



Substrate Complexity Drives Hermit Crab (Diogenidae) Diversity and Ecological Flexibility Across Sand, Rubble, and Coral Habitats in Tarahan Island, Indonesia

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ABSTRACT

Research on the role of benthic substrates in shaping hermit crab communities along coastlines remains relatively limited, despite the important role this group plays in coastal benthic ecosystems. This study conducted in April 2025, aimed to examine the relationship between substrate characteristics sand, coral rubble, and coral reefs and the distribution and community structure of hermit crabs of the family Diogenidae along the northwestern coast of Tarahan Island, Indonesia. A total of 58 individuals consisting of 9 hermit crab species were identified across the three habitat types, with the highest species richness and abundance found in the rubble habitat, which exhibited high porosity and microhabitat heterogeneity. Community analysis using ANOSIMS showed R value of -0.002 and a p-value of 0.48 revealed an overlap in species composition among habitat types however, SIMPER analysis certain species such as *Clibanarius striolatus* consistently dominated habitats with high structural complexity, while others like *Clibanarius signatus* showed a specific preference for coral-sand habitats. This variation in habitat preference reflects a spectrum of ecological strategies, ranging from specialists to generalists, within the hermit crab community studied. The findings highlight the importance of substrate diversity and integrity in supporting the ecological flexibility, stability, and sustainability of hermit crab communities in dynamic coastal ecosystems.

Introduction

Hermit crabs play a crucial ecological role in coastal ecosystems, particularly along beaches and mangrove areas (Barnes, 2001; Fitriani *et al.*, 2024). As detritivores and omnivores, hermit crabs significantly contribute to the decomposition of organic matter, including dead organisms and plant debris, thereby accelerating nutrient recycling in coastal environments (Laidre *et al.*, 2015). Their feeding activity helps maintain substrate and water quality (Fitriani *et al.*, 2024), while also sustaining energy flow in the food chain (Alcaraz and García-Cabello, 2017; Teoh and Chong, 2015). Furthermore, hermit crabs serve as indicators of environmental health, as changes in their

distribution and population abundance can reflect ongoing ecosystem conditions caused by either anthropogenic pressure or natural changes (Sogabe and Takatsuji, 2021; Zhao *et al.*, 2024). Hermit crabs also support biodiversity by acting as prey for birds, fish, and small mammals. Moreover, their use of empty gastropod shells contributes to the dynamics of other shell-utilizing organisms (Lima *et al.*, 2018; Nott and Nicolaidou, 1994; Zhao *et al.*, 2024). Thus, hermit crabs are a key component in maintaining the balance and stability of coastal ecosystems that play an important role in maintaining the ecological function of coastal ecosystems by recycling nutrients through the decomposition of organic matter, improving sediment and water quality,

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supporting food webs and their population trends serve as indicators of environmental health, detecting human impacts or natural shifts.

Tarahan Island is a coastal region featuring diverse substrate types, including sandy flats, coral rubble, and various coral reef formations. Substrate diversity and microhabitat availability in this area are key factors shaping benthic macrofaunal communities, including hermit crabs (Fantucci *et al.*, 2009; Leite *et al.*, 1998). The substrate plays an important role in determining species richness and abundance. The presence of crevices or shelters within the substrate provides both refuge and foraging areas for crustaceans, particularly hermit crabs (Atmaja *et al.*, 2023). Such shelters are commonly found in sandy and muddy habitats (Teoh and Chong, 2015), especially for species such as *Pagurus maclaughlinae*, *Pagurus longicarpus*, *Pagurus pollicaris* (Strasser and Price, 1999), and *Diogenes nitidimanus* (Asakura, 1991). These substrate types facilitate movement for feeding and protection from currents and waves. In contrast, movement on coral substrates tends to be limited due to narrow crevices that restrict hermit crab mobility (Benvenuto *et al.*, 2003; Teoh and Chong, 2015).

Previous studies from Bama and Kajang Beaches, reported Diogenidae dominance in complex substrates (Muzaki and Rifsanjani, 2019), and a study from Serangan Island, Bali, identifying *Clibanarius infraspinus* as a generalist species in the intertidal zone (Sinamo *et al.*, 2020).

Considering the essential role of hermit crabs in maintaining coastal ecosystem balance and the influence of substrate variation on their distribution and community structure, this study of hermit crab communities on Tarahan Island is highly important. This research specifically aims to analyze the relationship between substrate characteristics as microhabitats and hermit crab community structure in the region, while providing a scientific foundation for sustainable coastal policy in understudied tropical regions.

