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First Report on the Proliferation of Vermetid Gastropods in Southeast Sulawesi: Synergistic Effects of Nickel Mining Sedimentation and Destructive Fishing on Coral Reef Degradation

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ABSTRACT

Coral reef ecosystems in Southeast Sulawesi, particularly in Pomalaa, face dual anthropogenic pressures: massive sedimentation from nickel mining overburden and physical destruction from blast fishing. This study presents the first report on the anomalous proliferation of vermetid snails in nickel-impacted areas and investigates the environmental drivers behind this community shift. We assessed gastropod community structures and physicochemical parameters across a spatial gradient, ranging from high-impact mining and fishing zones to relatively undisturbed reference sites. Our findings reveal a significant phase-shift characterized by a massive abundance of vermetid snails in degraded zones. The synergistic effect of overburden-induced "smothering and clogging" and the structural collapse caused by destructive fishing has cleared vast areas of live coral cover, providing vacant, opportunistic substrates for vermetid colonization. In these high-turbidity environments, vermetids exhibit high resilience, whereas their natural competitors and predators are largely absent. Conversely, reference sites with high coral rugosity and low sediment stress show significantly lower vermetid density. This "local defaunation" of corals and the subsequent dominance of vermetids serve as a critical bioindicator of severe ecosystem stress. This study underscores the urgent need for integrated coastal management to address the compounding impacts of terrestrial mining runoff and illegal fishing practices in Indonesia's marine biodiversity hotspots.

Keywords: Ecological phase-shift, Local defaunation, Coral reef degradation, Opportunistic colonization

1. Introduction

Coral reef ecosystems in the Indo-Pacific region, particularly within the waters of Southeast Sulawesi, are currently in a critical state due to the convergence of various chronic and acute anthropogenic stressors (Hughes et al., 2003; Burke et al., 2012; Pelasula et al., 2025). One of the epicenters of this degradation is located in the coastal waters of Pomalaa, Kolaka Regency, where large-scale nickel mining activities have fundamentally altered the marine ecosystem landscape through the uncontrolled discharge and runoff of overburden material (Wulandari et al., 2022; Pelasula et al., 2025). This lateritic overburden, rich in iron oxides and heavy metal residues, enters the water column and creates a sediment load that exceeds the biological tolerance thresholds of coral organisms (Fabricius, 2005; Gillmore et al., 2020; Shah, 2021). This massive sedimentation process triggers a dual damage

mechanism known as "smothering" (physical burial of living tissue) and "clogging" (blockage of feeding and respiratory apparatuses), which collectively cause mass mortality in scleractinian corals (Rogers, 1990; Erftemeijer et al., 2012; Zill et al., 2017).

Simultaneously, these chemically stressed ecosystems must contend with destructive mechanical disturbances from blast fishing activities, which remain prevalent (Fox & Caldwell, 2006; Nurdin et al., 2021; Pelasula et al., 2025). The use of explosives instantaneously shatters the complex three-dimensional reef architecture built over centuries into flat, unstable expanses of coral rubble (Knowlton et al., 2021; Lamont et al., 2025; Samudra et al., 2025). The synergy between mining sediment pollution and physical destruction has created extreme environments that trigger local defaunation across most sensitive marine taxa (Jackson et al., 2001; Fabricius, 2005; Pelasula et al., 2025).

However, amidst this widespread ecological collapse, an anomalous biological phenomenon has emerged, previously undocumented in this region, which we present as a "First Report" from Southeast Sulawesi (Shima et al., 2010; Phillips et al., 2014; Pelasula et al., 2025). Paradoxically, the areas experiencing the most severe degradation exhibit an extraordinary population explosion of vermetid tube snails (Gastropoda: Vermetidae) (Shima et al., 2013; Brown & Osenberg, 2018; Zill et al., 2017). These sessile organisms, typically found solitarily and in limited numbers on healthy reefs, now form massive colonies that nearly cover the entire surface of dead substrates (Safriel, 1975; Phillips et al., 2014; Shima et al., 2025). This uncontrolled vermetid proliferation indicates a highly concerning ecological phase-shift, where natural coral reef succession has been hijacked by opportunistic species (Done, 1992; Bellwood et al., 2004; Shima et al., 2025).

