 doi:10.20944/preprints202204.0195.v1

Crab species-specific excavation and architecture of burrows in restored mangrove habitat

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Abstract

Burrowing crabs are considered to be the ecosystem engineers in mangrove ecosystems because they have impact on the ecosystem functioning through bio-geochemical transformations. This process depends on the size and shape of burrows. The present study analysed architecture of burrows, constructed by crabs in a restored mangrove habitat. Fourteen crab species were found to construct the burrows of 13 different shapes with predominance of 'I','J','L'. The burrow shape was diverse in *Metopograpsus messor,* followed by *Austruca occidentalis, Gelasimus vocans,* and *A. annulipes.* The burrow structural complexity was higher during summer in *Avicennia* or open zone. Sesarmids were larger in size than fiddlers, making the burrows of wider opening. Fiddlers were relatively smaller in size and they constructed complex burrows at vertical position, making longer and deeper burrows, in contrast to sesarmids, which formed simple burrows at horizontal position, digging shorter and shallower burrows. The sesarmids have smaller burrows without branching in mangrove zones, whereas the fiddler crabs (except *Austruca variegata*) have larger burrows with or without branching in open and *Avicennia* zones. The fiddler crabs especially *Austruca occidentalis* and *A.annulipes* have separate openings and passage for exit and entry as an adaptation against predators. The present work identified *Austruca occidentalis* and *A. annulipes* as the most potent bio-turbating crab species for restored mangrove habitats due to their efficiency in soil excavation and large sized burrows.

Keywords: crabs, fiddlers, sesarmids, burrowing, bioturbation, mangrove restoration

Introductión

Crabs are the keystone species of mangrove forest ecosystems (Smith et al., 1991), actively involved in burrowing; during which, sediments are excavated and mixed that can alter the physical, chemical and biological aspects, and this process is known as bioturbation. This activity aerates sediment, flushes soil, reduces pore-water salinity, increases nutrient availability, reduces toxic sulphide levels and creates microhabitats for benthic organisms (Smith et al., 1991; Lee, 1998; Sarker et al., 2020). The bioturbating crabs are considered to be the ecosystem engineers in mangrove ecosystems because they have considerable impact on the ecosystem functioning through bio-geochemical transformations in the water-sediment interface of mangrove habitats (Dahdouh-Guebas et al. 2002; Cannicci et al., 2008; Kristensen, 2008; Penha-Lopes et al., 2009;Sarker et al., 2020).

Crab burrow architecture is species-specific, but the crabs can modify the architecture to adjust a wide range of conditions that prevail in different habitats. The crabs display significant inter-specific variations in their burrow morphologies in relation to different environmental and biological factors of their biotopes (Morrisey et al., 1999; Lim and Diong, 2003). The burrows vary in shape and size, depending on biological factors such as crab species, size, sex and reproductive stages (Lim and Diong, 2003, Lim 2006, Sen and Sumit, 2016). The burrow architecture is also dependent on abiotic factors, such as sediment composition, vegetation, shore elevation, tidal variation, sub-surface root system and human disturbances (Penha-Lopes et al., 2009). The burrows serve as refuge against environmental adversity and as shelter for food storage and reproduction (Sen and Sumit, 2016). This is a major bioengineering effect that alters physical and chemical processes in mangrove forests (Kristensen and Alongi, 2006). The burrow functionality varies with architecture, differently constructed by crab species (Machado et al., 2013).

Burrow morphology varies between brachyuran crabs and hence composition of burrowing crabs has potential to impact ecosystem differently (Agusto et al., 2020). The burrow morphologies can also provide estimates of bioturbative activities by crabs from burrow volume and burrow depth (Machado et al. 2013). Most species within sesarmids and fiddlers are involved in burrowing of mangrove sediments (Kristensen, 2008). The burrow morphologies have been extensively studied in different species of the fiddler crabs: *Uca rapax*, *U. pugnax*, *U. longisignalis*, *U. spinicarpa*, *U. vocator*, *U. subcylindrica*, *U. tangeri*, *U. annulipes* and *U. vocans* (e.g. Sen and Sumit, 2016).

