




Temporal shifts in key mangrove crab species linked to biotic and abiotic factors at a latitudinal range limit

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ABSTRACT

Mangroves in South Africa occur at a southern latitudinal limit (33°12'51" S, 27°34'54" E) where distribution is influenced by global climate change. Mangroves are experiencing poleward expansion, affecting the distribution of associated macrofauna. Monitoring surveys have been conducted for South African mangrove macrofauna, with research focusing on drivers of ocypodid crabs rather than grapsoid crabs, despite the key role of grapsoids in this ecosystem. Using uni- and multivariate models, we investigated (i) changes in brachyuran community over time (2016 vs 2023), (ii) the potential biotic (food availability, brachyuran diversity and abundance) and abiotic (sediment, water and geographic parameters) factors influencing occurrence and abundance of three co-occurring mangrove crabs (*Austruca occidentalis*, *Neosarmatium africanum* and *Cristarma eulimene*) along the east coast of South Africa, and (iii) the potential distribution of these three species under climate change scenarios. Brachyuran community structure changed significantly over time (2016–2023) at all mangrove sites sampled ($df = 1$, pseudo- $f = 13.95$, $p < 0.05$). Overall, the presence and abundance of all three species were influenced by total brachyuran abundance and diversity, with latitude also influencing the occurrence of these crabs. Specifically, *A. occidentalis* occurrence was correlated with sediment organic matter and importance values of mangrove tree species to forest structure, while temperature, salinity and sediment moisture influenced their abundance. The presence and abundance of both sesarmids were driven by microphytobenthos and salinity, while temperature influenced abundance. Both climate change scenarios (SSP245 and SSP585) projected future shifts in distribution of all three crab species, with warmer temperatures and increased rainfall patterns expanding habitat suitability of sesarmids in a poleward direction while contracting fiddler crab ranges. This study highlights the ongoing and future impacts of climate change in South African mangroves and their associated macrofauna, suggesting a projected poleward expansion in response to climate change. Additionally, this study highlights future distributional shifts of mangrove associated crabs that can likely alter coastal ecosystem dynamics.

1. Introduction

Occurring along coastlines at tropic and subtropic latitudes, mangrove forests are ideal indicators of rapid climate change (Alongi, 2015; Hickey et al., 2017). Mangroves are woody trees and shrubs that form highly productive forest (Friess et al., 2023). However, due to climate change (i.e. rising temperatures and sea-levels), mangroves are experiencing a poleward shift in distribution and extending latitudinally in regions such as North and South America (Comeaux et al., 2012; Raabe et al., 2012; Bianchi et al., 2013; Osland et al., 2013; Yao et al., 2022) and countries such as Australia (Rogers et al., 2005; Williamson et al., 2011), New Zealand (Stokes et al., 2010), China (Durango-Cordero et al., 2013) and South Africa (Saintilan et al., 2014; Adams and Rajkaran, 2021; Raw et al., 2022).

In South Africa, mangrove forests occur in sheltered low energy estuaries from subtropical Kosi Bay in the north, to the temperate Tyolomnqa at their southernmost distributional limit (Naidoo, 2016; Rajkaran and Adams, 2016; Peer et al., 2018a). These mangrove forests

provide essential ecosystem services (Rajkaran and Adams, 2016), such as coastal protection (Donato et al., 2011), improvement of water quality (McLeod et al., 2011), sequestration of carbon (Johnson et al., 2020) and serve as refugia and a nursery habitat for many birds, fish and invertebrates (Raw et al., 2017; Whitfield, 2017; Peer et al., 2018a, Keur et al., 2019). Despite their protection status and socioecological importance, South African mangroves experience major anthropogenic setbacks such as wood harvesting, reduction of freshwater inputs, urbanisation, damaging agricultural practices, cattle grazing and pollution (Naidoo, 2016; Adams and Rajkaran, 2021). These impacts, along with the effects of climate change can alter the quality and quantity of ecosystem services offered and impacts biodiversity of associated fauna, especially macrofauna. Furthermore, climate-induced changes, such as sea-level rise and increased storm frequency, threaten the structural integrity of mangroves, leading to potential habitat loss (Gilman et al., 2008; Alongi, 2015). Shifts in temperature and precipitation patterns may also disrupt growth, reproduction, and the distribution of mangrove species, further compromising their resilience (Alongi, 2015;

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Osland et al., 2017; Fazlioglu et al., 2020)

Mangrove forests host abundant macrofauna, with the dominant groups being molluscs and brachyurans (true crabs) (Lee, 2008). These groups are important for ecological functioning of mangroves and serve as essential food links in estuarine food web structures (Lee, 1998, 2008; Werry and Lee, 2005; Nerot et al., 2009). Brachyuran crabs are the most diverse group and are key species in shaping mangrove forests (Cannicci et al., 2008), as they aerate soil, aid in mangrove tree establishment, recycle nutrients and contribute to the overall biodiversity of mangrove forests (Steinke et al., 1993; Lee, 2008). Macnae (1963) conducted the first review of South African mangroves and described crab community structures at various zones within mangrove forests. Almost fifty years later, Peer et al. (2018a) conducted a second review, recording poleward shifts in mangroves and associated macrofauna, and highlighting the need for continued monitoring of these habitats occurring at their latitudinal range limits to understand changes occurring amidst global climate change. Poleward expansions of mangroves have been recorded along the east coast of South Africa (Quisthoudt et al., 2013; Whiffeld et al., 2016; Peer et al., 2018a; Adams and Rajkaran, 2021; Raw et al., 2022), with mangroves often encroaching into adjacent saltmarshes (Saintilan et al., 2014; Adams, 2020; Yando et al., 2021; Adams and Rajkaran, 2021). However, there are only a few records of the poleward expansion of mangrove-associated macrofauna (Peer et al., 2015; van Niekerk et al., 2022). These include the molluscs *Cerithidea decollata* and *Littoraria subvittata* (Peer et al., 2018a), and crabs *Austruca occidentalis*, *Tubuca urvillei*, *Macrophthalmus grandidieri*, *Neosarmatium africanum* and *Cristarma eulimene* (Branch et al., 2017; Peer et al. 2015, 2018a; Ma and McQuaid, 2021).

Mangrove brachyurans comprise of two superfamilies: Ocypodoidea crabs (i.e. fiddler crabs) and Grapsoidea crabs (i.e. sesarmids) (Nobbs, 2003). The spatial distribution of these crabs in South Africa is generally well known (Macnae, 1963; Peer et al., 2014; Peer et al., 2018a). However, studies understanding factors that influence their spatial distribution are limited. Additionally, the few studies that have been conducted only considered fiddler crabs, whose local spatial distribution patterns can be attributed to both biotic and abiotic factors (Peer et al., 2018b; Theron et al., 2022). Whereas factors influencing local spatial distribution patterns of grapsoid crabs i.e. sesarmids remain largely unknown. Sesarmids are generally more abundant and diverse compared to ocypodid crabs in mangrove ecosystems (Lee, 1998) and are considered key species as they can alter both the substrate and mangrove tree structure (Dahdouh-Guebas et al., 1997), facilitate energy recycling (Gao et al., 2024) and nutrient flow (Lee, 1998). Sesarmid species such as *Neosarmatium africanum* and *Cristarma eulimene* are common crabs in east African mangroves and often co-occur with the fiddler crab *Austruca occidentalis*. These three species are found on the landward fringe of mangrove forests, where *C. eulimene* spends more time on the surface alongside *A. occidentalis*, while *N. africanum* spends most of their time in their burrows (Peer et al., 2019). These sesarmids, specifically *N. africanum*, are known to predate, compete and even intimidate this fiddler crab, however, interactions between these key species have rarely been studied (Peer et al., 2019).

Aside from local drivers, climate-induced changes in precipitation and temperature are expected to influence mangrove distribution (Gilman et al., 2008; Ward et al., 2016; Ximenes et al., 2016; Osland et al., 2017; Simard et al., 2019). It is likely that these changes will also influence the distribution of associated macrofauna. Many studies have shown that climate-induced changes can influence the distribution of mangrove crabs (Fusi et al., 2015; Cannizzo and Griffen, 2016; Riley and Griffen, 2017; Mos et al., 2017; Sharifian et al., 2020; Sharifian et al., 2021a,b; Yousefi and Naderloo, 2022; Gu et al., 2023). However, little is known about the future projection of mangrove-associated crabs in the face of climate change in South Africa.

