

## Impact of fiddler crab activity on microphytobenthic communities in a South African mangrove forest

Nasreen Peer<sup>a,\*</sup>, Nelson AF. Miranda<sup>a,b</sup>, Renzo Perissinotto<sup>b</sup>

<sup>a</sup> Department of Botany and Zoology, Stellenbosch University, Stellenbosch, 7600, South Africa

<sup>b</sup> Coastal and Marine Research Institute, Nelson Mandela University, Port Elizabeth, 6031, South Africa



### ARTICLE INFO

#### Keywords:

Microalgae  
Community composition  
Grazing effects  
Lake St Lucia  
Brachyura

### ABSTRACT

Microphytobenthos (MPB) are important primary producers in mangroves, where they are an important source of food for fiddler crabs. The St Lucia mangroves are currently disconnected from the sea and thus considered a non-tidal mangrove ecosystem. Fiddler crabs occur close by, along with sympatric sesarmid crabs. This study examined the foraging effects of the fiddler crab *Austruca occidentalis* on MPB biomass and composition. The effects of two dominant sesarmids, *Chiromantes eulimene* and *Neosarmatium africanum*, on *A. occidentalis* were also investigated as sesarmids are known to interfere with fiddler crab surface activities such as foraging and burrow maintenance.

*In situ* experimental plots contained fiddler crabs at three different densities, combinations of fiddler crabs and sesarmids, and controls with no crabs. The biomass of three main microalgal groups were measured (i.e. diatoms, cyanobacteria and green algae) using a fluoroprobe and overall MPB biomass was measured using acetone extraction analysis.

*Austruca occidentalis* affected cyanobacteria and diatoms, allowing green algae to increase in biomass during the experimental period. The presence of sesarmids was shown to affect cyanobacteria biomass more than either of the other two algal groups. Overall, MPB biomass was unaffected by fiddler crab density or sesarmid presence, suggesting that abiotic factors played a more important role in controlling biomass while biotic grazing and interference only affected microalgal group composition.

### 1. Introduction

Microphytobenthos (MPB), consisting of microalgae and cyanobacteria, are important primary producers in a range of aquatic habitats, including 'unvegetated' ecosystems such as mudflats and sandy shores (MacIntyre et al., 1996). In these habitats, they are an important source of food for microheterotrophs, macrobenthos and even pelagic organisms such as fish. In mangroves, MPB productivity is usually minimal compared to that of mangrove trees but they nevertheless constitute an invaluable food source to meiofauna, gastropods and brachyurans (Dye and Lasiak, 1986; Ribeiro and Iribarne, 2011; Alongi, 2012). They are even thought to offset carbon dioxide emissions in these habitats (Alongi, 2012; Chen et al., 2019). Despite this, MPB communities in mangrove ecosystems remain understudied with little understanding of the top-down and bottom-up controls on these populations despite the important role they play in sustaining key mangrove macrobenthos.

The importance of examining both abiotic and biotic drivers of MPB

biomass and composition has been highlighted in recent years (Klanderud et al., 2015; van der Sande et al., 2017; Savelli et al., 2018). Although challenging, this requires investigation at many levels to more accurately model productivity and carbon flux, especially under climate change and anthropogenic disturbance scenarios.

MPB growth and species composition is influenced by numerous factors including nutrient availability (Hillebrand and Sommer, 1997), physico-chemical fluctuations (Kristensen et al., 2008), seasonal and tidal influence (Ribeiro and Iribarne, 2011), disturbance of the substratum (Booth et al., 2019) and grazing pressure (Jaschinski et al., 2009). Fiddler crabs (Family Ocypodidae) occur globally in tropical, subtropical and temperate ecosystems (Mouton and Felder, 1995). They are regarded as flagship species in mangroves, tidal flats and sandy beach intertidal habitats where they occur in colonies. Previously collectively included within the genus *Uca*, the fiddler crab group has been subject to a vast number of studies on various aspects including taxonomy, molecular, ecological, behavioural, physiological and environmental. These species sometimes occur at high densities (Gordon, 1958)

\* Corresponding author.

E-mail address: [peer.nasreen@gmail.com](mailto:peer.nasreen@gmail.com) (N. Peer).

and can thus have profound impacts on the habitats in which they reside. Activities such as foraging, feeding and burrowing alter sediment nutrient levels and topography along with associated microbial, phyto-benthic and meiofaunal communities (Katz, 1980; Dye and Lasiak, 1986; Cuellar-Gempeler and Munguia, 2013; Mchenga and Tsuchiya, 2008).

Fiddler crab species feed largely on microphytobenthos (MPB), microheterotrophs and detrital matter, although it is predominantly heterotrophs and MPB that are assimilated (Dye and Lasiak, 1986; Wolfrath, 1992; Ribeiro and Iribarne, 2011). Milner et al. (2010) described the feeding habit of these species, where sediment is scooped up using the minor cheliped and moved to the mouth where digestible material is retained within the buccal chamber. All indigestible particles are later released as feeding pellets which cause disruption to microbiota and increases substratum erosion (Botto and Iribarne, 2000). Furthermore, it is understood that bioturbation of sediment occurring during the construction and maintenance of burrows promotes sediment drainage and aeration allowing for the movement of nutrients and elements through the soil and the removal of waste products (Botto and Iribarne, 2000; McCraith et al., 2003; Lim and Rosiah, 2007; Mokhtari et al., 2016) and oxygenation of the substratum (Katz, 1980; Mouton and Felder, 1996; Booth et al., 2019).

*Austruca occidentalis* (Naderloo, Schubart and Shih, 2016) is a Western Indian Ocean species of fiddler crab. The mangroves of South Africa represent the southernmost limit of the species distribution. They commonly occur here in high abundance and often sympatrically with other fiddler crab species and the common mangrove sesarmids (Peer et al., 2018). Interactions between fiddler crabs and other brachyuran species have not been extensively examined in South Africa. Here, previous observations have indicated that fiddler crabs are occasionally predated upon by the sesarmid *Neosarmatium africanum* (Steinke et al., 1993), and similar interactions with other sesarmids species have been observed more recently (pers. obs.)

The St Lucia mangroves have been disconnected from the ocean since the last overtopping event in 2007 (Hoppe-Speer et al., 2013), although in the current process of rehabilitation overwashing has occurred frequently and freshwater continues to feed in from the adjacent Mfolozi River (N. Forbes, pers. comm.). The lack of tidal influence and marine connectivity is unfavourable for many mangrove and mangrove-associated species, including fiddler crab populations which require an open connection to the ocean to complete their life cycle. Fiddler crabs were last recorded in St Lucia by Millard and Broekhuysen (1970) and have since been absent from the mangroves. In recent years, however, fiddler crabs have been observed moving towards the lake (Peer et al., 2015). It is speculated that connectivity between the adjacent Mfolozi River and the St Lucia system, along with the recent recovery from drought conditions experienced by the system, allows for recruitment and recolonisation of the St Lucia fiddler crab community from the Mfolozi populations. As the system has not been subject to the usual influence of fiddler crabs, it is uncertain to what extent the possible recolonisation of these species would affect the mangrove substratum within which the species reside and its associated biota. Furthermore, this presents a unique opportunity to examine the effect of grazers on a largely undisturbed habitat.