Vegetation influence the spatial distribution, abundance and burrowing activities of crabs within mangroves (Cannicci et al., 2008). The fiddler crabs construct lesser number of burrows on exposed beaches (non-mangroves) than that under mangrove canopy according to food availability. However, the number of crab burrows under mangrove canopy decreases as the canopy cover increases, and this is evident by a negative relationship between crab burrow density and mangrove canopy cover. Such studies are mostly confined to natural mangrove habitats rather than to restored mangroves (Wei et al., 2015). In a place along south east coast of India, no crabs were found to be present, but they got well-established over a period of mangrove restoration in that place (Ajmal Khan et al., 2005). However, there is no data on the crab burrow architecture in that restored mangrove habitat, and this information is required to get insight into the functional aspects of the crabs in the restored mangrove area. Hence, the present work was undertaken to deal with species-specific burrow excavation and architecture so as to identify the most influential functional species for restored mangrove ecosystems.

2. Materials and methods

2.1 Study area

The study area is at a mangrove vegetation artificially raised along the northern banks of Vellar estuary in southeast coast of India (Lat. 11^{0}.29'N; Long. 79^{0}.46'E; Fig.1). The Vellar estuary is influenced by tidal water from the Bay of Bengal and fresh-water inflow from adjoining backwaters and irrigation channels, extending upstream to a distance of 16 km from the river mouth. The average depth of estuary ranges from 2 m at low tide, and 6 meters during high tide. Average width and depth of the estuary are 100 m and 2.5 m respectively. The mangroves forest is about 25 years old covering an area of about 5 hectares, colonized with *Rhizophora* zone towards estuary and *Avicennia* zone towards landward and a non-vegetated open zone in upper intertidal area.

2.2 Sampling and analyses

Sampling was made for three intertidal zones namely, *Rhizophora*, *Avicennia*, and open zone for three seasons: monsoon (Nov. 2019), post-monsoon (Feb., 2020) and summer (June 2020). Crab burrow casts were made using plaster of Paris in four randomly selected burrows in a quadrat of 1 sq. m laid for each of the intertidal zones.

Crab burrow studies: Burrow casts were prepared using an aqueous solution of plaster of Paris, made in a ratio of 3:1 for plaster of Paris powder and water. This solution was poured into the crab burrows by using a syringe until the burrows were completely filled (Warburg & Shuchman, 1978). After 3 hours of drying, the burrow casts were carefully dug

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up manually or using a spade if the substrate was hardy. The burrow casts were cleaned using a brush and thoroghly washed with distilled water to remove all debris from their surface. Each cast was measured for architecture in terms of burrow opening diameter (BOD), total burrow length (TBL), total burrow depth (TBD) and burrow shape (BS). Soil excavation activity was measured in terms of burrow volume (BV) using water displacement method based on Archimedes principle. The complexity of burrow architecture was calculated as the ratio between TBL and TBD.

Crab studies: The crabs emerged out of burrows while adding plaster of Paris were collected manually and transferred to laboratory in polythene bags. The crabs were individually detected for sex and measured for their size in terms of body weight as well as carapace length and width using a venire calliper. The crabs were then identified based on morphological characters by following World Register of Marine Species (WORMS).

Statistical analyses: The data was subjected to statistical analysis for testing the significance between crab species for crab size or burrow architectures. Levene's test was conducted to test for equality of variance and covariance. Since it was non-significant, further multivariate analysis was made along with Post-Hoc and Tukey test to determine the significant differences for pair-wise comparison of different species. Pearson correlation coefficients were calculated flagging with significance at 1% and 5% levels respectively at $p<0.01$ and $p<0.05$ to determine the relationship among measures of crabs and burrow characteristics.

There was a significant difference between crab species when considered jointly on the variables of crab size or burrow architecture with Wilk's Lambda value of 0, F value (130,168) of 2.98, p value of 0.00 and partial Eta Squared value of 0.62. A separate ANOVA was then conducted for each dependent variable and the evaluated at alpha level of 0.025. However, there was no significant difference between sexes in crab size or burrow architecture except burrow shape.

There was significant difference between seasons when considered jointly on the variables of crab size or burrow architecture with Wilk's Lambda value of 0.33, F value (16, 66) of 3.1, p value of 0.001 and partial Eta Squared value of 0.43. A separate ANOVA was then conducted for each dependent variable and the evaluated at alpha level of 0.025. All variables were significant except crab weight, carapace width, burrow opening diameter, burrow volume and burrow shape.

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Similarly, there was significant difference between intertidal zones when considered jointly on the variables of crab size or burrow architecture with Wilk's Lambda value of 0.35, F value (16, 66) of 2.85, p value of 0.001 and partial Eta Squared value of 0.41. A separate ANOVA was then conducted for each dependent variable and the evaluated at alpha level of 0.025. All variables were significant except total burrow length, total burrow depth and burrow shape.

