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Simple and complex burrow morphology in two *Macrophthalmus* species on the intertidal mudflats of Barr Al Hikman, Sultanate of Oman

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Abstract

Burrowing Ocypodoidea crabs are an abundant component of many tropical and temperate coastal areas and central to the ecosystem functioning, for instance because they recycle nutrients, are important food for many shorebirds and alter the sediment by their burrowing behaviour. The burrow morphology of these crabs may differ between and within species, often correlated with differences in habitat preferences, crab morphology and life-history traits. Here we studied the burrow morphology and complexity of *Macrophthalmus sulcatus* and *Macrophthalmus depressus*, by means of casts (n = 7 and 10 respectively) and burrow excavations (n = 17 and 16 respectively) at the pristine intertidal mudflats of Barr Al Hikman in the Sultanate of Oman. We found that *M. sulcatus* construct simple burrows that were in all but one case inhabited by a single crab. By contrast, all burrows of *M. depressus* were complex with multiple entrances and many (deep-reaching) branches. There was a strong relation between *M. sulcatus* carapace width and burrow entrance size, indicating that the simple burrows are adapted to, and made by the occupant. There was no relation between *M. depressus* carapace width and burrow entrance size, and in six burrows more than one crab was encountered, suggesting that the complex burrows are not made by, and adapted to a single occupant. The complex burrows were found close to the shore whereas the simple burrows were found at the intermediate tidal zone. We speculate that the striking differences in burrow morphology may be explained by difference in habitat selection of the studied crabs, which most importantly relates to differences in sediment structure and tidal height. Also, crab morphology and life-history traits of the studied crabs could account for the observed difference in burrow morphology.

Keywords: burrow size, carapace width, *Macrophthalmus sulcatus*, *Macrophthalmus depressus*, Ocypodoidea, tidal zone

Introduction

Crabs of the Ocypodoidea superfamily (families Macrophthalmidae Ocypodidae, Ucididae, Dotillidae) are a diverse and abundant faunistic group of coastal areas in the tropics, subtropics, and temperate regions (Shih et al., 2016), well-known for their burrowing behaviour (Vannini 1980). In many areas, these crabs are central to the ecosystem functioning, among others because they are important prey species for shorebirds and important for nutrient recycling (Qureshi & Saher, 2012; Bom et al., 2020). Moreover, by their burrowing behaviour Ocypodoidea crabs can significantly modify their habitat because the burrows increase the water and air content in the sediment (Bertness & Miller, 1984; Chan et al., 2006; Qureshi & Saher, 2012).

Burrows of Ocypodoidea crabs have several adaptive functions as they can serve as a refuge from predators, as a protection from waves and extreme temperatures, as a place for moulting and mating and as a place to retain access to water (Nye, 1974; Lim & Diong, 2003; Chan et al., 2006; Yong et al., 2011; Sal Moyano et al., 2012; Qureshi & Saher, 2012). Most Ocypodoidea crabs construct relatively simple burrows, for instance in the shape of a J, S, U or Y (Christy, 1982; Chan et al., 2006; Yong et al., 2011). A few Ocypodoidea crabs, mainly larger ghost crabs, were observed to construct more complex burrows with multiple entrances and connected tunnels and sometimes with up to 3 m long and more than 1 m deep rooting branches (Vannini, 1980; Koo et al., 2005; Qureshi & Saher, 2012; Vachhrajani & Trivedi, 2016; Odhani & Saher, 2017). Differences in burrow morphology has been related to interspecific differences in crab morphology, crab life-history traits and to (interspecific) differences in habitat occupation (Vannini 1980; Lim 2006). Concurrently, differences in burrow morphology can affect the way in which crabs modify their habitat (Bertness & Miller, 1984).