This study was, therefore, designed to determine the effects that foraging, feeding and burrowing of *A. occidentalis* have on the composition and abundance of MPB in the St Lucia-Mfolozi mangrove forest. The aims of this study were to determine: (1) the effects of fiddler crab density on microphytobenthic community composition and biomass; and (2) whether or not the presence of common sesarmids influences the effects of fiddler crabs on MPB. It was expected that fiddler crabs would significantly reduce MPB biomass but that they would feed indiscriminately on different microalgal groups. It was also expected that the presence of sesarmids would lead to a decrease in fiddler crab surface activity (feeding, foraging, burrow maintenance) and thus mitigate the impacts of fiddler crabs on MPB biomass.

## 2. Materials and methods

### 2.1. Study site

The Island located at Honeymoon Bend in the St Lucia Narrows ( $28^{\circ}23'14''$  S  $32^{\circ}24'10''$  E) Fig. 1 was used as the experimental site as the presence of *A. occidentalis* was noted here in previous literature (Millard and Broekhuysen, 1970). Plots were set up in a mangrove habitat consisting of *Bruguiera gymnorhiza* and *Avicennia marina* where no fiddler crabs were present.

### 2.2. Experimental setup

*In situ* experiments were conducted over a period of 12 days. Plots were constructed with wooden stakes and mesh to form  $50 \times 50$  cm enclosures. The mesh extended 20 cm below the surface to account for burrowing of the crabs while a 10 cm strip of clear plastic encircled the top edge of the mesh to prevent crabs from escaping the plots. For the density experiment (experiment 1), each treatment consisted of 5 replicates and was set up as follows: control with no crabs (CON), three crabs present (A), five crabs present (B) and ten crabs present (C). Densities of approximately 20 individuals  $\text{m}^{-2}$  were observed in the field. The number of individuals present in each plot was based on this value so that treatments consisted of low (12 ind.  $\text{m}^{-2}$ ), average (20 ind.  $\text{m}^{-2}$ ) and high (40 ind.  $\text{m}^{-2}$ ) densities. For the sesarmid-presence experiment (experiment 2), each treatment contained 5 replicates and was set up as follows: control with no crabs (CON), average fiddler crab density (20 ind.  $\text{m}^{-2}$ ) with no sesarmids present (B), average fiddler crab density with 5 *Chiromantes eulimene* present (D), average fiddler crab density with 1 *Neosarmatium africanum* present (E). These two sesarmid species were selected based on their co-occurrence with *Austruca occidentalis* in the drier, landward mangrove edges and abundance was modelled on abundance observed in the field. Introduced crabs adapted to the plot environment, burrowed immediately and resumed feeding, maintenance as well as both intraspecific and interspecific interactions.

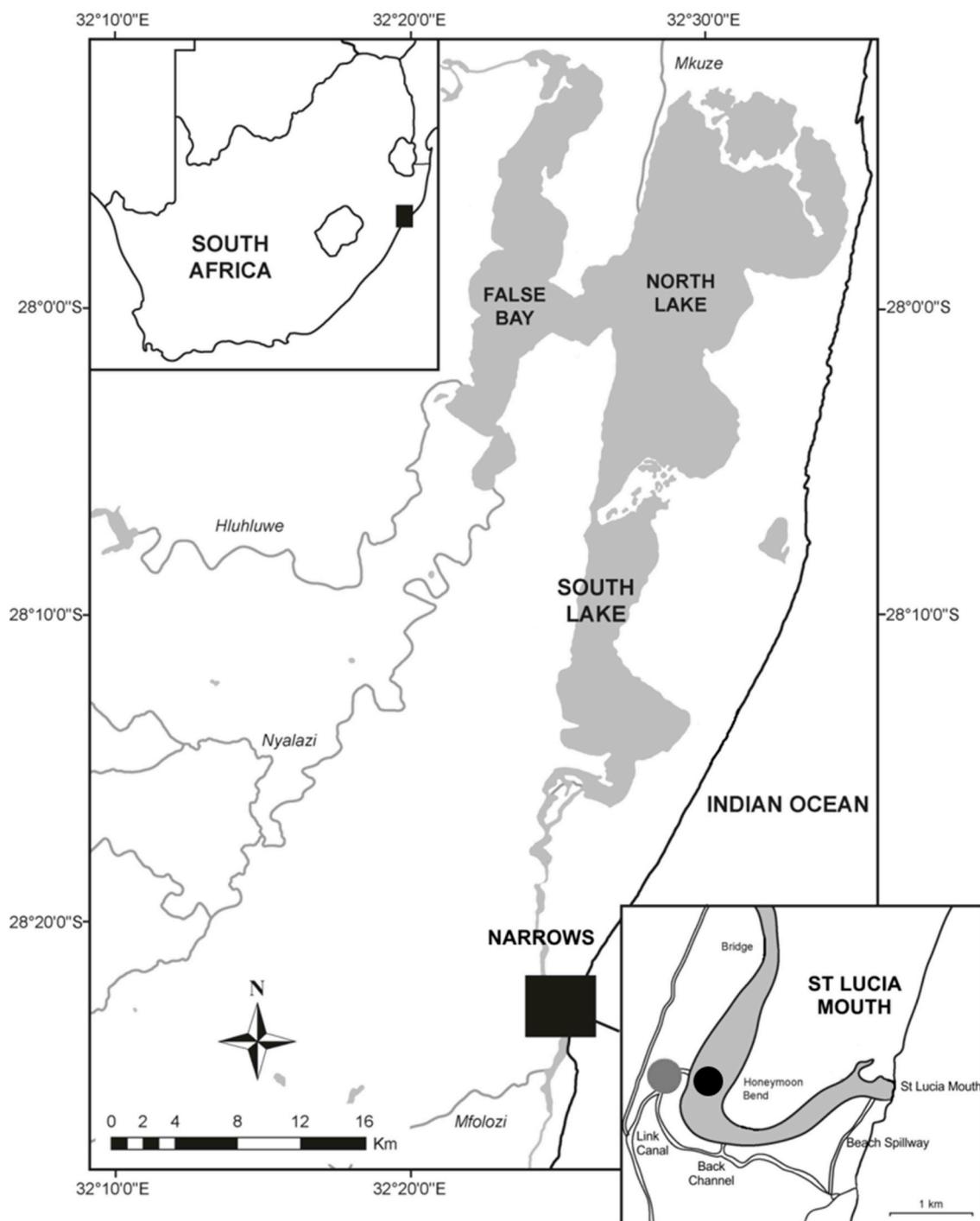
Physico-chemical variables, including water temperature, pH and salinity were recorded daily using a YSI 6600-V2 multiprobe system (YSI Inc., Yellow Springs, OH, USA) to measure three replicates. No deaths of either fiddler crabs or sesarmids were noted for the duration of the experiment.

