



Factors Affecting Population Density and Mound Distribution of Mud Lobsters, *Thalassina* spp.

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Abstract

This study is the first to investigate factors affecting population density and mound distribution of mud lobsters, *Thalassina* spp., in Southern Thailand. Mud lobsters are essential for nutrient cycling and maintaining mangrove ecosystems through their bioturbation activities. This study was conducted by establishing three transect lines in a 5×350 m² area beginning 100 m from the edge of the river towards inland and composed of six subplots with 50-m intervals (i.e., 100, 150, 200, 250, 300, and 350-m subplots). Numbers of mounds were recorded, and mound height and diameter basal area in each subplot were measured. Soil samples were collected, and moisture, grain size distribution, and pH were measured. The results showed that soil grain size was mostly less than 250 μm with an average soil pH of 4.48. The mound density and mound height increased with increased distance from the river (i.e., 267 mounds per hectare at 100 m increased to 1,734 mounds per hectare at 350 m from the river edge) and with decreased soil moisture (72.6% to 65.9%). This indicated that the mud lobsters preferred to build more and higher mounds farther away from the river edge, where they were less affected by the tide and the soil was drier. Findings also indicated that mud lobsters used resource partitioning to reduce intraspecific competition. This study is the first to show that mounds associated with prop roots had greater heights than mounds without prop roots nearby.

Keywords:

Mud Lobster;
Mangrove Frost;
Soil Moisture;
Marine Biology;
Mound Density.

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1- Introduction

Bioturbation plays a vital role in mangrove ecosystems through fauna activities such as feeding, burrowing, and ventilation [1–6]. Bioturbation in mangrove ecosystems is carried out by fauna that directly or indirectly affects sediment matrices [1, 7]. Bioturbation can preserve and bury organic matter in deeper sediment layers, increase the amount of food availability in the sediment, enhance sediment oxygenation, and promote nutrient cycling [8–10]. Mud lobsters (*Thalassina* spp.) are ecosystem engineers abundant in mangrove ecosystems in the Indo-Western Pacific region [11–15]. They consume mud, clay, and organic matter in the soil as food during the mound-building process [16–18]. Burrow structures serve as refuge from predators, perturbation, and harsh environmental conditions such as high temperatures and dryness and are also locations for feeding, breeding, and moulting [7, 15].

The mud lobsters' soil excavation plays a crucial role in aerating deep soil and trapping, recycling, and enhancing the retention of organic matter, organic carbon, and nutrients in the mangrove ecosystem [15, 19–23]. This is caused by the movement of soil from deeper below to the soil surface by the mud lobster, resulting in a significantly higher content of organic matter and total carbon in freshly excavated mud than in older mud in the mound [24]. Moreover,

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the burrowing process also effectively increases macronutrients (including $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, P, and Na concentrations) and Fe, Cu, and Zn concentrations in the surface soil [19]. Dissanayake and Chandrasekara [25] have described that mangrove soils are typically brackish and acidic. The presence of mud lobsters affects pH in mangrove forests as the soil they excavated is rich in sulphur content, which acidifies strongly upon oxidation and develops low pH soil on the surface [19].

Eleven species of mud lobsters have been described worldwide [11–14]. Four species of mud lobsters are reported in the Kampuan mangrove forest, Southern Thailand: *Thalassina anomala* [26], *Thalassina spinosa* [12], *Thalassina krempfi* [12], and *Thalassina squamifera* [16]. However, only one specimen each of *T. krempfi* and *T. squamifera* has been caught at this site, whereas several specimens of *T. anomala* and *T. spinosa* have been caught due to their high prevalence in the area. Mud lobsters are essential in maintaining ecosystems; however, little is known about the factors affecting mud lobster density. This is the first study investigating factors affecting population density, mound size, and its distribution of mud lobsters (*T. anomala*) in Southern Thailand. In this study, three research questions were investigated: (1) how does distance from the river edge affect mud lobster mound density and size?; (2) what is the relationship between mud lobster mound density, size, and soil moisture?; and (3) what is the relationship between lobster mound height and mangrove prop roots?

Figure 1 shows the flowchart of the research methodology through which the objectives of this study were achieved.

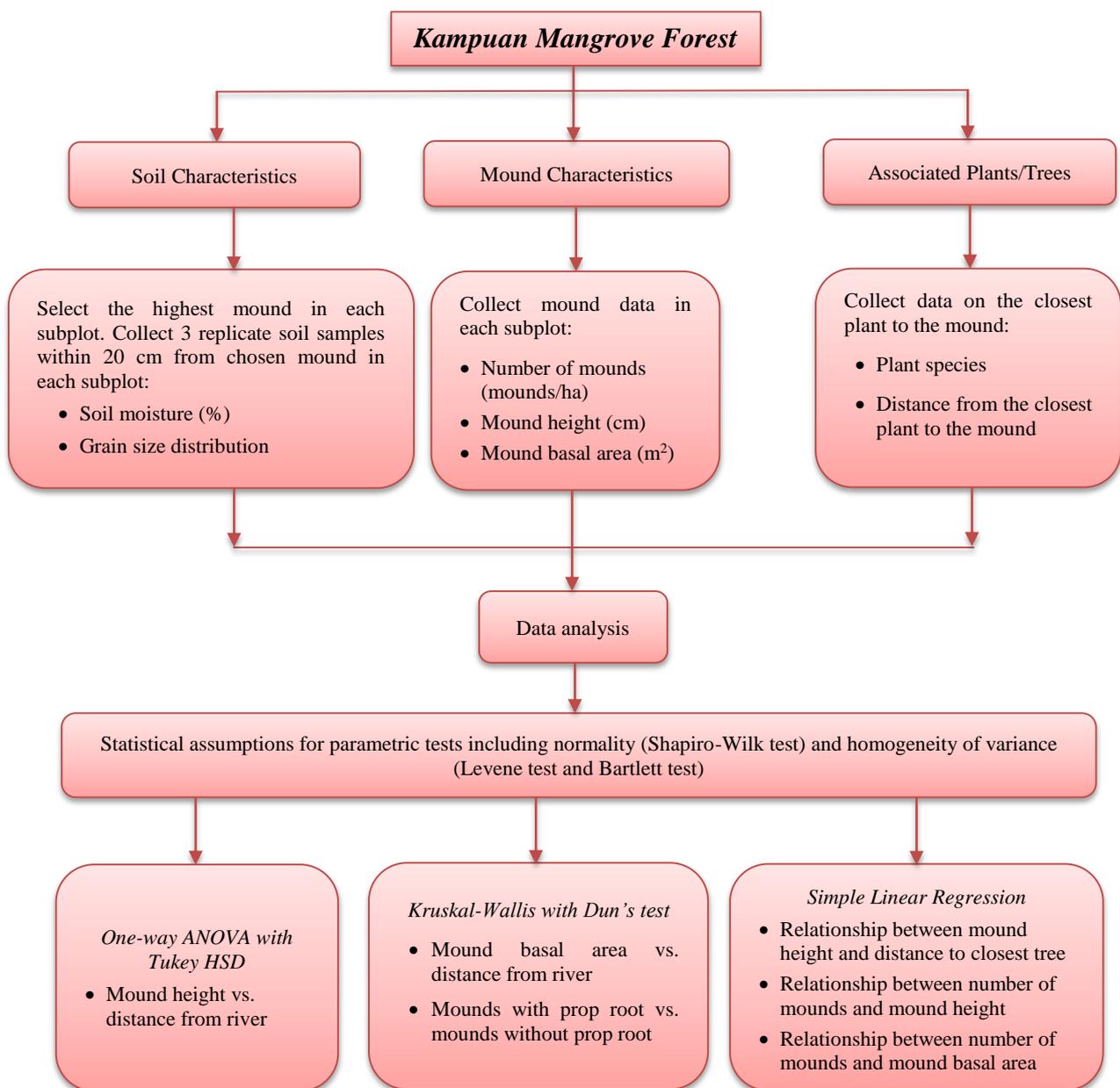


Figure 1. Research methodology schema for factors affecting population density and mound distribution of mud lobsters, *Thalassina* spp., in the Kampuan Mangrove Forest in Southern Thailand

