



Burrowing crabs in arid mangrove forests on the southwestern Arabian Gulf: Ecological and biogeographical considerations



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ABSTRACT

Many species of mangrove crabs are essential in the formation of mangrove ecosystems, and the bioturbation resulting from the excavation of their underground chambers is directly correlated with substrate oxygenation and carbon and nitrogen cycling within the ecosystem. This study examines the ecological and biogeographical characteristics of bioengineering crab assemblages that inhabit the environmentally challenging arid mangroves in the southwestern Persian-Arabian Gulf. Results demonstrated that a hyper-arid environment could directly impact crab diversity, reducing it to only one species per niche or coastal zone. A biogeographic comparison revealed an exclusive divergence of species composition in each Gulf region. Variations in seasonal temperatures were found to have a direct influence on the abundance of species and how the zonation is driven by sediment composition and trophic relations. Two crabs – *Nasima dotilliformis* in the salt march (supratidal zone) and *Macrophthalmus (Mareotis) depressus* in the intertidal – were considered to be the most influential functional species for this hyper-arid ecosystem due to their abundance, size, bioturbation potential and niche specificity for the intertidal zone. The limited number of species within the arid mangrove system emphasised the biogeographic pressure and inherent importance of the few active bioengineering species present and adapted to the harsh conditions, indicating that the dominant crabs within the biotope are directly related to the successful evolutionary establishment of these hyperarid mangroves. The study highlights important implications for future forest management strategies of the only forest ecosystem that tolerates the extremes of the southwestern Persian-Arabian Gulf area.

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1. Introduction

The highest global concentration of arid and hyper-arid mangrove ecosystems is in the Middle East desert regions, an area subject to extreme environmental conditions (Edgell, 2006; Khan et al., 2010; Zahed et al., 2010; Almahasheer et al., 2016; Vaughan et al., 2019). These ecosystems are unique, as they are the only mangrove systems not formed within a freshwater connective estuarine catchment (Almahasheer et al., 2016; Al-Khayat et al., 2019). They contain the only natural evergreen forest in the Persian-Arabian Gulf (PAG) and, consequently, are of considerable economic and environmental importance (Al-Khayat et al., 2019; Burt and Bartholomew, 2019). Increasing coastal urbanisation is threatening the forest (Al-Khayat et al., 2019; Burt and Bartholomew, 2019), even though the coastal marine habitat is advancing its range despite anthropogenic pressures, including climate change (Almahasheer et al., 2016).

The biogeography of ecosystems and species in the PAG are driven mainly by high temperature and salinity, and as a semi-closed basin, it is dependent on water input from the Indian Ocean, supplied on the Gulf's southeast coast (Riegl and Purkis, 2012; Vaughan et al., 2019). The majority of the PAG is within the northern end of the range of global mangrove distribution (25°–30°N), mangroves that are limited by lower temperatures (Almahasheer et al., 2016; Osland et al., 2017). Because of this peculiar distribution pattern, the large mangrove forests with high species richness in the PAG are found south of 25°N, and closer to the open-sea area on the East coast (Zahed et al., 2010; Almahasheer et al., 2016; Naderloo, 2017; Osland et al., 2017). Under this biogeographical scenario (north of 25°N, and isolated from the water input from the Indian Ocean), these mangroves experience extreme hypersaline (>50 psu) and hyperthermic water (>40 °C), and hot air (>55 °C) (Riegl and Purkis, 2012; Almahasheer et al., 2016; Giraldes et al., 2016, 2019). The entire mangrove forest is formed exclusively by the plant *Avicennia marina* (Forssk.) Vierh., an 'ecosystem-builder' species peripherally limited by the salt marshes that separate the forest seascape from the desert landscape (Zahed et al., 2010; Almahasheer et al., 2016; Burt and Bartholomew, 2019).

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Considered one of the most diverse taxa in marine ecosystems, the decapod is described as a niche specialist, with entire families and species groups inhabiting specific coastal zones and similar ecological niches worldwide (Giraldes et al., 2017; Naderloo, 2017). Therefore, within a particular habitat such as the arid mangrove in the northeast Indian Ocean, it is expected that a specific group of crabs would fill the associated ecological niches within the intertidal and supratidal zones (Naderloo, 2017).

Among the mangrove intertidal macrofauna, one of the most influential groups is the bioturbating engineer crabs. These crabs create numerous cavities in the sediment and are directly responsible for substrate oxygenation and carbon and nitrogen cycling in the development of mangrove systems (Vopel and Hancock, 2005; Otani et al., 2010; Penha-Lopes et al., 2009, 2010, 2012). Therefore, the engineering crabs can be considered key-stone functional species that operate synergistically within the mangrove systems.

To understand the effects of abiotic factors on the hyper-arid mangroves on the southwestern coast of PAG, the present study assesses the assemblage of target functional species and describes how the abiotic factors drive species composition, distribution and abundance in a mangrove setting in Qatar. The results could assist in developing sustainable forestation and management of this unique regional mangrove ecosystem.

2. Materials and methods

2.1. Study area

The survey was undertaken in the Al-khor coastal region on the southwestern coast of PAG (25°41'29.2"N, 51°33'15.7"E) in the only naturally occurring mangrove system in Qatar (Al-Khayat and Jones, 1999) (Fig. 1). The study area was divided into four sampling sites (Fig. 1B): site 1, in the supratidal zone in a salt marsh with unique vegetation (*Sabha*); site 2, in the salt marsh in a sandy supratidal zone void of vegetation; site 3, in the mangrove in the high intertidal zone, near the salt marsh; and site 4, in the mangrove, in the lower intertidal zone with connectivity to tidal channels. Mangrove tree height was measured using a graduated pole for a qualitative differentiation between sites 3 and 4.