3. Results

Burrow types: The shape-based burrow types found in crab species across intertidal zones of restored mangrove habitat under different seasons are given in table 1. Totally 14 burrowing crab species that include fiddlers (7 spp.) and sesarmids (7 spp.) were collected from the study area. A total of 48 burrow casts was prepared and categorised into 13 types based on shape, and these were J, Y, L, C, I, CS, U, LL, V, X, S, CL, and JU types (Fig. 2). The burrows were predominantly 'I' shaped contributing to 35.4% of total casts, followed by 'J' (18.8%) and 'L' shaped (16.7%). Other types were 'Y' shaped (6.3%), LL (4.2%), V (4.2%) and the remaining ('C', 'CS', 'U', 'X', 'S', 'CL' and 'JU' shaped) each contributed to only 2.1%.

Burrow shape varied with crab species. *Metopograpsus messor* displayed the maximum of 6 types of burrow shape (L,I, CS, C, CL,J) followed by 4 types in *Austruca occidentalis* (L,JU,Y, X), *Gelasimus vocans* (I,S, J,V) and *A. annulipes* (I,LL,J,Y). Two types of burrows were found in *A. lactea* (L, I), *A. variegata* (I,J), *Parasesarma plicatum* (L,J) and *P. pictum* (LL,J). Only one type of burrow was found in *Austruca cryptica* (I), *Parasesarma bidens* (U), *Uca victoriana* (L), *P. guttatum* (L), *Episesarma mederi* (V), and *E. vesicolor* (Y).

Crabs burrowing varied with intertidal zones and seasons in the restored mangrove habitat. *Metopograpsus messor* constructed burrows only in mangrove zones, interestingly in *Rhizophora* zone during monsoon and in *Avicennia* zone during post-monsoon and summer. Thus there was a shift in the burrow construction from *Rhizophora* to *Avicennia* during monsoon to summer. *Parasesarma pictum* constructed burrows only in *Avicennia* zone during summer and monsoon. Similarly, *Austruca lactea* formed burrows only in *Avicennia* in all seasons and there was a shift in the shape from I to L from monsoon to summer. *Austruca variegata* constructed burrows only in mangrove zones, and there was also a shift in the shape from I to J from monsoon to postmonsoon. *Austruca occidentalis* produced burrows

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only in monsoon at *Avicennia* and open zones, whereas *Gelasimus vocans* made burrows in *Avicennia* and open zones in all seasons. *Austruca annulipes* produced burrows in *Avicennia* and open zones in monsoon and summer (Table 1).

Burrow structural complexity was measured as the ratio between TBL and TBD. This ratio varied with burrow shape being higher than the value of 1 for 'V' (1.22) and 'Y' shape (1.06); but lesser than 1 for JU, J shape (0.98); I,X,LL,S (0.97); L (0.96);U, C (0.94); and, for CS (0.91). The ratio also varied with crab species, ranging from 0.93 to 1.06 in fiddlers: 1.06 in *Gelasimus vocans,* 0.99 in *Austruca annulipes,* 0.97 in *A. occidentalis,* 0.95 in *A. lactea,* 0.94 in *Uca victoriana,* 0.94 in *A. variegata* and 0.93 in *A. cryptica.* In the case of sesarmids, the ratio was in a range of 0.93 – 0.98, being the highest in *Parasesarma pictum* (0.98)*,* followed by *Metopograpsus messor* (0.97)*, P. plicatum* (0.97)*, P. guttatum* (0.96)*, P. bidens* (0.94)*, Episesarma vesicolo***r** (0.94) and in *E. mederi* (0.93). It is interesting to note that the ratio was found high exceeding the value of 1 only in summer with *Avicennia* or open zones for the burrow shapes of I, J, Y, V (Table 1).

Size of crab species:

The crab size in terms of weight, carapace length and width of 14 species is shown in Fig. 3. Crab weight varied from 0.17 to 0.36 g for fiddlers, and from 0.22 to 0.90 g for sesarmids. It was the highest in *Austraca occidentalis* and *Episesarma vesicolor* and the lowest in *Gelasimus vocans* and *Metopograpsus messor*. The crab weight was correlated with carapace width (r= 0.95), carapace length (r= 0.93), BOD (r=0.92), MBL (r=0.48), TBL (r=0.44), TBD (r=0.44), and BV (r=0.38).

