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Seagrass density correlates with burrow abundance and size in the Zebra Mantis Shrimp (Stomatopoda: Lysiosquillidae)

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ABSTRACT

Introduction: Mantis shrimps are ecologically and economically important organisms in marine ecosystems. However, there is still a lack of information about their habitat, in particular, their burrows.

Objective: To analyze how dense and sparse mantis shrimp burrows differ in abundance, size, sediment grain size, and water quality.

Methods: We counted burrows in 10 x 10 m^2 random plots in sparse and dense seagrass (ten plots per density), around Barrang Lompo Island, South Sulawesi, Indonesia. Sampling took place at spring low tide from August to September 2017.

Results: Two mantis shrimp species were observed: *Lysiosquillina maculate* and *L. sulcata*. Dense and sparse seagrass burrows did not differ in wall grain size or water parameters, both inside and outside of burrows ($P > 0.05$). Similarly, there was no correlation between burrow depth and diameter in either dense ($P > 0.05$; $r = 0.27$) or sparse ($P > 0.05$; $r = 0.33$) seagrass. However, larger burrows tend to occur in denser beds, but there were more burrows in denser seagrass (*t*-test, $P < 0.05$).

Conclusions: There seems to be a preference for dense seagrass beds, especially by larger mantis shrimps. The correlation between shrimp burrow abundance and seagrass density highlights the importance of conserving the quality as well as the extent of seagrass habitat.

Key words: Zebra mantis shrimp; burrows; seagrass; intertidal; Barrang Lompo Island; Indonesia.

Mantis shrimps (Phylum Crustacea, Order Stomatopoda) are common and economically important coastal fisheries targets in Europe, and even more so in Asia (Ragonese et al., 2012; Wortham, 2009). They are used for consumption, animal feed, and also for environmental biomonitoring (Wortham, 2009). Despite their economic importance, there is very little information on the habitat factors that determine their abundance, distribution and size. In tropical Asia, these shrimps are principally harvested in shallow seagrass beds and other soft-sediment habitats (Mili et al., 2013; Taylor & Patek, 2010), in which they inhabit burrows. Hence, understanding the importance of these burrows for mantis shrimp abundance, distribution and size will be valuable for managing sustainable harvesting.

Mantis shrimps are known as predatory burrowing crustaceans. These animals can be found over a wide depth range, from shallow and intertidal waters to subtidal areas tens of meters deep (Poupin & Poupin, 2008). Like other burrowing animals, their burrows provide protection from predators and space for reproduction (Mead & Minshall, 2012; Morgan & Goy, 1987). The burrows also serve an aeration function, preventing anaerobic conditions by increasing the area of the water-sediment interface and ventilating the lower sediment layer with oxygen-rich water (Kinoshita, 2002). A limited number of studies have been carried out on mantis shrimp burrows. For example, chemical communication related to cavity occupation in *Gonodactylus festai* (Caldwell, 1979), burrow opening size of the mantis shrimp *Squilla empusa* (Mead & Minshall, 2012), occupation of natural and artificial burrows by Japanese mantis shrimp (*Oratosquilla oratoria*) (Matsuura & Hamano, 1984), aggressive territorial defense behavior of *Gonodactylus bredini* (Dingle & Caldwell, 1969). But none of these studies focus on mantis shrimp abundance in seagrass beds or the factors influencing their abundance.

Seagrass beds are well known as an important habitat harboring a variety of fauna (Nadiarti et al., 2015), providing food, protection, shelter, and living space (Christianen et al., 2013; Jackson et al., 2001; Jackson et al., 2006; Vonk et al., 2010). The seagrasses located in the intertidal zone are more frequently exposed to anthropogenic stress (Benjamin et al., 2008; Crowe et al., 2000) and seagrass in Indonesia have experienced widespread degradation and loss (Nadiarti et al., 2012; Unsworth et al., 2018). Associated organisms in this ecosystem, including mantis shrimps, are therefore coming under pressure and potentially threatened.

Zebra mantis shrimp can be found in a variety of habitat types, including soft substrate such as mud (Reaka, 1987) bare sandy bottoms, seagrass beds and coral rubble-dominated areas (Priosambodo et al., 2014), as well as in coral reef ecosystems (Barber et al., 2011). However, information is still extremely limited on their dwellings (burrows) in general, in seagrass beds in particular, and specifically with respect to seagrass density. Therefore, in this study we ask the following questions: i) does the density of seagrass beds influence burrow abundance; ii) does the sediment grain size affect burrow wall construction in seagrass beds of different density; iii) does water quality (dissolved oxygen, pH and temperature) differ between the outside and inside of mantis shrimp burrows in seagrass beds of different density. To answer these questions, we analyzed the differences between dense and sparse seagrass beds in burrow abundance, burrow size distribution and correlation between diameter and depth of the burrows, as well as the differences in water quality (dissolved oxygen, pH and temperature) outside and inside mantis shrimp burrows.