2- Material and Methods

2-1- Study Area

The study was conducted at the Kampuan mangrove forest (Latitude 9.371697°N, Longitude 98.401798°E) in Ranong Province, Southern Thailand (Figures 2-a and 2-b). Ranong Province has an average annual rainfall of 2,625 mm and an average temperature of 26.1 °C. The warmest month of the year is April, with a monthly average temperature of 27.6 °C, and the coldest month of the year is December, with a monthly average temperature of 25.4 °C. At the Kampuan mangrove forest, there were 11 plant species present (*Aegiceras corniculatum*, *Avicennia alba*, *Bruguiera cylindrica*, *Bruguiera parviflora*, *Ceriops tagal*, *Cytisus pinnatus*, *Heritiera littoralis*, *Rhizophora apiculata*, *Rhizophora mucronata*, *Xylocarpus granatum*, and *Xylocarpus moluccensis*). The dominant species were *R. apiculata* (61.98%), *R. mucronata* (18.38%), and *B. cylindrica* (10.78%), with an Importance Value Index of 160.6, 66.14, and 33.02, respectively.

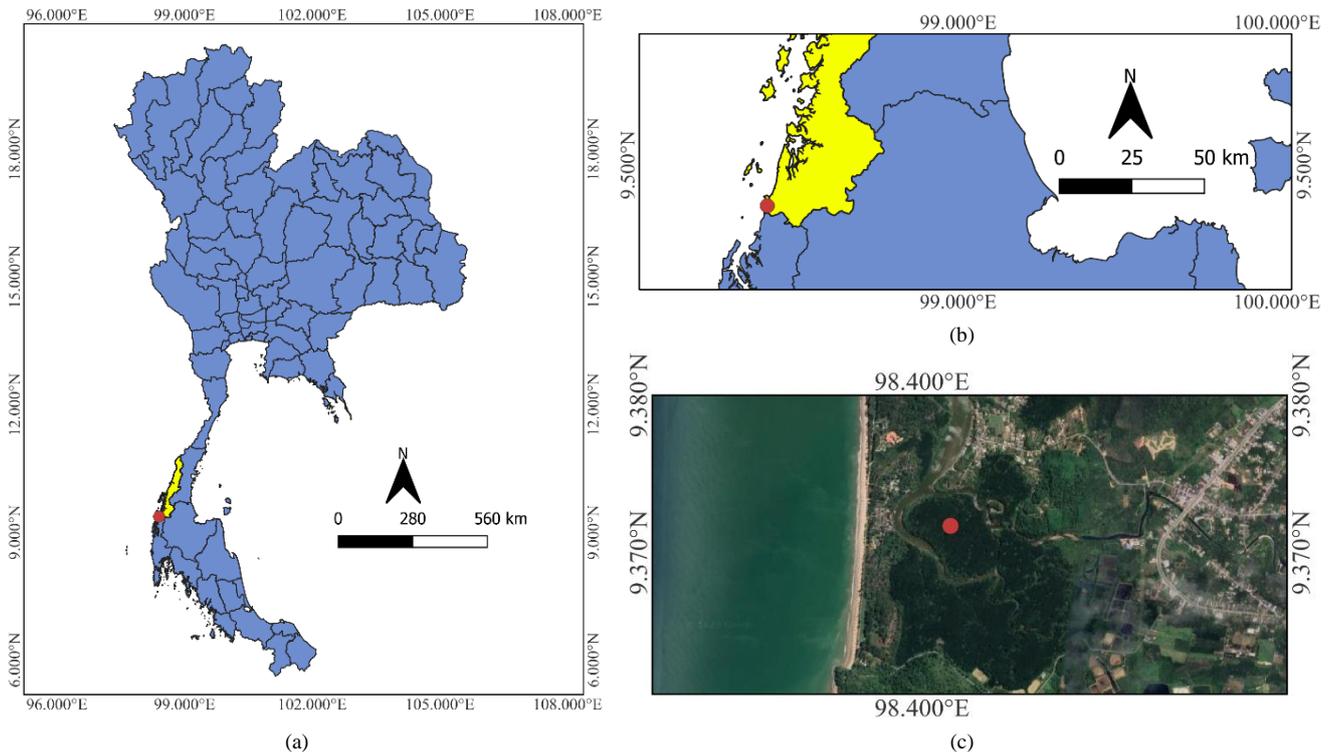


Figure 2. Thailand map and study site. (a) Thailand map with Ranong Province marked with yellow color, (b) Ranong Province represented with yellow color and study site represented with red dot, and (c) satellite image of study site marked with red dot.

2-2- Data Collection

In this study, three permanent transect lines were created in a 5×350 m² area with six subplots of 5×10 m² at 50-m intervals in each transect, for a total of 18 subplots. Each transect line started at 100 m from the river edge to 350 m inward in the mangrove forest (i.e., 100, 150, 200, 250, 300, and 350-m subplots) (Figure 3).

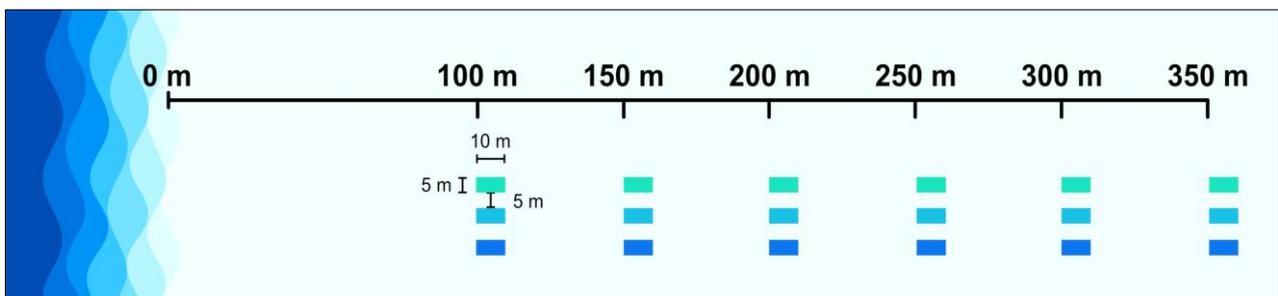


Figure 3. A schematic profile of sampling procedure at 100 m from the river edge to 350 m inward in the mangrove forest. Three transects were created in a 5×350 m² area with six subplots of 5×10 m² at 50-m intervals in each transect with a total of 18 subplots, each transect line starting at 100 m from the river edge to 350 m inward in the mangrove forest (i.e. 100, 150, 200, 250, 300, and 350-m subplots).