This study aimed to (i) investigate changes in mangrove brachyuran community structure following the last dedicated survey from Peer et al. (2018a), (ii) investigate biotic and abiotic drivers of three key

co-occurring crab species (*Austruca occidentalis*, *Neosarmatium africanum* and *Cristarma eulimene*), and (iii) determine the future distributional shifts in these three crabs under two different climate change scenarios. It was hypothesized that.

- (i) Brachyuran community structure has significantly changed over time (2016 (Peer et al., 2018a) vs 2023).
- (ii) Occurrence and abundance of three key crab species are influenced by both biotic (microphytobenthos, tree density, pneumatophore density, total abundance and diversity of crabs) and abiotic (canopy cover, water and soil characteristics, latitude) factors
- (iii) The distribution of the three key crab species expands further south in response to projected climate change scenarios.

2. Methods and materials

2.1. Study sites

Eight mangrove sites were surveyed along the east coast (KwaZulu-Natal and Eastern Cape provinces) of South Africa (Fig. 1), representing a latitudinal gradient of faunal and floral diversity. These sites were selected with the aim of replicating a past survey (Peer et al., 2018a). Mangrove sites, ranging between 1.3 and 118 ha in area, occur within four different estuarine types, with *Avicennia marina*, *Bruguiera gymnorhiza* and *Rhizophora mucronata* being the three dominant mangrove species (Table S1). From these eight estuaries, five fall within protected areas. The largest mangrove site in this study was Mngazana while the smallest mangrove site was Tyolomnqa. Although six mangrove stands occur naturally, two (Nahoon and Tyolomnqa) are planted mangrove stands (Hoppe-Speer et al., 2015). Sampling was carried out during the summer (February) and the winter (August) of 2023. In the summer (January) of 2024, only one site (Tyolomnqa) that was not sampled in the summer of 2023 was revisited. Within each site, five subsites were chosen to account for variation within sites. All data were collected during low tide.

2.2. Field work and laboratory analysis

2.2.1. Mangrove tree characteristics

The point-center quarter method was used to gather mangrove tree data (Mitchell, 2010; Theron et al., 2022). A 30 cm pole was randomly placed in each subsite, and the four closest mangrove trees to this pole were included in the field sample. The mangrove species, distance from the point (m), height (m), and circumference at breast height (CBH in m) of each mangrove tree was recorded. The distance from the pole and height of the mangrove trees were measured using a retractable measuring tape while CBH was measured at 1.3 m above the ground using a measuring tape (Theron et al., 2022). The CBH was converted to diameter at breast height (DBH in cm) (Mitchell, 2010). Thereafter, the relative dominance (%), relative frequency (%) and relative density (%) was derived to determine the importance value (IV) of each mangrove species, which represents how dominant each species in relation to each other (Mitchell, 2010; Theron et al., 2022). The IV can range between 0 and 300, with the highest values indicating that a species is well represented either through size or density (Mitchell, 2010). At each subsite, three 50 × 50 cm quadrats were randomly placed to measure pneumatophore density, expressed as pneumatophores per m². The canopy cover of each subsite was determined by taking three photographs from beneath the canopy, with the angle of the camera perpendicular to the soil. These images were then converted into binary images on ImageJ to determine the canopy cover percentage (Theron et al., 2022).

2.2.2. Physicochemical variables

At each subsite, a sediment corer was used to excavate to a minimum

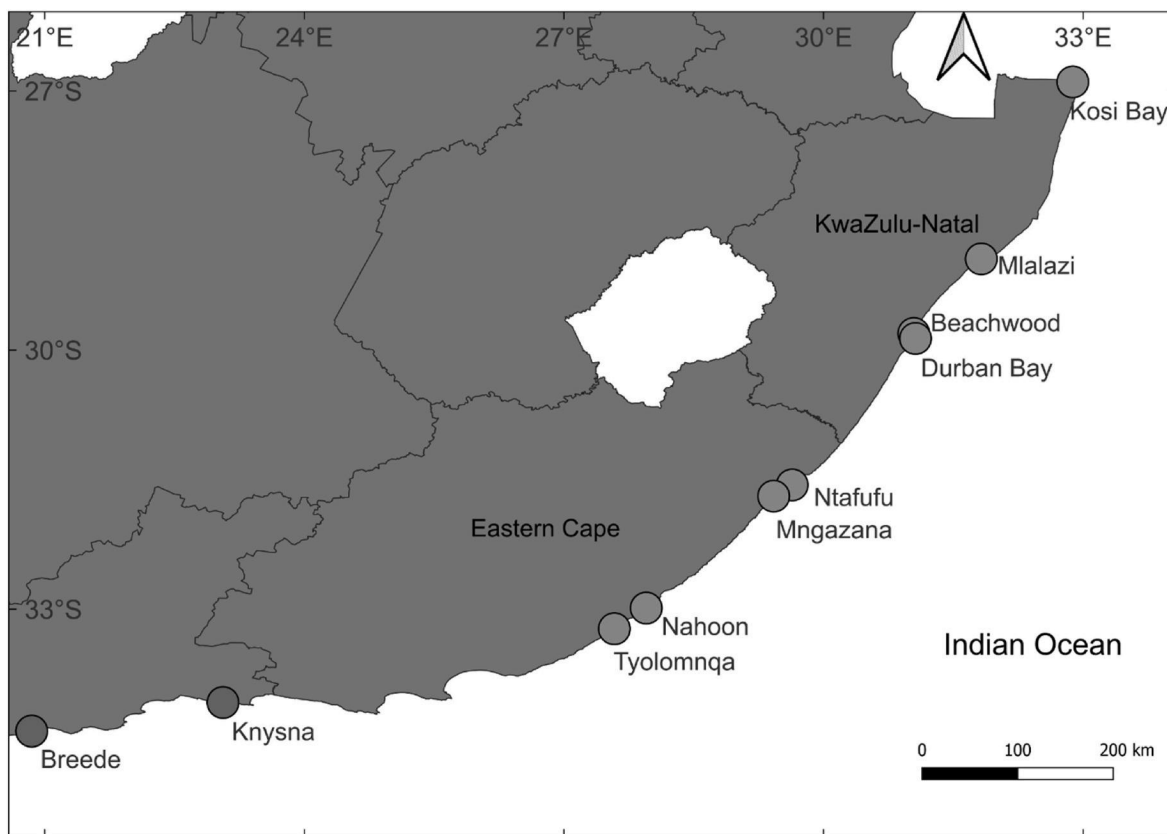


Fig. 1. Mangrove sites (represented by blue circles) located in the Eastern Cape and KwaZulu-Natal provinces and other sites mentioned in this study (represented by green circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

depth of 15 cm to collect porewater data (pH, salinity and temperature) using a Hanna HI9829 multiparameter probe (Hanna Instruments, Woonsocket, RI). Approximately 100 g of surface sediment was collected in a Ziplock bag and kept in a cool, dark place until laboratory analyses of sediment grain size, sediment organic matter, sediment moisture content, pH and salinity were done (following protocol from Rajkaran and Adams, 2012; Adams and Human, 2016). Sediment grain size was ranked from 1 to 5 based on percentage contribution of grain sizes, i.e. 1 = clay, 2 = clay/silt, 3 = silt, 4 = silt/sand, 5 = sand (Peer et al., 2018a).

To determine microphytobenthic (MPB) chlorophyll-a concentrations, three sediment cores (approximately 2 cm deep) were collected at each subsite using a 2 cm diameter corer and kept frozen until laboratory analysis. In the laboratory, 15 ml of 95% ethanol was added to each sediment sample, thereafter, chlorophyll-a was extracted for 12 h in a cold, dark room ($\sim 2^{\circ}\text{C}$). The extract was filtered through a 1.2- μm glass

microfibre filters (Munktell® MGC) to remove any sediment. The absorbance of the filtered extract before and after acidification with 1N of HCl, was read using a Thermo Scientific GENESYS 10S UV-Vis spectrophotometer at a wavelength of 665 nm.

2.2.3. Mangrove macrofauna data

Mangrove brachyurans were sampled using three randomly placed 50×50 cm quadrats within each subsite at all sites. Crabs within each quadrat were identified and counted, and their densities were standardized to individuals per m^2 , then averaged for each subsite. Tree-climbing brachyurans were counted on the four closest mangrove trees (Theron et al., 2022). The World Register of Marine Species (<https://www.marinespecies.org/>, accessed October 2023) was used to verify species names. The three mangrove-associated crabs being investigated in this study are presented in Fig. 2.2. *Austruca occidentalis* is a widely distributed fiddler crab species in the Indo-West Pacific

a. *Austruca occidentalis*



b. *Neosarmatium africanum*



c. *Cristarma eulimene*



Fig. 2. Three mangrove-associated crabs (a–c) being investigated in this present study. All photos are listed on iNaturalist (<https://www.inaturalist.org/>).