MATERIALS AND METHODS

Field sampling and data collection: Mantis shrimp burrows were identified during field observation when the mantis shrimp was visible in the burrow and following previously described burrow characteristics (Ramsay & Holt, 2001). Shrimp burrows were studied at two seagrass sites within the intertidal waters around Barrang Lompo Island (5º03’ S-119º19’ E, 1.5 m.s.n.m) in the Spermonde Archipelago, South Sulawesi, Indonesia (Fig. 1). Sampling took place at spring low tide from August to September 2017, i.e. during the calm season at this site, to ensure good visibility and accessibility for taking measurements of both the burrow dimensions and water quality parameters.

At site 1 on the West coast (50 x 300 m), the seagrass beds were classified as sparse (20-50 % cover), while at site 2 on the Southwest coast (50 x 300 m) the seagrass beds were classified as dense (> 80 % cover). The species present were also identified following McKenzie (2003). The seagrass percentage cover at each site was estimated using a standard

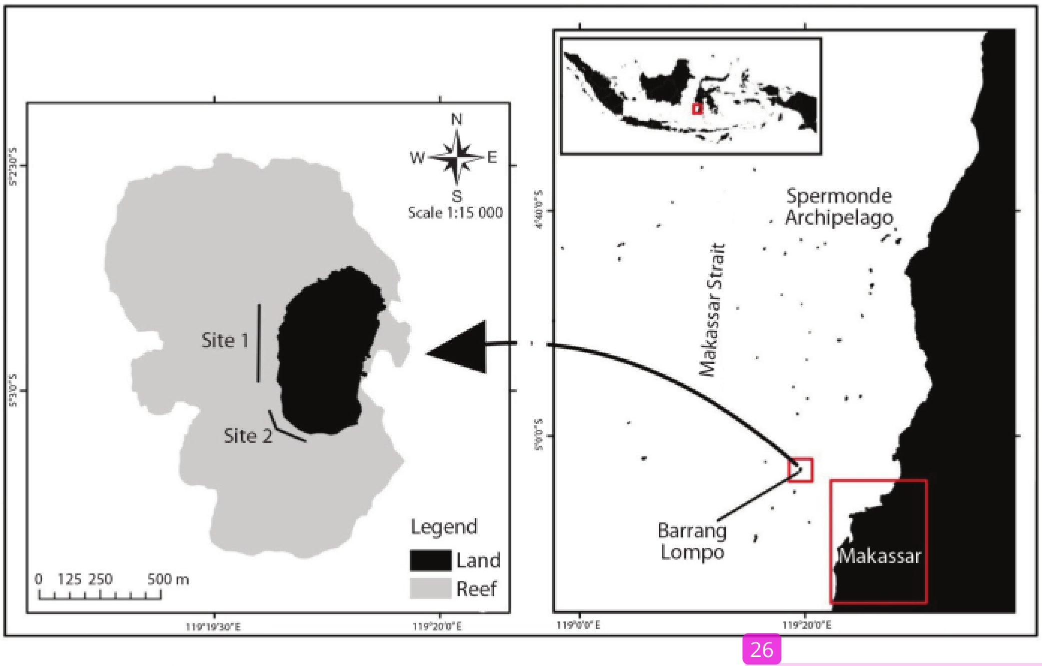

Fig. 1. Location of the sparse (site 1) and dense (site 2) seagrass study sites around Barrang Lompo Island, Spermonde Archipelago, South Sulawesi, Indonesia. The map of the Spermonde Archipelago was adapted from Stapel (2001).

percentage cover photography-based method (Mckenzie, 2003).

Shrimp species identification is important for controlling and managing the exploitation of mantis shrimps. Mantis shrimps were not extracted from their burrows or caught; however, all mantis shrimps seen in the study area (inside or outside the burrows) were identified based on the descriptions and keys in Ahyong (2001), Ahyong and Randall (2001) and Manning (1978). Particular features of interest for identification were the number of teeth on the dactylus of the raptorial claw and the coloration of the distal end of the uropodal endopod.