Coastal zonation within the arid mangrove of Qatar follows a recognised division with well-defined supratidal and intertidal areas, which was apparent in the Al-Khor profile (Fig. 1C). The hyper-arid mangrove in the lower intertidal zone (site 4) had larger *A. marina* (several specimens > 4 m), while site 3 in the higher intertidal zone was represented by smaller shrubs such as *A. marina* (most specimens < 1.5 m). Site 1 in the salt marsh had the two common sub-shrub plants for *Sabhas* *Arthrocnemum macrostachyum* (Moric.) K. Koch and *Halocnemum strobilaceum* (Pall.) Bieb. (Abdel-razik and Ismail, 1990; Sukhorukov and Nilova, 2016).

Sample sites were also characterised by sediment type. Ten sediment samples (core of approximately 30 cm) were collected 10 m apart within a 100-m transect at every sample collection site. All samples were collected during low tide within the same month. Using a Mastersizer© 2000 (Malvern Instruments, Malvern, UK), grain size was identified, and samples were categorised by type (sand %, silt % and clay %) per sample area.

2.2. Seasonal abiotic data

Abiotic data was surveyed on a seasonal (spring, summer, autumn and winter) basis from March 2013 to February 2014. Abiotic parameters – including pH, dissolved oxygen, temperature and salinity – were measured using a waterproof hand-held

Oakton© WD-35632-PD 300 logger and a VEE GEE© Model STX-3 refractometer (Kingwood, Texas, USA). All seasonal surveys were conducted at low tide at mid-day in the riparian zone, with water parameters measured in the tidal channels (site 4), and air parameters closer to the tidal channel, at the forest canopy. Surveys were conducted at site 1 during the peak summer months for control comparisons and for determining extreme conditions, with salinity and temperature measured in tidal pools at low tide in close proximity to the salt marshes. In addition, and also during the peak summer months, air and ground (30 cm below surface) temperatures were measured at site 1 within the bioturbated zone (the most exposed sector) of the arid mangrove in an attempt to establish the temperature within the crab burrows.

2.3. Ecological and biological data

Using two transect guidelines of 50 m crossing through the centre of each schematic area, 5 (1-m²) quadrats were placed per transect (1 quadrat per 10 m), totalling 10 quadrats monthly per sample site. Within each quadrat, the substrate was excavated to a depth of 20–30 cm, and the sediment collected was filtered through a 0.5-cm mesh. All crabs were captured manually and visually identified in situ, based on characteristics described in the appropriate taxonomic keys (Jones, 1984; Naderloo, 2017). Voucher specimens of each species were identified in the laboratory to confirm in situ identification. The remaining samples were returned to the collection site to minimise sampling disturbance.

2.4. Data analysis

Each sample area was evaluated based on richness (number of species per area), relative abundance (percentage of specimens per area) and abundance per m². The average (%) grain size (sand, mud and clay) of sediment was determined. Abiotic data such as pH, dissolved oxygen, temperature and salinity are presented in charts for visual comparisons. Statistical differences of each species between the sites (1, 2, 3 and 4) and seasons (spring, summer, autumn and winter) were determined.

After testing for normality, the data was standardised (square root), and a Kruskal–Wallis one-way ANOVA on ranks with 95% CI and a significance level of 5% ($p < 0.05$) was employed. Statistical analyses were performed using Past3© and SigmaPlot©. Based on the average abundance, (m²) boxplot charts were produced to illustrate the populational differences of each species per site and season. Aiming to demonstrate the bioturbation potential of each species in the mangrove and the *Sabha*, a bioturbation area (m²) was estimated based on the carapace size of each species (defined as the diameter of each burrow) multiplied by each species abundance (m²), assuming the burrow area was comparable with the carapace sizes, and each burrow contained one animal.

3. Results

3.1. Site characterisation

The average sediment composition was different at each sample site (Fig. 1D), with a clay-enriched substrate at site 1, a sand-dominant substrate at site 2 and a muddy substrate at sites 3 and 4. Sandbanks were observed in the channels of site 4 and peripherally in site 3.