(Naderloo et al., 2016). While *Neosarmatium africanum* and *Cristarma eulimene* are Western Indian Ocean sesarmid species (Guerao et al., 2011; Ragionieri et al., 2012) distributed along the east coast of Africa. The largest of the three crabs is *N. africanum* with a carapace width between 20 and 50 mm followed by *C. eulimene* (15–35 mm) and *A. occidentalis* (15–25 mm) (Branch et al., 2017).

2.2.4. Statistical analysis

To quantify the abundance of brachyurans, counts from 50 × 50 cm quadrats were converted to individuals per m². Quadrats were averaged per subsite, with the subsite as a replicate to account for variation within each mangrove forest. To compare brachyuran community structure between past (Peer et al., 2018a) and present data at all sites, a permutational multivariate analysis of variance (PERMANOVA) (Anderson et al., 2013, Anderson et al., 2017) was performed (R Core Team, 2024, R version 4.3.3. “Angel Food Cake”). These data were checked for homogeneity. The data were square root transformed, thereafter, a Bray-Curtis resemblance matrix was generated. The two factors considered were time (2016, 2023) and sites (Kosi Bay, Mlalazi, Beachwood, Durban Bay, Ntafufu, Mngazana, Nahoon and Tyolomnqa). Where significant values were found amongst sites, a pairwise comparison was conducted. Species richness, Shannon-Wiener diversity (*H'*) and Pielou's evenness (*J'*) were also calculated for each site and year.

To investigate factors that influence the distribution of three selected crab species (*A. occidentalis*, *N. africanum* and *C. eulimene*), the presence/absence and abundance data were analysed. The factors considered as possible drivers of the presence/absence and abundance of these three crabs—porewater, sediment and mangrove tree characteristics, brachyuran data, food availability, estuarine dynamics, and geographic location—are presented in Fig. 3. Of these factors, estuarine dynamic data were obtained from the Council of Scientific and Industrial Research national database through SANBI (<https://bgis.sanbi.org/>, accessed April 2024) (Raw et al., 2022). These factors were included as they have been found to influence mangrove tree establishment within estuaries (Raw et al., 2022) and would likely influence the distribution of their associated macrofauna (Meijer et al., 2021).

A variance inflation factor (VIF) analysis was conducted to test for collinearity amongst variables. Variables with a VIF above 3 were removed from the main model (Zuur et al., 2009), with the exception of

the importance values of trees (IVA, IVB, IVR) and tree density. Variables removed were brachyuran richness, porewater and sediment pH, daily flushing rate, mean annual runoff, estuary mouth state (opened or closed) and floodplain area (>3). Thereafter, no variables showed collinearity. To determine which factors influenced the abundance and presence or absence of these three crabs, a generalised linear model (GLM) was performed, with univariate models used to determine species-specific relationships (Wang et al., 2012; Peer et al., 2018b). Multivariate abundance and presence data were analysed using the ‘mvabund’ package (Wang et al., 2012). For the abundance data, the ‘negative.binomial’ family was used while for the presence/absence data, the ‘(binomial.(link = “logit”))’ family was used. Model assumptions were evaluated by examining plots of residuals versus fitted values to assess normality and homogeneity (Wang et al., 2012). Akaike Information Criterion (AIC) scores were compared across various models, and the model with the lowest AIC was chosen as the revised ‘full’ model (abundance = 2440.06; presence/absence = 370.77) (Zuur et al., 2009).

2.2.5. Maxent distribution

To model distribution shifts of the three selected species under current and future (SSP245 and SSP585) climate change scenarios, maximum entropy (Maxent) modelling was utilized (Phillips, 2005). The SSP245 scenario is where protection measures are undertaken with medium challenges to adaptation and mitigation, while the SSP585 can be termed the ‘high road’ where there are low adaptation and high mitigation challenges (Riahi et al., 2017). Maxent, a species distribution model software, has been used worldwide to model current and future distributions of numerous marine species (Shahparian et al., 2017; Silva et al., 2019; Wang et al., 2018; Sharifian et al., 2021a,b; Yousefi and Naderloo, 2022; Lawson et al., 2023). In this study, maxent models were used to predict possible future habitats that are suitable for each species and distribution of the three selected crabs under climate change scenarios, to better manage and conserve mangrove macrofauna and mangrove ecosystems. A species distribution model such as Maxent only requires two data inputs: species occurrence data and environmental data. Species occurrence data (*A. occidentalis*, *N. africanum* and *C. eulimene*) were collected during this study, from published papers (Macnae, 1963; Peer et al., 2018a; Theron et al., 2022) and from the

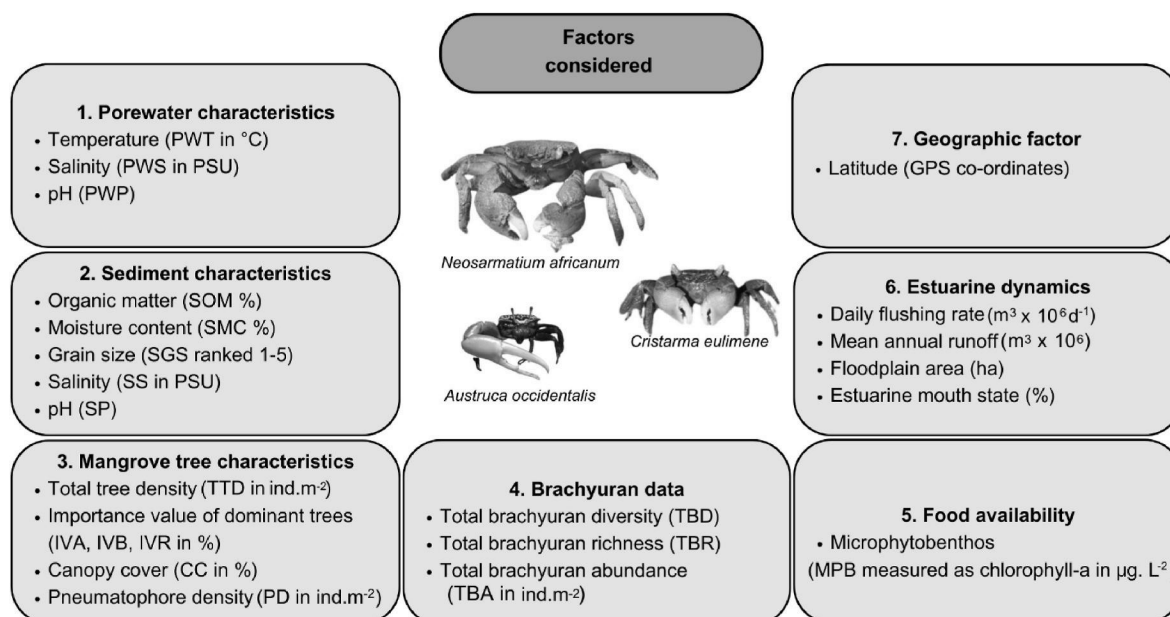


Fig. 3. Factors considered to influence the occurrence and abundance of three selected key crab species (*Austruca occidentalis*, *Neosarmatium africanum* and *Cristarma eulimene*) in South African mangroves (Peer et al., 2018b; Theron et al., 2022).

Global Biodiversity Information Facility (GBIF) platform (<https://www.gbif.org/>, accessed March 2024). The environmental data for the current and future (SSP245 and SSP585) conditions consisted of the max, min and mean for both temperature and precipitation. The current conditions were downloaded from WorldClim and the future projection conditions were obtained for the year 2050 (2041–2060) under the Shared Socioeconomic Pathways SSP245 and SSP585 (https://www.worldclim.org/data/cmip6/cmip6_clim5m.html, accessed May 2024). All environmental data were downloaded at 5-min arc. These data were obtained as GeoTiff files, cropped with a South African extent and converted into ASCII files using the “raster” package in R (Hijmans, 2024) before being used in model simulations in Maxent v 3.4.1 (Phillips, 2005).