### 2.3. Selective feeding and grazing impact

A bbe Moldaenke FluoroProbe was used to measure the relative concentrations of the three main microphytobenthic classes i.e. diatoms, cyanobacteria and green microalgae (Underwood, 2001; Beutler et al., 2002; Kring et al., 2014) in  $\mu\text{g.cm}^{-2}$  (indication of bioturbation effects and selectivity of feeding). These *in situ* measurements were conducted on the initial day of the experiment and every 3rd day thereafter taking triplicate measurements from each plot. Changes in MPB biomass over the 12 day experimental period were measured as  $\mu\text{g}$  of chlorophyll pigment per unit area. Triplicate cores were removed every three days from each treatment with a 20 mm internal diameter corer and placed into falcon tubes containing 8 ml of 90% acetone solution for the extraction of chlorophyll-a and phaeopigment. After a 48 h refrigeration period, the pigments were measured using a Turner Designs 10-AU fluorometer, fitted with a narrow band, non-acidification system (Welschmeyer, 1994) and combined to form a total pigment value (chl-a plus phaeopigments).

### 2.4. Statistical analyses

Plot effects were measured by comparing the total microphytobenthic biomass and biomass of each algal group between plot controls (CON) and no-plot controls (NPC) using a mixed linear model



**Fig. 1.** Map of the St Lucia estuarine lake on the east coast of South Africa. The experimental location (the Island) is indicated by a black dot while a grey dot indicates the location of closest *Austruca occidentalis* population. Figure adapted from Peer et al. (2015).

('lmer' in package 'lme4'). Plots were found to have no significant impact ( $F_{\text{condition}} = 1.76$ ,  $\text{df} = 1$ ,  $p = 0.18$ ) and no-plot controls were thus eliminated from analyses.

Mixed linear models were run in R to detect significant changes of fiddler crab impact on the biomass of each algal group as well as the total microphytobenthic biomass over time. For the 1st experiment, the impact of density over time was measured, with 'density' and 'time' as fixed, continuous variables while 'plot' was used as a random factor. For the 2nd experiment, 'treatment' (B, D, E, CON) was regarded as a fixed categorical factor and 'time' as a fixed continuous factor, while 'plot' was used as a random factor. Mixed models were subject to analysis of

variance (ANOVA), run using the package 'car' to obtain F-ratios, degrees of freedom and p-values.

### 3. Results

Physico-chemical variables remained stable for the duration of the experiment (Table 1). An increase in salinity and a decrease in dissolved oxygen were noted on the last day, most likely influenced by the rainfall at the time.

Although crab density did not significantly affect total microphytobenthic (MPB) biomass (Table 2), it did affect the biomass of all 3

**Table 1**  
Temperature, salinity, pH and dissolved oxygen of the adjacent channel.

Date	temperature (°C)	salinity	pH	dissolved oxygen (%)
20-Feb-14	29.8 ± 0.5	5.2 ± 0.2	8.0 ± 0.1	89.0 ± 5.3
23-Feb-14	28.8 ± 0.3	6.8 ± 0.2	8.0 ± 0.1	85.2 ± 10.6
26-Feb-14	28.8 ± 0.1	7.5 ± 0.1	8.0 ± 0.1	85.0 ± 2.1
01-Mar-14	28.9 ± 0.4	6.3 ± 0.2	8.1 ± 0.1	75.8 ± 21.1
04-Mar-14	28.1 ± 0.2	10.7 ± 0.1	8.0 ± 0.1	69.1 ± 12.8

algal classes with an even more pronounced effect over time experienced by diatoms and cyanobacteria.

Fig. 2 (a) and (b) show how biomass decreased over time for diatoms and cyanobacteria compared to the control. Green algae had the lowest biomass and appeared to fluctuate independently of crab density

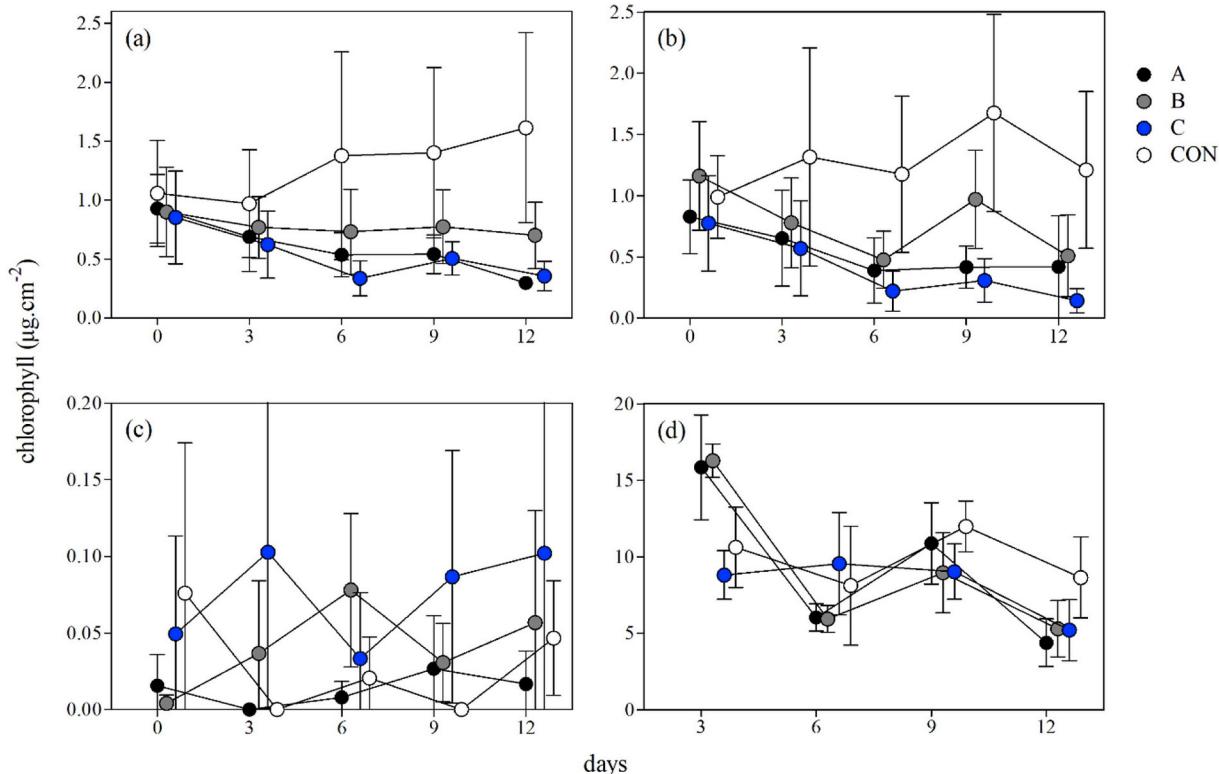
(Fig. 2c). MPB decreased over time consistently across all treatments and the control (Fig. 2d) and was unaffected by crab density.