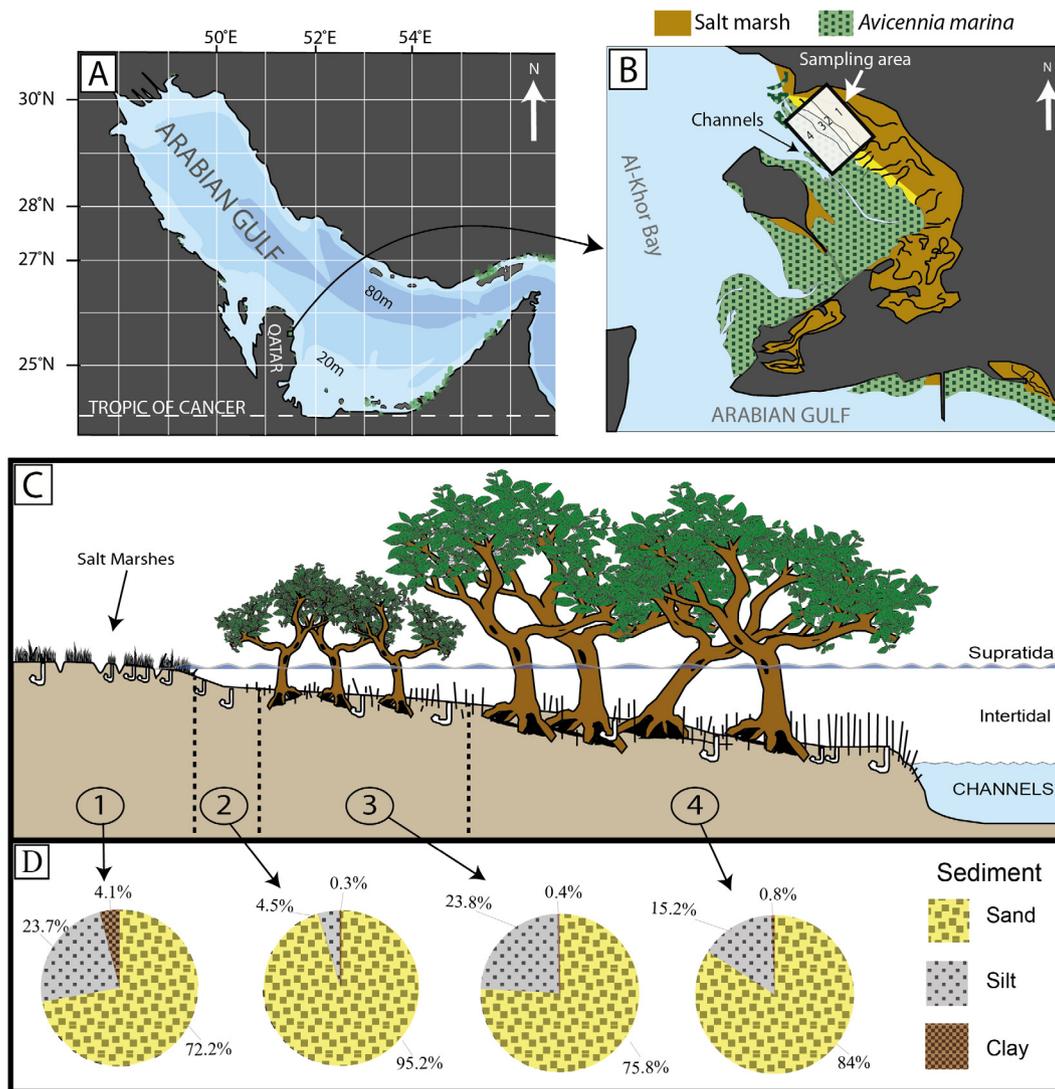


Fig. 1. (A) Position of the studied arid mangrove in Qatar, Southwestern PAG, highlighting the position of the global range limits of mangroves (25° and 30°N); (B) the sampling area in the mangrove of Al-Khor, with the position of the sampling sites within the *Avicennia marina* forest [1,2], in the sand bar [3] and the salt marsh [4]; (C) the schematic profile of the study sites 1–4, according to the intertidal and supratidal zones; (D) the composition [%] of sediment [sand, clay and silt] per site.

3.2. Species composition and zonation

A total of 6747 specimens from four bioengineering crab species were observed, and abundance was inversely proportional to crab size (Fig. 2), with 2900 specimens of *Scopimera crabicauda* Alcock, 1900; 2117 *Nasima dotilliformis* (Alcock, 1900); 637 *Macrophthalmus (Mareotis) depressus* Rüppell, 1830; and 93 *Eurycarcinus orientalis* Milne-Edwards, 1867. The fifth intertidal species commonly observed and collected several times while occupying the cavities of other crabs was *Metopograpsus messor* (Forskaal, 1775). However, *M. messor* was not included in this study because it is considered a tree climber and not an engineering bioturbating crab (Giraldes et al., 2019).

The analysed species presented a significant difference in sizes, and, consequently, the associated burrows (degree of bio-turbation) varied in size. The smaller 0.6-cm carapace width *S. crabicauda* burrows were characterised by the presence of sand balls spread around its associated burrows (Fig. 2E). The burrows of *N. dotilliformis* (2-cm carapace width) were identifiable by conical chimney formations above the sediment (Fig. 2A–D). The two larger species, *M. depressus* (3-cm carapace width) (Fig. 2G, H) and *E. orientalis* (5 cm) (Fig. 2I, J), were associated with simple

burrow holes in the sediment, devoid of any specific shape or characteristics.

The abundance of species by site (Fig. 3) highlights the zonation and the relationship between species and substrate type. The supratidal zone contained the highest density of specimens, with 2156 crabs associated with the clay enriched site 1 (93% *N. dotilliformis*). The sand substrate of site 2 accommodated 1702 individuals (98% *S. crabicauda*). The intertidal zone with muddy substrate contained the lowest density of specimens, with 524 at site 3 and 984 at site 4. However, the intertidal zone (sites 3 and 4) was the only coastal zone where *M. depressus* was recorded, representing 37% and 45% of the recorded specimens, respectively. The small *S. crabicauda* was the dominant species at all sites, with a direct correlation to a sandy substrate and a low correlation to clay-enriched sediment. *Eurycarcinus orientalis* was the least dominant, constituting < 4% at all sites.