Ten plots (10 m x 10 m each) were placed randomly in each of the two sites. Distance between plots was determined based on the number of steps obtained from a Random Integer Generator (RIG). In each plot, the mantis shrimp burrows were counted and their diameter and depth recorded with a folding plastic ruler which was narrow enough to avoid touching or disturbing the sides of the burrow. A yabbie pump was not used in order to avoid undue disturbance to the burrow or the shrimp. Some mantis shrimps have U-shaped burrows (Matsuura & Hamano, 1984), although the diagram in Faulkes (2013) indicates a straight burrow for the genus *Lysiosquilla*. The ruler was inserted gently into the burrow until the bottom or (if present) the U bend of the burrow was encountered. In order to compare characteristics inside and outside burrows, we measured sediment grain size composition and water quality parameters (temperature, pH, and dissolved oxygen) inside and outside each burrow.

Sediment samples (to a depth of ca. 15-20 cm) from outside the burrows were collected using a homemade yabbie pump; and sediment samples from inside the burrows (wall lining) were taken to depths of between 6-15 cm (depending on burrow depth) using a homemade small tube with a fine screen at the bottom of the tube. All visible animal and plant fragments were removed from the sediment samples prior to aeration. Classification of grain size based on Wen-worth Class and grain size composition of sediment (outside burrows) and burrow lining material (inside burrows) was analyzed after shaking the dried sediment sample for 10 minutes on a series of test sieves (Din 4188 Pruf-sieb) with mesh sizes of 2, 1, 0.5, 0.25, 0.1, and 0.063 mm.

Dissolved oxygen, pH, water temperature outside and inside burrows were measured in-situ using a CellOx 325 sensor head and a SenTix 21 sensor head, respectively. Both sensor heads were connected to a WTW Multi 340i Multimeter.

Data analysis: The number of burrows per plot gave burrow abundance per 100 m^2. Statistical analyses were conducted in SPSS 25 (IBM Corp., 2017), and the summary statistics presented as mean ± standard error (SE). The significance of differences in mean value and variance of burrow abundance between dense and sparse seagrass beds was determined using a Student's *t*-test.

Non-parametric Spearman correlation analysis was used to evaluate the significance of correlation between burrow diameter and depth. Burrows size distributions in the dense and sparse seagrass beds were compared using a Student's *t*-test. Sediment grain size composition both outside and inside burrows, in dense and sparse seagrass beds, were compared using a factorial MANOVA analysis.

The measured water parameters were pooled together for outside and inside burrows from both seagrass beds. Water quality parameters (DO concentration, pH, and water temperature) outside and inside burrows in sparse and dense seagrass beds were analyzed using a factorial MANOVA analysis.

RESULTS

Out of the 16 seagrass species reported from Indonesia (Yasir & Moore, 2021), six were observed at the study sites. Four species were present at both sites: *Cymodocea rotundata*, *Enhalus acoroides*, *Syringodium isoetifolium*, and *Thalassia hemprichii*. *Halophila ovalis* was found only in the sparse seagrass beds (Site 1) and *Halodule uninervis* in the dense seagrass beds (Site 2). At the sparse site, the most visually prominent feature was the high canopy formed by the large leaves of *E. acoroides*. At the dense site isolated small stands of *E. acoroides* were present but the general canopy height was much lower, with *Thalassia hemprichii* the visually dominant species.

A total of 77 mantis shrimp burrows were identified during the study. The number of burrows can be considered a good indication of relative abundance, as most of the burrows found during the study were occupied by mantis shrimps. Zebra mantis shrimps were often visible in their burrow openings and sometimes came out from their burrows, enabling identification as members of the genus *Lysiosquillina*. However, only six individuals (mostly from larger burrows 4-6 cm in diameter) could be observed in sufficient detail to determine the species, comprising five *Lysiosquillina maculata* and one *L. sulcata*. The abundance of mantis shrimp burrows in sparse and dense seagrass beds was significantly different (t = 2.3, d.f. = 18, P < 0.05), being around twice as high in the dense seagrass beds as in the sparse seagrass beds (Fig. 2).

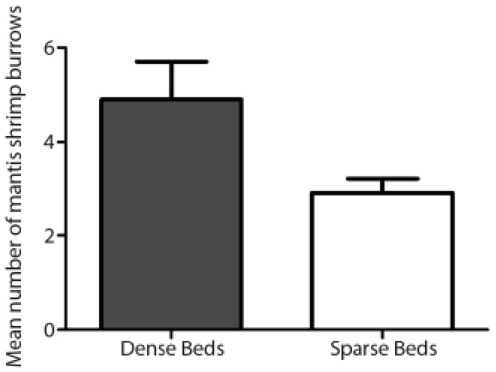

Fig. 2. Mean number of mantis shrimp burrows in 10 × 10 m plots (100 m^2) with different seagrass densities (Error bars represent standard error).