The coastal area bordering the Barr Al Hikman Peninsula in the Sultanate of Oman is an example of a tropical soft-sedimented intertidal ecosystem where Ocypodoidea crab species are abundant, especially species of the *Macrophthalmus* genus (Bom *et al.*, 2018; Bom *et al.*, 2020). This relative pristine intertidal ecosystem is acknowledged for its high biodiversity, among others because it hosts a large number of shorebirds and is an important nursery area for fish and crustaceans (de Fouw *et al.*, 2017; Bom *et al.*, 2020). The area consists of several tidal zones, ranging from a zone close to the shore that is only flooded with spring tide, to an intermediate zone that is flooded and exposed with every high tide, i.e. twice per lunar day, to a subtidal zone that is only exposed during spring tides. The tidal zones are associated with differences in sediment structure and seagrass densities and faunistic assemblages, including *Macrophthalmus* species (Bom et al., 2020). The most abundant *Macrophthalmus* species is *Macrophthalmus sulcatus*, which lives in the intermediate zone in sandy sediments where it occasionally reaches densities of up to 100 crabs/m^2. *Macrophthalmus depressus* is less abundant and lives close to the shore in silty sediments (Bom et al., 2020). These different crab species and tidal habitats may be associated with different burrow morphology but this remains unaccounted for (Naderloo et al 2011).

In this study we investigate if burrow morphology and complexity differ between *M. sulcatus* and *M. depressus* at Barr Al Hikman. In addition, to better understand differences in burrow morphology and complexity, we investigate burrow-morphological characters (burrow diameter) in relation to characteristics (size and sex) of the crab(s) found inside. To this end we expect a relationship between burrow diameter and crab carapace width if the retrieved crab constructed and maintain its own burrow. We found that the two species construct strikingly different burrows and discuss potential explanations for the differences in burrow morphology.

Methods & Material

Study area & study species

The present study was conducted at the intertidal mudflats at the east coast of the Barr Al Hikman Peninsula in the Sultanate of Oman (N20.68°, E58.65°, Fig. 1a and 1b). This is the most pristine part of the area, presumably because it is difficult to access, and, except for some local fisherman, there is limited disturbance. *M. sulcatus* is the most abundant crab in the area. The species occurs in a zone of around 1 km broad at intermediate distance from the coastline (Fig. 1c and 1d) where it burrows in medium grained sediments (median grain size ~ 250 μm), often in association with seagrass beds (Bom et al. 2020). *M. depressus* is less abundant than *M. sulcatus,* and occurs mainly in a zone within 100 m from the coastline in fine-grained sediments (median grain size ~ 150 μm, Fig. 1c and 1d, Bom et al. 2020). This zone is flooded with spring tides only, approximately 12 times per lunar cycle (Fig. 1d).

Burrow morphology

We studied the burrow morphology of *M. sulcatus* and *M. depressus* by means of casting and by excavating and visually inspecting burrows. On 16 December, 2014, we poured Krone Moulding Plaster into the entrances of seven *M. sulcatus* burrows and ten *M. depressus* burrows. After 30 minutes the resulting casts were excavated using a small spoon (Fig. 2). In case we found (one or more) entombed crabs the sex and carapace width was noted. We further manually excavated nine burrows of *M. sulcatus* in December 2009 and eight burrows of *M. sulcatus* and 16 burrows of *M. depressus* in December 2014. Also for these burrows the burrow size at entrance was measured as well as the sex and carapace width of the crab(s) found inside. For all excavated burrows the general morphology of the burrows was noted. We also measured the depth and length of the casted burrows of *M. sulcatus*. The latter was not possible for *M. depressus* as these burrows were found to be complex and consisted of multiple branches (see results). Burrow size and carapace width were measured using a pair of vernier calliper and was recorded to the nearest 0.1 mm. We tested the relation between burrow size at entrance and carapace width using linear regression models. This analysis was done using the R software (R Development Core Team, 2021).