3.3. Environmental parameters

The air and water temperatures collected in site 4 were high in the summer (peaks of 44 °C and 33 °C, respectively) and low in the winter (peaks of 19 °C and 21 °C, respectively) (averages

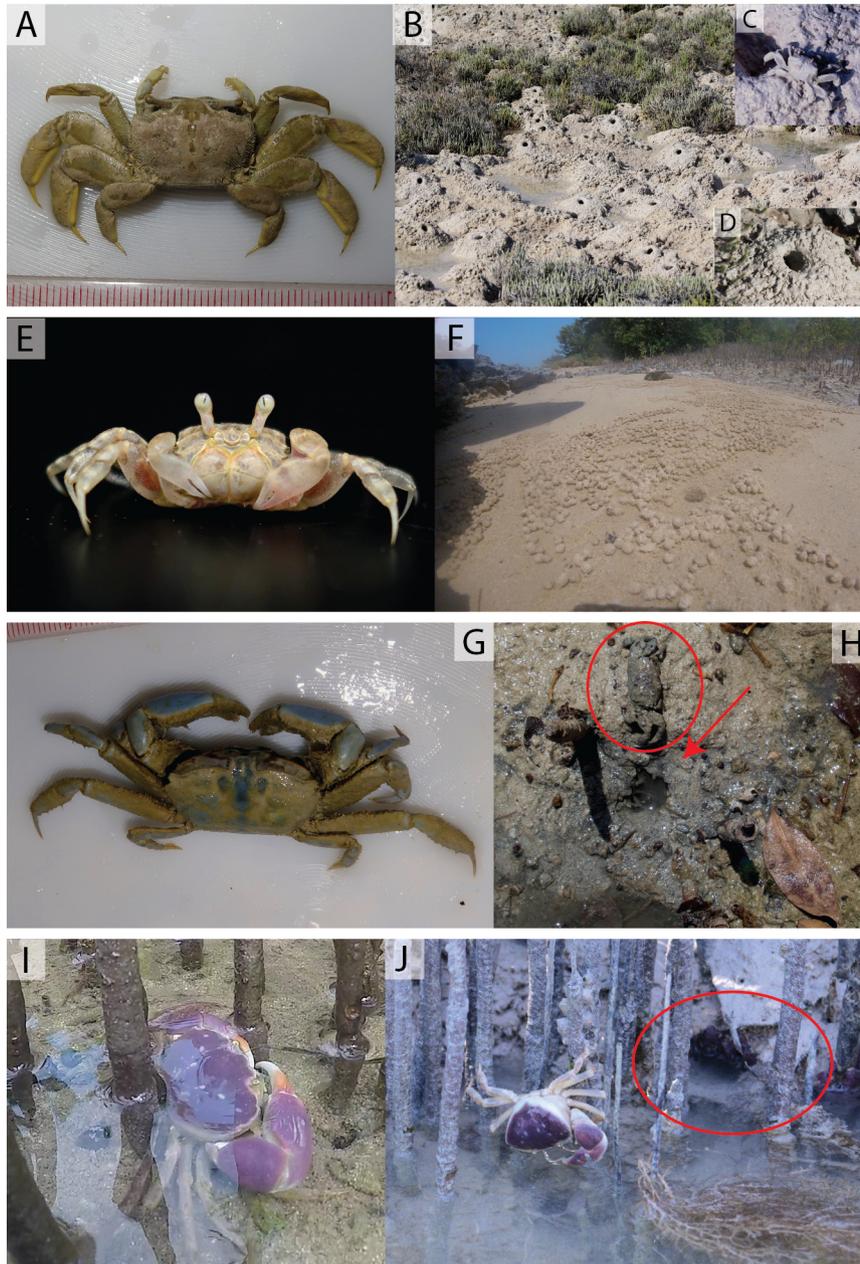


Fig. 2. Illustrations: (A) a clean, alive *N. dotilliformis*; (B) the bioturbation of this species, with several chimneys in the salt marsh; (C) specimen covered by clay; (D) the chimney shape; (E) *S. crabicauda*, with the second with the red pigmentation in the breathing legs; (F) the sandy-bar, with its sand bubbles and burrow shape; (G) a clean, alive male of *M. depressus*, with the large, blue cheliped, and (H) a female covered by mud near its burrow; (I) *E. orientalis* foraging and (J) a specimen closer to its cavity..

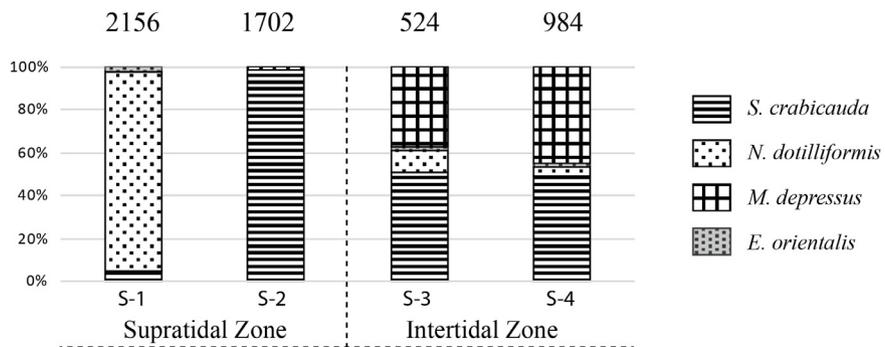


Fig. 3. Dominance (%) of the studied species in each study site (S) 1–4, with the total abundance of specimens per site.