There was a significant difference between the sparse and dense seagrass beds in both burrow diameter (t= [illegible], d.f.= 76, P < 0.0001) and burrow depth (t= 2.7, d.f.= 76, P < 0.05). Burrows in the sparse seagrass beds were, on average, smaller compared to those in the

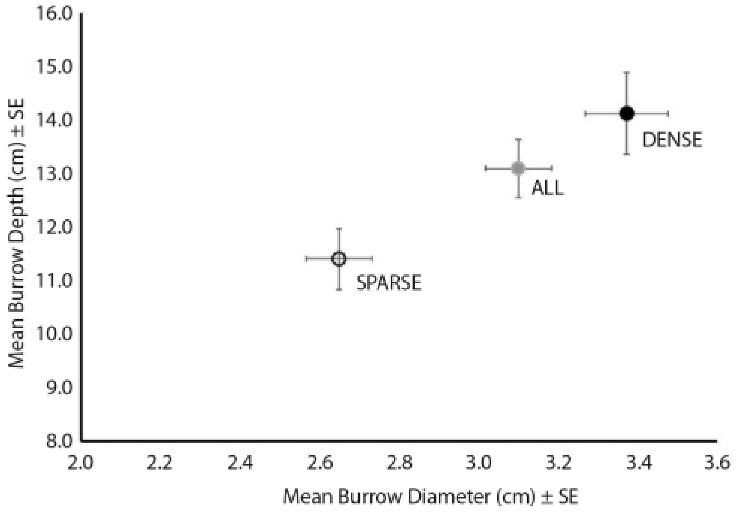

Fig. 3. Distribution of burrows based on mean diameter (cm) and mean depth (cm). Error bars represent standard error.

dense beds (Fig. 3). Burrow diameter and depth ranges were 1.3-2.5 cm and 7.0-19.0 cm in the sparse seagrass beds and 2.5-6.0 cm and 5.0-26.0 cm in the dense seagrass beds. However, there was no significant correlation (P > 0.05) between burrow diameter and depth within either the dense or sparse seagrass beds, or indeed for the combined burrow dataset.

Overall, the sediment comprised sand, coral rubble, and shell fragments; however, we did not analyze the proportion of each component. Factorial MANOVA analysis showed that the grain size composition differed significantly between the sparse and dense seagrass beds as well as between the burrow lining materials and the sediment outside the burrows in both seagrass beds (Fig. 4). Inside the burrows, the overall pattern was similar in both seagrass beds, although there were significant differences between dense and sparse seagrass beds in the proportions of three grain size classes: > 2 mm, < 0.13 mm, and < 0.063 mm. The proportion of coarse particles (> 2 mm) in the burrow lining was significantly higher in the sparse seagrass bed while the proportions of fine particle classes (< 0.13 mm and > 0.063 mm) were higher in the dense seagrass bed. Outside the burrows, the grain size distribution was noticeably different between the two seagrass beds, and the sediment grain size composition patterns were reversed between the dense and sparse seagrass beds. There was a significantly higher proportion of relatively coarse grain classes (> 2 mm and > 0.5 mm) in the sparse seagrass bed, while the proportion of smaller grain size classes (> 0.25 mm and > 0.13 mm) was significantly higher in the dense seagrass bed.

The water quality parameters measured (DO concentration, pH, temperature) (Table 1) did not differ significantly (factorial MANOVA) between the water column (outside

TABLE 1
Water parameters outside and inside burrows in dense and sparse seagrass beds. Values are presented as mean ± SE (n)

Seagrass beds	Burrows	O_2 (mg l^{-1})				pH				Temperature (°C)			
Dense	Outside	4.51	±	0.51	(10)	7.66	±	0.03	(9)	30.16	±	0.14	(10)
	Inside	4.03	±	0.58	(10)	7.59	±	0.03	(9)	30.25	±	0.10	(10)
Sparse	Outside	5.37	±	0.56	(7)	7.79	±	0.08	(7)	30.28	±	0.12	(8)
	Inside	3.79	±	0.77	(7)	7.77	±	0.04	(7)	30.29	±	0.09	(8)