Carapace length ranged from 0.4 to 0.8 cm for fiddlers and from 0.4 to 2.3 cm for sesarmids. It was the maximum in *Uca victoriana* and *Episesarma vesicolor,* and minimum in *Austraca variegata* and *Parasesarma pictum* (Fig. 3). The carapace length had correlation with carapace width (r=0.93), BOD (r= 0.92), MBL (r= 0.40), TBD (r=0.30) and TBL (r=0.30).

Carapace width varied between 0.72 and 1.14 cm for fiddlers and from 0.7 to 2.5 cm for sesarmids, being the maximum in *Austraca occidentalis* and *Episesarma vesicolor* and the minimum in *Gelasimus vocans* and *Parasesarma plicatum* (Fig. 3). The carapace width was correlated with BOD (r= 0.99), MBL (r=0.47), TBD (r=0.40), TBL (r=0.40) and BV (r=0.32).

Burrow architecture of crab species

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Soil excavation activity in terms of burrow volume in different crab species is shown in Fig. 4. Burrow volume (BV) varied from 3.52 to 45.6 cm^3 for fiddler and from 1.95 to 24.0 cm^3 for sesarmids, being the highest in *Austruca occidentalis* and *Episesarma vesicolor* and the lowest in *Austruca lactea* and *Parasesarma plicatum.* The BV had correlation with TBL (r=0.81), TBD (r=0.81) and burrow shape (r= 0.44) (Fig.5).

Burrow measures for 14 crab species are given in fig. 6. Total burrow length (TBL) ranged from 1.3 to 12.72 cm for fiddlers, and from 2.6 to 9.75 cm for sesarmids being the highest in *Austruca occidentalis* and *Parasesarma pictum* and the lowest in *Austruca cryptica* and *Parasesarma plicatum*. The TBL had correlations with TBD (0.99), BV (r= 0.81), BOD (r= 0.40) and burrow shape (r=0.38), crab weight (r=0.44), carapace width (r=0.4) and length (r=0.30).

Total burrow depth (TBD) varied from 1.4 to 13.16 cm for fiddler and from 2.7 to 10 cm for sesarmids being the highest in *Austruca occidentalis* and *Parasesarma pictum* and the lowest in *Austruca cryptica* and *Parasesarma plicatum* (Fig. 6). The TBD was correlated with TBL (r=0.99), BV (r=0.81), BOD (r=0.39) and burrow shape (r=0.36), crab weight (r=0.44), carapace width (r=0.40) and carapace length (r=0.30).

Burrow opening diameter (BOD) varied from 0.78 to 1.16 cm for fiddlers and from 0.7 to 2.5 cm for sesarmids, being the maximum in *Austruca occidentalis* and *Episesarma vesicolor* and the minimum in *Gelasimus vocans* and *Parasesarma plicatum* .The BOD was correlated with carapace width (r=0.99), crab weight (r=0.92), carapace length (r=0.92), TBL (r= 0.40), TBD (r=0.39) and BV (0.31) (Fig.7).

Discussion

Crabs are key bioturbating organisms in mangrove habitats. Among the crabs, sesarmids and fiddlers are the most prominent groups, affecting biogeochemical transformation in mangrove soil (Kristensen et al., 2008). Not all crab species do construct burrows (Gillikin and Kamanu, 2005). Similarly, the present study recorded 14 burrowing crab species and 4 non-burrowing species. These were *Selatium brockii*, *Nanosesarma batavicum*, *U.boninensis, Paraleptuca chlorophthalmus.* The present study assessed the crab bio-turbation activity in restored mangrove habitat by evaluating the burrow architecture in 14 crab species. The burrow architecture was measured in terms of burrow shape, burrow opening diameter, total burrow length and total burrow depth, whereas the volume of soil excavated was evaluated in terms of burrow volume.

Sesarmids are of larger size than fiddlers (Kristensen, 2008) as evident in the present work by crab weight, carapace length and width (Fig.3), and this could be attributed to the stage of the crabs as juveniles or matured ones that were collected in the study area. Large-sized crabs excavate more volume of soil thereby making longer and deeper burrows with broader burrow opening so as to enable them to enter into the burrow chamber and to reside in spacious burrow (Lim and Diong, 2003; Lim 2006). Sesarmids are larger in size than fiddlers. The larger sized sesarmids displayed the burrows of wider opening, but relatively shorter and shallower burrows as found in *Episesarma mederi, E. vesicolor, Parasesarma pictum* and *P.guttatum*. The fiddlers were efficient in soil excavation and also in making deeper and longer burrows as found in *Austruca occidentalis* and *A. annulipes*. Smaller-sized crabs were poor in soil excavation and constructed only shorter and shallower burrows with narrow opening, as found in the species of fiddlers (*Gelasimus vocans, Austruca lactea, Austruca cryptica*) and sesarmids (*Parasesarma plicatum, Metopograpsus messor*).