This phenomenon raises fundamental questions regarding the biological mechanisms that allow vermetids not only to survive but to dominate environments containing abrasive and toxic nickel sediments (Gillmore et al., 2020; Shah, 2021; Shima et al., 2025). Therefore, this study underscores the importance of understanding the interaction between blast fishing remnants as space providers and mining sedimentation as a natural selection agent favoring vermetids (Fox & Caldwell, 2006; Zill et al., 2017; Lamont et al., 2025). Through this research, we aim to reveal how severe environmental degradation in Pomalaa has created a new ecological niche exclusively occupied by these tube gastropods, which in turn serves as a visual indicator of the total failure of natural reef recovery systems (Shima et al., 2010; Erftemeijer et al., 2012; Pelasula et al., 2025).

2. Methods

2.1. Study Site and Habitat Categorization

This research was conducted in the coastal waters of Pomalaa, Southeast Sulawesi, from October 2025 to February 2026, targeting areas confirmed to have undergone chronic degradation due to nickel mining overburden accumulation and destructive fishing activities (Wulandari et al., 2022; Pelasula et al., 2025). Observation stations were categorized into two primary environmental regimes to compare the biological responses of gastropods across an anthropogenic pressure gradient (Done, 1992; Jackson et al., 2001; Pelasula et al., 2025).

- Degraded Reef Matrix (DRM): Sites exhibiting substrate coverage by nickel silt (sedimentation) >60% and extensive coral rubble fields resulting from blast fishing (Fox & Caldwell, 2006; Erftemeijer et al., 2012; Samudra et al., 2025).



Figure 1. Visual Profile of the Degraded Reef Matrix (DRM) in the Pomalaa Coastal Area. The image illustrates an ecosystem undergoing massive structural degradation characterized by extensive coral rubble from blast fishing activities, exacerbated by nickel silt (overburden) coverage on the substrate surface exceeding 60% **(Source: Doc. Risfandi & Sudarno, 2025)**.

- Comparative Reference Site (CRS): Areas with intact reef architecture and minimal terrestrial sediment accumulation, used to establish the baseline community structure of benthic gastropods **(Rogers, 1990; Fabricius, 2005; Pelasula et al., 2025)**.



Figure 2. Visual Profile of the Comparative Reference Site (CRS) in Kolaka Coastal Waters. The photograph depicts an ecosystem with intact reef architecture, high three-dimensional structural complexity, and minimal terrestrial sediment accumulation, serving as a baseline for determining gastropod community structure under optimal environmental conditions **(Source: Doc. Risfandi & Sudarno, 2025)**.

2.2. Specification and Characterization of Study Object: Family Vermetidae

The primary biological object in this study is the sessile gastropod from the family Vermetidae (Rafinesque, 1815), morphologically characterized by irregular calcium carbonate tubular shells permanently cemented to hard substrates (Safriel, 1975; Shima et al., 2010; Phillips et al., 2014). Target species were identified based on specific taxonomic attributes, including aperture diameter, deconsolidated helical growth patterns, and the presence of an operculum serving as a mechanical defense mechanism (Safriel, 1975; Kappner et al., 2000; Shima et al., 2025). Unlike mobile gastropods, vermetids in the Pomalaa ecosystem act as ecosystem engineers capable of altering reef topography through the formation of massive aggregations or biogenic crusts in areas that have undergone physical and geochemical degradation (Shima et al., 2013; Zill et al., 2017; Brown & Osenberg, 2018).