2-2-1- Mound Data Collection

Mound density (the number of mounds per hectare) was used as an index of population density and was determined by counting the number of mounds with freshly excavated soil in each 5x10 m² subplot, and mound size was determined by measuring the mound height (cm) and basal diameter for both width and length in each subplot. The mound basal area (cm²) was calculated using an ellipse area formula.

2-2-2- Soil Data Collection

Soil core samplers were used to collect three soil samples to a depth of 20 cm from the soil surface per subplot at a 20-cm distance from the mound opening. The soil samples were transported to the laboratory to be analyzed for soil moisture [27]. For soil particle size distribution, a wet sieve methodology was used with 5 sieve sizes of >1,000 µm, 500-1,000 µm, 250-500 µm, 125-250 µm, and 63-125 µm. Soil pH was analyzed by mixing 50 grams of dried soil samples with 50 mL of distilled water, stirring for 30 mins, then allowing the mixture to sit for 30 mins, and then measuring the pH of the supernatant with a pH meter.

2-2-3-Plant Data Collection

The plant species and root types (i.e., prop root and other root) that were found closest to the mud lobster mounds were recorded, and the distance from the apex of the mound to the closest tree in each subplot was measured.

2-3-Data Analysis

One-way ANOVA with post-hoc Tukey HSD test or Kruskal-Wallis tests with Dunn's test for multiple comparisons were used to analyze: (1) the mean mound height and basal area differences from the river edge to 350 m upward in the mangrove forest (i.e., 100, 150, 200, 250, 300, and 350-m subplots); and (2) the mean mound height differences between mounds with prop roots and without prop roots. Simple linear regression tests were used to examine: (1) the relationship between the mound height and distance from the closest tree; (2) the relationship between the number of mounds and the mound height; and (3) the relationship between the number of mounds and the mound basal area.

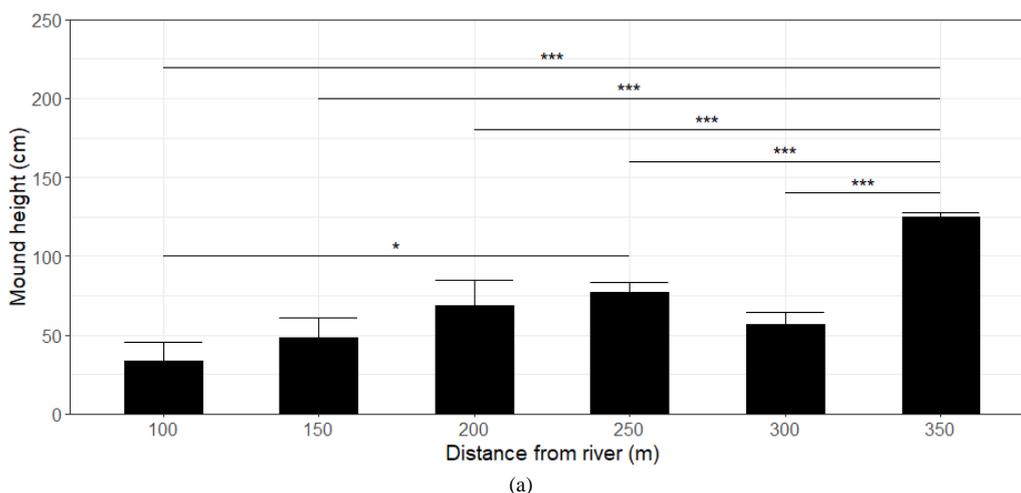
3- Results

3-1-Soil Conditions in the Kampuan Mangrove Forest

Soil moisture from the river edge to 350 m upward in the mangrove forest at Kampuan decreased as the distance from the river edge increased (i.e., 72.6% (100 m), 71.7% (150 m), 73.1% (200 m), 69.8% (250 m), 68.3% (300 m), and 65.9% (350 m). Soil particle size was mostly less than 250 µm, which was fine sand, very fine sand, and silt, respectively. The soil pH ranged from 4-6, with an average of 4.48.

3-2-Mound Density, Height, Basal Area, and Plant Association

Mound density from the river edge to 350 m inward in the mangrove forest increased as the distance from the river edge increased (267 mounds/ha (100 m), 267 mounds/ha (150 m), 400 mounds/ha (200 m), 734 mounds/ha (250 m), 867 mounds/ha (300 m), and 1,734 mounds/ha (350 m). Mound height significantly differed among distances from the river (one-way ANOVA: $F_{(5,55)} = 28.21$, $P < 0.001$), and the post-hoc Tukey HSD test for multiple comparisons showed that the mound height at 350 m from the river was significantly higher than at other distances ($P < 0.001$, Figure 4-a). Mound basal area differed significantly among distances from the river (Kruskal-Wallis tests: $H_{(5)} = 23.34$, $P < 0.001$, Figure 4-b), and Dunn's test for multiple comparison showed that the mound basal area at 350 m was significantly smaller than at other distances ($P < 0.05$, Figure 4-b).