More specifically, an increase in grazing density affected the composition of the algal community (Fig. 3), which consisted of 43.6–52.3% diatoms, 46.2–56.2% cyanobacteria and 0.2–3.6% green algae at the start of the experiment. At a natural density of 20 individuals. m<sup>-2</sup> (B), cyanobacteria contributed 56.2% of total algal biomass on the first day (day 0). This decreased to 40.2% on the last day (day 12). Conversely, green algae shifted from 0.2% on the first day to 4.5% by the last day. A similar, more intense pattern was seen for a higher density of 40 individuals. m<sup>-2</sup> (C) (Fig. 3), where cyanobacteria representation decreased from 46.2% to 23.8% over the duration of the experiment, while green algae representation increased from 2.9% to 17.0% during the same time. A small decrease from 46.5 to 42.2% was seen for cyanobacteria in the control group, while green algae also

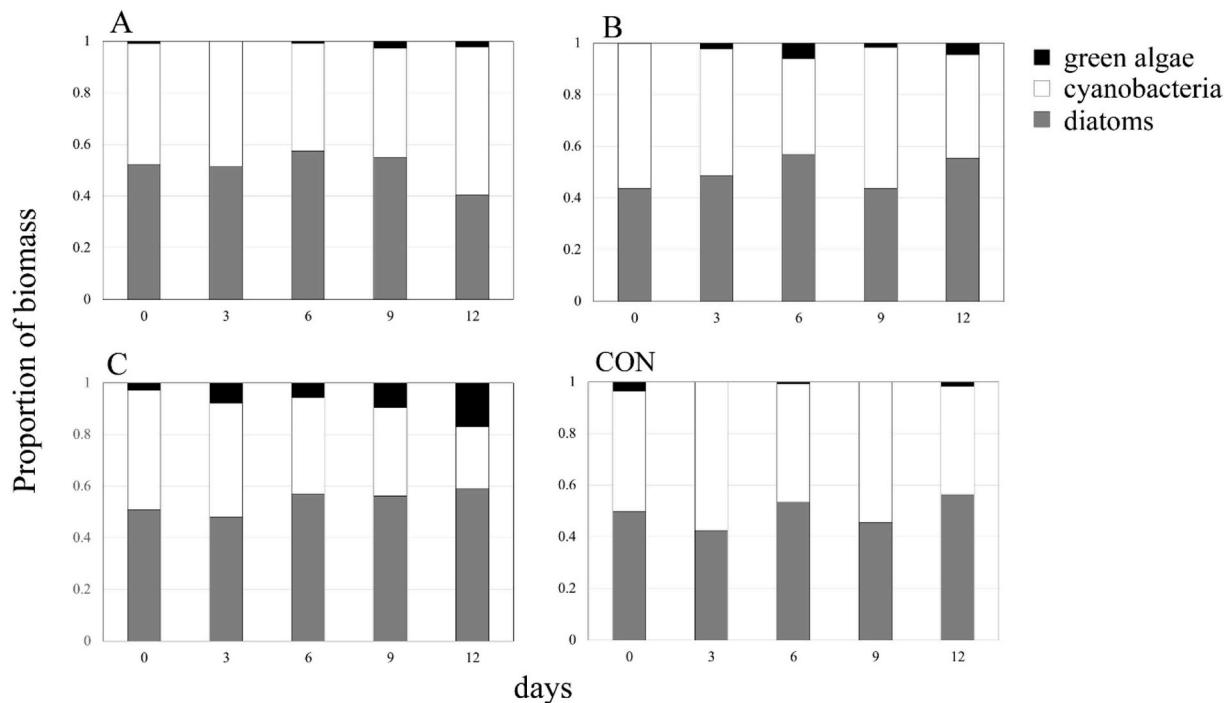
**Table 2**

Impacts of fiddler crab density and presence of sesarmids on the biomass of microphytobenthos and each algal class (diatoms, blue-green algae and green algae). F-ratios and degrees of freedom from ANOVAs on mixed linear models of Experiments 1 and 2 are presented here. Significance codes as follows: \*\*\*\* p < 0.001; \*\*\*, p < 0.01; \*\* p < 0.05; \* p < 0.1.

	algal classes				total microphytobenthos	
	df	diatoms	cyanobacteria	green algae	df	microphytobenthos
<u>Experiment 1</u>						
Density	1	2.77*	3.60*	5.49**	3	0.91
Time	4	1.49	4.01**	1.26	3	43.41****
Density*Time	4	6.69***	4.34**	0.18	9	0.72
<u>Experiment 2</u>						
Treatment	3	1,7	2,72*	1,9	3	0.77
Time	1	6,82***	0,71	1,26	3	17.61****
Treatment*Time	3	3,16**	0,19	0,15	9	0.68



**Fig. 2.** Decrease in biomass ( $\mu\text{g chlorophyll. cm}^{-2}$ ) of (a) diatoms, (b) cyanobacteria, (c) green algae and (d) microphytobenthos under different *Austruca occidentalis* densities over the 12 day experimental period. Treatment A contained only three individuals while B consisted of five individuals, C of 10 and CON had no crabs. Values represented here are means and with standard error bars. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

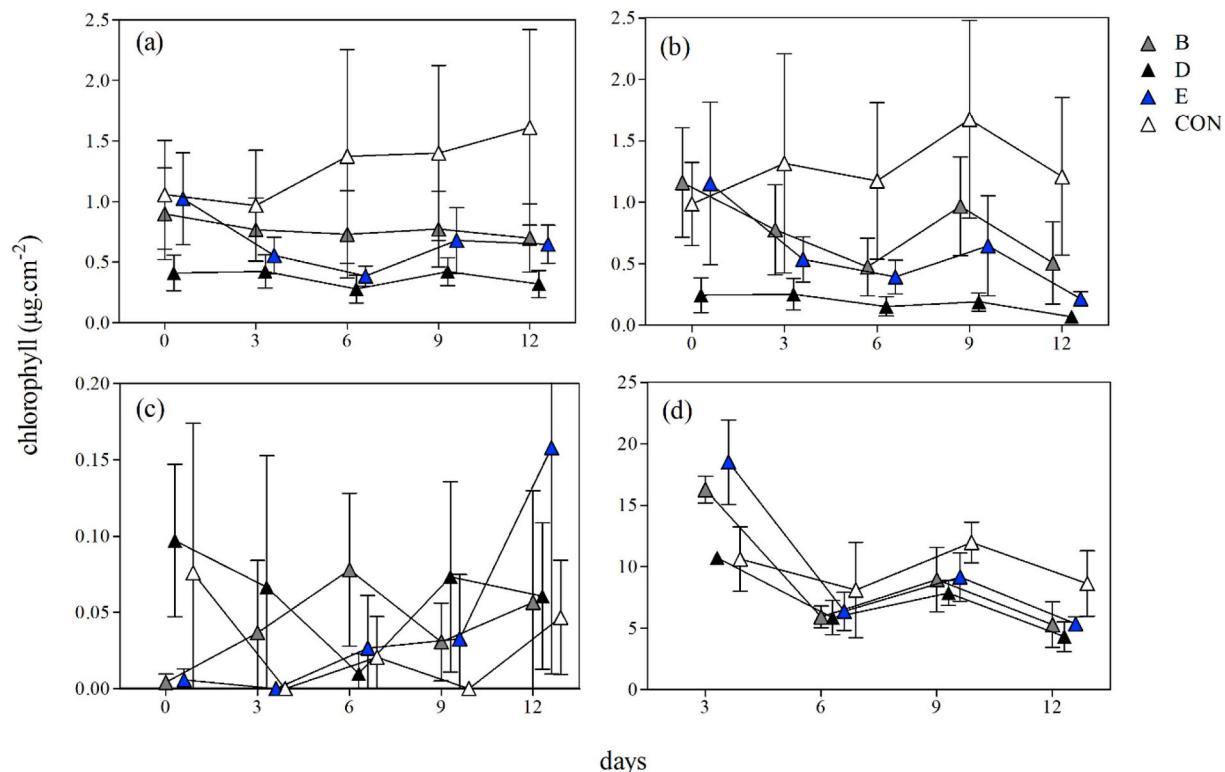


**Fig. 3.** Class composition of microphytobenthos over the experimental period for each density treatment (A, B, C) and the control (CON). Chlorophyll was measured in  $\mu\text{g}$  per  $\text{cm}^{-2}$ .