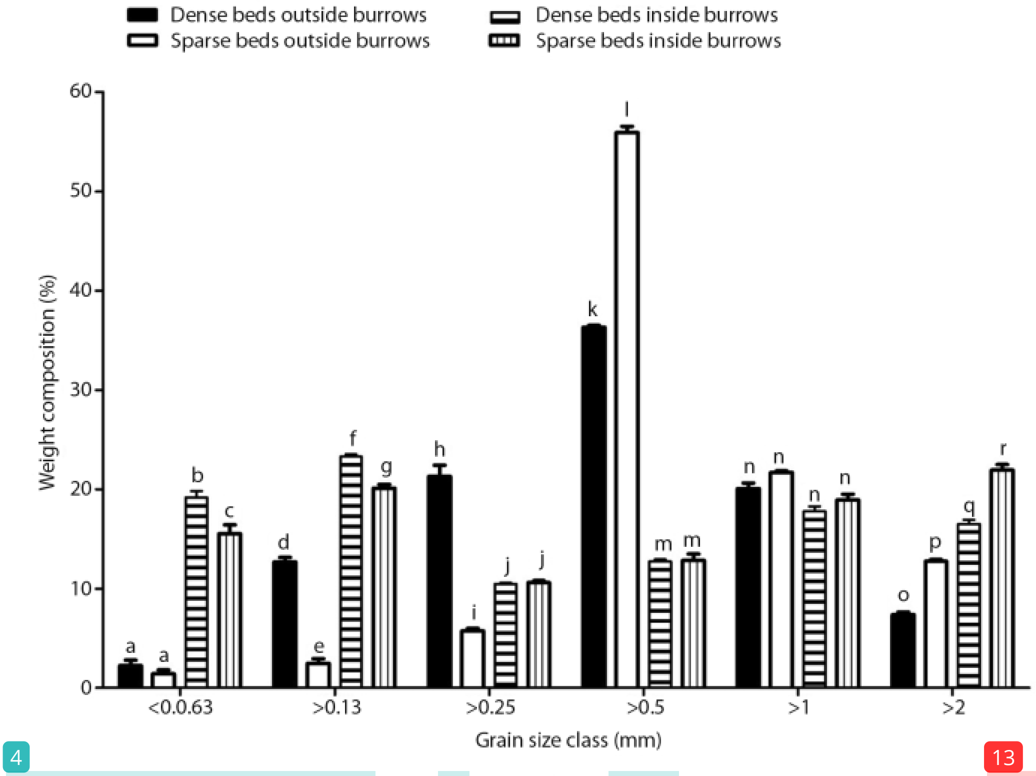

Fig. 4. Grain size composition of sediment inside and outside shrimp burrows in dense and sparse seagrass beds. Error bars represent standard error. Different letters above error bars indicate significant differences.

burrows) and in the burrow water (inside burrows) or between the two seagrass bed types (sparse and dense).

DISCUSSION

The two species observed at the study site are spearers. In contrast with the smasher mantis shrimp that live in pre-existing cavities within hard substrate, the spearers live in burrows that they excavate themselves, typically in soft substrates (Hernáez et al., 2011). Spearer mantis shrimp are ambush predators with elongated spear-like appendages used to ambush soft-bodied evasive prey (deVries et al., 2012; deVries, 2017). Spearing appendages are more commonly found in lysiosquillids, but also in the squillid, bathysquillid, and some gonodactylid mantis shrimps (Caldwell and Dingle, 1975). While *Lysiosquillina maculata* is a widespread and frequently abundant across the Indo-Pacific (Ahyong, 2001), including some areas of Indonesia (e.g. Dini et al., 2013), *L. sulcata* is only reported from a few locations; however, these range from the Pacific to Madagascar and Zanzibar including one Indonesian site in Ambon (Manning, 1978); French Polynesia, including Moorea (Patek et al., 2012) and Rangiroa (Lecchini et al., 2010); and Australia, including One Tree Island, Australia (Courtney et al., 1999; Courtney et al., 2007). While the literature on *L. sulcata* is extremely limited, it has been reported as sympatric with *L. maculata* (Manning, 1978; Lecchini et al., 2010). Like other spearer mantis shrimps, the species *L. maculata* is the object of targeted fisheries (Ahyong et al., 2017; Abduho & Madjos, 2018; Baigtu & Echem, 2018) and caught as by-catch in other fisheries (Babu et al., 2022; Courtney et al., 1999; Courtney et al., 2007). The zebra mantis shrimps including *L. maculata* (and perhaps *L. sulcata* as they are very similar) are commonly found in big seafood restaurants in Bali and Batam, Indonesia (Pers. Obs.). However, in general little is known of the social behavior of lysiosquilloid mantis shrimps.