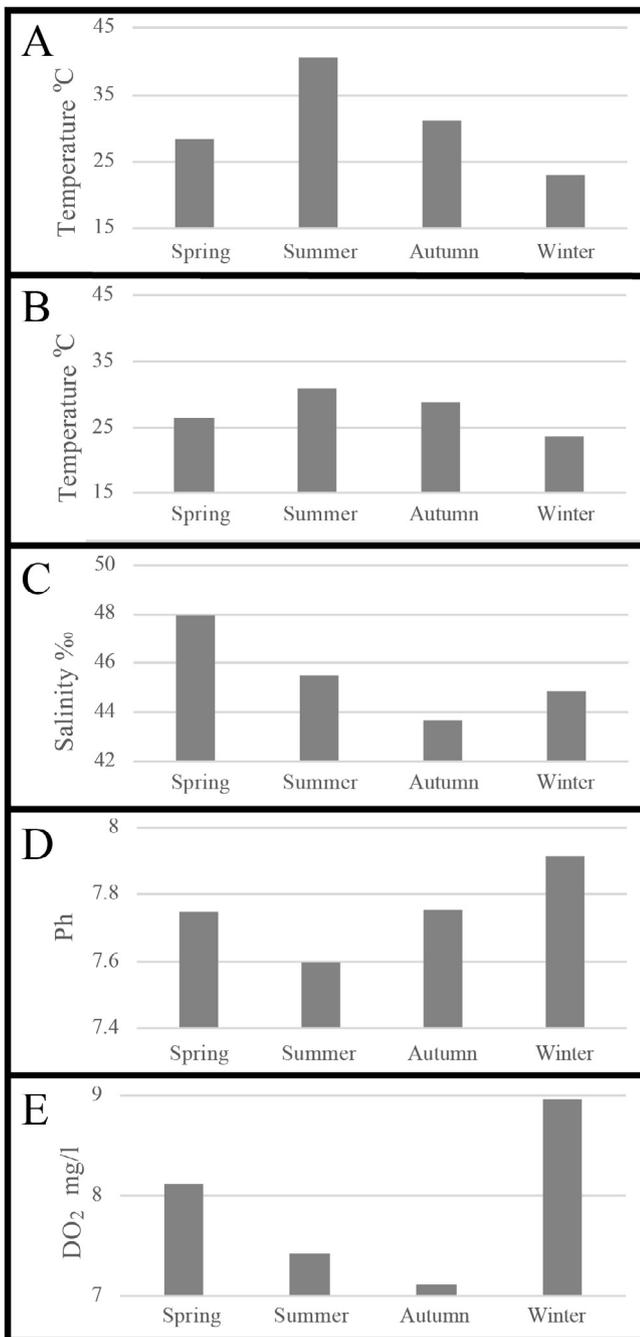


Fig. 4. Averages of the seasonal abiotic data in a year: (A) water and (B) air temperatures [°C], (C) salinity [‰], (D) pH and (E) the dissolved oxygen [mg/l].

in Fig. 4A, B). Salinities were 41–51 psu, with smaller values in the autumn and winter (Fig. 4C). Dissolved oxygen (DO) was 7.2–10.8 mg/l and pH 7.5–8.14, with the lowest values for both measurements observed during summer months (Fig. 6D, E). A visible seasonal pattern was observed, whereby levels of pH and DO were reduced as temperature increased.

At the supratidal zone in contact with the desert ecosystem (site 1), in summer, air temperature reached 56°C, water temperature 48 °C and salinity 74 psu, and the below-ground (30 cm) temperature was 29°C. Therefore, in summer, comparing sites 1 and 4, a significant temperature decrease was observed in the mangrove near the channels (site 4), decreasing ≈ 12 °C in air

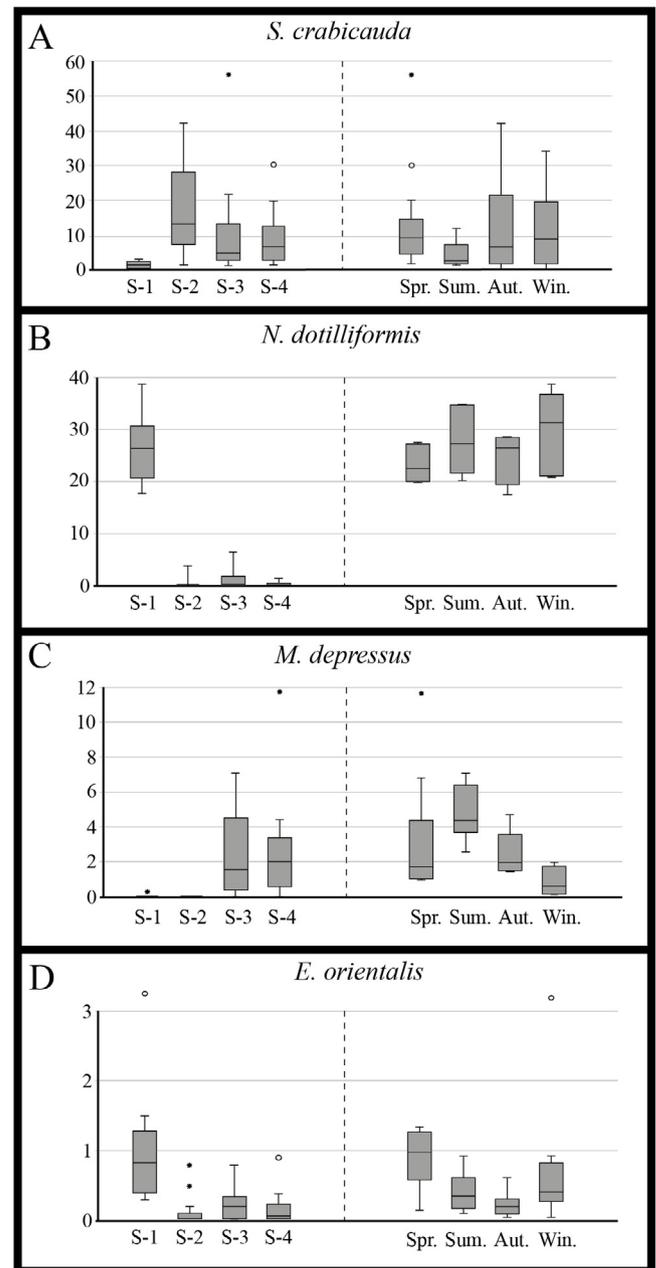


Fig. 5. Boxplots of the abundance [specimen/m²] of each studied species (A, B, C, D) presented in boxplot per study sites (S) 1–4 and seasons (spring, summer, autumn and winter).

and 15 °C in water. In addition, the air temperature was approximately 27 °C higher than the temperature underground in the supratidal zone (site 1), highlighting significant thermic isolation for crabs in burrows in the site that separates the mangrove system from the desert habitat.