Results

Macropthalmus sulcatus

All casted and excavated burrows of *M. sulcatus* were single tunnelled (Fig. 3). The casted burrows showed one or two sharp curves at the beginning, with no specific direction, after which the tunnel continued into one direction. The end of each burrow consisted of a small pool of water in which in all but one cast a single crab was entombed by the plaster. The mean length of the casted burrows was 21.3 cm (SD ± 5.2; range 11.2 – 26.6 cm) and the mean depth was 10.3 cm (SD ± 1.5; range 8.3 – 12.5 cm). In one of the casted burrows two relatively large crabs were found; a male and a female (Fig. 4). In total 24 crabs were entombed or captured of which we identified 13 as males and 11 as females. There was a positive relation between burrow size at entrance and the carapace width of the crab caught inside ($t = 8.972$, $P < 0.01$, $R^2 = 0.79$, Fig. 4). The regression equation was $Y = 4.51 + 1.16X$

Macrophthalmus depressus

The casted burrows of *M. depressus* were complex, with multiple entrances and branches (Fig. 2 and 3). In fact, we never managed to make a complete cast of an entire burrow as the tunnels always continued where the plaster stopped. One burrow appeared to have five entrances and another had two entrances (the ten burrow entrances into which plaster was poured ultimately belonged to five burrows). Branches were observed in every direction and tunnels had various slopes and angles. Maximum depth of a cast was 35 cm, at which the water level was reached. In two casted burrows a single crab was found. In the three other burrows the crabs could probably escape, as the burrows were more extensive than our casts. The 16 excavated burrows were similarly complex as the casted burrows. In six of the 16 excavated burrows more than one crab per burrow was encountered (up to four crabs per burrow, Fig. 4). In total 27 crabs were captured of which we identified 7 as males and 8 as females. Sex could not be convincingly determined in 12 smaller individuals. There was no relation between burrow size at entrance and crab size ($t = 1.109$, $P = 0.28$, $R^2 = 0.01$, Fig. 4).

Discussion

This study shows that within the intertidal mudflats of Barr Al Hikman, the burrow morphology of two closely related crab species can be strikingly different, ranging from rather simple burrows in *M. sulcatus* to complex burrows in *M. depressus*. The simple burrows which were, in all but one case, occupied by just one individual, and the size at entrance of the simple burrows strongly matched with the size of the crab found inside. This indicates that the burrows of *M. sulcatus* are adapted to the size of (and made by) the single occupant. By contrast, complex burrows consisted of multiple interconnected branches and entrances and were occupied by multiple individuals from various size classes. There was no relation between crab size and the burrow size at entrance, indicating that these burrows are not adapted to a single occupant and perhaps have a live span that exceeds the live span of individual crabs.

The complexity of the burrows of *M. depressus* is noteworthy, as it differs from the simple, single-tunnelled burrows described in almost all Ocypodoidea crabs (Vannini 1980). In fact, many of the 'complex' burrows that have been described in Ocypodoidea crabs may be simpler than the complex burrows we found in *M. depressus*. For instance, the complex burrows described in *M. japonicus* had 1.7 openings per burrow and had a few tunnels only (Koo et al. 2005) whereas the complex, multi branched tunnels in *Ocypode ceratophthalmus* were not interconnected to other burrows and occupied by a single crab (Vachhrajani and Trivedi 2016). The complex burrows of *Uca chlorophthalmus* have multiple entrances and interconnected burrows (albeit the pictured casts do not show such complexity) and thus may be more similar to the complex burrows that we found (Qureshi and Saher, 2012). Outside the Ocypodoidea superfamily, complex burrow morphology that resemble the burrows that we found in *M. depressus* have been described for a few species including the tunnelling mud crab *Helice crassa* (Morrisey et al. 1999) and the angular crab *Goneplax rhomboides* (Rice and Chapman 1971). Similar complex, highly interconnected burrows have been found in other crustaceans such as the Norwegian lobster *Nephrops norvegicus* (Rice and Chapman 1971) and thalassinidean shrimps *Callianassa* sp. (Nickell and Atkinson, 1995).