Sesarmids constructed simple and horizontal burrows due to hard and compact mangrove substratum that prevented deep-digging, whereas the fiddlers formed complex and vertical burrows due to porous soil substratum without interference of sub-surface root structures. Thus, the fiddlers were found much more efficient in constructing the burrows of different shapes than the sesarmids, as the fiddlers require the burrow construction to avoid predation, environmental and human disturbance, whereas the sesarmids stay protected on complex structure of mangrove vegetation, however, they require burrows mainly for storing and processing the mangrove litter (Lim and Diong, 2003). For example, *Episesarma vesicolor* stays underneath of mangrove roots and then moves to stems especially during high tide and hence they did not construct a deeper and longer burrow. However it makes larger burrow opening, facilitating the entry of the larger sized crabs.

The size of burrows is attributed to sex of crabs. Males dig and reside in larger burrows due to spatial requirement for their larger body size and cheliped; but the large chelipeds prevent the males to move easily into the burrows as compared to females with smaller chelipeds (Lim and Diong, 2003). Females and smaller males are better at burrowing than larger males because due to enlarged chelipeds are of limited use in burrowing (Morrisey et al., 1999). Females of *Uca dussumieri* and *U. vocans* were reported to have longer burrows with larger opening than the males (Sen and Sumit, 2016). However, the present study did not find any statistical significance between crab sexes in burrow construction.

Burrow architecture was diverse with crab species. *Metopograpsus messer* displayed the maximum of 6 different types of burrows, followed by 4 types in *Gelasimus vocans, Austruca occidentalis* and *A. annulipes*. The burrow structural complexity as measured by the ratio between total burrow length and total burrow depth was higher in the fiddlers than the sesarmids. This could be attributed to the instability of burrows due to structural collapse, which requires a continuous construction and reworking efforts. Contrary to our observation, the sesarmids are reported to create a wide range of complex and irregular burrow shapes as compared to the fiddlers (Lim and Diong, 2003; Thongtham and Kristensen, 2003; Kristensen, 2008; Wang et al., 2015). It is interesting to note in the present study that the burrow structural complexity ratio exceeded the value of 1 during summer. Hence, the diversity of burrow structure might be a response to higher stress factors such as high temperature, as well to avoid the intensity predatory pressure (Micheli et al., 1991; Stieglitz et al., 2000; Thongtham and Kristensen, 2003).

Crabs constructed burrows simply by starting with an elongated shaft of 'I' shaped which is further modified to J, L and other shapes according to their functional requirements. The present study found predominance of I, J, L shaped burrows. Branching of burrows is required to avoid heavy predatory pressure and to accommodate more juveniles and parents together. Similarly more number of openings facilitates the crabs to escape easily from predators. Open ending of burrow casts indicate the presence of molluscan shells on which the burrow is constructed. Twin burrows recorded for the first time of this study in *Gelasimus vocans* perhaps for accommodating separately the individual crabs of same or different sexes. Thus the burrow construction is need-based. Crab species such as *Paraseseama guttatum* burrows only in dry soils where no other shelter is available to hide (Gillikin and Kamanu, 2005). The burrows of 'I' shape nurture juveniles, while that of 'Y' shaped support adults of *Metaplax* crabs (De, 2019) and thus there is an ontogenic differences in burrow shape. The present study observed a shift in burrow shape from I to L from monsoon to summer in the case of *Austruca lactea* and a similar shift was also found from *Rhizophora* to *Avicennia* by *Metopograpsus messor* (Table 1).

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There was a specific association of crab burrows and mangroves. *Parasesarma pictum* and *P. plicatum* constructed burrows only in *Avicennia* zone because of cannibalistic behaviour of the species, attacking small crabs that are abundantly available in that zone. *Austruca variegata* constructed burrows only in mangrove zones, but not in open zone. Sesarmids were found to construct burrows mostly in *Rhizophora* zone, while fiddlers in *Avicennia* or open zones. The burrows shapes, specific to crab species were 'JU' to *Austruca occidentalis,* 'S' to *Gelasimus vocans,* 'U' to *Parasesarma bidens* and CS, C, CL to *Metopograpsus messor.*

The species-specific burrow characteristics provide insight into different bioengineering role of crab species, which are critical to functioning and health of mangrove ecosystem (Agusto et al., 2020). The present work identified *Austruca occidentalis* and *A. annulipes* as the most potent bio-turbating crab species for restored mangrove habitats, similar to *Macrophthalmus* (Mareotic) *depressus* for hyper arid ecosystems (Arid Al-Khayat and Giraldes, 2020) and *Uca rosea* for Sundarban mangroves (Sen and Sumit, 2016).