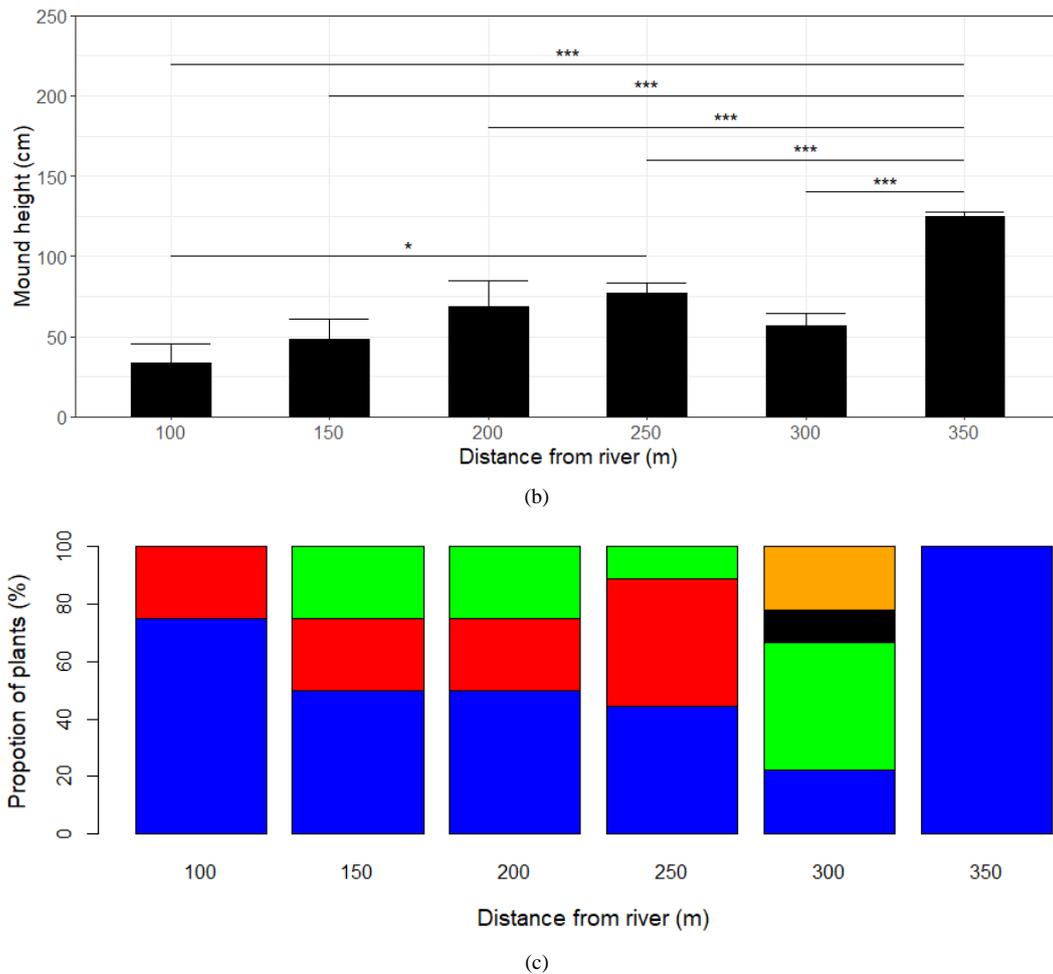
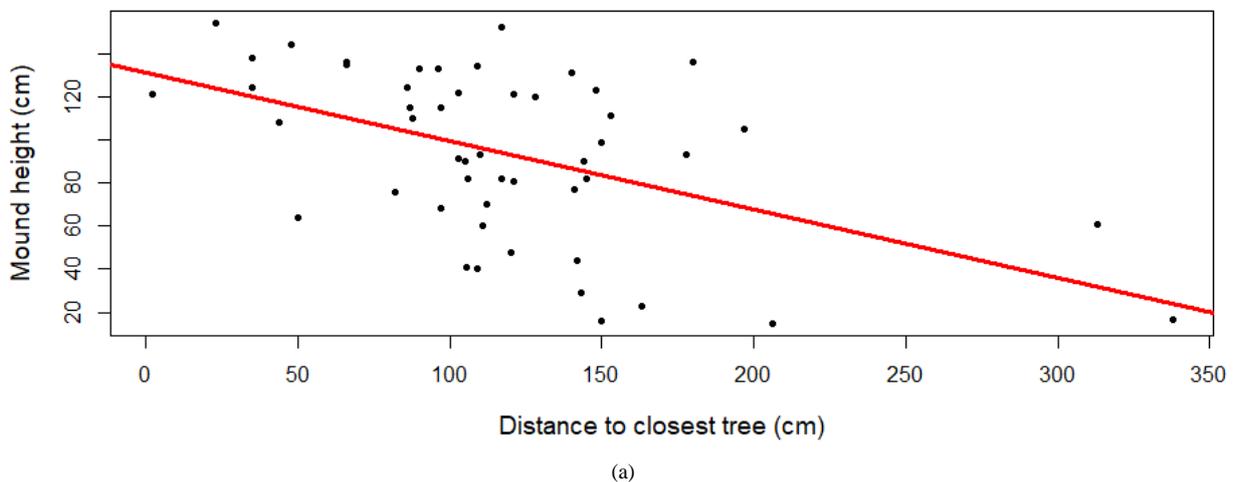


Figure 4. Mound characteristics with distance from river: (a) mound height (cm), (b) mound basal area (cm²), and (c) proportion of plants associated with the mounds (blue represents *R. apiculata*, red represents *R. mucronata*, green represents *B. cylindrica*, black represents *C. tagal*, and orange represents *X. granatum*) (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

3-3-Relationship between Mound Characteristics and Mound Distance to the Closest Tree and Resource Partitioning

Mounds associated with prop roots ($\bar{X} \pm SD = 95.11 \pm 37.46$) were taller than mounds without prop roots ($\bar{X} \pm SD = 53.17.11 \pm 28.11$) (Kruskal-Wallis test: $H_{(1)} = 10.433$, $P < 0.005$). Mound height significantly decreased as distances increased between the mounds and the prop roots (Simple linear regression test: $R^2 = 0.2498$, $F_{(1,48)} = 15.98$, $P < 0.001$, $y = -0.3177x + 131.15$, Figure 5-a), but with significant increase in mound density (Simple linear regression test: $R^2 = 0.2782$, $F_{(1,14)} = 5.397$, $P < 0.05$, $y = 0.0244x + 48.05$, Figure 5-b). There was no relationship between mound density and mound basal area (simple linear regression test: $F_{(1,14)} = 0.1682$, ns , Figure 5-c).