A projection model was run with a 25% testing set and 75% training set, using the current distribution of the three crabs as a baseline simulation, and the two future climate change scenarios (SSP245 and SSP585) as the projection layers. The model was run with linear, quadratic and hinge features, with a ‘logistic’ output. Jack-knife tests of variable importance were used as a measure of model performance as well as the area under the curve (AUC). To map the distribution, Maxent logistic outputs (ASCII) were overlaid with estuarine location data (csv file), from Kosi Bay in the north to Breede River further south (total number of estuaries included = 255). Breede River Estuary was chosen as it occurs approximately 200 km away in a SE direction from Knysna Estuary where a fiddler crab (*A. occidentalis*) was previously observed (Peer et al., 2016). Logistic output values (0–1) were extracted for each estuary and mapped in QGIS. To determine the expansion, contraction or stability of each species (*A. occidentalis*, *N. africanum*, *C. eulimene*), the maximum sum of specificity and sensitivity (MaxSSS) was used under the three climate conditions (current, SSP245, SSP585) (Lawson et al., 2023). Logistic values for each estuary (n = 255) that were greater than the MaxSSS for each species under each climate condition were considered as suitable habitat for expansion, contraction or stability. This was converted into a percentage of suitable habitats (McQuillan and Rice, 2015; Lawson et al., 2023).

3. Results

3.1. Temporal changes in brachyuran community structure

Overall, 19 species of brachyurans were recorded in South African mangroves between past and present surveys (Table 1). However, only 14 species were recorded from the eight mangrove sites sampled during this study (Table 1). The most common species found at all sites was *N. africanum*, while the least common species were *Macrophthalmus grandidieri* and *Eurycarcinus natalensis*, occurring only at Mngazana. The species that had the highest abundance at half (4 out of 8) of the sites was *A. occidentalis*, except for in Beachwood and Durban Bay where *N. africanum* and *Parasesarma capensis* dominated respectively, and in Nahoon and Tyolomnqa where *A. occidentalis* was absent. Most notably, this study recorded a new southern distributional limit for two fiddler crab species, *Paraleptuca chlorophthalmus* and *Tubuca urvillei*, at Tyolomnqa Estuary (Table 1).

Generally, the mean abundance (no. ind. m⁻²) of brachyurans was higher in the present study compared to the past survey, except for three sites i.e. Ntafufu, Nahoon and Tyolomnqa (Table 1). The fiddler crab *Gelasimus hesperiae*, that was previously observed in Mlalazi, Durban Bay and Mngazana during the past survey was not found at these sites during this present study. The fiddler crabs *A. occidentalis*, *P. chlorophthalmus* and *T. urvillei* observed in Nahoon (past) were also absent from this site in this present study. Other species that were absent during this present study were *Metopograpsus thukuhar* and *Metopograpsus messor*.

A PERMANOVA revealed that brachyuran community structure changed significantly (df = 1, Pseudo-F = 13.946, p = 0.001) over time (2016 vs 2023). A pairwise comparison revealed that brachyuran

communities at all sites were also significantly different (p < 0.05). Community structure was also different amongst all sites (df = 7, Pseudo-F = 13.923, P = 0.001).

3.2. Biophysical drivers of three selected species

The significant abiotic and biotic factors influencing the occurrence and abundance of *A. occidentalis*, *N. africanum* and *C. eulimene* are displayed in Table S2. In terms of tree-associated variables, *A. marina* and *B. gymnorhiza* both had importance values reaching 300, while *R. mucronata* only reached a maximum of 275. Sediment moisture content and sediment organic matter ranged from 12% to 63% and 8.9% and 83% respectively. The lowest temperature was 18 °C and the highest was 26 °C. Salinity had a maximum of 38 PSU and minimum of 1 PSU.

From the species-specific univariate GLM (Table 2), latitude, total brachyuran diversity and abundance positively influenced the presence/absence of all three species (*A. occidentalis*, *N. africanum* and *C. eulimene*). Microphytobenthos and salinity only influenced the two sesarmids (*N. africanum* and *C. eulimene*), with microphytobenthos having a positive correlation with both species, and salinity having a positive relationship with *C. eulimene* and negative relationship with *N. africanum*. In terms of tree-related variables, tree density and IVB were significant for the presence of *C. eulimene* while IVA was an important variable for *N. africanum* and *A. occidentalis*, explaining 7% and 25% of the total deviance respectively.

The abundance of all three species was influenced by temperature, salinity, total brachyuran diversity and abundance (Table 3). Salinity and total brachyuran diversity had a positive correlation with all species, with total brachyuran diversity contributing to the highest deviance in *A. occidentalis* (40%) and *N. africanum* (16%). Sediment moisture only influenced the abundance of *A. occidentalis* with a deviance of 6%. *Cristarma eulimene* was the only species to be influenced by sediment grain size, specifically, clay/silt and silt textures had a negative correlation with abundance and silt/sand had a positive correlation (Fig. 4b). Microphytobenthos had a significantly negative influence on the abundance of *N. africanum* and *C. eulimene* but did not have any significant influence on the abundance of *A. occidentalis* (Fig. 4a). Mangrove tree characteristics (tree density, canopy cover, importance values of mangrove trees and pneumatophore density) had no significant influence on the abundance of these three species.

3.3. Current and future distribution of three selected species

To understand the relative importance of each environmental predictor (temperature and precipitation), the permutation importance values (%) for each species under each climate scenario is presented in Table S3. Under the current climatic scenarios, precipitation had the highest permutation importance for both sesarmids, *Neosarmatium africanum* (56.7 %) and *Cristarma eulimene* (85.3 %), while temperature had the highest permutation importance for the fiddler crab, *Austruca occidentalis* (100 %). However, under the SSP245 and SSP585 climate scenarios, precipitation had the highest permutation importance for all three crab species.

Under the current climate scenario, the fiddler crab *A. occidentalis* has the most suitable habitats available from Kosi Bay in the north to Breede in the southeast, whereas the sesarmids, *N. africanum* and *C. eulimene*, share similar suitable habitats, ranging from Kosi Bay to Tyolomnqa (Fig. 5a, b, c). Under the SSP245 climate scenario, the suitable habitats for *A. occidentalis* decreases, while the suitable habitats for the two sesarmids, *N. africanum* and *C. eulimene* increases in a southeasterly direction (Fig. 5d, e, f). Although suitable habitats for *A. occidentalis* decreases, four estuaries further south from still remain suitable for this species, namely, Lottering, Bloukrans, Sout-Oos and Groot-Wes. These four estuaries are also suitable habitats for *N. africanum* and the former two estuaries (Lottering and Bloukrans) are suitable habitats for *C. eulimene*. However, under the SSP585 climate

Table 1
 A comparison of crab abundances (no. ind. m⁻²) between past (2016) and present (2023) data sets at eight sampled sites. Past data obtained from Peer et al., (2018a). Species richness, Shannon-Wiener diversity (H) and Pielou's evenness (J') are displayed for each site and year. P indicates the presence of a species where no quadrat data was available.