3.4. Seasonal and spatial distribution

Scopimera crabicauda abundance differences were statistically significant among sites ($P < 0.001$), with higher abundance at site 2 (average of 17.2 specimens/m²), but they were not statistically significant ($P = 0.618$) among the seasons (Fig. 5A), with lowest abundance in the summer (average of 3.3 specimens/m²). The difference in *N. dotilliformis* abundance was also statistically significant among the sites ($P < 0.001$) and the seasons ($P =$

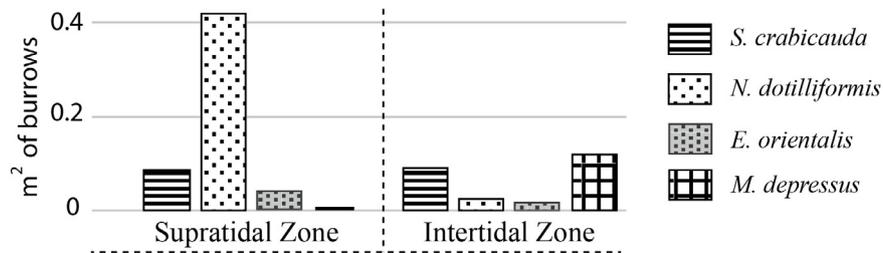


Fig. 6. An estimated bioturbation potential of each studied species in the supratidal zone and intertidal zone, based in the area (m^2) of burrows per square metre of soil.

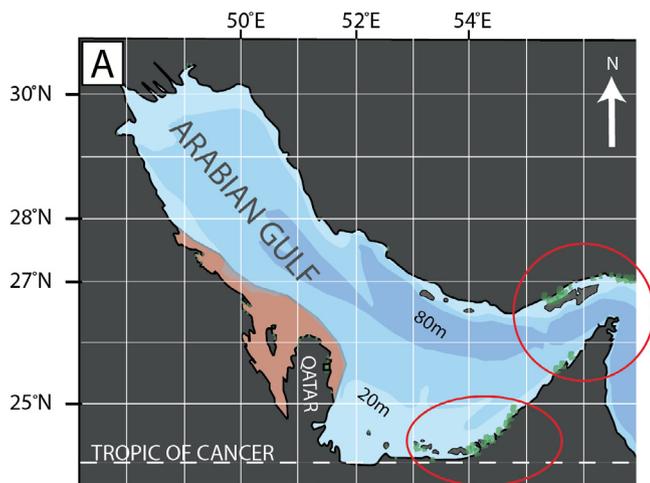


Fig. 7. A schematic illustration of the southwestern province in the Arabian Gulf, illustrating the areas with higher mangrove concentration and species diversity (red circles), the area below $25^\circ N$ and in the areas closer to the opening area of the Gulf.

0.020), which was primarily observed at site 1 (average of 26.1 specimens/ m^2), with higher abundance in the summer and the winter (averages of 25.5 and 30.2 sp/ m^2 , respectively) (Fig. 5B). Abundance of *M. depressus* was also significantly different among the sites ($P = <0.001$) and the seasons ($P = <0.001$), with averages of 2.3 and 2.6 sp/ m^2 in sites 3 and 4, respectively, and higher abundance in summer, with an average of 4.5 sp/ m^2 in site 4 (Fig. 5C). Abundance of *E. orientalis* was significantly different among the sites ($P = <0.001$) and the seasons ($P = 0.004$), with higher abundance in site 1 (0.9 sp/ m^2), and lower abundance after the summer (0.3 sp/ m^2) (Fig. 5D).

3.5. Bioturbation

Greater bioturbation in the Sabha (supratidal) was provided by *N. dotilliformis* (Fig. 6), which alone contributed $0.42 m^2$ of burrows per square metre of soil surface. The greatest bioturbation contribution in the mangrove forest was by *M. depressus*, with an average of $0.12 m^2$ of burrows (Fig. 6). The abundant, but relatively small, *S. crabicauda* contributed $0.09 m^2$ of burrows per square metre in the sandy beaches of the Sabha and the mangrove. The larger engineer crab *E. orientalis* presented the largest burrows, but as it was less abundant, contributed only $0.04 m^2$ of burrows per square metre in the Sabha.

4. Discussion

4.1. Sediment type and zonation

The engineering crabs followed the ecological equivalent of zonation, driven by sediment type (Kristensen, 2008; Naderloo,

2017). The small *S. crabicauda* followed the habitual niche of the 'sand bubbler crabs' from genera *Scopimera* and *Dotilla*, inhabiting the sandy substrate (Hartnoll, 1973; Maitland, 1986). *Nasima dotilliformis* followed zonation typical of the Camptandriidae family, namely, in the intertidal zones in mangrove ecosystems (Hartnoll, 1973; Tan and Ng, 1999; Naderloo, 2017). *Macrophthalmus (Mareotis) depressus*, with mouthparts adapted to feeding in muddy substrates, was found where the family Macrophthalmidae might be expected (Hartnoll, 1973; Naderloo, 2017). *Eurycarcinus orientalis* and all other species from this genus inhabit muddy substrates associated with *A. marina* mangroves (Dahdouh-Guebas et al., 1999; Gillikin, 2000; Naderloo, 2017; Ng et al., 2018). Thus, a sediment association is directly related to a physiological and anatomical adaptation associated with mouth anatomy, sediment grain size and diet (Hartnoll, 1973).