Acknowledgements

The authors are thankful to DST-TWAS for Post-Doc. Fellowship (WWM; FR No. 3240306336) and to the authorities of Annamalai University, India for providing facilities.

Conflict of Interests

The authors do not have any conflict of interest.

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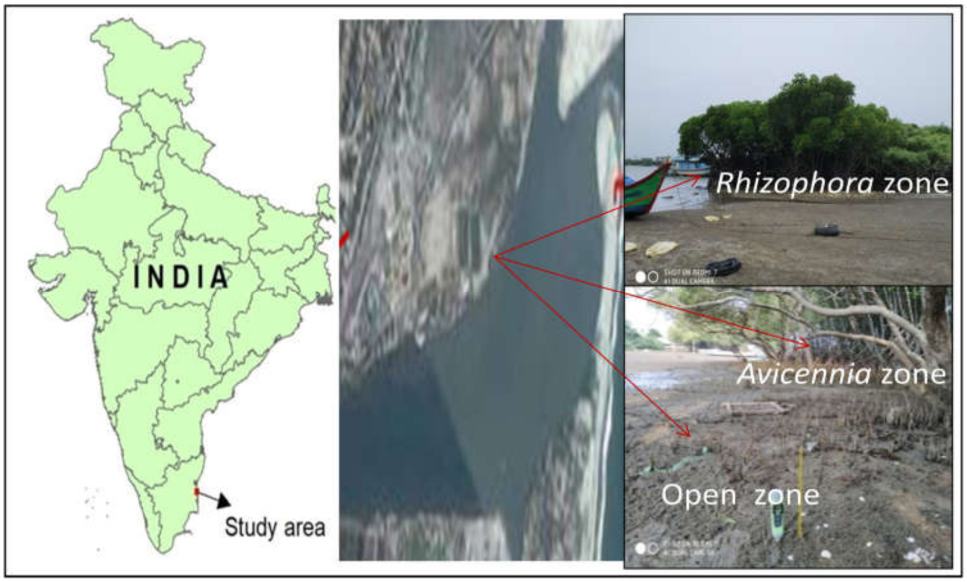


Fig.1. Study area along a restored mangrove forest in Vellar estuary, southeast of India

Austraca occidentalis and types of burrows (JU, L, Y, X)

A. annulipes and types of burrows (LL, Y, J, I)

Gelasimus vocans and types of burrows (S, I, V, J)

doi:10.20944/preprints202204.0195.v1

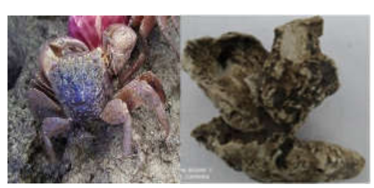

A.variegate and types of burrows (J, I) *A. cryptica* and type of burrow (I)


A lactea and types of burrows (L, I) *Uca victoriana* and types of burrow (L)

Metopograpsus messor and types of burrows (CS, I, CL, J, L, C)


Parasesarma pictum and type of burrow (LL, J) *P. guttatum* and type of burrow(L)


P. plicatum and types of burrow (L,J) *P. bidens* and type of burrow (U)

Episesarma versicolor and type of burrow (Y) *E. mederi* and type of burrow(V)

Fig. 2. Crab burrow architectures found in restored mangrove habitat

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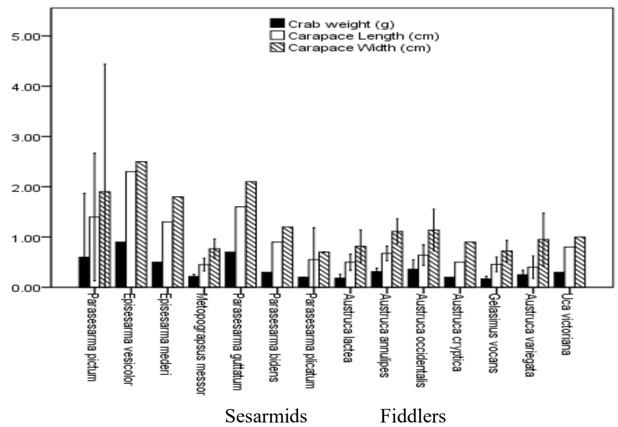