Species	Kosi Bay		Mlalazi		Beachwood		Durban Bay		Ntatufo		Mngazana		Nahoon		Tyolomnqa	
	2016	2023	2016	2023	2016	2023	2016	2023	2016	2023	2016	2023	2016	2023	2016	2023
Grapsoidae -																
<i>Neosarmatium africanum</i>	3.2 (1.27)	1.2 (0.73)	0.26 (0.18)	10.7 (2.13)	1.25 (0.49)	22.4 (3.92)	0.2 (0.14)	1.33 (1.07)	9.3 (1.22)	5.07 (5.07)	0.4 (0.16)	5.47 (2.78)	2.8 (0.51)	1.87 (0.87)	0.58 (0.43)	0.53 (0.31)
<i>Parasesarma capensis</i>	1.1 (0.62)	60.7 (10.2)	0.3 (0.3)	0.67 (0.65)	1.25 (0.57)	4.27 (2.8)	0.2 (0.14)	22.67 (4.68)	-	-	1.3 (0.54)	38.8 (8.15)	-	-	-	-
<i>Parasesarma catenatum</i>	-	-	1.4 (1)	4 (2.1)	-	-	-	12.93 (4.61)	15.6 (4.68)	12.13 (2.94)	10.5 (1.74)	26.27 (7.27)	4.5 (0.85)	15.06 (5.52)	5.58 (2.09)	12.64 (7.02)
<i>Parasesarma leptosoma</i>	-	-	-	-	-	-	-	-	-	9.07 (4.03)	-	2.13 (0.99)	-	-	-	-
<i>Cristarma eulimene</i>	-	-	3.2 (1.47)	7.5 (3.53)	12.08 (4.82)	13.3 (3.6)	1.3 (0.89)	1.2 (0.83)	3.1 (1.1)	1.07 (1.04)	1.3 (0.55)	-	-	-	-	-
<i>Metopograpsus messor</i>	-	-	-	-	-	-	-	-	-	-	0.7 (0.33)	-	1.7 (0.92)	-	-	-
<i>Metopograpsus thukuhar</i>	5.8 (2.53)	-	0.2 (0.18)	-	0.3 (0.18)	-	-	-	-	-	-	-	-	-	-	-
<i>Cyclograpsus punctatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.66 (0.23)	1.06 (1.04)	0.4 (0.19)	1.89 (0.68)
Ocypodoidea -																
<i>Austraca occidentalis</i>	3 (1.52)	87.8 (11.6)	7.4 (2.7)	29.3 (9.1)	4.5 (2.39)	12.4 (4.02)	7.4 (3.7)	10.8 (4.67)	10.6 (4)	16.93 (4.09)	4.6 (2.2)	127.46 (31.29)	6.6 (1.73)	-	-	-
<i>Paraleptuca chlorophthalmus</i>	1.6 (0.79)	10 (2.8)	9.2 (2.17)	4 (1.7)	6.9 (4.03)	2.67 (1.86)	8.3 (2.58)	4.4 (1.71)	7.8 (3.58)	6.93 (2.89)	7.2 (1.98)	53.33 (13.67)	3.7 (1.03)	-	-	P
<i>Tubuca urvillei</i>	-	-	2 (0.67)	-	-	-	0.5 (0.37)	1.06 (1.05)	1.2 (0.47)	1.6 (0.87)	1.2 (0.46)	16.53 (8.24)	0.11 (0.11)	-	-	1.96 (1.43)
<i>Gelasimus hesperiae</i>	-	-	1.5 (0.83)	-	-	-	2.2 (1.36)	-	-	-	0.6 (0.36)	-	-	-	-	-
<i>Macrophthalmus grandidieri</i>	-	-	-	-	-	-	-	-	-	-	1 (0.68)	1.07 (0.72)	-	-	-	-
<i>Dotilla fenestrata</i>	-	-	0.6 (0.6)	4 (2.7)	-	-	-	1.6 (1.57)	-	-	0.73 (0.73)	-	1.4 (0.72)	11.73 (6.03)	-	7.26 (5.28)
<i>Daniellia edwardsii</i>	-	-	-	-	-	-	-	-	-	-	-	-	6.7 (1.83)	54.53 (13.31)	65.3 (14.8)	42.16 (16.75)
Pilumnoidea -																
<i>Eurycarcinus natalensis</i>	0.3 (0.12)	-	-	-	-	-	-	-	-	-	-	1.6 (0.87)	-	-	-	-
Portunoidea -																
<i>Scylla serrata</i>	-	0.5 (0.5)	0.06 (0.06)	0.67 (1.63)	0.08 (0.08)	1.06 (0.72)	-	0.27 (0.18)	-	P	0.26 (0.11)	2.13 (1.64)	-	-	0.33 (0.14)	-
<i>Thalassina crenata</i>	0.2 (0.10)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cardisoma carnifex</i>	-	-	0.06 (0.06)	-	-	-	-	-	-	-	-	-	-	-	-	-
Species richness	7	5	12	8	7	6	7	9	6	8	12	10	9	5	5	7
Species diversity (H')	0.71	0.72	0.73	0.67	0.76	0.55	0.71	0.49	1.5	0.44	1.26	1.03	1.53	0.41	0.46	0.48
Species evenness (J')	0.92	0.93	0.93	0.96	0.93	0.96	0.88	0.96	0.94	0.97	0.94	0.92	0.97	0.91	0.65	0.91

Table 2

Results of species-specific generalised linear model output, showing the effects of the most parsimonious predictor variables on three co-occurring crab presence/absence. Coefficient estimates (C) with standard error (SE) in brackets, proportion of deviance explained (D%) and the test significance values (p) are presented. AO – *Austruca occidentalis*, NA – *Neosarmatium africanum*, CE – *Cristarma eulimene*. Mangrove tree species; AM – *Avicennia marina*, BG – *Brugeria gymnorhiza*. Values in **bold*** are significant.

Presence/absence	AO			NA			CE		
	C (SE)	D %	p	C (SE)	D %	p	C (SE)	D %	p
Microphytobenthos	0.001 (0.008)	2.93	0.12	−0.001 (0.006)	21.68	0.001*	−0.02 (0.02)	22.00	0.001*
Temperature	−0.15 (0.08)	5.08	0.08	0.11 (0.06)	3.51	0.12	−0.09 (0.12)	0.31	0.57
Salinity	−0.01 (0.02)	0.91	0.33	−0.04 (0.02)	17.45	0.001*	0.06 (0.04)	5.38	0.04*
Sediment pH	−0.95 (0.59)	0.16	0.70	0.66 (0.48)	5.23	0.07	−0.56 (1.12)	2.90	0.18
Sediment grain size		6.73	0.17		4.78	0.19		10.26	0.06
Clay/Silt	2.14 (0.93)			−1.05 (0.76)			−2.62 (1.87)		
Silt	1.12 (0.86)			−0.61 (0.78)			−1.14 (1.37)		
Silt/Sand	1.26 (0.84)			−0.63 (0.75)			1.39 (1.27)		
Sediment organic matter	−0.005 (0.01)	9.19	0.01*	0.01 (0.009)	1.06	0.54	0.01 (0.01)	0.003	0.96
Total brachyuran diversity	4.03 (0.77)	79.11	0.001*	3.18 (0.68)	19.83	0.001*	5.30 (1.41)	20.48	0.001*
Canopy cover	−0.01 (0.01)	3.20	0.22	0.01 (0.009)	1.7	0.22	0.04 (0.01)	3.47	0.22
Total brachyuran abundance	0.01 (0.004)	16.78	0.002*	−0.008 (0.003)	12.90	0.004*	−0.02 (0.01)	10.87	0.005*
Importance Value of AM	−0.01 (0.005)	24.81	0.001*	0.001 (0.004)	7.20	0.02*	0.10 (0.26)	2.24	0.16
Importance Value of BG	−0.01 (0.005)	7.79	0.03*	0.006 (0.004)	2.74	0.22	0.10 (0.26)	1.49	0.29
Tree density	−0.48 (0.22)	3.36	0.18	−0.25 (0.19)	1.68	0.25	0.99 (0.41)	7.08	0.046*
Pneumatophore density	−0.003 (0.001)	4.09	0.20	−0.002 (0.001)	2.68	0.27	−0.002 (0.003)	0.27	0.66
Latitude	0.74 (0.21)	14.28	0.008*	0.30 (0.15)	4.08	0.04*	1.14 (0.54)	7.66	0.03*

Table 3

Results of species-specific generalised linear model output, showing the effects of the most parsimonious predictor variables on three co-occurring crab abundances. Coefficient estimates (C) with standard error (SE) in brackets, proportion of deviance explained (D %) and the test significance values (p) are presented. Crab species; AO – *Austruca occidentalis*, NA – *Neosarmatium africanum*, CE – *Cristarma eulimene*. Mangrove tree species; AM – *Avicennia marina*, BG – *Brugeria gymnorhiza*, RM – *Rhizophora mucronata*. Values in **bold*** are significant.

Abundance	AO			NA			CE		
	C (SE)	D	p	C (SE)	D	p	C (SE)	D	p
Microphytobenthos	−0.0009 (0.005)	0.25	0.47	−0.005 (0.004)	8.69	0.002*	−0.002 (0.01)	14.01	0.002*
Temperature	−0.01 (0.04)	7.09	0.007*	0.14 (0.057)	5.27	0.01*	0.03 (0.10)	4.42	0.02*
Salinity	0.03 (0.01)	3.91	0.04*	0.0004 (0.02)	10.33	0.002*	0.04 (0.04)	3.09	0.04*
Sediment salinity	−0.06 (0.97)	2.00	0.26	−0.94 (1.28)	0.34	0.61	1.85 (2.20)	0.62	0.61
Sediment grain size		2.42	0.56		0.97	0.75		10.03	0.04*
Clay/Silt	−0.35 (0.66)			−0.22 (0.70)			−5.49 (2.40)		
Silt	−0.66 (0.66)			−1.34 (0.77)			−3.66 (1.54)		
Silt/Sand	−0.83 (0.68)			−0.42 (0.76)			2.33 (2.13)		
Sediment moisture content	−0.02 (0.01)	5.89	0.05*	0.01 (0.02)	0.01	0.98	0.17 (0.05)	0	0.98
Sediment organic matter	−0.003 (0.007)	0.05	0.94	0.02 (0.008)	2.33	0.34	−0.01 (0.01)	−0.004	0.98
Total brachyuran diversity	2.91 (0.37)	39.78	0.03*	3.84 (0.55)	16.39	0.03*	6.75 (1.09)	21.95	0.03*
Canopy cover	0.006 (0.008)	0.09	0.93	0.03 (0.01)	2.05	0.46	0.07 (0.02)	0	0.97
Total brachyuran abundance	0.005 (0.001)	17.94	0.02*	−0.01 (0.002)	6.75	0.02*	−0.02 (0.009)	25.08	0.02*
Importance Value of AM	−0.002 (0.005)	7.99	0.24	0.07 (1.81)	15.29	0.23	0.03 (1.13)	0.41	0.54
Importance Value of BG	−0.007 (0.005)	8.43	0.16	0.07 (1.81)	3.01	0.23	0.02 (1.13)	0.82	0.50
Importance Value of RM	0.001 (0.004)	0.29	0.53	0.09 (1.81)	6.35	0.17	0.07 (0.98)	1.26	0.34
Tree density	−0.08 (0.11)	0.12	0.75	0.06 (0.24)	0.49	0.75	1.55 (0.40)	3.45	0.44
Pneumatophore density	0.0002 (0.0008)	0.58	0.71	0.001 (0.001)	1.27	0.71	−0.008 (0.004)	0.87	0.71
Latitude	−68.40 (93.41)	13.67	0.23	−0.05 (13.18)	0.64	0.72	−281 (77.09)	0	0.96