Intraspecific and interspecific differences in burrow morphology in intertidal Ocypodoidea crabs has mainly been attributed to differences in sediment coarseness and tidal height (i.e. inundation time, and note that tidal height and sediment coarseness are often correlated.). For instance, *Uca pugnax* was found to construct limited burrows in fluid substratum and more extensive burrows in more solid sediments (Bertness and Miller 1984) and also the burrow depth decreased with increasing tidal height (Bertness and Miller 1984). In Mozambique, *0. ceratophthalmus* were observed to shift their burrows in accordance with the consistency of the sand, which is related to the length of submersion (Hughes 1966). Likewise, in Hong Kong *0. ceratophthalmus* was found to construct more complex and deeper burrows closer to the shore in order to ensure continuous access to water during prolonged periods of drought (Chan et al., 2006). We speculate that also in our study system sediment and tidal height can (at least partly) explain the observed difference in burrow morphology: The simple burrows of *M. sulcatus* were found in coarse (sandy) sediments (Bom et al. 2020) which could limit the possibilities for complex burrow morphology due to soil instability. Although we did not quantify sediment compaction (eg, using a sediment penetrometer), we noted that during excavation, several burrows of *M. sulcatus* collapsed before a crab was encountered (these burrows are not included in this study). By contrast, the complex burrows of *M. depressus* were found close to the shore, a zone that is consists of fine (silty) sediments, which may allow for construction of complex burrows. This zone is not flooded daily and the deep rooting burrows may ensure a continuous access to water. Interestingly, it was found that *M. depressus* construct rather-simple U-shaped burrows in India (Silas and Sankarankutty 1967). Like in our system, these burrows were found close to the shore, but contrary to our system, these burrows were found in sandy and muddy sediments. This further indicates that sediment may be an important factor to explain differences in burrow morphology (Vanninni 1980), and also suggest that tidal zonation ultimately explain the distribution of this species. Yet, given that the observed burrows in *M. depressus* is more complex than has been described in any related species we argue that it is unlikely that sediment composition is the only factor that determines burrow morphology in this species.

Several other non-mutually exclusive aspects might further explain the observed differences in burrow morphology. Importantly, differences in burrow morphology may be related to differences in crab morphology. For instance, differences in burrow structure in *Uca annulipes* and *U. vocans* were attributed to differences in carapace proportions and cheliped shape (Lim, 2006, Lim et al 2015). In our study species, the cheliped shape does not differ substantially between the species, but notably *M. sulcatus* has a larger carapace-width/carapace-length ratio (2.3) than *M. depressus* (1.5) (Naderloo et al., 2011). *M. depressus* is thus less elongated and more manoeuvrable, which indeed may facilitate more complex burrow constructions (Lim 2006). In addition, burrow morphology was found to be related to feeding behaviour in deposit-feeding thalassinidean shrimps, where species constructing complex burrows were observed to forage on organic material that has drifted inside (Nickell and Atkinson 1995). Similarly, and speculatively, the complex burrows of *M. depressus* may facilitate the capture of food items in the same way. This could benefit the species as it lives close the shore in an area that is often deprived of food (i.e. the organic material that flourish from the water brought with the flooding tide; Schuwerack et al. 2006). Furthermore, complex burrow constructions have been explained by the need for oxygen of developing embryos (Rice and Chapman 1971) and, in *Gonoplax* crabs, were linked to the highly developed social behaviour (Atkinson 1974). Diverse social behaviour is also found in *Macrophthalmus* crabs (Kitaura et al. 2006), but it is unclear to what extent the social lives of the two studied crabs differ, and thus, whether social behaviour could explain the difference in burrow complexity.

Burrow morphology was also found to be affected by structural elements in the substratum such as grass stems, small mussels and pneumatophores (Bertness and Miller 1984, Lim and Heng 2007, Lim and Rosiah 2007). In our study all burrows were studied in bare sediments so structural elements cannot explain the observed differences. Another explanation for differences in burrow morphology was given by Yong et al. (2011), who speculated that *0. ceratophthalmus* constructed more complex burrows in response to higher predation pressure. At Barr Al Hikman, *Macrophthalmus* crabs are an important prey for many shorebirds in the area (Bom et al., 2018), but we have no indication that the different crabs are exposed to different levels of predation pressure. Moreover, we presume that it is unlikely that the observed complexity in burrows in *M. depressus* is caused by extensive predation pressure, because it is not supposed to lead to the high complexity observed (Vaninni 1980).