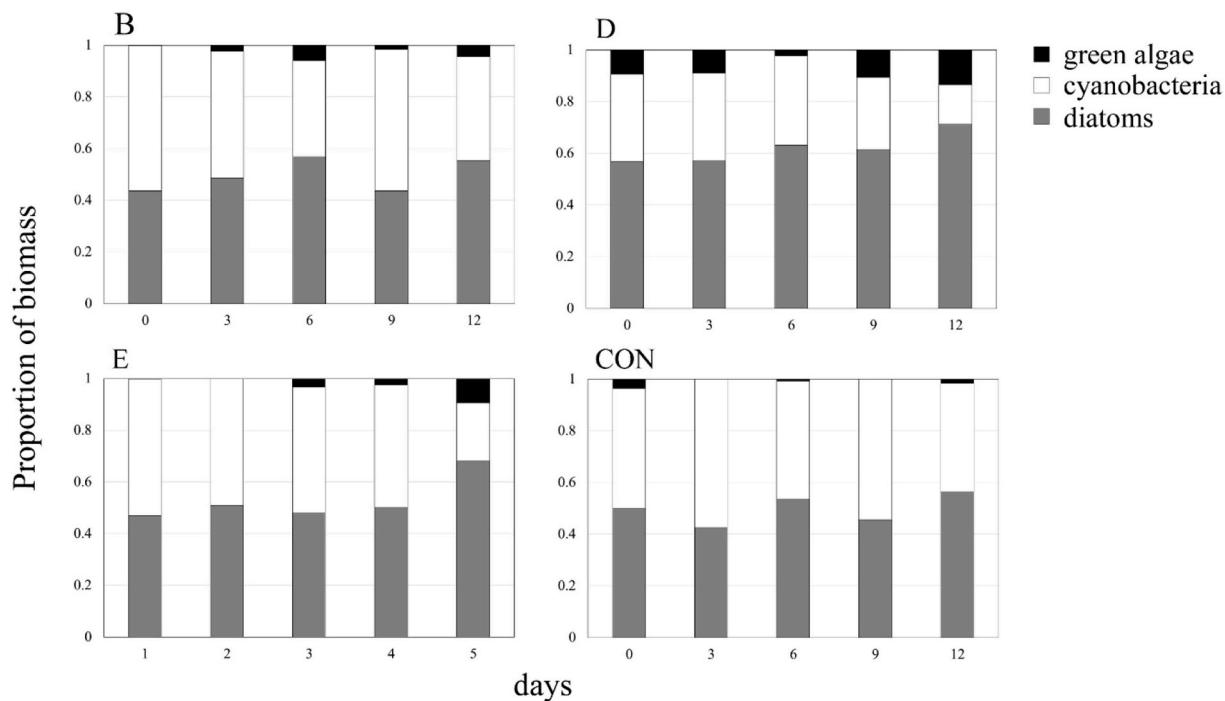
decreased from 3.6 to 1.6% during the experiment.

The effects of sesarmid presence were not as clear, as cyanobacteria were significantly affected by their presence (Table 2), while time had more of a significant impact on diatom and total MPB biomass. Fig. 4

shows the change in biomass over time. MPB decreased consistently over time in all experimental groups and the control. The biomass of diatoms and cyanobacteria increased in the control group over time, but not in any of the experimental treatments. Both diatom and



**Fig. 4.** Decrease in biomass ( $\mu\text{g chlorophyll.cm}^{-2}$ ) of (a) diatoms, (b) cyanobacteria, (c) green algae and (d) total microphytobenthos with and without the presence of sesarmid crabs over the 12 day experimental period. Treatment B contained only five fiddler crabs, while D consisted of five fiddler crabs and three Chiromantes eulimene individuals, and E consisted of five fiddler crabs and one *Neosarmatium africanum* individual. CON plots had no fiddler crabs. Values represented are means with standard error bars. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 5.** Class composition of microphytobenthos over the experimental period for each sesarmid treatment. B – only *Austruca occidentalis*, D – *A. occidentalis* and *Chiromantes eulimene*, E – *A. occidentalis* and *Neosarmatium africanum*, and CON – control with no crabs. Chlorophyll was measured in  $\mu\text{g per cm}^{-2}$ .

cyanobacteria biomass decreased in treatments B (sesarmids absent) and E (*N. africanum* present), but remained stable under treatment D (*C. eulimene* present). Green algae once again fluctuated independently of sesarmid presence/absence (Fig. 4d).

In terms of algal composition (Fig. 5), both sesarmid experimental treatments (D with *C. eulimene* and E with *N. africanum*) showed a higher proportion of green algae by the end of the experiment, with increases of approximately 9% and 4% respectively. The natural density treatment B showed a 4% increase in green algae, similar to treatment E, while the control showed a decrease in the green algal component of total biomass. In treatments B and D, cyanobacteria decreased in proportion from 56 to 40% and from 34 to 15% respectively. A larger decrease in proportion was seen in treatment E, from 53% to 23%, while a much smaller decrease (47–42%) was measured in the control.

#### 4. Discussion

Despite the shift in microalgal group composition with an increase in crab density, there was no significant impact of crab density on overall MPB biomass (Fig. 2d, Table 2). While MPB significantly decreased over time in all populated plots (Table 2, Figs. 2d and 4d), there was no difference between treatments, either in the density experiment or the sesarmid presence experiment. This suggests that as fiddler crabs feed on more dominant algal groups (in this case cyanobacteria and diatoms), they facilitate the growth of other microalgal groups such as green algae. Fig. 3c shows algal composition at the highest fiddler crab density and indicates a significant decrease in cyanobacteria composition allowing the proportion of green algae to increase.

So while fiddler crabs alter the composition of microalgal groups possibly through selective feeding, it is unlikely that they significantly reduce overall MPB biomass. It is more likely that abiotic factors influenced MPB biomass in this study. For example, a sharp decrease was noted for MPB biomass across treatments A, B, D, and E from day 3 to day 6. The reason for this is unclear although most likely due to an abiotic factor that was unaccounted for in this experiment e.g. rainfall was noted intermittently during the experimental period and possibly led to an increase in inorganic nutrients with the freshwater inflow.

Other known important drivers of MPB biomass are light availability (Kristensen et al., 2008), inorganic nutrients (Bourgeois et al., 2010), tidal movements (Ribeiro and Iribarne, 2011) and seasonality (Pülmans et al., 2016), all constituting abiotic factors.