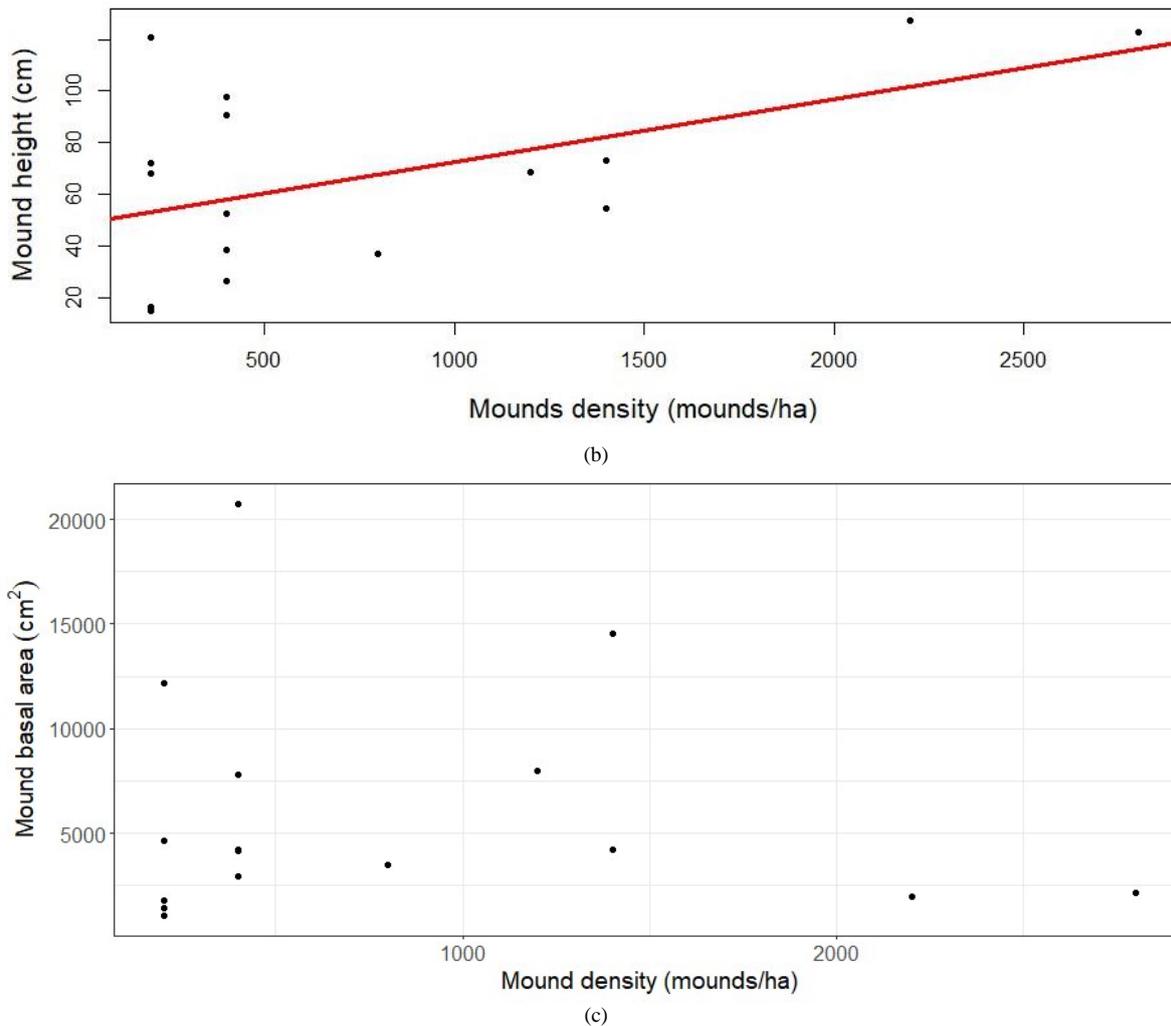


Figure 5. Mound density and mound characteristics: (a) distance to closest tree (cm) and mound height (cm), (b) mound density (mounds/ha) and mound height (cm), and (c) mound density (mounds/ha) and mound basal area (cm²) (Note: Figure 5 needs to be moved up under Results right after Figure 4. Right now it is showing under the Discussion which does not directly refer to Fig 5 like it does in the Results).

4- Discussion

4-1- Soil Condition

Four species of mud lobsters were found in the Kampuan mangrove forest: *T. anomala*, *T. spinosa*, *T. krempfi*, and *T. squamifera*, with *T. anomala* as the most common one reported [16]. Our results showed that the percentage of soil moisture in the *T. anomala* mounds in the Kampuan mangrove forest ranged from 68.3-73.1%. The percentage of soil moisture in mangrove forests could be affected by the frequency of tidal inundation, the amount of freshwater input, mangrove vegetation, rainfall, evaporation, transpiration, soil characteristics, and the mud lobster density and mound size [21, 28]. Our results indicated an inverse relationship of percent soil moisture with mud lobster mound density and mound size. In the high mud lobster mound density, soil was drier because mud lobsters can excavate large complex branching tunnels, allowing water circulation during high tides [29]. Their mounds, tunnels, and aeration associated with mounds may result in an increase in the water drainage of the high mound density areas [21, 28]. This has also been observed in *Helograpsus haswellianus*, where the greatest burrow densities occurred in drier substrates, not in waterlogged soils [30–32]. In addition, Moh [33] reported the soil moisture of *T. anomala* on Carey Island, Malaysia, to range from 20–50%, while Macintosh et al. [34] reported the soil moisture of *T. anomala* mounds at the mangrove rehabilitation site in Klong Ngao, Ranong Province, Thailand, to range from 30.7–50.7%. The soil moisture content from these studies is lower than that found in our study. The reasons for the higher soil moisture content at our study site could be due to a greater frequency of tidal inundation, heavy rainfall during the sampling period, and/or high freshwater input from the river [35].

Our study results showed that the soil grain size distribution in the Kampuan mangrove forest was less than 250 μm , mainly composed of sand, fine sand, and silt. Mud lobsters prefer to occupy fine grain sizes of less than 250 μm [33]. Similar soil grain size distributions for *T. anomala* mounds have been reported in many countries, e.g., Thailand [16],

Malaysia [33, 36], Indonesia [37], and Fiji [38]. Similar to our study, previous studies in Thailand, Malaysia, and Fiji have indicated that the majority of soil grain size distribution was also less than 250 μm and consisted of sand and fine sand [14, 36, 38]. Alternatively, *T. anomala* in Indonesia occupies clayish soil [37]. Finer soil grain size is likely a more suitable substrate for mud lobsters due to three reasons: (1) this finer grain size can retain more water than coarse grains [39], (2) the water table in finer grain size soil stays higher due to greater capillarity [39], and (3) finer grains have a higher cohesive nature, allowing mud lobsters to build extensive and more complex burrows [33, 40, 41].

Our results also showed that the soil pH in the Kampuan mangrove forest ranged from 4.0–6.0, which was within the range reported by other researchers. Mud lobsters have been reported to occupy soil with a substantial pH range starting from pH 2.7–7.3 in many countries, e.g. *T. anomala* inhabits soil with a pH ranging from 2.7–6.2 in Thailand [42], 2.7–7.3 in Carey Island and Kelanang Shore, Malaysia [33], 4.6–6.9 in Sematan Mangrove Forest, Sarawak, Malaysia [21], 3.5–4.6 in Tanjung Jabung Barat, Jambi, Sumatra, Indonesia [37], and 5.0–7.2 in Sungai Reuleung Leupung Aceh Besar, Indonesia [15]. Interestingly, all other studies have reported that mud lobster mounds were found in low pH soil because the mud lobsters' sediment excavation activity brought up the sulfide-rich soil, increased aeration, and caused oxidation [19–20, 33], as well as the respiration and decomposition of organic matter, which could also decrease the pH in the soil [21, 33, 43]. Similar findings have reported that the excavated soil from crabs has exposed more anoxic soil to air, causing the soil to become acidified by oxidation [44].

4-2- Mound Density, Size, and Resource Partitioning

Our results showed that the mound density of *T. anomala* ranged from 200–2,800 mounds/ha (800.0 ± 838.37 mounds/ha). Two studies on the *T. anomala* mound densities in Malaysia have reported 3,900–4,500 mounds/ha at Kelanang Beach, Carey Island [36] and 1,250–6,875 mounds/ha at Sarawak [21]. One study in Indonesia has reported 360–530 mounds/ha in Tanjung Jabung Barat, Jambi, Sumatra [24]. The mound density at our site was lower than the two sites in Malaysia but higher than the site in Indonesia. One possible reason is that our study site consisted of mostly sandy soil, which might not be as suitable for *T. anomala*. Our results also showed that mound densities were higher in the inward direction of the mangrove forest, where daily tide had less effect on burrow excavation activity, resulting in hardened burrow construction [36, 45]. A previous study indicated that mud lobsters inhabited an inland mangrove area at a distance of 100–200 m from the water boundary [42].