Research Methods

Time and Sampling Sites

This research was conducted in April 2025 along the northwestern coast of Tarahan Island, Banten, Indonesia. The study area covered three habitat types: sand, coral rubble, and coral reef.

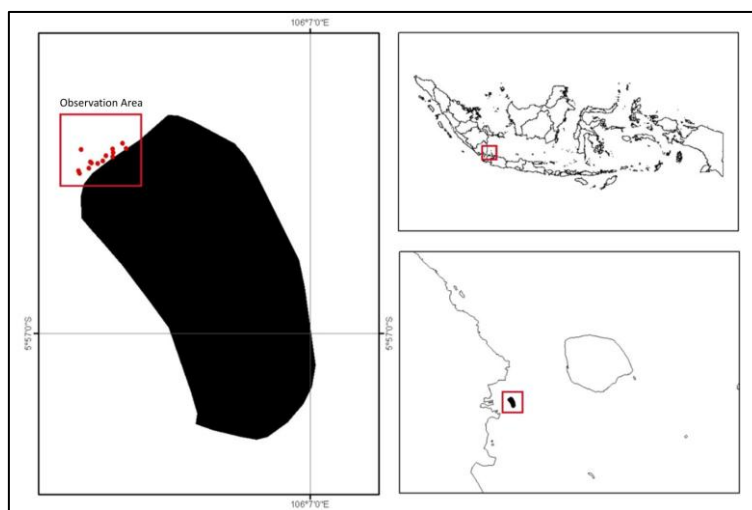


Figure 1. Location of Research (Tarahan Island, Banten, Indonesia)

Hermit Crab Sampling Method

Hermit crabs were collected using direct hand-picking methods based on purposive sampling (Gilchrist and Abele, 1984; Strasser and Price, 1999). Systematic searches were conducted across the intertidal to shallow subtidal zones to locate individuals. Each specimen encountered was recorded and documented, including habitat type. Sampling was performed within an imaginary 50 × 50 cm area, followed by photography and identification, with five replicates per session.

Documentation and Identification Procedures

A total of 58 individual hermit crab specimens collected from three habitat types: sand, coral rubble, and coral reef were documented in the laboratory following standard procedures. To minimize movement during documentation, each hermit crab was placed in a clean petri dish. Specimens measuring 3–7 cm were photographed using a digital camera with a macro lens and additional lighting. Each specimen was photographed outside its shell against a black

cloth background to highlight morphological details. The identification process referred to relevant identification keys and taxonomic literature, including the primary reference book *Crustacea: Guide of the World* (Debelius, 2001).

Data Analysis

Data analysis in this study integrated multivariate statistical techniques to test structural differences in hermit crab communities across habitats. The analytical framework was built on modern quantitative ecological paradigms, combining visual exploration, ecological ordination, and comparative hypothesis testing. The analysis was implemented using R Studio (v4.3.2) and the vegan package (v2.6-4) (Oksanen *et al.*, 2013), which is effective for biodiversity analysis.

Species abundance data were analyzed in stages to comprehensively evaluate distribution patterns and community structure. Initial visualization was performed using boxplots to show species abundance distributions across habitats (McGill *et al.*, 1978). Non-metric Multidimensional Scaling (NMDS) based on Bray-Curtis distance was used to represent ecological relationships among samples in low-dimensional space (Oksanen *et al.*, 2013). Community composition differences were tested using Analysis of Similarities (ANOSIM) (Clarke *et al.*, 2016), with the Global R value indicating the strength of community differences and a significance level ($P < 0.05$) confirming non-random differences (Somerfield *et al.*, 2021). The Similarity Percentage (SIMPER) analysis identified species contributing most to community dissimilarity across habitats and calculated each species' relative contribution to cumulative differences (Clarke, 1993). This integration of analytical methods enabled a thorough interpretation of hermit crab community structure in terms of spatial distribution patterns and species-specific contributions across habitat types.

Results

Species Distribution of Diogenidae Hermit Crabs in Various Habitat Types on Tarahan Island

The species composition of Diogenidae hermit crabs across the three coastal habitats of Tarahan Island sand, rubble, and coral revealed complex distribution patterns with species-specific habitat preferences. Nine species were identified, with the rubble habitat showing the highest richness (7

species), followed by coral (5 species) and sand (5 species) Table 1.