Of the microphytobenthic groups, green algae made up the smallest portion of biomass (0–17% - Fig. 3) during the experiment. Cyanobacteria and diatoms dominated equally at the start of the experiment but by the end diatoms were dominant in all treatments and the control except treatment A, which had the lowest density of fiddler crabs at 12 ind.  $\text{m}^{-2}$  (Figs. 3 and 4). Generally microalgal production is limited in mangroves, where it is accepted that light availability has greater influence over microalgal growth in mangroves compared to nutrient availability (Alongi, 1988; Kristensen et al., 2008). Despite this, MPB is not a limiting food source in the St Lucia mangroves (Peer et al., 2015) or elsewhere (Ribeiro and Iribarne, 2011; Pülmans et al., 2016), although it has been demonstrated that the replenishment of MPB is dependent on tidal fluctuations (Ribeiro and Iribarne, 2011). Since the St Lucia estuary is considered a non-tidal mangrove habitat (Peer et al., 2018), it is possible that MPB consumption by fiddler crabs would be unsustainable and this suggests that fiddler crab adult populations cannot survive in some areas unless tidal fluctuations are restored when the mouth is breached.

In contrast, fiddler crabs have been shown to facilitate primary production of microalgae and macro flora by aerating the substratum and influencing nutrient availability (Smith et al., 2009; Gittman and Keller, 2013). The role of faecal pellets in nutrient-enrichment has been documented for sesarmids which feed primarily on mangrove leaves. These crabs facilitate decomposition increasing the availability of organic matter and nutrients for food production and primary consumption Lee (1997), Werry and Lee (2005). However, the role of fiddler crab faecal production on primary production still remains unclear. The deposition of fiddler crab faecal pellets enhances available carbon and facilitates nutrient regeneration (Hargrave, 1976) which is beneficial to primary producers in nutrient-poor mangrove soils (Reef et al., 2010). Furthermore, Cuellar-Gempeler and Munguia (2013) demonstrated how certain bacteria are able to survive within fiddler crab digestive tracts, being ejected through faecal pellets and how in this way, fiddler

crabs can influence dispersal and dominance of certain bacterial groups.

Fiddler crab density appeared to reduce the biomass of cyanobacteria and diatoms and increase green algal biomass over time. Robertson et al. (1981) experimented on the sand fiddler crab *Leptuca pugilator* and found that feeding was stimulated by the availability of both diatoms and cyanobacteria (blue-green algae). The authors speculated that the preference for these two groups over bacteria and ciliates was either due to the palatability of stimulatory compounds in mucoid sheaths of diatoms and cyanobacteria, or to more efficient extraction of these two groups from the sediment. The reduction of diatoms and cyanobacteria could create more available resources for green algae, which indeed increased in biomass under treatments B and C in this study. It is unclear whether this group is affected by fiddler crab activity, as it was only present in small amounts.

*Austruca occidentalis* often occurs at the landward fringe of mangrove habitats with sesarmid species i.e. *C. eulimene* and the much larger *N. africanum*. These species are all tolerant to drought conditions and freshwater dominance. Field observations show that *C. eulimene* are much more abundant (most likely due to their smaller size) and active on the surface compared to *N. africanum*, which spend most of their time in their burrows emerging only to collect fallen leaves. It was thus expected that *C. eulimene* would have a more notable effect on *A. occidentalis* compared to *N. africanum*. Fiddler crabs often seek shelter in burrows or stop feeding/movement when *C. eulimene* or *N. africanum* individuals move closer (N. Peer, pers. obs.). Thus fiddler crabs are more likely to display surface activity in the presence of *N. africanum* than in the presence of *C. eulimene*, since the latter species spends more time on the surface. The presence of *C. eulimene* should also indirectly influence MPB biomass more positively compared to *N. africanum*, as it inhibits fiddler crab surface activity. However, *C. eulimene* did not have any significant effects on MPB biomass compared with either treatment B (*A. occidentalis* only) or E (*A. occidentalis* and *N. africanum*) (Table 2). Fig. 4 shows similar trends in the decrease of diatoms and cyanobacteria in both treatments B (*A. occidentalis* only) and E (*A. occidentalis* and *N. africanum*), suggesting a similar level of activity both in the presence and absence of *N. africanum*. While there was a smaller overall decrease in cyanobacteria and diatoms in treatment D (*A. occidentalis* and *C. eulimene*), these algal groups had lower levels of biomass to begin with (Fig. 4a and b).

However, while *N. africanum* may pose less interference (and thus indirectly affect MPB biomass), this detritivorous species mostly feeds on fallen mangrove leaves (Steinke et al., 1993; Dahdouh-Guebas et al., 1999) and does not directly affect MPB biomass through surface feeding. Conversely, the feeding habits of *C. eulimene* appear to be more generalist. Although these have not been studied previously, field observations show that this species feeds on detritus, small molluscs and sediment, directly affecting different algal groups. Feeding of *C. eulimene* in D plots could have contributed to consumption/disturbance of microalgal groups subsequently confounding the results of this experiment.

Fiddler crabs have been shown to influence mangrove soil biogeochemistry and productivity through different activities. Burrow construction of mangrove crabs affects both sediment structure (Botto and Iribarne, 2000), sediment composition (Mokhtari et al., 2016), and benthic microbial structure (Booth et al., 2019). Reinsel (2004) also investigated the impacts of fiddler crab feeding on the reduction of MPB and meiofaunal densities and found that these effects were seasonally influenced. Seasonal feeding experiments conducted on the same population (Peer et al., 2015) revealed that *A. occidentalis* feeds less and displays less surface activity in winter compared to summer. Thus it is expected that fiddler crabs would exert a lower pressure on MPB populations during winter compared to summer.

In this study, we show how MPB biomass modulates and supports crab populations with a shift in species composition instead of

reduction in overall MPB biomass. The top-down interaction between fiddler crabs and the MPB community appears to be a complex balance which requires more investigation perhaps over a longer experimental period and in a variety of habitats. Mchenga and Tsuchiya (2008) discussed the delicate balance of production and decomposition of organic matter by primary producers and crabs respectively, highlighting the disruption that occurs with anthropogenic input.

As we are already observing effects of global climate change and associated sea level rise, we consider their potential impacts in the scenario of this study. Although there is a definite effect of sea level rise on tides globally, this response is a non-linear response with fluctuations and amplitudes either increasing or decreasing depending on geomorphology, riverine input, anthropogenic activities and ocean currents (Devlin et al., 2017; Pickering et al., 2017). Devlin et al. (2017) predicted that areas with river flow will experience a decrease in tidal amplitude. Since mangrove habitats occur most frequently around estuaries, it can be assumed that with sea level rise, these habitats will experience less tidal input. Without this tidal input, MPB communities will have less chance to recover from grazing activities so the effects of grazing may be exacerbated. These changes will also reduce ecosystem stability in the face of environmental disruptions or anthropogenic input. These effects could involve alteration of the microalgal species composition to favour less palatable groups or overall depletion of MPB standing stocks.

Lastly, when considering benthic communities, results can also include other groups such as microbial communities and meiofauna which were not considered in this study. Abdullah and Lee (2016) found that fiddler crabs indirectly interfere with other species through physical disturbance of the sediment. However, it is also possible that, by changing the MPB composition and availability of specific algal groups, fiddler crabs interfere with food availability to meiofauna. Either way, the indirect effect of fiddler crabs on all benthic communities (i.e. microbiota and meiofauna) as well as sediment properties through the consumption of MPB and shift in algal composition has broader implications for the study of mangrove ecosystem productivity. Although it well-established that fiddler crabs feed mostly on MPB, this study is the first to demonstrate the selective impacts of this feeding behaviour and provides more insight into MPB community dynamics in mangrove forests where they are poorly studied.