Mud lobsters excavate the deeper sediment layers, transport them to the surface, forming the mud mound above the ground [19]. Our study showed that the mound heights of *T. anomala* ranged from 15.0–154.0 cm (86.87 ± 39.39 cm). *T. anomala* mound heights have gained a great interest and been studied in many countries, e.g., in Thailand, mound heights were reported to be 3.0–40.0 cm (19.4 ± 10.9 cm) [16] and 20–180 cm [33], in Malaysia, mound heights were reported to be 50.0–101.2 cm (83.60 ± 17.66 cm) [33] and 11.58–58.50 cm (25.69 ± 3.48 cm) [20], and in Indonesia, mound heights were reported to be 13.2–56.3 cm [11] and 22.40–49.50 cm [46]. Surprisingly, mound height ranges seem to differ among sites and countries. In our study, the mound height range was wider compared to those in other studies. The possible reason could be due to the plant community that the mud lobsters associate with. Previous studies have reported that mud lobsters were associated with mangrove vegetation such as *Bruguiera* sp., *Rhizophora* sp., *Xylocarpus* sp., and other mangrove plants [21, 37]. Previous study has shown mound heights that ranged from 3.0–40.0 cm [16], but at our site, the mound heights ranged from 15.0–154.0 cm. At their site, there were eight plant species: *I. cylindrica*, *A. ilicifolius*, *A. alba*, *F. maritima*, *D. trifoliata*, *C. decandra*, *R. apiculata*, and *R. mucronata*. *R. apiculata* and *R. mucronata* were planted within less than two years with a tree height of less than 1.0 m and with 2–3 prop roots per tree. However, at our study site, the mangrove trees were 30 years old, with an average tree height of 12–20 m and with more than 20 prop roots per tree. Previous studies [19, 33, 36, 47] have mentioned that prop roots might have provided some structure and supported mound construction. However, there has been no previous experiment to test the association between the function of prop roots and mound height. The results of our study are the first to show that mounds that were associated with prop roots had greater height than mounds without prop roots nearby.

The basal area of *T. anomala* mounds ranged from 0.03–2.76 m^2 (0.5 ± 0.6 m^2) in our study. Other researchers have reported that *T. anomala* mound basal areas had a great variation ranging from 0.01–29.91 m^2 (i.e., 0.01–29.91 m^2 (1.24 ± 1.53 m^2) [16], 0.28–15.60 m^2 [33], and 0.03–0.87 m^2 (0.17 ± 0.06 m^2) [21]. The possible factor that might influence mound basal areas is the presence of mangrove trees. Mangrove structural complexity is produced by a multi-dimensional net of mangrove trunks, branches, and prop roots that provide substrate for recruitment and predator refuge [48–50]. Our results clearly demonstrated that the mangrove trees provide mechanical support for the mud lobsters, building more abundant and taller mounds. However, a highly dense mangrove forest could have a negative effect on the mound basal area in a way that it restricts the space available for mud lobsters to build mounds. Our results also showed that mud lobster mounds in high prop root areas built small mound basal areas. It is possible that prop roots, underground root structures, and other plant matter in the sediment might be obstructions for mud lobsters to build large basal mounds [51]. Previous studies have reported that extensive mangrove roots can limit the space for mud lobsters to construct their burrows [33, 38]. Intermediate root density and fine sediments have been suggested to

be critical for burrow supports and longevity due to roots' mechanical supports and finer sediments' cohesive nature [40, 41, 52]. In addition, mud lobsters display aggressive and interference competition by competing for habitat space and defending for food resources and mates within the territory [16, 22, 33]. In a previous study, aggressive behavior was displayed, and fighting began immediately [16]. The results of our study showed that mud lobsters exhibited some resource partitioning by reducing the mound basal area and increasing the mound height in places where there were numerous mounds. This strategic behavior of mud lobsters is needed to reduce intraspecific competition, helping them coexist more effectively.

4-3-Future Outlook

To better understand the influence of mangrove prop roots on mud lobster characteristics and their burrowing activities, further studies are needed that take into account the complexity of underground prop root structures, their interactions with mud lobsters, and their functions in mangrove ecosystems.

5- Conclusion

This study is the first to elucidate the influence of factors such as distance from the river edge, soil water moisture, and the presence of tree prop roots on mud lobster (*Thalassina* spp.) population density and mound characteristics, e.g., height and basal area, in the Kampuan mangrove forest in Southern Thailand. Results indicate that mud lobster mound density increases as the distance from the river increases. This may be due to the decreased impacts of the water during high tide, allowing the mud lobsters to build more and higher mounds. However, not only did the water during high tide affect the mound height, but so did soil moisture and the type of vegetation. As soil moisture decreased with an increase in distance from the river (drier soil at 350 m from the river), the mud lobster density and the mound height increased, but the mound basal area decreased. When mud lobster mounds were close to plants with prop roots, the mound heights were significantly higher than those mounds close to plants without prop roots. Also, as the distance increased between the mud lobster mound and the closest plant with prop roots, the mound height significantly decreased, indicating the decreased influence of the prop roots. This study is the first to show the impact of prop roots on mound heights. In addition, mud lobsters exhibited some resource partitioning in terms of conserving space by building higher mounds instead of wider mounds, which may be helpful in reducing intraspecific competition and increasing effective coexistence capabilities.

6- Declarations

6-1-Author Contributions

Conceptualization, K.J.; methodology, K.J., S.D., and M.J.; formal analysis, K.J., S.D., and M.J.; investigation, K.J.; data curation, S.D.; writing—original draft preparation, K.J. and S.D.; writing—review and editing, K.J., P.B., M.J., and E.S.; project administration, K.J.; funding acquisition, K.J. All authors have read and agreed to the published version of the manuscript.

6-2-Data Availability Statement

The data presented in this study are available on request from the corresponding author. Due to confidentiality agreements, supporting data can only be made available to bona fide researchers subject to a non-disclosure agreement. Details of the data and how to request access are available from Assoc. Prof. Dr. Krisanadej Jaroensutasinee, PI at Center of Excellence for Ecoinformatics, Walailak University, Thailand.

6-3-Funding

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6-4-Acknowledgements

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6-5-Institutional Review Board Statement

The animal study protocol was approved by the Walailak University Institutional Animal Care and Use Committee (WU-IACUC), based on the Code of Ethical Practice for the Care and Use of Animals for Scientific Purposes, Institute of Animals for Scientific Purposes Development (IAD), National Research Council of Thailand (NRCT) (protocol code: WU-ACUC-66007 and date of approval: 31 January 2023)." for studies involving animals.

6-6-Informed Consent Statement

Not applicable.

6-7-Conflicts of Interest

The authors declare that there is no conflict of interest regarding the publication of this manuscript. In addition, the ethical issues, including plagiarism, informed consent, misconduct, data fabrication and/or falsification, double publication and/or submission, and redundancies have been completely observed by the authors.