Fig 3. Crab weight, carapace width and length in 14 burrowing crab species; values significant between crab species at 1% level

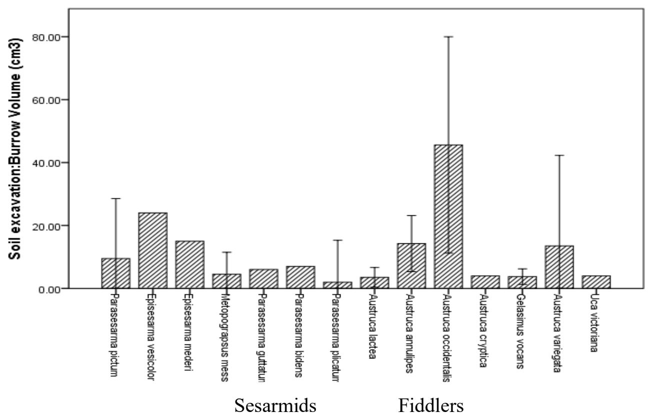

Fig 4. Crab species-specific soil excavation activity in terms of burrow volume (cm^3) ; values significant between crab species at 1% level

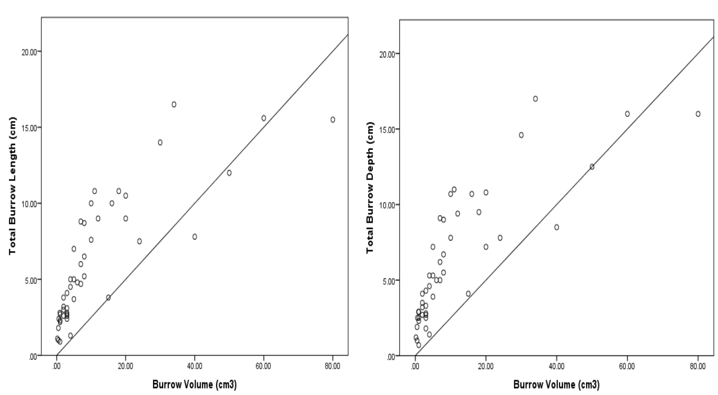

Fig 5. Relationship between burrow volume and total burrow length(r=0.81) or total burrow depth (r=0.81)

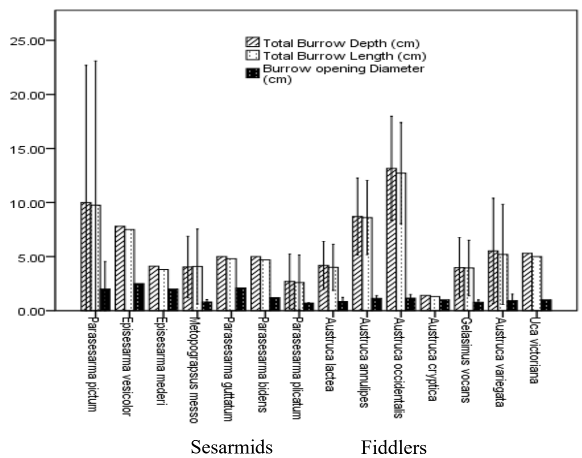

Fig 6. Crab species-specific burrow opening diameter, length and depth of burrows; values significant between crab species at 1% level

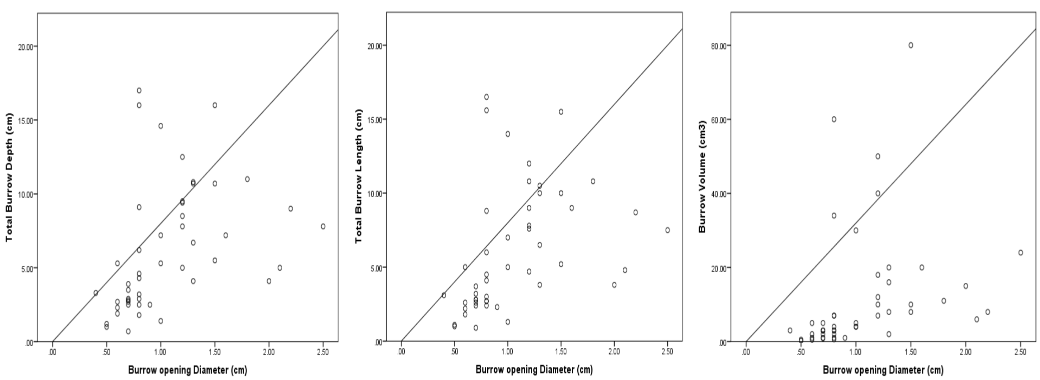

Fig 7. Relationship between burrow opening diameter and total burrow length (r= 0.40) or total burrow depth(r=0.39) at 1% level or burrow volume (r=0.31; p<0.05)