## Acknowledgements

The authors are grateful to Jackie Raw for field assistance, and to Mandy Jones and Nicola Carrasco for lab assistance. Funding for this project was provided by the National Research Foundation (grant no. 84375), Nelson Mandela University and The Ernst and Ethel Eriksen Trust. This work is based on the research supported by the South African Research Chairs Initiative of the Department of Science and Technology and NRF. Any opinion, finding and conclusion or recommendation expressed in this material is that of the author(s) and the NRF does not accept any liability in this regard.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2019.106332>.

## References

- Abdullah, M.M., Lee, S.Y., 2016. Meiofauna and crabs in mangroves and adjoining sandflats: is the interaction physical or trophic? *J. Exp. Mar. Biol. Ecol.* 479, 69–75. <https://doi.org/10.1016/j.jembe.2016.03.004>.
- Alongi, D.M., 2012. Carbon sequestration in mangrove forests. *Carbon Manag.* 3, 313–322.
- Alongi, D.M., 1988. Bacterial productivity and microbial biomass in tropical mangrove sediments. *Microb. Ecol.* 15, 59–79.

- Beutler, M., Wiltshire, K.H., Meyer, B., Moldaenke, C., Lüring, C., Meyerhöfer, M., Hansen, U.P., Dau, H., 2002. A fluorometric method for the differentiation of algal populations in vivo and in situ. *Photosynth. Res.* 72 (1), 39–53. <https://doi.org/10.1023/A:1016026607048>.
- Booth, J.M., Fusi, M., Marasco, R., Mbobo, T., Daffonchio, D., 2019. Fiddler crab bioturbation determines consistent changes in bacterial communities across contrasting environmental conditions. *Sci. Rep.* 9, 3479. <https://doi.org/10.1038/s41598-019-40315-0>.
- Botto, F., Iribarne, O., 2000. Contrasting effects of two burrowing crabs (*Chasmagnathus granulata* and *Uca uruguensis*) on sediment composition and transport in estuarine environments. *Estuar. Coast Shelf Sci.* 51, 141–151. <https://doi.org/10.1006/ecss.2000.0642>.
- Bourgeois, S., Hochard, S., Pringault, O., 2010. Subtidal microphytobenthos: effects of inorganic and organic compound supplies on migration, production, and respiration in a tropical coastal environment. *Aquat. Microb. Ecol.* 61, 13–29.
- Chen, S., Chmura, G.L., Wang, Y., Yu, D., Ou, D., et al., 2019. Benthic microalgae offset the sediment carbon dioxide emission in subtropical mangrove in cold seasons. *Limnol. Oceanogr.* 64, 1297–1308. <https://doi.org/10.1002/lo.11116>.
- Cuellar-Gempeler, C., Munguia, P., 2013. Fiddler crabs (*Uca thayeri*, Brachyura: Ocypodidae) affect bacterial assemblages in mangrove forest sediments. *Community Ecol.* 14, 59–66. <https://doi.org/10.1556/ComEc.14.2013.1.7>.
- Dahdouh-Guebas, F., Giuggioli, M., Oluoich, A., Vannini, M., Cannicci, S., 1999. Feeding habits of non-ocypodid crabs from two mangrove forests in Kenya. *Bull. Mar. Sci.* 64 291–197.
- Devlin, A.T., Jay, T.A., Talke, S.A., Zaron, E.D., Pan, J., et al., 2017. Coupling of sea level and tidal range changes, with implications for future water levels. *Sci. Rep.* 7, 17021. <https://doi.org/10.1038/s41598-017-17056-z>.
- Dye, A.H., Lasiak, T.A., 1986. Microbenthos, meiobenthos and fiddler crabs: trophic interactions in a tropical mangrove sediment. *Mar. Ecol. Prog. Ser.* 32, 259–264.
- Gittman, R.K., Keller, D.A., 2013. Fiddler crabs facilitate *Spartina alterniflora* growth, mitigating periwinkle overgrazing of marsh habitat. *Ecology* 94, 2709–2718.
- Gordon, H.R.S., 1958. Synchronous claw-waving of fiddler crabs. *Anim. Behav.* 134, 238–241. [https://doi.org/10.1016/0003-3472\(58\)90057-5](https://doi.org/10.1016/0003-3472(58)90057-5).
- Hargrave, B.T., 1976. The central role of invertebrate faeces in sediment decomposition. In: Anderson, J.M., Mann, H.K. (Eds.), *The Role of the Terrestrial and Aquatic Organisms in Decomposition Processes*. Blackwell Scientific Publications, Oxford, UK, pp. 301–321.
- Hillebrand, H., Sommer, U., 1997. Response of epilithic microphytobenthos of the Western Baltic Sea to *in situ* experiments with nutrient enrichment. *Mar. Ecol. Prog. Ser.* 160, 35–46. <https://doi.org/10.3354/meps160035>.
- Hoppe-Speer, S.J.L., Adams, J.B., Rajkaran, A., 2013. Response of mangroves to drought and non-tidal conditions in St Lucia Estuary, South Africa. *Afr. J. Aquat. Sci.* 38, 153–162. <https://doi.org/10.2989/16085914.2012.759095>.
- Jaschinski, S., Aberle, N., Gohse-Reimann, S., Brendelberger, H., Wiltshire, K.H., Sommer, U., 2009. Grazer diversity effects in an eelgrass-epiphyte-microphytobenthos system. *Oecologia* 159, 607–615. <https://doi.org/10.1007/s00442-008-1236-2>.
- Katz, L.C., 1980. Effects of burrowing by the fiddler crab, *Uca pugnax* (Smith). *Estuar. Coast Mar. Sci.* 11, 233–237. [https://doi.org/10.1016/S0302-3524\(80\)80043-0](https://doi.org/10.1016/S0302-3524(80)80043-0).
- Klanderud, K., Vandvik, V., Goldberg, D., 2015. The importance of biotic vs. abiotic drivers of local plant community composition along regional bioclimatic gradients. *PLoS One* 10, e0130205. <https://doi.org/10.1371/journal.pone.0130205>.
- Kring, S.A., Figary, S.E., Boyer, G.L., Watson, S.B., Twiss, M.R., 2014. Rapid in situ measures of phytoplankton communities using the bbe FluoroProbe: evaluation of spectral calibration, instrument intercompatibility, and performance range. *Can. J. Fish. Aquat. Sci.* 71 (7), 1087–1095. <https://doi.org/10.1139/cfias-2013-0599>.
- Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: a review. *Aquat. Bot.* 89, 201–219. <https://doi.org/10.1016/j.aquabot.2007.12.005>.
- Lee, S.Y., 1997. Potential trophic importance of the faecal material of the mangrove seasmarine crab *Sesarma messa*. *Mar. Ecol. Prog. Ser.* 159, 275–284.