To further understand the causes and consequences of (differences in) burrow morphology of *Macrophthalmus* at Barr Al Hikman, detailed observations and experiments are needed, for instance by means of transplantation experiments and by studying burrow morphology across space and time. Likewise, it will be interesting to study how the different burrow structures modify the complexity of the sediments (Lim and Heng 2007). This is especially relevant in the light of the changes that are expected to alter the area in the near future. Currently, an extensive aquaculture project is planned in the area (Times of Oman 2020), which undoubtedly will affect the area in many ways, including sediment flows, nutrient input, and anthropogenic noise (Bom et al. 2020). This may have far-reaching consequence for the crabs and their burrows in the area.

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Data on burrow entrance size in relation to crab size will be made available at the NIOZ Digital Archive System.

The authors declare that they have no conflicts of interest.

Figures

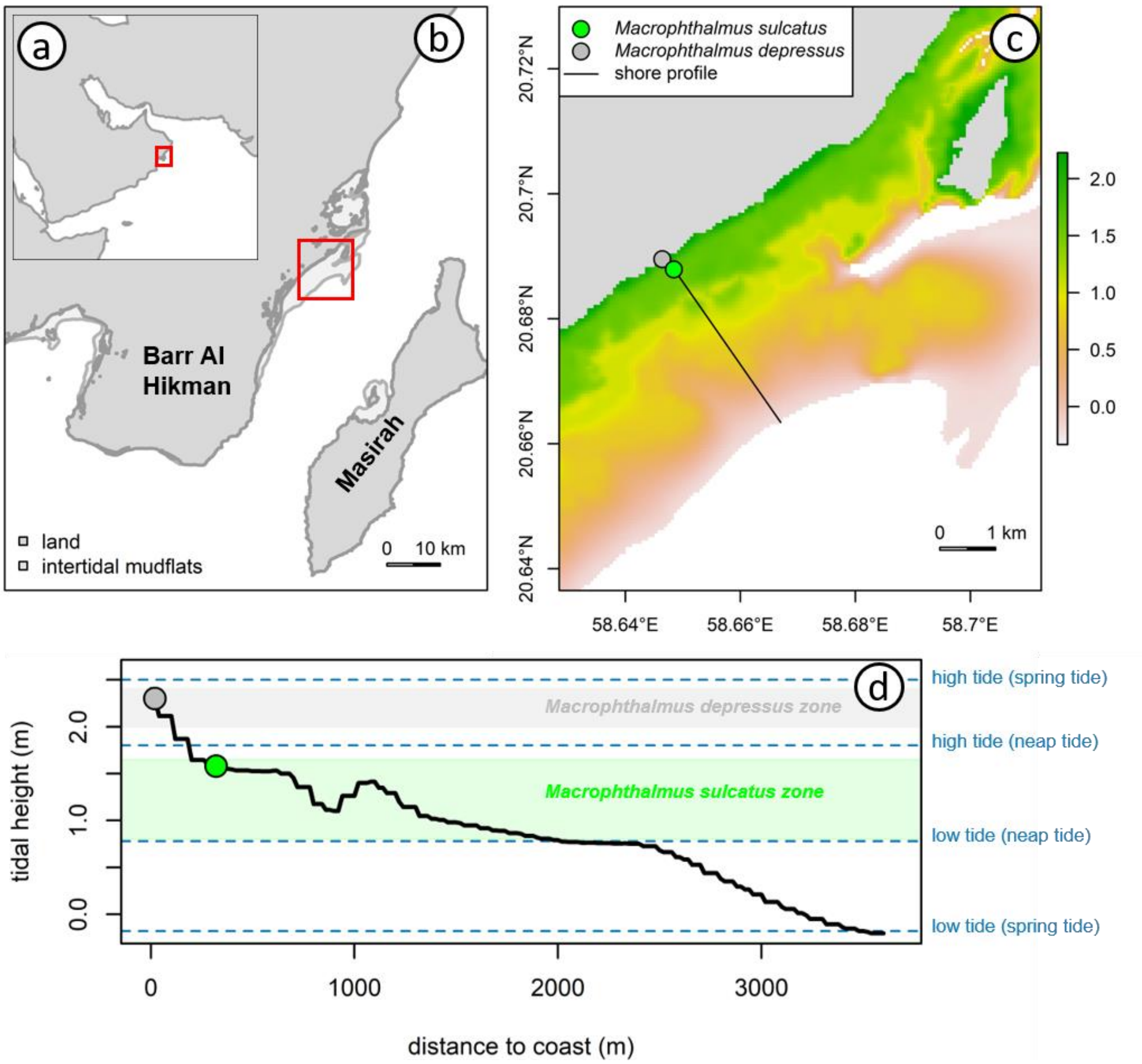

Figure 1. a) The Arabian Peninsula with Barr Al Hikman in the red square. b) Barr Al Hikman. The red square indicates the boundaries of the map given in c. c). Bathymetry map showing part of the intertidal mudflats of Barr Al Hikman based on Bom et al. (2020). The locations of burrow excavation and the shore profile are also given. c) shoreprofile (tidal height) as function of distance to the coast at the sampling locations (see figure d). The sampling locations and the zone in which *M. depressus* and *M. sulcatus* can be found are indicated (see Bom et al. (2020) for a detailed distribution map of *M. sulcatus*). Also the high and low tide waterlines for both spring tides and neap tides are given. They correspond with the highest high tide during spring tide and the lowest high tide and highest low tide and the lowest low tide in November 2012.

Figure 2. Cast of a burrow of *Macrophthalmus depressus*. Note that the two casts were connected and broke during excavation.