This study found that dense seagrass beds harbor a higher abundance of zebra mantis shrimp burrows than sparse seagrass beds. This reinforces the view that seagrass beds are an important habitat for economically important animals (Nadiarti et al., 2015; Torre-Castro et al., 2014), including mantis shrimps (Jayabarathi et al., 2013), with seagrass density as an important factor with regards to the abundance of these animals. Other studies have reported higher faunal abundance in denser seagrass beds, in general or in specific taxa (e.g. Nadiarti et al., 2015; Nadiarti et al., 2021; Pogoreutz et al., 2012; Vonk et al., 2008), although the correlation can be weak for some taxa (Priosambodo, 2015). Furthermore, seagrass community composition can also be an important factor influencing faunal biodiversity and abundance. For example, Nienhuis et al. (1989) report that the density of selected macrofauna was positively correlated with *T. hemprichii* density but not with overall seagrass density or the density of other seagrass species.

The seagrass species present at the study site were the same as reported from seagrass beds in this area by Nadiarti et al. (2021) who considered the sea urchin and macroalgae community composition were most likely influenced by the identity and relative abundance of the seagrass species present, in particular differences in canopy structure and hence habitat niches available, as well as feeding preferences and predator-prey relationships. As mantis shrimps are carnivorous, predominantly piscivorous, ambush predators (de Vries et al., 2012), burrow surroundings are likely an important factor with respect to the capture of prey. Habitat characteristics related to seagrass community composition which might influence mantis shrimp burrow site choice, as well as individual growth and survival, include the canopy structure (Pogoreutz et al., 2012), root and rhizome structure (Kiswara et al., 2009), and abundance of suitable prey (Jackson et al., 2001).

Larger (diameter and/or depth) mantis shrimp burrows were more common in the denser seagrass beds and smaller burrows were more common in sparse seagrass beds. This pattern may indicate that larger mantis shrimps prefer denser seagrass beds. A similar pattern of larger individuals mostly found in denser seagrass beds has been observed in seagrass associated fishes (Nadiarti et al., 2015; Pogoreutz et al., 2012). The higher abundance of mantis shrimp burrows in the dense seagrass beds may be related to the structure of the seagrass canopy and/or to root and rhizome structure. As predators, mantis shrimps may prefer dense seagrass cover which could provide a more effective hiding place and make it easier to ambush their prey than in a more exposed area (sparse seagrass beds), as has been suggested for predatory fishes (Schultz et al., 2009). The denser and more structured seagrass beds could provide better cover for the mantis shrimp to ambush their prey from their burrow openings; however, information about their activity in their burrows and the surrounding areas is extremely limited, calling for further studies on mantis shrimp behavior and ecology.

Although the percentage cover was much higher in the dense seagrass area, the seagrass canopy was much taller in the sparse seagrass area which was dominated by *Enhalus acoroides,* the largest seagrass species found in Indonesia. The thick rhizomes and long black bristly cord-like roots of *E. acoroides* are closely interwoven and more deeply embedded into the substrate than the root and rhizomes of other seagrass species, and could be a challenge for the zebra mantis shrimps when making their burrows. In the dense seagrass area, the dominant seagrasses were *Cymodocea rotundata* and *Thalassia hemprichii*, both of which have shorter canopies with smaller rhizomes and roots, among which it would most likely be easier for zebra mantis shrimps to create large (wide and/or deep) and stable burrows. On the other hand, seagrass root systems can stabilize sediment (Mcleod et al., 2011) and it is possible that, in stabilizing sediment, the roots may also help to stabilize burrow walls. A more stable burrow will be better for the mantis shrimp, since the burrow functions as a shelter, a place for processing prey, and a safe home for mating and for the guarding of eggs and larvae (Vetter & Caldwell, 2015). The higher abundance of mantis shrimp burrows in dense seagrass beds compared to in sparse seagrass beds may be influenced by these factors, although further study is needed to test whether burrows are more stable in dense seagrass areas, and to elucidate the causal mechanisms for the observed difference in burrow size and abundance.