Table 1. Species Distribution of the Family *Diogenidae* in Sand, Rubble, and Coral Habitats

Species	Habitat		
	Sand	Rubble	Coral
<i>Clibanarius taeniatus</i>	+	+	+
<i>Clibanarius signatus</i>	+	+	-
<i>Clibanarius englaucus</i>	+	+	+
<i>Clibanarius striolatus</i>	-	+	+
<i>Clibanarius merguensis</i>	+	+	-
<i>Clibanarius vittatus</i>	+	+	+
<i>Clibanarius longitarsus</i>	+	+	-
<i>Clibanarius erythropus</i>	-	-	+
<i>Dardanus woodmasoni</i>	-	-	+

Note : (-) Absent, (+) Present

ANOSIM analysis showed significant differences in hermit crab abundance were observed among the three habitat types: coral, rubble, and sand, with $p < 0.05$. The rubble habitat recorded the highest abundance (5–8 individuals), followed by sand (1–5 individuals), and coral (1–4 individuals) Figure 2. These results challenge the common assumption that coral habitats are always the most productive zones, indicating the influence of more complex ecological factors beyond physical habitat structure (Barnes, 1997).

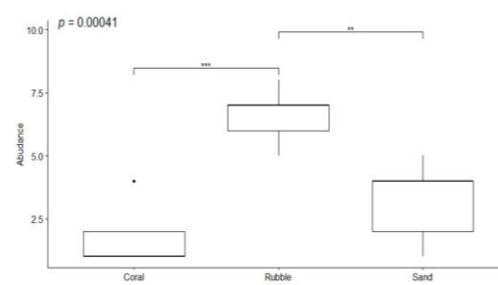


Figure 1. Abundance of hermit crabs on (a) sand, (b) rubble, and (c) coral on Tarahan Island

The abundance of hermit crabs on Tarahan Island was highest in the rubble habitat, ranging from 5–8 individuals, followed by sand (1–5 individuals) and coral (1–4 individuals).

Hermit Crab Community Structure on Tarahan Island

The hermit crab communities in sand, rubble, and coral habitats on Tarahan Island exhibited overlapping distribution patterns, indicating high species composition similarity among the three

habitat types [Figure 3](#). This was supported by ANOSIM analysis, which produced an R value of -0.002 and a p-value of 0.48, suggesting no significant differences in community structure across habitats. Based on these results, it can be seen that habitat characteristics do not affect the composition of hermit crab species.

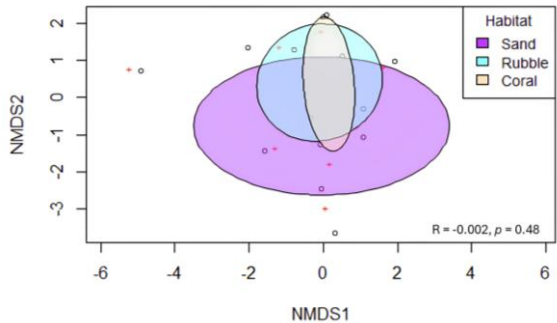


Figure 2. Distribution Pattern of Hermit Crab Community in Various Habitat Types Based on NMDS Analysis on Tarahan Island

SIMPER analysis confirmed heterogeneous species responses to different habitat characteristics. *Clibanarius striolatus* consistently dominated structurally complex habitats (coral-rubble and rubble-sand), while *Clibanarius signatus* showed a specific preference for coral-sand habitats. Variations in significance levels (0.01 to 0.72) reflect a spectrum of habitat preferences, from highly specialized to generalist strategies. These findings support the hypothesis that the hermit crab community at the study site exhibits high ecological flexibility, with some species showing specific habitat preferences while others are generalists.

Table 1. SIMPER Analysis (C= Contribution, CC= Cumulative Contribution, *p* = significant)

Species	C	CC	P
Coral >< Rubble			
<i>Clibanarius striolatus</i>	0.32	0.34	0.04*
<i>Clibanarius englaucus</i>	0.23	0.59	0.27
<i>Clibanarius longitarsus</i>	0.12	0.73	0.54
Coral >< Sand			
<i>Clibanarius signatus</i>	0.17	0.18	0.01*
<i>Clibanarius englaucus</i>	0.17	0.37	0.72
<i>Clibanarius taeniatus</i>	0.11	0.48	0.20
Rubble >< Sand			
<i>Clibanarius striolatus</i>	0.27	0.31	0.26
<i>Clibanarius englaucus</i>	0.20	0.55	0.44
<i>Clibanarius longitarsus</i>	0.12	0.69	0.41

Note : *Significantly different

Discussion

Distribution and Abundance Patterns Relative to Habitat Characteristics

The distribution of Diogenidae species on Tarahan Island strongly correlates with the physical complexity of the substrate. Rubble habitats, with high porosity and microhabitat heterogeneity ([Barnes, 1997](#); [Turra & Denadai, 2002](#)), supported seven species, including *Clibanarius striolatus* and *Clibanarius merguiensis*, which were absent from sandy habitats. These characteristics provide protection from predation and environmental fluctuations while enhancing feeding efficiency and shell acquisition ([Teoh et al., 2014](#)). Similar studies in Bama and Kajang Beaches reported Diogenidae dominance in complex substrates enriched with seagrass and organic debris, which create ideal conditions for hermit crab activities ([Muzaki and Rifsanjani, 2019](#)).