This study focused on the adaptive behavior of vermetids toward extreme environmental stress through mucus net feeding mechanisms (Kappner et al., 2000; Ribak et al., 2005; Zill et al., 2017). This apparatus allows the study objects to exploit suspended organic particles (seston) and detrital material in waters with high nickel sediment loads a functional advantage providing metabolic resilience compared to scleractinian corals (Fabricius, 2005; Bissett et al., 2020; Shima et al., 2025). Ecologically, vermetid snails in this study are positioned as bioindicators of phase-shifts, where their presence on dead substrates is quantified to map the extent to which natural coral reef succession has been disrupted by anthropogenic activities (Done, 1992; Bellwood et al., 2004; Pelasula et al., 2025).

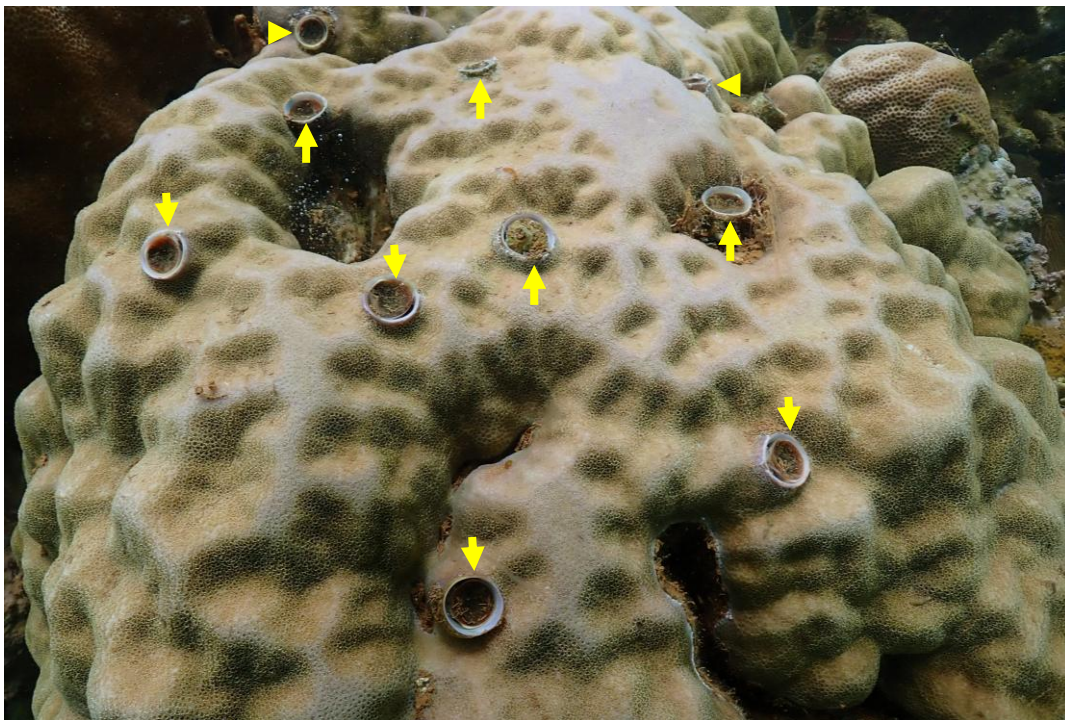


Figure 3. Colonization of vermetid tube snails on the surface of massive coral colonies under environmental stress. The image illustrates several vermetid opercula protruding above the coral surface, which is increasingly obscured by a layer of fine sediment (Source: Doc. Risfandi & Sudarno, 2025).

2.3. Quantitative Mapping of Vermetid Proliferation

To investigate how vermetid snails exploit these degraded habitats, high-resolution benthic censuses were conducted using the Multi-scale Quadrat technique (Lechene et al., 2019; Pelasula et al., 2025; Shima et al., 2025).