The differences in burrow size are most likely related to the size of the occupant, indicating that burrows in the dense seagrass tended to be occupied by larger mantis shrimps compared to those in sparse seagrass. This may indicate an ontogenetic shift in habitat preference between the two seagrass habitats, but could also be related to the species present. Once possible explanation could be that juveniles are more abundant further offshore, and will tend to move to the more favorable (presumably more productive) dense seagrass habitat as they grow larger and are more capable of constructing and defending their burrows. The burrows not only serve as refuges and for ambushing prey but also play a key role in mantis shrimp reproduction (Mead & Caldwell, 2010; Matsuura & Hamano, 1984; Wortham-Neal, 2002), as female mantis shrimps remain in the burrow while brooding their eggs. The juveniles of gonodactyloid smasher mantis shrimps in the Caribbean live in deeper offshore reefs and migrate to more productive inshore waters as they grow larger and are able to fight for occupancy of the limited pre-existing cavities where reproduction can take place (Reaka, 1987). However, in general, spearer mantis shrimps are less aggressive than the smasher mantis shrimps (Reaka and Manning, 1981). As they can construct their own burrows, competition for burrows could be less of an issue, although territorial behavior may occur and could limit density and/or give rise to competition over prime habitat. Further studies are needed to elucidate the social behavior of spearer mantis shrimps, including with respect to their occupation of different habitats at each life stage.

Although larger burrows (wider diameter and deeper in depth) tend to occur in the dense seagrass beds and small burrows in sparse seagrass beds, there was no correlation between diameter and depth. This indicates that the inhabitants (mantis shrimp) of each burrow construct dwellings of very different shapes and sizes. Several studies show that burrow dimensions and diameter size tend to be correlated with the size of the inhabitant (Atkinson et al., 1997; Mead & Caldwell, 2010; Matsuura & Hamano, 1984) as in some gobies (Dinh et al., 2014), while size can also be correlated with different species, as in fiddler crabs (Qureshi & Saher, 2012). Caldwell & Dingle (1975) found different species of mantis shrimp can create burrows of different shapes and sizes, with burrow depth generally proportional to the length of the mantis shrimp. Therefore, the different burrow shapes may be related to mantis shrimp size and/or species. During our study we only found two zebra mantis shrimp species (*Lysiosquillina maculata* and *L. sulcata*); furthermore, mantis shrimps caught by local fishers during the study period were all identified as one of these two species. However, were unable to verify which burrows were inhabited by which species, and further studies are needed to ascertain whether the smaller burrows belong to smaller (possibly juvenile or slow growing) zebra mantis shrimps or belong to other mantis shrimp species.

The differences in burrow abundance and size do not appear to be due to differences in sediment between the dense and sparse seagrass beds. Despite significant differences in some grain size classes both within and outside the burrows, the overall substrate composition pattern within all burrows was similar in both seagrass bed types, with coarse and fine particles more dominant than the medium particles both in absolute terms and relative to the composition of the surrounding substrate. These data indicate that the mantis shrimps were selective in the materials they used to construct their burrows, in particular the inner wall lining. Grain size selectivity in burrow construction has been reported in several burrowing marine invertebrates including crustaceans (Sumida et al., 2020; Zorn et al., 2010).

The sediment outside and inside zebra mantis shrimp burrows, in both sparse and dense seagrass beds, was dominated by sand, rubble and shell fragments (> 90 %) with the remainder composed of silt and clay. This means that the substrate of the zebra mantis shrimp habitat in the study area is predominantly sandy, similar to the substrate characteristics described by Nurdin et al., (2019) in the same study area. Outside the burrows, coarse sand (0.25-0.5 mm) was more abundant in sparse than in dense seagrass beds; conversely, medium sand (0.13-0.25 mm) was more abundant in sparse than in dense seagrass beds. These differences in sediment composition were most probably due to the higher hydrodynamic energy in sparse seagrass beds compared with dense seagrass beds. Seagrasses reduce hydrodynamic energy compared to unvegetated areas (Contti Neto et al., 2022; Lanuru et al., 2018; Potouroglou et al., 2017).

Furthermore, seagrasses have a differential effect on the transportation process for particles of different sizes (Conley & Austin, 2017); in particular, the seagrass foliage may reduce water movement and wave energy and hence lower the effective transport rates of coarser sediment particles with a higher settling velocity, while turbulence generated by the seagrass canopy can cause the resuspension of finer particles. The higher proportion of coarse particles in the area with sparse seagrass compared to that with denser seagrass vegetation could seem counterintuitive. However, this result is most likely related to the canopy structure. The taller *E. acoroides* stands in the sparse seagrass area most likely have a greater effect in precipitating the deposition of coarse particles; however, the higher velocities further from the seabed and the greater distances between shoots and patches may also enhance turbulence which could facilitate the resuspension of finer particles and account for the lower proportion of fine sediment. On the other hand, the lower growing species in the dense seagrass beds would be less likely to cause the precipitation of larger particles higher in the water column; however, with very little exposed substrate they are likely more effective in reducing near-ground turbulence and retaining medium and relatively fine particles. The proportion of the largest grain sizes (> 1 mm and > 2 mm), mostly comprised of coral rubble and shell fragments, was similar in both seagrass bed types, reflecting the proximity of these seagrass beds to the coral reefs fringing the island and that fact that they both harbor various shellfish.