7- References

- [1] Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C. O., & Banta, G. T. (2012). What is bioturbation? the need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series*, 446, 285–302. doi:10.3354/meps09506.
- [2] Guimond, J. A., Seyfferth, A. L., Moffett, K. B., & Michael, H. A. (2020). A physical-biogeochemical mechanism for negative feedback between marsh crabs and carbon storage. *Environmental Research Letters*, 15(3), 34024. doi:10.1088/1748-9326/ab60e2.
- [3] Xiao, K., Wilson, A. M., Li, H., Santos, I. R., Tamborski, J., Smith, E., Lang, S. Q., Zheng, C., Luo, X., Lu, M., & Correa, R. E. (2021). Large CO₂ release and tidal flushing in salt marsh crab burrows reduce the potential for blue carbon sequestration. *Limnology and Oceanography*, 66(1), 14–29. doi:10.1002/lno.11582.
- [4] Xiao, K., Pan, F., Santos, I. R., Zheng, Y., Zheng, C., Chen, N., Lu, Z., Wang, F., Li, Z., & Li, H. (2022). Crab bioturbation drives coupled iron-phosphate-sulfide cycling in mangrove and salt marsh soils. *Geoderma*, 424(2022), 115990. doi:10.1016/j.geoderma.2022.115990.
- [5] Farrell, E. M., Beermann, J., Neumann, A., & Wrede, A. (2023). The interplay of temperature and algal enrichment intensifies bioturbation of the intertidal amphipod *Corophium volutator*. *Journal of Experimental Marine Biology and Ecology*, 559(2023), 151837. doi:10.1016/j.jembe.2022.151837.
- [6] Giorgini, M., de Astarloa, C. D., Esquius, K. S., Miguez, A., Fanjul, E., Escapa, M., & Iribarne, O. (2023). Discriminating the effects of bioturbation and herbivory by the intertidal burrowing crab *Neohelice granulata* on microphytobenthic assemblages of SW Atlantic mudflats. *Journal of Experimental Marine Biology and Ecology*, 567. doi:10.1016/j.jembe.2023.151928.
- [7] Correia, R. R. S., & Guimarães, J. R. D. (2016). Impacts of crab bioturbation and local pollution on sulfate reduction, Hg distribution and methylation in mangrove sediments, Rio de Janeiro, Brazil. *Marine Pollution Bulletin*, 109(1), 453–460. doi:10.1016/j.marpolbul.2016.05.028.
- [8] Braeckman, U., Foshtomi, M. Y., Van Gansbeke, D., Meysman, F., Soetaert, K., Vincx, M., & Vanaverbeke, J. (2014). Variable Importance of Macrofaunal Functional Biodiversity for Biogeochemical Cycling in Temperate Coastal Sediments. *Ecosystems*, 17(4), 720–737. doi:10.1007/s10021-014-9755-7.
- [9] Zhang, W., Wirtz, K., Daewel, U., Wrede, A., Kröncke, I., Kuhn, G., Neumann, A., Meyer, J., Ma, M., & Schrum, C. (2019). The Budget of Macrobenthic Reworked Organic Carbon: A Modeling Case Study of the North Sea. *Journal of Geophysical Research: Biogeosciences*, 124(6), 1446–1471. doi:10.1029/2019JG005109.
- [10] Kristensen, E. (2000). Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia*, 426(1), 1–24. doi:10.1023/A:1003980226194.
- [11] Moh, H. H., & Chong, V. C. (2009). A new species of *Thalassina* (Crustacea: Decapoda: Thalassinidae) From Malaysia. *Raffles Bulletin of Zoology*, 57(2), 465–473. doi:10.5281/zenodo.4509163.
- [12] Ngoc-Ho, N., & de Saint Laurent, M. (2009). The genus *Thalassina* Latreille, 1806 (Crustacea: Thalassinidea: Thalassinidae). *The Raffles Bulletin of Zoology*, 20, 121–158.
- [13] Sakai, K., & Türkay, M. (2012). A review of the species of the genus *Thalassina* (Thalassinidea, Thalassinidae). *Crustaceana*, 85(11), 1339–1376. doi:10.1163/15685403-00003114.
- [14] Lin, F. J., Komai, T., & Chan, T. Y. (2016). A new mud lobster of the genus *Thalassina* Latreille, 1806 (Crustacea: Decapoda: Gebiidea: Thalassinidae) from marine seagrass beds in Dongsha (Pratas) Island, South China Sea. *Raffles Bulletin of Zoology*, 64.
- [15] Ali, M. S., Zulfikar, Saputri, M., & Frias, J. C. (2020). Bioturbation of *Thalassina anomala* and microhabitat in mangrove ecosystem at Sungai Reuleung Leupung Aceh Besar. *Journal of Physics: Conference Series*, 1460(1), 12063. doi:10.1088/1742-6596/1460/1/012063.
- [16] Ngokoed, N., & Ratmuangkhwang, S. (2020). Some biological aspects of mud lobsters, *Thalassina* spp. in Kampuan mangrove forest, Ranong province. *Andaman Coastal Research Station for Development, Faculty of Fisheries, Kasetsart University, Bangkok, Thailand*.

- [17] Johnson, D. S. (1961). The Food and Feeding of the Mud-Lobster, *Thalassina anomala* (Herbst). *Crustaceana*, 2(4), 325–326. doi:10.1163/156854061X00455.
- [18] Vatcharanon, P., & Naiyanetr, P. (1987). Habitat and morphological adaptation of mud lobster *Thalassina anomala* (Herbst, 1804). Proceedings of the 25th Kasetsart University Conference, Fisheries Section 3-5 February, 1987, Bangkok, Thailand.
- [19] Hossain, M. S., Bujang, J. S., Kamal, A. H. M., Zakaria, M. H., & Muslim, A. M. (2019). Behavioural response of the mud lobster, *Thalassina anomala* Herbst, 1804 (Decapoda, Gebiidea), to different trapping devices. *Crustaceana*, 92(3), 353–371. doi:10.1163/15685403-00003869.
- [20] Andriessse, J. P., Van Breemen, N., & Blokhuis, W. A. (1973). The influence of mudlobsters (*Thalassina anomala*) on the development of acid sulphate soils in mangrove swamps in Sarawak (East Malaysia). *Acid sulphate soils. Proceedings of the International Symposium, 13-20 August, 1972, Wageningen, Netherlands.*
- [21] Ashton, E. C., & Macintosh, D. J. (2002). Preliminary assessment of the plant diversity and community ecology of the Sematan mangrove forest, Sarawak, Malaysia. *Forest Ecology and Management*, 166(1–3), 111–129. doi:10.1016/S0378-1127(01)00673-9.
- [22] Dubey, S. K., Choudhury, A., Chand, B. K., & Trivedi, R. K. (2012). Ecobiological study on burrowing mud lobster *Thalassina anomala* (Herbst, 1804) (Decapoda: Thalassinidea) in the intertidal mangrove mudflat of deltaic Sundarbans. *Exploratory Animal and Medical Research*, 2(1), 70-75.
- [23] Havanond, S. (1987). Effects of mud lobsters *Thalassina anomala* Herbst on plant succession in mangrove forests, Thailand. *Bulletin of Marine Science*, 41(2), 635-636.
- [24] Hossain, M. S., Bujang, J. S., & Alam, S. M. R. (2020). Microclimate and distribution of mangrove soil carbon in mud lobster (*Thalassina anomala* Herbst 1804) mounds. *Regional Studies in Marine Science*, 40, 101540. doi:10.1016/j.rsma.2020.101540.
- [25] Dissanayake, N., & Chandrasekara, U. (2014). Effects of Mangrove Zonation and the Physicochemical Parameters of Soil on the Distribution of Macrobenthic Fauna in Kadolkele Mangrove Forest, a Tropical Mangrove Forest in Sri Lanka. *Advances in Ecology*, 2014, 1–13. doi:10.1155/2014/564056.
- [26] Herbst, J. F. W. (1782). *Attempt at a natural history of crabs and crabs: along with a systematic description of their species / by Johann Friedrich Wilhelm Herbst. Gottlieb August Lange, Berlin, Germany.* doi:10.5962/bhl.title.62813.
- [27] Voroney, P. (2019). *Soils for Horse Pasture Management. Horse Pasture Management, 65–79, Academic Press, Cambridge, United States.* doi:10.1016/b978-0-12-812919-7.00004-4.
- [28] Macnae, W. (1969). A General Account of the Fauna and Flora of Mangrove Swamps and Forests in the Indo-West-Pacific Region. *Advances in Marine Biology*, 6(C), 73–270. doi:10.1016/S0065-2881(08)60438-1.
- [29] Stieglitz, T., Ridd, P., & Müller, P. (2000). Passive irrigation and functional morphology of crustacean burrows in a tropical mangrove swamp. *Hydrobiologia*, 421(1), 69–76. doi:10.1023/A:1003925502665.
- [30] Higginbottom, K. B. (1982). Behavioural ecology of the mud crab *Helograpsus haswellianus*: agonistic behaviour and burrow. Honours Thesis. University of Adelaide, Adelaide, Australia.
- [31] Marsh, JA (1982): Aspects of the ecology of three saltmarshes of the Derwent Region and an investigation into the role of the Burrowing Crab *H. haswellianus* (Whitelegge, 1889), BSc (Honours) thesis, University of Tasmania, Hobart.
- [32] Richardson, A. M. M., Swain, R., & Wong, V. (1997). The crustacean and molluscan fauna of Tasmanian saltmarshes. *Papers and Proceedings - Royal Society of Tasmania*, 131, 21–30. doi:10.26749/rstpp.131.21.
- [33] Moh, H. H. (2016). Taxonomy, ecology and control of *Thalassina* mud lobsters on Carey Island and Kelanang shore (Peninsular Malaysia)/Moh Heng Hing. Ph.D. Thesis, University of Malaya, Kuala Lumpur, Malaysia.
- [34] Macintosh, D. J., Ashton, E. C., & Havanon, S. (2002). Mangrove rehabilitation and intertidal biodiversity: A study in the Ranong mangrove ecosystem, Thailand. *Estuarine, Coastal and Shelf Science*, 55(3), 331–345. doi:10.1006/ecss.2001.0896.
- [35] Zou, Y., & van der Ploeg, M. (2012). A study to determine the soil moisture and temperature dynamics. Bachelor Thesis, Wageningen University, Wageningen, Netherlands.
- [36] Moh, H. H., Chong, V. C., & Sasekumar, A. (2015). Distribution and burrow morphology of three sympatric species of *Thalassina* mud lobsters in relation to environmental parameters on a Malayan mangrove shore. *Journal of Sea Research*, 95, 75–83. doi:10.1016/j.seares.2014.10.006.
- [37] Kartika, W. D., & Patria, M. P. (2012). Nest characteristics of mud lobster *Thalassina anomala* (Herbst 1804) in Tanjung Jabung Barat, Jambi, Sumatra, Indonesia.
- [38] Pillai, G. (1989). Environmental factors limiting the distribution of the mangrove lobster (*Thalassina anomala*). *Agricultural Development in the Pacific Islands in the 90's, University of the South Pacific Library, Suva, Fiji.*