4.2. Biogeography and ecology

In 480 quadrats in one of the most established mangrove ecosystems on the southwestern coast of PAG, only four bioengineer crab species were recorded actively excavating burrows in the tidal zone. Interestingly, some of the mangrove associated crabs, viz., *Manningis arabicum* (Jones and Clayton, 1983), *Ilyoplax frater* (Kemp, 1919), *Serenella leachii* (Audouin, 1826) and *Metaplax indica* (H. Milne and Edwards, 1852), which were previously recorded in the Qatari mangroves (Al-Khayat and Jones, 1999), were absent. These species, however, may be rare and do not have a resident population directly associated with the mangroves in the study area. Alternatively, the influence of historical and recent anthropogenic impacts in the region (Sheppard et al., 2010; Riegl and Purkis, 2012; Smyth et al., 2016) may have affected the population density of these species.

Comparing the species richness of the engineer crabs associated with mangroves, more than 30 species were recorded in the PAG. In contrast, on the southwestern coast, only eight total species were recorded (Al-Khayat and Jones, 1999; Naderloo, 2017), with just four actual residents. This highlights how *N. dotilliformis* and *M. arabicum* are the only species from the family Camptandriidae, which presents 4 species recorded in the muddy intertidal from eastern PAG (Naderloo, 2017). *Scopimera crabicauda* is the only 'sand bubbler crab', while the other two species from genus *Dotilla* do not occur on the southwestern coast of PAG (Naderloo, 2017). *Macrophthalmus (Mareotis) depressus* is the only representative from family Macrophthalmidae recorded in the PAG and Gulf of Oman (Naderloo, 2017). Remarkably, the absence of target intertidal engineer crabs intimately associated with mangrove ecosystems such as the fiddler crabs from genera *Cranuca*, *Austruca* and *Gelasimus* do not occur on the southwestern coast of PAG (Naderloo, 2017). The absence of certain species highlights the existence of a biogeographic barrier that limits the establishment of a greater diversity of engineer crabs that naturally inhabit mangrove ecosystems only a few hundred kilometres away, in eastern PAG, at a similar latitude (Fig. 7).

In the biogeographical distribution of species, it is expected that the seasonal low and high temperatures affect the population of each species, especially in the hyper-arid ecosystems in the northern latitudinal limit of global mangrove distribution (25–30°N) (Almahasheer et al., 2016; Osland et al., 2017). In this study, the abundance of *S. crabicauda* and *E. orientalis* were negatively influenced by high temperatures. In contrast, *M. depressus* and *N. dotilliformis* appeared to be adapted to the challenging conditions of the ecosystem, as population densities increased under the extreme summer temperatures. The seasonal high peaks of abundance recorded in this study might be related to population recruitment, and low peaks to a reduction of food resources or the result of mass mortality under stressful environmental conditions such as has been suggested for gastropods in this region (Al-Maslamani et al., 2015).

One notable observation of this study is the important role that the *A. marina* canopy played in providing a heat attenuator by creating a more habitable environment. The canopy reduced the temperature by more than 10 °C in summer compared to that in Sabha, which has no forest shade. This suggests the presence of favourable environmental conditions for *M. depressus* that mainly inhabit this mangrove zone. Extreme temperatures have a negative effect on the population ecology of this species. On the India coast, for example, in stable tropical conditions, *M. depressus* was recorded in densities of 82 specimens/m² (Pandya and Vachhrajani, 2010), while in the present study, the maximum density recorded was only 2.6 specimens/m², a considerable reduction in abundance. However, the heat attenuation provided by the *A. marina* canopy might be related to the increase in abundance observed in *M. depressus* during the summer high temperatures. An engineer crab evolutionarily adapted to the extreme summer in the local arid mangrove, which presents a biological cycle with population recruitment during the summer and a population reduction during the low temperatures of the winter.

The Sabha associated with the mangrove can be considered to be the most environmentally exposed portion of the biotope that links the desert landscape with the coastal ecosystem. In this scenario, the present study highlights how the underground temperature was markedly reduced compared to that of the air. The higher levels of clay in this zone may reduce the substrate temperature, as the combination of salt, organic matter and clay are considered efficient thermal insulators (Abu-Hamdeh and Reeder, 2000). In this area, the higher bioturbation contribution is attributed to *N. dotilliformis*. This species is the most elaborate habitat modifier, building conical chimneys with holes in the top (Fig. 3L, M), creating a characteristic landscape peripheral from the mangrove forest. A characteristic bioturbation landscape scenario was observed mainly in the Sabha that surrounds the mangroves (Pers.Obs. BWG and JAK). Indeed, *N. dotilliformis* was not recorded in the Sabha in planted mangroves (Al-Khayat and Jones, 1999; Al-Khayat et al., 2019), demonstrating its close relationship with the Sabhas located in the supratidal mangrove ecosystem.