The abundance of hermit crab on Tarahan Island indicate a higher abundance compared to studies conducted at Sindangkerta Beach, West Java (1–2 individuals) ([Permana et al., 2018](#)), and Lhokseumawe, Aceh (1–5 individuals) ([Fitriani et al., 2024](#)). However, these findings are still lower than those recorded at Leuweung Sancang Beach, Garut Regency, which reported a density of up to 15.73 individuals/m² ([Fau et al., 2023](#)).

The highest abundance in rubble habitats (5–8 individuals) contradicts traditional expectations about coral ecosystem productivity. The analysis revealed that rubble not only offers shelter but also acts as a dynamic "shell bank" due to the accumulation of dead coral fragments—ideal substrates for mollusc ([Turra and Denadai, 2002](#)). The availability of empty shells reduces intraspecific competition, enabling more stable population densities compared to sand or coral habitats ([Barnes, 1997](#)). Conversely, coral habitats are limited by predation pressure from reef fish and the scarcity of suitable shells ([Abrams, 1980](#); [Tran et al., 2014](#)).

Hermit Crab Community Structure

ANOSIM analysis with R = -0.002 (*p* = 0.48) indicates no significant differences in hermit crab community structure across the three habitat types (sand, rubble, and coral). The near-zero negative R value highlights the high overlap in species composition, as visualized through NMDS ([Figure 4](#)). This aligns with ecological theory suggesting that communities with high homogeneity tend to show ecological flexibility and adaptability to environmental variation ([Chapman and Underwood, 1999](#)). The homogeneous environment and high

mobility of hermit crabs allow them to move between habitats without showing strong preferences (Teoh and Chong, 2015).

SIMPER analysis revealed heterogeneity in hermit crab species responses to habitat variation. *Clibanarius striolatus* consistently dominated structurally complex habitats such as coral-rubble and rubble-sand, indicating adaptation to coarse substrates and structural crevices that offer protection and abundant resources (Malay *et al.*, 2018). On the other hand, *Clibanarius signatus* exhibited a more specific preference for coral-sand habitats, reflecting a higher degree of specialization (Clarke and Warwick, 1994). The variability in significance levels (from 0.01 to 0.72) indicates a spectrum of habitat preferences ranging from high specialization to generalization, suggesting high ecological flexibility among hermit crab communities at the study site (Barnes, 1997). Some species depend on specific habitat characteristics, while others can broadly adapt to various substrate conditions. These findings align with theories of hermit crab ecological diversity and flexibility, allowing them to optimize resource use across different habitats depending on availability and environmental pressures (Teoh *et al.*, 2014). Additionally, this heterogeneity supports the concept that hermit crab communities are dynamic and capable of adapting to habitat variation, which is a crucial survival strategy in diverse and changing environments (Lee, 2018). Thus, the analysis reinforces the understanding that hermit crab communities exhibit high ecological flexibility, with some species having specific habitat preferences while others are generalists, enabling survival and growth across varying habitat conditions.

Conclusion

This study demonstrates that the complexity and characteristics of the benthic substrate play a crucial role in shaping the distribution and community structure of hermit crabs in coastal areas. The highest abundance in rubble habitats showed habitats with higher physical heterogeneity and porosity support greater species richness and abundance. Hermit crab adaptations to microhabitat variation are reflected in species capable of utilizing various substrate types, while others show specific habitat preferences, resulting in dynamic and flexible communities in response to environmental changes. These findings highlight the importance of maintaining substrate diversity and integrity as key factors for sustaining the stability and resilience of hermit crab communities in dynamic coastal

ecosystems. Consequently, conservation and coastal habitat management efforts should prioritize the protection of structurally complex substrates, including rubble zones, to preserve biodiversity and ecological functions in benthic communities. Future studies should explore long-term responses of hermit crab populations to habitat degradation and climate-induced changes, as well as assess the role of substrate restoration in enhancing benthic community resilience.

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