- The transect protocol involved three 50-meter lines deployed parallel to the shoreline at a depth of 5 meters to ensure accurate spatial representation (Giyanto & Soedarma, 2010; Nurdin et al., 2015; Pelasula et al., 2025).
- Quadrat sampling used 0.5 x 0.5 m² frames (n=10 per transect), focusing on "secondary substrates" such as dead coral skeletons and rubble fragments covered by nickel sediment (Fox & Caldwell, 2006; Zill et al., 2017; Samudra et al., 2025).
- Physical removal of fine sediment layers was performed manually using soft brushes to ensure that vermetid tube shells attached to the underlying substrate could be counted with high precision (Erftemeijer et al., 2012; Zill et al., 2017; Pelasula et al., 2025).

2.4. Assessment of Structural and Substrate Damage

This study measured existing physical damage using the Point Intercept Transect (PIT) method at 0.5-meter intervals to obtain detailed benthic composition data (Ivkić et al., 2023; Pelasula et al., 2025; Samudra et al., 2025).

- Smothering levels were recorded as the percentage of benthos covered by fine reddish lateritic sediment (a direct indicator of nickel overburden pollution) (Fabricius, 2005; Erftemeijer et al., 2012; Gillmore et al., 2020).
- Mechanical damage was quantified through the ratio of coral rubble to consolidated reef framework to assess the historical impact of blast fishing (Fox & Caldwell, 2006; Knowlton et al., 2021; Lamont et al., 2025).
- Niche availability was measured based on the surface area of dead coral not yet fully buried, serving as the primary habitat for vermetid colonization (Phillips et al., 2014; Zill et al., 2017; Shima et al., 2025).

2.5. Biological Indicators and Community Metrics

For each vermetid cluster found, population density was calculated as the number of individuals per square meter (ind/m²) to determine proliferation levels (Shima et al., 2010; Zill et al., 2017; Pelasula et al., 2025).

- Aggregation patterns were analyzed to determine if vermetids formed "biogenic mats" in response to the loss of living coral competitors (Safriel, 1975; Brown & Osenberg, 2018; Shima et al., 2025).
- Gastropod diversity was assessed using the Shannon-Wiener Index (H') and Evenness (J') to evaluate the correlation between vermetid dominance and the loss of other gastropod functional groups in degraded areas (Jackson et al., 2001; Pelasula et al., 2025; Shima et al., 2025).

2.6. Statistical Analysis

Statistical analyses were performed to evaluate the significance of habitat type on vermetid snail abundance using parametric One-Way Analysis of Variance (ANOVA) (Lechene et al., 2019; Pelasula et al., 2025; Shima et al., 2025). Non-parametric Kruskal-Wallis procedures followed by Dunn's post-hoc tests were applied if normality assumptions were not met (Giyanto & Soedarma, 2010; Pelasula et al., 2025; Shima et al., 2025). Redundancy Analysis (RDA) modeling was implemented to dissect complex interactions between

sediment coverage intensity, overburden thickness, and rubble density against vermetid population fluctuations (Rice et al., 2019; Pelasula et al., 2025; Shima et al., 2025). RDA ordination and Principal Component Analysis (PCA) were used to visualize the grouping of observation sites based on environmental degradation profiles (Rice et al., 2019; Pelasula et al., 2025; Shima et al., 2025).

3. Results

3.1. Comparative Analysis of Vermetid Population Structure: From Solitary Distribution to Massive Biogenic Crusts

Comparative analysis between the Comparative Reference Site (CRS) and the Degraded Reef Matrix (DRM) reveals a significant ecological dichotomy in the colonization patterns of sessile gastropods in Pomalaa waters. In the CRS ecosystem, the intact reef architecture creates a highly competitive environment that limits niche availability for opportunistic species. With terrestrial sediment accumulation at basal levels, scleractinian corals maintain spatial dominance, resulting in vermetid populations being found only in solitary distribution patterns with extremely low densities. This ecological stability is statistically confirmed by the position of the Reference Site (RS) cluster in the Redundancy Analysis (RDA) ordination (Figure 9), which projects diametrically opposite to all anthropogenic pressure vectors.

