out in several southern African TOCEs have demonstrated that the maximum estimates of biology are typically attained during the closed phase of the system following freshwater inflow [4,26,52–54]. The estimates of total microphytobenthic alga biomass and macrobenthos abundance and biomass recorded during the current study were reduced compared to previous studies conducted in TOCEs in the same region [26,53]. The lower estimates can likely be attributed to the prolonged mouth closure which limited the recruitment of marine breeding species into the system and low macronutrient availability conferred by the low freshwater inflow resulting from the prolonged drought within the region [54,55]. The macrobenthic community structure observed during the present study is in agreement with previous investigations both within the same estuary and indeed, inTOCE's within the same biogeographic region [4,47,49,52,54]

The increased rates of bioturbation recorded with the increase in the density of *C. kraussi* observed during the caging experiment is not unexpected and likely contributed to the decline in the total microphytobenthic algal concentrations within the cages (Figure 1(b)). A notable exception was recorded in Treatment 1, where a significant increase in microphytobenthic algal concentration was recorded over the duration of the caging experiment. The reduced microphytobenthic algal concentrations observed in Treatments 2 and 3, can likely be ascribed to the re-suspension of sediments by the burrowing activities of the prawn which creates an unfavourable light environment and ultimately bury the microphytobenthic algae [4,8,53]. The burrowing activities of sand prawn have been demonstrated to modify nutrient cycles in the sediments and water column of shallow water ecosystems [24]. Thus, the observed increase in microphytobenthic algal concentrations in Treatment 1 can possibly be attributed to the increased availability of macronutrients due to the burrowing activities of the sand prawn.

Total macrofaunal abundances and biomass within the different treatments generally decreased with increased sand prawn density (Figures 3 and 4). Again, a notable exception was recorded in Treatment 1 where the values increased. The observed patterns in Treatments 2 and 3 can possibly be ascribed to reduced food availability (microphytobenthic algae) or an attempt of macrofauna to avoid being buried by settling sediment due to the bioturbating activities of sand prawns [2,11]. Indeed, it is worth noting that differences in the groupings identified with the numerical analyses could largely be attributed to changes in the abundances of mobile components of the macrobenthos including the tick shell, *Nassarius kraussianus* and the isopod, *Exospheroma hylocoetes*. The decrease in macrofaunal abundance and biomass due to increased sand prawn densities during this investigation corresponds with similar studies conducted in other shallow water ecosystems and indeed within the same system [4,28,53,57]. For instance, [10] proposed that the reduction in surface microalgal development brought about by *C. kraussi's* reworking of sediments resulted in enhanced food intake by *N. kraussianus* and decreased food uptake by *E. paupercula*. This is because the physical disturbance of the sediment surface, direct consumption, and competition for nutrients create an environment that is less favorable for microalgal growth, which ultimately results in a reduction in microalgal biomass.

The elevated concentrations of microphytobenthic algae in the Control and Treatment 1 coincided with elevated abundances and biomass of the macrofauna (figure 1 a, b, c, and d). (Figures 5 and 6). Bioturbation generated by sand prawns at low densities has been demonstrated to enhance macrofaunal abundances and species richness [58]. The increase in abundances and biomass of macrofauna observed in Treatment 1 could mainly be attributed to an increase in the abundance of *N. kraussianus* which were likely sustained by the elevated biomass of microphytobenthos [4,10].This result suggests that the effect of *C. kraussi* burrowing activities in shaping macrofauna within the study estuary was density-dependent [46]. Therefore, at higher sandprawn densities, production declines which in turn decreases the macrofauna in the experimental cages [59–61].

7. Conclusions

In agreement with previous studies, the results of the caging experiment indicate that the sand prawn can be considered a key ecological engineer in TOCE along the South African coastline. Importantly the caging experiments suggest that the burrowing activities of the sand prawn at low/medium densities may locally mitigate the adverse effects of prolonged mouth closure of TOCE by contributing to increased concentrations of microphytobenthic algae which sustain elevated abundances and biomass of macrofauna.

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Conflicts of Interest: There is no conflict of interest to declare.

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