scenario, these four estuaries are no longer suitable for any of these three crab species (Fig. 5g, h, i). The suitable habitats for *A. occidentalis* and *N. africanum* decrease from the SSP245 to the SSP585 scenarios. The sesarmid, *C. eulimene* has more suitable habitats in the SSP585 climate scenario compared to the current and SSP245 climate scenario.

The sum of sensitivity and specificity method (MaxSSS) was used (Lawson et al., 2023) to determine the predicted distribution range outcome of each species under the each climatic scenario (Fig. 6). *Austruca occidentalis* contracts its range under both future projections (SSP245 and SSP585), while *C. eulimene* expands under the same future projections. *Neosarmatium africanum* expands its distribution under the SSP245 climate projection but contracts under the SSP585 projection, however, still having more available habitat than the current climate scenario. The greatest habitat suitability for *A. occidentalis* occurs in the current climate projection, while *N. africanum* and *C. eulimene* has the most suitable habitat under the SSP245 and SSP585 climate condition, respectively.

4. Discussion

Analysing macrofaunal community structure is a useful tool for understanding temporal changes, especially in dynamic and coastal environments, such as mangroves as they face both aquatic and terrestrial extremities (Joseph and Nandan, 2020). In this study, brachyuran community structure has changed over time (2016 vs 2023) supporting hypothesis 1 (Brachyuran community structure has significantly changed over time (2016 (Peer et al., 2018a) vs 2023). Changes in community structure can generally be attributed to both anthropogenic and natural habitat changes (Ashton et al., 2003; Satheeshkumar 2012; Joseph and Nandan, 2020). For example, anthropogenic changes such as coastal development (Zabbey et al., 2021), deforestation (Bernardino et al., 2018; Barbanera et al., 2022), pollution (Kamalifar et al., 2016) and introduction of invasive species (Demopoulos and Smith, 2010) influenced community structure of macrofauna occurring in those mangrove forests. In turn, natural habitat changes such as estuarine

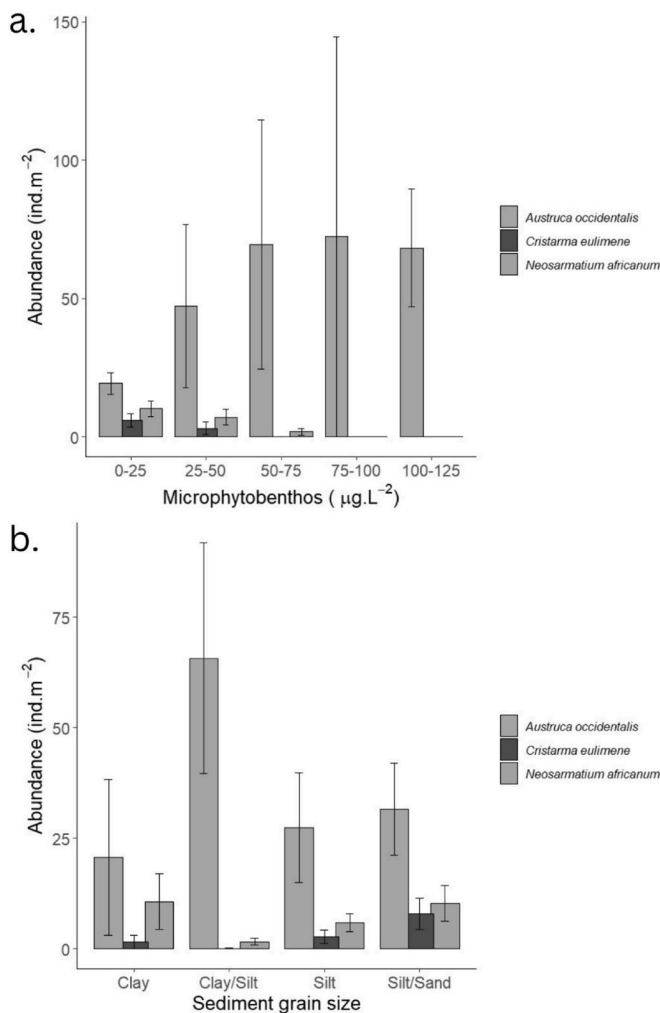


Fig. 4. Average abundance (ind. m^{-2} + SE) of three mangrove crab species across varying (a) microphytobenthos and (b) sediment grain size categories.

mouth closures (Peer et al., 2014), mangrove community succession (Demopoulos and Smith, 2010), shifts in vegetation (Smee et al., 2017) and seasonality (Li et al., 2022) are known to alter macrofaunal community structure.

The most noteworthy change observed between past (Peer et al., 2018a) and present studies was the presence or absence of fiddler crab species. During this study, two fiddler crab species, *Paraleptuca chlorophthalmus* and *Tubuca urvillei*, were observed for the first time at a new southernmost distributional limit in Tyolomnqa. This new finding adds to and supports local (Peer et al., 2015; Peer et al. 2018a; Peer et al. 2018b; Ma and McQuaid, 2020; Theron et al., 2022) and international studies (Salvadeo et al., 2011, Johnson, 2014; Schoeman et al., 2015; Caswell et al., 2020, Pinsky et al., 2020) that have investigated poleward expansions in marine macrofauna. On the other hand, three fiddler crab species (*Austruca occidentalis*, *P. chlorophthalmus* and *T. urvillei*) previously observed in Nahoon (Peer et al., 2018a) were absent in this present study. It is likely that the absence of these fiddler crabs at Nahoon are due to temporal and seasonal cycles of emergence that these crabs are known to go through (Reaney and Backwell, 2007; Al-Musawi and Wagner, 2012). Fiddler crabs were found to change their activity (i.e emergence for foraging, courting and burrow maintenance) in response to changing ambient temperatures throughout different seasons (Al-Musawi and Wagner, 2012), suggesting the important role temperature plays in the biological clocks of these crabs. This pattern of seasonal emergence coupled with a strong latitude association (Peer et al., 2018b) could be a reason why the fiddler crab *Gelasimus hesperiae*, was

not observed at all in this present study, even though sites were sampled in both summer and winter, accounting for temporal variation. Nevertheless, this highlights the importance of routine biodiversity monitoring in order to detect seasonal changes vs more large-scale boom-and-bust type changes in species occurrence and abundance.