A few species of small size inhabiting the mangrove could possibly be associated with extreme temperatures because small body size is related to the physiological adaptation required to survive under extreme high-temperature conditions (Angilletta et al., 2004). This is especially so when compared with large engineer crabs in tropical mangroves worldwide such as *Cardisoma guanhumii* Latreille, 1828 and *Ucides cordatus* (Linnaeus, 1763) (Melo-Filho, 1996). The inverse relationship between body size and abundance that we observed in this study also supports the concept that high temperatures negatively influence the size of species.

The intense higher temperature and salinity in the tidal channels that reach the Sabha (creating tidal pools during the low

tides) highlight the importance of tidal variation and topography for the species distribution in this arid mangrove. The low-tide period between the flood tides directly influences the evaporation processes throughout the shore zones, especially during the extremely hot summer conditions. This creates daily gradients of salinity and temperature that certainly affect the internal distribution of arid mangrove species.

The composition of species and their zonation patterns discussed in this study highlights the existence of biogeographic barriers that limit the ecosystem and species distribution in the PAG, a small semi-closed sea. The region north of 28–29°N is limited by low winter temperatures, with a virtual absence of mangrove forests (Almahasheer et al., 2016; Osland et al., 2017). Two regions with more favourable environmental conditions and significantly higher species diversity are located in the Gulf in (1) the region south of 25°N and closer to the opening area in the PAG, and (2) the region on the eastern coast of PAG (north of 26°N), the deepest area in the Gulf receiving direct water influx from the Indian Ocean with more tropical environmental conditions. The favourable conditions in those two regions are reflected by the concentration of almost 90% of the mangrove forest in the Gulf and a higher diversity of species, including the presence of another major mangrove plant in the mangrove ecosystem (Zahed et al., 2010; Almahasheer et al., 2016; Naderloo, 2017; Osland et al., 2017) and not only *A. marina*, as was recorded in the studied arid mangrove. Therefore, the present study supports the concept of the existence of a shallow marine province on the southwestern coast of PAG (Fig. 7) with a biogeographic barrier, governed by hyperthermic and hypersaline water conditions, that isolates marine ecosystems and their associated indigenous diversity. The presence of an abundant endemic shrimp that has thus far only been recorded in the mangroves of Qatar (De Grave and Al-Maslamani, 2006; Giraldez et al., 2019) also supports this concept.

4.3. Influence of biotic factors

Eurycarcinus orientalis is an engineer crab that belongs to a genus of crab predators (Dahdouh-Guebas et al., 1999; Giraldez et al., 2019). Therefore, its low abundance within the survey sites may be related to prey-predator proportions and not exclusively to abiotic factors such as substrate and temperatures. The most abundant engineering crabs in this study are grazers of microbial mats: *N. dotilliformis* grazes on benthic diatoms present in the Sabha, and *M. depressus* grazes on cyanobacteria filaments in the mangrove (Al-Zaidan et al., 2006; Cannicci et al., 2018). In other words, the higher abundance of *E. orientalis* in site 1 could possibly be a reflection of the prey-predator-driven high abundance of *N. dotilliformis*, and the predator abundance in the mangrove (sites 3 and 4) related to the abundance of *M. depressus*. The abundant but small *S. crabicauda* apparently has no trophic relation with *E. orientalis*, due to the virtual absence of this predator in site 2, which is dominated by the 'sand bubbler crab'.

4.4. Engineer crabs, forestation and management implications

The present study suggests that the roles of the two main bioturbating species in this study – the intertidal *M. depressus* and the supratidal *N. dotilliformis* – are beyond that of an engineer, and closer to that of an environmental manager directly related to the establishment of the arid mangrove ecosystem on the southwestern coast of PAG. With the higher bioturbation potential, those two functional species are the only bioengineer crabs evolutionarily adapted to mangroves in the southwest province. In mangrove ecosystems worldwide, engineer crabs are recognised as vital components in the instigation of substrate oxygenation,

nitrogen and carbon cycling (Vopel and Hancock, 2005; Otani et al., 2010; Penha-Lopes et al., 2009, 2010, 2012), and therefore warrant systemic management in any forest establishment. This research suggests that these two habitat-shaping species may contribute to advancements in reforestation and forest introductions of hyper-arid mangrove ecosystems on the southwestern coast of PAG. An introduction of local target functional species may be used as an environmental management strategy to increase the biomass of the only evergreen forest in a desert region. Given that these unique mangroves are threatened by historical deforestation and vigorous human development, restoration and reforestation efforts are needed to protect their only forest habitat (Al-Khayat et al., 2019).

5. Conclusion

This study demonstrated that extreme conditions in a hyperthermic and hypersaline environment reduce the diversity of niche-restricted species and functional species responsible for the biological functionality of a forest. In the case of the hyper-arid mangrove on the southwestern coast of the Arabian-Persian Gulf, only two species, one species per niche, is responsible for the biological functionality of the only evergreen forest in a desert region. The crabs studied are a group of niche-restricted species, with coastal zonation driven by sediment type and diet, and with a peculiar population dynamic driven by the seasonal environmental conditions. The study also demonstrated how the shade of the forest canopy (intertidal) and the clay enrichment in the saltmarshes reduce the temperature for those functional species during the extreme summer conditions. The populations of the bioengineer decapods associated with the mangroves of the Arabian-Persian Gulf compared in this study supports the existence of a marine biogeographic province on the southwestern coast.

CRedit authorship contribution statement

Jassim A. Al-Khayat: Conceptualization, Methodology, Writing - original draft, Resources, Investigation, Validation. **Bruno Welter Giraldes:** Writing - review & editing, Visualization, Funding acquisition, Resources, Investigation, Validation, Methodology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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