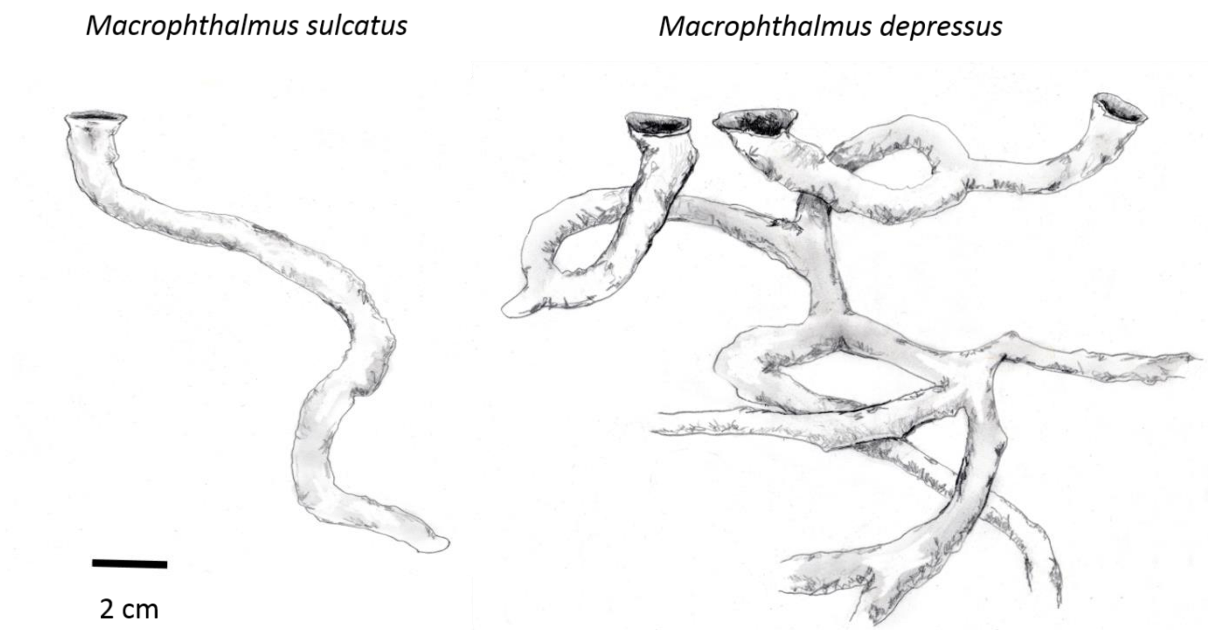

Figure 3. Drawing of a typical cast of the burrow of the two crabs studied. The burrow ends of the burrow of *Macrophthalmus depressus* are open as the burrows were more extensive than our casts.

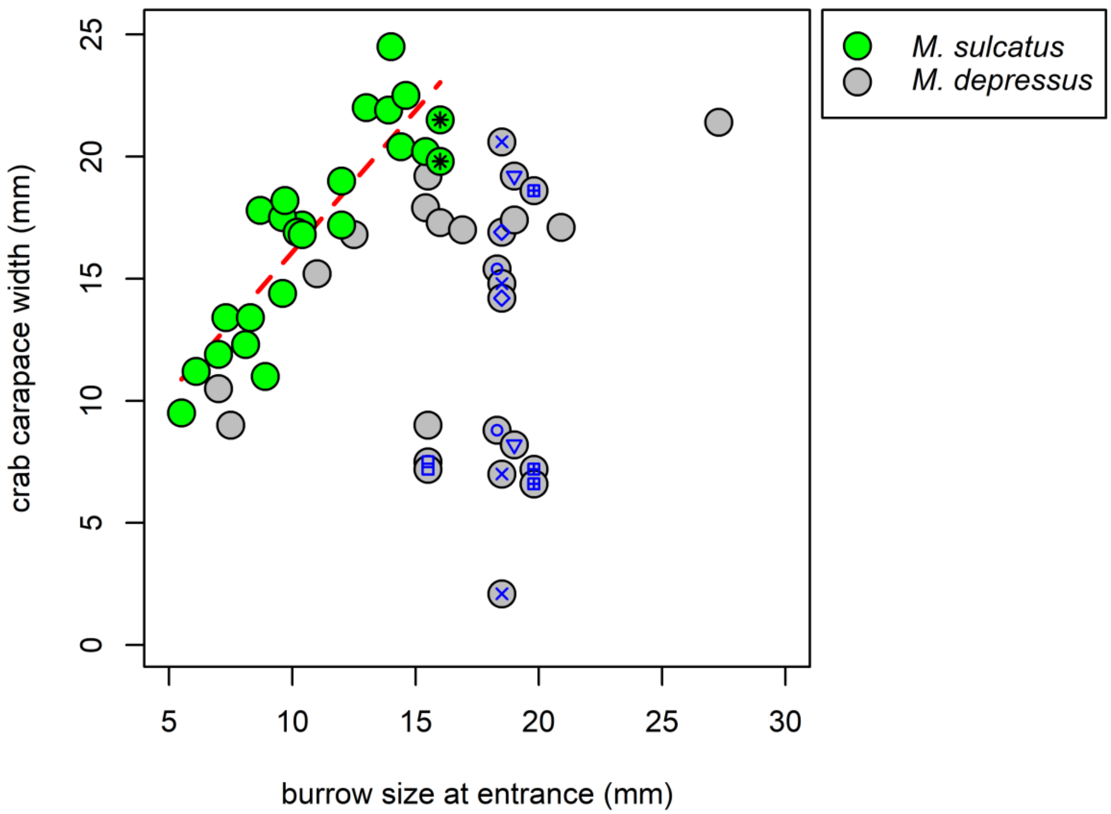

Figure 4. Relationship between crab carapace width and burrow size at entrance for the two studied crab species. The dashed red line gives the significant linear model relating *Macrophthalmus sulcatus* carapace width to burrow size at entrance. Symbols within the points refer to burrows in which more than one crab was encountered; similar symbols refer to the same burrow.

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