Although few local studies have investigated drivers of *A. occidentalis* (Peer et al., 2018b; Theron et al., 2022), no local studies have explored which factors influence the occurrence and abundance of grapsoids such as the sesarmids *N. africanum* and *C. eulimene*. Since both biotic and abiotic factors influenced the presence and abundance of all three crabs, hypothesis 2 (both biotic and abiotic factors influence crab distribution) was accepted. The total brachyuran diversity positively influenced the presence and abundance of all three crab species, highlighting how a diverse community of brachyuran crabs can enhance the establishment of these three crab species and vice versa. This in turn, promotes mangrove biodiversity, stability and health (Peer et al., 2018b). Microphytobenthos had a negative correlation with both the occurrence and abundance of both sesarmids, contradictory to Peer et al. (2019) who found no correlation between MPB biomass and occurrence of both *N. africanum* and *C. eulimene*. It is likely that other mangrove-associated crabs are more abundant where there is increased MPB food source, leading to a higher total abundance of crabs, which negatively influences the occurrence and abundance of both sesarmids, as they are highly territorial and would avoid 'crowded' areas (Cannicci et al., 2018). *Neosarmatium africanum* is a large species known to compete with other mangrove crabs, preventing them from establishing and colonising certain parts of the mangrove forests (Cannicci et al., 2018). This territorial behaviour was also observed in *Neosarmatium smithi* in Sri Lankan mangroves (Cannicci et al., 2018), where interference competition was found to shape spatial distribution of sesarmids. The positive correlation between *N. africanum* and the importance value of *Avicennia marina* (IVA) is possibly because of the palatability of the mangrove leaves to *N. africanum*. These crabs are known to emerge from their burrows to collect fallen mangrove leaves (Peer et al., 2019). Whereas *A. occidentalis* had a negative correlation with IVA, likely to reduce predation and competition pressure from *N. africanum*, which have been observed harassing fiddler crabs (Peer et al., 2019). *Austruca occidentalis* was also negatively correlated with the importance value of *Bruguiera gymnorhiza*, supporting findings from Theron et al. (2022). Fiddler crabs are likely negatively correlated with mangrove trees, as they generally prefer open clearings where they can rely on visual displays for mating signals (Nobbs and Blamires, 2015). In contrast, sesarmid crabs, which do not exhibit this behaviour, are often found in vegetated areas (Cannicci et al., 2008), with tree density influencing the occurrence of *C. eulimene* in this study.

Many studies have researched the influence of sediment and pore-water characteristics on mangrove macrofauna (Sasekumar 1974, Frusher et al., 1994, Chapman and Tolhurst, 2007, Tolhurst et al., 2010, Kon et al., 2011, Rohit et al., 2016, Hadiyanto et al., 2018). Other studies found that the distribution of *A. occidentalis* can be affected by factors such as sediment grain size, sediment organic matter and moisture content, pneumatophore and tree density and presence of mangrove vegetation (Mokhtari et al., 2008; Mokhtari et al., 2015; Peer et al., 2018b; Theron et al., 2022). Similarly, in this study, the occurrence and abundance of *A. occidentalis* was influenced by sediment organic matter and sediment moisture content, respectively. In the same light, the abundance of the sesarmid, *C. eulimene* was influenced by sediment grain size, where these crabs preferred silt/sand substrate types. Pore-water characteristics such as salinity and temperature can play an important role in small scale distribution of burrowing crab species (Frusher et al., 1994). Contradictory to Frusher et al. (1994), who found that porewater salinity provided no explanatory power for any mangrove grapsoid species, this study found that porewater salinity influenced the abundance of all three crab species and the occurrence of *N. africanum* and *C. eulimene*. Sesarmids can change their osmoregulatory patterns in short periods of time (Lv et al., 2022), however, Gillikin

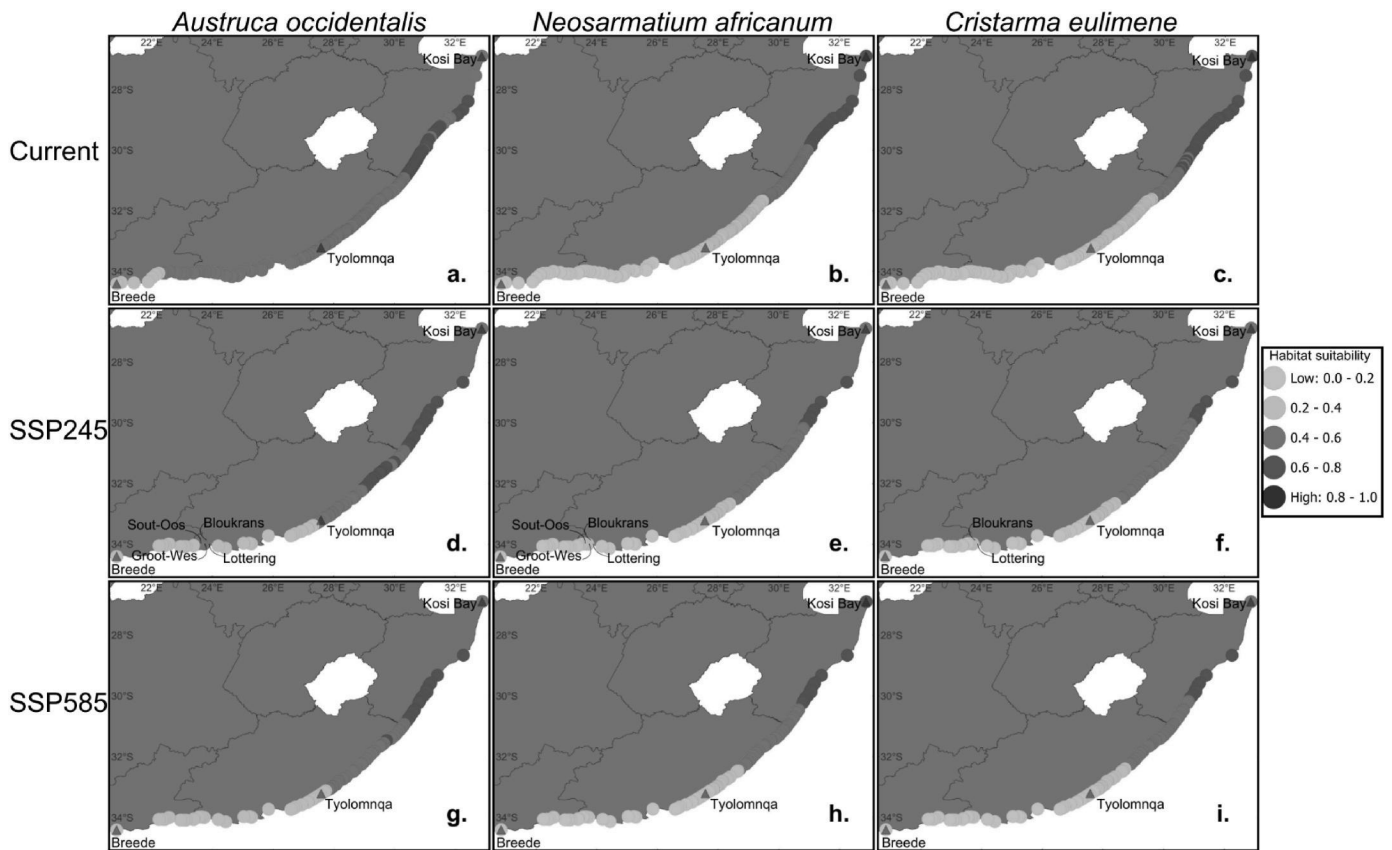


Fig. 5. Maxent logistic SDM maps, where cooler colours (blues) indicate higher habitat suitability for each of three selected crab species (*A. occidentalis*, *N. africanum* and *C. eulimene*), under three different climate scenarios current (a,b,c), SSP245 (d,e,f) and SSP585 (g,h,i), in South Africa. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