Table1. Burrow shape and its structural complexity ratio across three intertidal zones under three seasons of analysis in the restored mangrove forest

No	Species name	Season of Analysis	Inertidal Zone	Burrow Shape	Burrow structural complexity ratio (TBL/TBD)
1	*Metopograpsus messor*	Monsoon	*Rhizophora*	L	0.93
	Metopograpsus messor	Summer	*Avicennia*	J	1.14
	Metopograpsus messor	Monsoon	*Rhizophora*	I	0.93

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	Metopograpsus messor	Monsoon	*Rhizophora*	CS	0.91
	M. messor	Monsoon	*Rhizophora*	C	0.94
	M. messor	Post-monsoon	*Avicennia*	CL	0.96
			Mean	L,J.I,CS,C,CL	0.97
2	*Parasesarma guttatum*	Monsoon	*Rhizophora*	L	0.96
3	*Parasesarma plicatum*	Post-monsoon	*Avicennia*	L	0.97
	P.plicatum	Summer	*Avicennia*	J	0.96
			Mean	L,J	0.97
4	*Austruca occidentalis*	Monsoon	*Avicennia*	L	0.97
	A.occidentalis	Monsoon	*Avicennia*	L	0.96
	A.occidentalis	Monsoon	Open	Y	0.96
	A.occidentalis	Monsoon	Open	JU	0.98
	A.occidentalis	Monsoon	Open	X	0.97
			Mean	L,Y, JU,X	0.97
5	*A.lactea*	Monsoon	*Avicennia*	L	0.97
	A.lactea	Monsoon	*Avicennia*	L	0.94
	A.lactea	Monsoon	*Avicennia*	I	0.94
	A.lactea	Post-monsoon	*Avicennia*	I	0.95
	A.lactea	Post-monsoon	*Avicennia*	I	0.96
	A.lactea	Summer	*Avicennia*	I	0.96
			Mean	L,I	0.95
6	*Uca victoriana*	Monsoon	*Avicennia*	L	0.94
7	*Austruca variegata*	Monsoon	*Rhizophora*	J	0.92
	A.variegata	Monsoon	*Avicennia*	J	0.97
	A.variegata	Post-monsoon	*Rhizophora*	J	0.92
	A.variegata	Monsoon	*Rhizophora*	I	0.94
			Mean	I,J	0.94
8	*Parasesarma pictum*	Summer	*Avicennia*	J	0.98
	Parasesarma pictum	Monsoon	*Avicennia*	LL	0.97
			Mean	J,LL	0.98
9	*Gelasimus vocans*	Post-monsoon	*Avicennia*	J	0.92
	Gelasimus vocans	Summer	*Avicennia*	J	1.03
	Gelasimus	Monsoon	*Avicennia*	I	0.93

	vocans				
	Gelasimus vocans	Monsoon	*Avicennia*	I	0.95
	Gelasimus vocans	Monsoon	Open	I	0.98
	Gelasimus vocans	Post-monsoon	Open	I	1
	Gelasimus vocans	Summer	Open	I	1.29
	Gelasimus vocans	Monsoon	*Avicennia*	S	0.97
	Gelasimus vocans	Summer	*Avicennia*	V	1.5
			Mean	J,I,S,V	1.06
10	*Austruca annulipes*	Summer	*Avicennia*	J	0.97
	A.annulipes	Monsoon	*Avicennia*	I	0.95
	A.annulipes	Monsoon	*Avicennia*	I	0.93
	A.annulipes	Monsoon	*Avicennia*	I	0.97
	A.annulipes	Monsoon	*Avicennia*	I	0.96
	A.annulipes	Monsoon	*Avicennia*	I	0.93
	Austruca annulipes	Summer	*Avicennia*	Y	1.25
	A. annulipes	Monsoon	Open	LL	0.97
			Mean	J,I,Y,LL	0.99
11	*A.cryptica*	Summer	*Avicennia*	I	0.93
12	*Episesarma vesicolor*	Summer	*Rhizophora*	Y	0.96
13	*Episesarma mederi*	Post-monsoon	*Rhizophora*	V	0.93
14	*Parasesarma bidens*	Monsoon	*Rhizophora*	U	0.94