- [39] Webb, J. E. (1958). The ecology of Lagos Lagoon I. The lagoons of the Guinea Coast. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 241(683), 307–318. doi:10.1098/rstb.1958.0005.
- [40] Takeda, S., & Kurihara, Y. (1987). The effects of burrowing of *Helice tridens* (De Haan) on the soil of a salt-marsh habitat. *Journal of Experimental Marine Biology and Ecology*, 113(1), 79–89. doi:10.1016/0022-0981(87)90084-0.
- [41] Rudnick, D., Chan, V., & Resh, V. (2005). Morphology and impacts of the burrows of the Chinese mitten crab, *Eriocheir sinensis* H. Milne Edwards (Decapoda, Grapsoidae), in South San Francisco Bay, California, U.S.A. *Crustaceana*, 78(7), 787–807. doi:10.1163/156854005774445500.
- [42] Havanond, S. (2000). Effects of mud lobster (*Thalassina anomala*) mounds on mangrove succession in Thailand. PhD Thesis, Tokyo University of Agriculture, Tokyo, Japan. doi:10.11501/3170840.
- [43] Sasekumar, A. (1974). Distribution of Macrofauna on a Malayan Mangrove Shore. *The Journal of Animal Ecology*, 43(1), 51. doi:10.2307/3157.
- [44] Smith, T. J., Boto, K. G., Frusher, S. D., & Giddins, R. L. (1991). Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. *Estuarine, Coastal and Shelf Science*, 33(5), 419–432. doi:10.1016/0272-7714(91)90081-L.
- [45] Breitfuss, M. J., Connolly, R. M., & Dale, P. E. R. (2004). Densities and aperture sizes of burrows constructed by *Helograpsus haswellianus* (Decapoda: Varunidae) in saltmarshes with and without mosquito-control runnels. *Wetlands*, 24(1), 14–22. doi:10.1672/0277-5212(2004)024[0014:DAASOB]2.0.CO;2.
- [46] Grinang, J. ak, & Rusyaidi Amnah, A. F. (2021). Note on Historical Records, Geographical Distribution, and Ecological Characteristics of a Mud Lobster, *Thalassina anomala* (Herbst, 1804) (Decapoda, Gebiidea, Thalassinidae) in Sarawak, Borneo. *Borneo Journal of Resource Science and Technology*, 11(2), 19–29. doi:10.33736/bjrst.4058.2021.
- [47] Nakamura, T. (1998). Mangrove succession and mud lobster mounds in Ranong, Thailand. *Phuket Marine Biological Center Special Publication*, 20, 21–36.
- [48] Kiruba-Sankar, R., Krishnan, P., Dam Roy, S., Raymond Jani Angel, J., Goutham-Bharathi, M. P., Lohith Kumar, K., Ragavan, P., Kaliyamoorthy, M., Muruganandam, R., Rajakumari, S., Purvaja, R., & Ramesh, R. (2018). Structural complexity and tree species composition of mangrove forests of the Andaman Islands, India. *Journal of Coastal Conservation*, 22(2), 217–234. doi:10.1007/s11852-017-0588-3.
- [49] Tomiczek, T., Wargula, A., Lomónaco, P., Goodwin, S., Cox, D., Kennedy, A., & Lynett, P. (2020). Physical model investigation of mid-scale mangrove effects on flow hydrodynamics and pressures and loads in the built environment. *Coastal Engineering*, 162. doi:10.1016/j.coastaleng.2020.103791.
- [50] Nozarpour, R., Shojaei, M. G., Naderloo, R., & Nasi, F. (2023). Crustaceans functional diversity in mangroves and adjacent mudflats of the Persian Gulf and Gulf of Oman. *Marine Environmental Research*, 186, 105919. doi:10.1016/j.marenvres.2023.105919.
- [51] Katrak, G., Dittmann, S., & Seuront, L. (2008). Spatial variation in burrow morphology of the mud shore crab *Helograpsus haswellianus* (Brachyura, Grapsidae) in South Australian saltmarshes. *Marine and Freshwater Research*, 59(10), 902–911. doi:10.1071/MF08044.
- [52] Bertness, M. D., & Miller, T. (1984). The distribution and dynamics of *Uca pugnax* (Smith) burrows in a New England salt marsh. *Journal of Experimental Marine Biology and Ecology*, 83(3), 211–237. doi:10.1016/S0022-0981(84)80002-7.