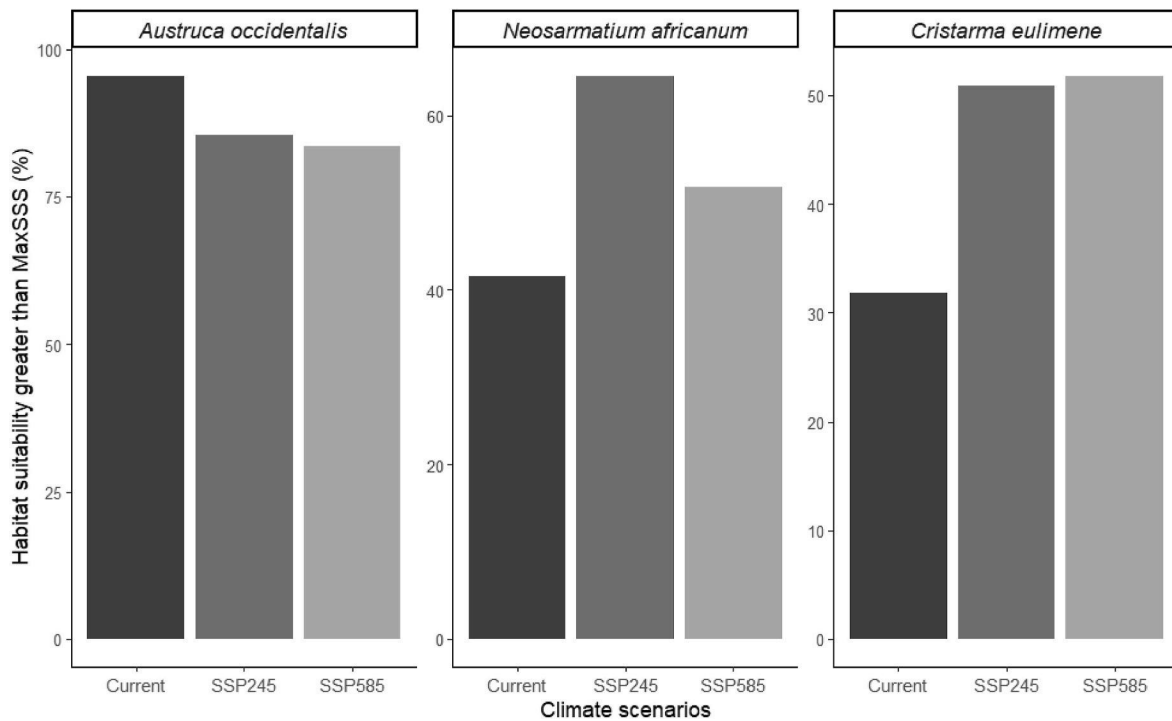


Fig. 6. The expansion and contraction of three mangrove crab species occurring in South Africa (*Austruca occidentalis*, *Neosarmatium africanum* and *Cristarma eulimene*) under three climate scenarios (Current, SSP245 and SSP585).

et al. (2004) showed that two different sesarmid species *N. africanum* and *N. smithi* had different responses to altered salinity regimes, with both species being negatively influenced by hypersaline conditions. This is probably the same case, as salinity was negatively correlated with occurrence of *N. africanum* and positively correlated with occurrence of *C. eulimene*. Both sesarmids and fiddler crabs are strong osmoregulators, but experience different salinity regimes as they often occur in different parts of the mangroves (Theuerkauff et al., 2018). Sesarmids are sporadically subjected to extreme fluctuations in salinity in their burrows, while fiddler crabs often create burrows near waterbodies and use a burrowing plug behaviour (Fusi et al., 2015) to minimize exposure to large variations in salinity (Theuerkauff et al., 2018). Porewater temperature influenced the abundance of all three crabs. Kawaida et al. (2017) similarly identified porewater temperature as a driver of mangrove crabs in Japan. The authors stated that temperature, salinity and vegetation are all influenced by latitude, which influenced the occurrence of all three species.

On a larger-scale, precipitation and temperature are critical drivers of the global distribution of crabs (Sharifian et al., 2020). Both precipitation and temperature are influenced by global climate change and latitudinal gradient, which in turn influences species occurrences of flora and fauna globally (Whitfield et al., 2016; Sharifian et al., 2020, Sathish et al. 2023). Under future climate change scenarios (SSP245 and SSP585), precipitation and temperature are expected to increase severely (Riahi et al., 2017). From this study, the distribution range of the fiddler crab *A. occidentalis* contracts under both climate change scenarios (SSP245 and SSP585), while the sesarmids *N. africanum* and *C. eulimene* expand their distribution latitudinally. Therefore, hypothesis 3 (selected crabs will expand their ranges in face of climate change) is partially accepted. Precipitation is more influential on all three crabs compared to temperature in both future climate change scenarios (SSP245 and SSP585), highlighting that temperature might not play such a large role at these species latitudinal limits. Increased precipitation, specifically rainfall, can lead to increased freshwater inputs in estuaries, resulting in changes in salinity, sediment composition and growth of mangrove vegetation (Gu et al., 2023; Sathish et al., 2023), which are all factors that influence distribution patterns of these three crabs. The contraction of *A. occidentalis* was unexpected, given that this species has a wide tolerance range to thermal and salinity stress compared to other species (Edney, 1961; Khanyile, 2012). This result contradicts a global study done by Sharifian et al. (2021a,b), who found that *A. occidentalis* expands its ranges under climate change scenarios. This present study used regional scale environmental data (temperature and precipitation), as South African estuaries are relatively small and also used land temperature rather than sea-surface temperature, which is likely why this study found a range contraction. Additionally, *A. occidentalis* occurs at its latitudinal range limit in South Africa and likely has reached its tolerance threshold, further explaining the contraction of this species. On the other hand, the expansion of the two sesarmids was expected as grapsoids generally show an ability to move into temperate climates (Hartnoll et al., 2002), which occur from the east to west coast of South Africa. This change in occurrence and abundance of ocypodid to grapsoid crabs will change energy flow dynamics in mangrove ecosystems from deposit feeders to leaf eaters (Hartnoll et al., 2002) changing ecosystem dynamics in these temperate estuaries.

South African estuaries host many coastal vegetated ecosystems, including mangroves, saltmarsh and seagrass (Adams et al., 2016). Already, climate change promotes both the poleward expansion (Raw et al., 2022) and encroachment of mangroves into adjacent habitats i.e. saltmarshes (Adams and Rajkaran, 2020). Mangrove encroachment has already been documented in South Africa (Hoppe-Speer et al., 2015, Adams and Rajkaran, 2020), with mangrove-associated macrofauna likely following the same shift, as seen in global studies (Whitfield et al., 2016; Cannizzo et al., 2018; Walker et al., 2019). As sesarmids are expected to expand their distribution ranges in the future, it is likely that

they will move into novel saltmarsh habitats as a result of global climate change (Cannizzo et al., 2018). As mangroves and saltmarshes differ in vegetation types, it is possible that burrowing crabs such as sesarmids will alter ecosystem dynamics (Walker et al., 2019), by influencing sediment composition (Kristensen, 2008) thereby altering growth and productivity of saltmarsh plants (Smith et al., 2013). However, limitations in this study, including restricted timeframes, a limited number of occurrence records for MaxEnt models, and the absence of fine-scale habitat features in environmental data, may have influenced our ability to fully capture the extent of these shifts. Therefore, it is critical to understand both local, regional and global drivers of mangrove-associated crabs to predict range shifts to provide management strategies and conservation for coastal ecosystems in the face of climate change.

5. Conclusion

The significant change in crab community structure over a seven year period, with the presence of two previously unrecorded fiddler crabs, *P. chlorophthalmus* and *T. urvillei*, at new southern distributional limit highlights ongoing poleward shifts in species distributions occurring in response to climate change. Additionally, our study identified factors that influence sesarmid crabs, *N. africanum* and *C. eulimene* for the first time in South Africa. The factors that influence sesarmids include porewater, sediment and mangrove tree characteristics, as well as ecological interactions between other mangrove crabs. Predictions made under future climate scenarios suggest contrasting responses among all three crab species, with sesarmids expanding and the fiddler crab contracting their ranges. It is likely that sesarmids will move into and alter ecosystem dynamics and functioning in novel habitats such as saltmarshes, as mangroves encroach into this adjacent habitat in the face of climate change. Additionally, the contraction of fiddler crabs could have serious effects in mangrove forests, by reducing soil aeration and nutrient turnover, thereby reducing propagule establishment and changing predator-prey dynamics. This highlights how routine biodiversity monitoring remains essential for comprehensively understanding these changes and informing effective conservation efforts. As mangroves expand polewards and encroach into saltmarshes, our research will help understand the consequences of shifting vegetation types on mangrove-associated macrofauna.

CRedit authorship contribution statement

Chaitanya Katharoyan: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Anusha Rajkaran:** Writing – review & editing, Supervision, Resources, Investigation, Funding acquisition, Conceptualization. **Nasreen Peer:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Nasreen Peer reports financial support was provided by National Research Foundation. Anusha Rajkaran reports financial support was provided by National Research Foundation. Chaitanya Katharoyan reports financial support was provided by National Research Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

For the assistance in the field, the authors acknowledge Emma

Rossouw, Jaime Johnson, Jake Mulvaney and Aiden Bossert. The authors are also grateful to Daniel Lemley for processing micro-phytobenthos samples, Susana Fietz and Megan Mathese for use of their equipment during laboratory processing and Caleb Thaver for assistance in transportation of sediment samples. Sampling permits were obtained from the Department of Forestry, Fisheries and the Environment of the Republic of South Africa (permit number Res2023-79), Ezemvelo KZN Wildlife (permit number MSP210) and thanks is given to iSimangaliso Wetland Park Authority. This work is based on research supported by the National Research Foundation of South Africa through a Thuthuka Grant (Grant reference TTK2204052094) and a Marine and Coastal Research Grant (Grant no. 136490). The authors acknowledge that opinions, findings and conclusions or recommendations expressed in this publication generated by the NRF supported research is that of the authors, and that the NRF accepts no liability whatsoever in this regard.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2024.109116>.

Data availability

Data will be made available on request.

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