The similarity in the grain size composition of particles lining the burrow walls of zebra mantis shrimps in the dense or sparse seagrass beds coupled with the marked difference between the burrow walls and the composition of the surrounding substrate in each seagrass area, indicates that the sediment particles present around the burrow have a limited influence on burrow wall construction, with purposive selection (retention or rejection) of excavated materials for use in burrow wall construction. We did not observe how the zebra mantis shrimps create their burrows, but we assumed that burrow creation by zebra mantis shrimps is similar to the way in which *Squilla empusa* create their burrows, using their pleopods for excavating and their maxillipeds for basketing sediment (Mead & Minshall, 2012). We based this assumption on morphological similarities between the species, both of which are spearers, sharing a similar raptorial appendage structure; the dactyl of both species is lined with sharp spines and the propodus is also spined (Dingle & Caldwell, 1978). The texture of the sediment from within the burrow (burrow linings) was more solid than outside the burrows, due to the mucus used in lining the burrow wall. This mucus-reinforced lining is essential in sandy sediment to support the otherwise readily collapsing walls of the burrow (Papaspyrou et al., 2005).

Differences in burrow abundance and size were not correlated with the water quality parameters measured (temperature, pH and DO), as none of these parameters differed significantly between sites. Although pH and DO (but not temperature) were somewhat lower within the burrows of mantis shrimp than outside the burrows (in both sparse and dense seagrass sites), the lack of statistical significance was most likely related to the high between-burrow variability reflected in the high standard error values (Table 1).

Although there was no significant correlation between mantis shrimp burrow size and seagrass density, the burrows were significantly more abundant and larger in the dense seagrass beds than the sparse seagrass beds. Seagrass conservation is increasingly recognized as crucial for climate mitigation, biodiversity protection, and food security (Cullen-Unsworth & Unsworth, 2018). In particular, seagrass beds provide vital habitat for various fauna with high economic value, including mantis shrimps. The results of this study highlight the importance of conserving the quality (e. g. density) of seagrass ecosystems as well as their extent in order to support seagrass-associated resources.

Ethical statement: the authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgements section. A signed document has been filed in the journal archives.

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RESUMEN

La densidad de los pastos marinos se correlaciona con la abundancia y el tamaño de las madrigueras de los camarones mantis cebra (Stomatopoda: Lysiosquillidae)

Introducción: Los camarones mantis son organismos ecológica y económicamente importantes en los ecosistemas marinos. Sin embargo, aún falta información sobre su hábitat, en particular sobre sus madrigueras.
Objetivo: Analizar cómo difieren las madrigueras de los camarones mantis en su abundancia, tamaño, tamaño de grano de los sedimentos y calidad del agua.
Métodos: Contamos las madrigueras en parcelas de 10 x 10 m^2 al azar (diez parcelas por densidad) en pastos marinos densos y poco densos, alrededor de la isla de Barrang Lompo, Sulawesi del Sur, Indonesia.
Resultados: Se observaron dos especies de camarones mantis: *Lysiosquillina maculata* y *L. sulcata*. El tamaño de grano de las paredes de las madrigueras y los parámetros de agua, tanto dentro y fuera de la madriguera no variaron ($P > 0.05$). Tampoco hubo correlación entre la profundidad y el diámetro de las madrigueras, tanto en praderas densas ($P > 0.05$; $r= 0.27$), como no densas ($P > 0.05$; $r= 0.33$). Sin embargo, las madrigueras más grandes tienden a aparecer en las praderas densas, además había más madrigueras en pastos densos (*t*-test, $P < 0.05$).
Conclusiones: Parece haber una preferencia por las praderas marinas densas, especialmente en los camarones mantis de mayor tamaño. La correlación entre la abundancia de madrigueras de camarones y la densidad de pastos marinos pone de manifiesto la importancia de conservar la calidad del hábitat de los pastos, así como su extensión.

Palabras clave: Camarón mantis cebra; madrigueras; pastos marinos; intermareal; isla de Barrang Lompo; Indonesia.

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