- Lim, S.S.L., Rosiah, A., 2007. Influence of pneumatophores on the burrow morphology of *Uca annulipes* (H. Milne Edwards, 1837) (Brachyura, Ocypodidae) in the field and in simulated mangrove micro-habitats. *Crustaceana* 80, 1327–1338. <https://doi.org/10.1163/156854007782605529>.
- MacIntyre, H.L., Geider, R.J., Miller, D.C., 1996. Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats: I. Distribution, abundance and primary production. In: Selected Papers from the First Annual Marine and Estuarine Shallow Water Science and Management Conference, vol 19. pp. 186–201. <https://doi.org/10.2307/1352224>.
- McCraith, B.J., Gardner, L.R., Wethey, D.S., Moore, W.S., 2003. The effect of fiddler crab burrowing on sediment mixing and radionuclide profiles along a topographic gradient in a southeastern salt marsh. *J. Mar. Res.* 61, 359–390. <https://doi.org/10.1357/002224003322201232>.
- Mchenga, I.S.S., Tsuchiya, M., 2008. Nutrient dynamics in mangrove crab burrow sediments subjected to anthropogenic input. *J. Sea Res.* 59, 103–113. <https://doi.org/10.1016/j.seares.2007.06.005>.
- Millard, N.A.H., Broekhuysen, G.J., 1970. The ecology of South African estuaries Part X. St Lucia: a second report. *Zool. Afr.* 5, 277–307. <https://doi.org/10.1080/00445096.1970.11447398>.
- Milner, R.N.C., Detto, T., Jennions, M.D., Backwell, P.R.Y., 2010. Hunting and predation in a fiddler crab. *J. Ethol.* 28, 171–173. <https://doi.org/10.1007/s10164-009-0156-x>.
- Mokhtari, M., Abd Ghaffar, M., Usup, G., Che Cob, Z., 2016. Effects of fiddler crab burrows on sediment properties in the mangrove mudflats of Sungai Sepang, Malaysia. *Biology* 5, 7. <https://doi.org/10.3390/biology5010007>.
- Mouton Jr., E.C., Felder, D.L., 1995. Reproduction of the fiddler crabs *Uca longisignalis* and *Uca spinicarpa* in a Gulf of Mexico salt marsh. *Estuaries* 18, 469–481.
- Mouton Jr., E.C., Felder, D.L., 1996. Burrow distributions and population estimates for the fiddler crabs *Uca spinicarpa* and *Uca longisignalis* in a Gulf of Mexico salt marsh. *Estuaries* 19, 51–61. <https://doi.org/10.2307/1352651>.
- Peer, N., Rajkaran, A., Miranda, N.A.F., Taylor, R.H., Newman, B., et al., 2018. Latitudinal gradients and poleward expansion of mangrove ecosystems in South Africa: 50 years after Macnae's first assessment. *Afr. J. Mar. Sci.* 40, 101–120. <https://doi.org/10.2989/1814232X.2018.1466728>.
- Naderloo, R., Schubart, C.D., Shih, H.T., 2016. Genetic and morphological separation of *Uca occidentalis*, a new East African fiddler crab species, from *Uca annulipes* (H. Milne Edward, 1837) (Crustacea: Decapoda: Brachyura: Ocypodidae). *Zool. Anz.* 262, 10–19.
- Peer, N., Miranda, N.A.F., Perissinotto, R., Raw, J.L., 2015. Feeding dynamics of the fiddler crab (*Uca annulipes*) in a non-tidal mangrove forest. *Mar. Freshw. Res.* 67, 556–565. <https://doi.org/10.1071/MF15038>.
- Pickering, M.D., Horsburgh, K.J., Blundell, J.R., Hirschi, J.M., Nicholls, R.J., Verlaan, M., Wells, N.C., 2017. The impact of future sea-level rise on the global tides. *Cont. Shelf Res.* 142, 50–68. <https://doi.org/10.1016/j.csr.2017.02.004>.
- Pülmanns, N., Mehlig, U., Nordhaus, I., Saint-Paul, U., Diele, K., 2016. Mangrove crab *Ucides cordatus* removal does not affect sediment parameters and stipule production in a one year experiment in northern Brazil. *PLoS One* 11, e0167375. <https://doi.org/10.1371/journal.pone.0167375>.
- Reef, R., Feller, I.C., Lovelock, C.E., 2010. Nutrition of mangroves. *Tree Physiol.* 30, 1148–1160. <https://doi.org/10.1093/treephys/tpq048>.
- Reinsel, K.A., 2004. Impact of fiddler crab foraging and tidal inundation on an intertidal sandflat: season-dependent effects in one tidal cycle. *J. Exp. Mar. Biol. Ecol.* 313, 1–17. <https://doi.org/10.1016/j.jembe.2004.06.003>.
- Ribeiro, P.D., Iribarne, O.O., 2011. Coupling between microphytobenthic biomass and fiddler crab feeding. *J. Exp. Mar. Biol. Ecol.* 407, 147–154. <https://doi.org/10.1016/j.jembe.2011.05.030>.
- Robertson, J.R., Fudge, J.A., Vermeer, G.K., 1981. Chemical and live feeding stimulants of the sand fiddler crab, *Uca pugilator* (Bosc). *J. Exp. Mar. Biol. Ecol.* 53, 47–64.
- Savelli, R., Dupuy, C., Barillé, L., Lerouxel, A., Guizien, K., et al., 2018. On biotic and abiotic drivers of the microphytobenthos seasonal cycle in a temperate intertidal mudflat: a modelling study. *Biogeosciences* 15, 7243–7271. <https://doi.org/10.5194/bg-15-7243-2018>.
- Smith, N.F., Wilcox, C., Lessmann, J.M., 2009. Fiddler crab burrowing affects growth and production of the white mangrove (*Laguncularia racemosa*) in a restored Florida coastal marsh. *Mar. Biol.* 146, 2255–2266. <https://doi.org/10.1007/s00227-009-1253-7>.
- Steinke, T.D., Rah, A., Holland, A.J., 1993. The feeding behaviour of the red mangrove crab *Sesarma meinerti* De Man, 1887 (Crustacea: Decapoda: Grapsidae) and its effect on the degradation of mangrove leaf litter. *S. Afr. J. Mar. Sci.* 13, 151–160. <https://doi.org/10.2989/025776193784287455>.
- Underwood, G.J.C., 2001. Microphytobenthos. In: Steele, J.H., Thorpe, S.A., Turekian, K.K. (Eds.), *Encyclopedia of Ocean Sciences*, second ed. Academic Press, Massachusetts, pp. 807–814.
- van der Sande, M.T., Peña-Claros, M., Ascarrunz, N., Arell, E.J., Licona, J.C., et al., 2017. Abiotic and biotic drivers of biomass change in a Neotropical forest. *J. Ecol.* 105, 1223–1234. <https://doi.org/10.1111/1365-2745.12756>.
- Welschmeyer, N.A., 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheophytins. *Limnol. Oceanogr.* 39, 1985–1992. <https://doi.org/10.4319/lo.1994.39.8.1985>.
- Werry, J., Lee, S.Y., 2005. Grapsid crabs mediate link between mangrove litter production and estuarine planktonic food chains. *Mar. Ecol. Prog. Ser.* 293, 165–176.
- Wolfrath, B., 1992. Field experiments on feeding of European fiddler crab *Uca tangeri*. *Mar. Ecol. Prog. Ser.* 90, 39–43. <https://doi.org/10.3354/meps090039>.