An extreme contrast was observed in the Degraded Reef Matrix (DRM), where an ecological phase-shift has occurred from coral-dominated communities to a near-monoculture of vermetids. Environmental conditions characterized by nickel silt coverage >60% (Smothering) and extensive rubble accumulation act as catalysts for exponential vermetid proliferation. In these areas, vermetid individuals are no longer solitary but form massive aggregations in the form of biogenic crusts covering dead substrates. This population outbreak is validated by a very strong linear correlation on the primary RDA axis, explicitly linking vermetid density with Total Suspended Solids (TSS) intensity, overburden thickness, and mechanical damage from blast fishing.

Functionally, the transition from the solitary patterns shown in Figure 5 to the massive colonization in Figure 4 represents a loss of ecosystem resilience and a drastic simplification of biodiversity. While the radar profile (Figure 6) indicates that the CRS site maintains high Gastropod Diversity (H') and live coral cover, the DRM area exhibits peaks in Vermetid Density and Abiotic Substrate variables. Thus, this comparison provides empirical evidence that vermetid snails in this region serve as specific indicators of chronic habitat degradation triggered by mining activities and destructive fishing.

Ecosystem conditions in zones with extreme anthropogenic disturbance show significant structural transformations, identified in this study as the Degraded Reef Matrix (DRM). The primary characteristic of this matrix is the loss of reef architectural complexity due to the destructive synergy between post-blast fishing mechanical damage and massive nickel sediment deposition. Data indicate that in these areas, nickel silt accumulation (overburden) has reached a critical threshold exceeding 60%, effectively killing scleractinian coral tissues through smothering mechanisms. This phenomenon creates functional vacant spaces subsequently exploited by opportunistic organisms. As visualized in Figure 4, such environmental degradation facilitates the sole dominance of sessile gastropods capable of adapting to high-turbidity conditions.



Figure 4. Massive colonization of vermetid tube snails on the Degraded Reef Matrix (DRM). The photograph illustrates the dominance of vermetids on a substrate subjected to synergistic disturbances: nickel silt accumulation (sedimentation >60%) and extensive coral rubble resulting from blast fishing activities (**Source: Doc. Risfandi & Sudarno, 2025**).

Visualizations in Figure 4 confirm an ecological phase-shift from healthy coral communities to the dominance of vermetid biogenic crusts. This massive colonization aligns with the Redundancy Analysis (RDA) results, where vermetid density shows a very strong positive correlation ($RDA1 = 94\%$) with Smothering and Rubble vectors. The dense distribution of vermetid opercula over sediment layers proves the ability of this taxa to maintain feeding activities via mucus nets despite being in environments with extreme Total Suspended Solids (TSS) loads. This condition stands in stark contrast to the Comparative

Reference Site (CRS), where gastropod diversity remains high (H') and vermetid density is at basal levels due to the dominance of intact live coral cover. Thus, Figure 4 serves as empirical evidence that the degraded reef matrix in Pomalaa has reached a disturbance saturation point that favors exponential vermetid proliferation.

Optimal ecosystem conditions are represented by the Comparative Reference Site (CRS), which serves as the baseline standard for gastropod community structure and coral reef health in Pomalaa waters. Fundamentally different from the impacted areas, this site is characterized by intact reef architecture with high Live Coral Cover dominance and preserved three-dimensional structural complexity. Anthropogenic pressure in this area is at minimal levels, where terrestrial sediment accumulation and smothering indicators do not show significant values for coral growth inhibition. In this stable environment, biological interactions are balanced, preventing the dominance of specific opportunistic species. As shown in Figure 5, the community profile at the reference site displays biota naturally dispersed without invasive biogenic crust formations.



Figure 5. Solitary distribution of vermetid tube snails at the Comparative Reference Site (CRS). The photograph displays a very low vermetid density, characterized by scattered individuals on healthy, live coral colonies. The reef architecture remains intact with minimal terrestrial sediment accumulation (**Source: Doc. Risfandi & Sudarno, 2025**).

Visualizations in Figure 5 confirm that under healthy environmental conditions, vermetid snail density is found at very low basal levels with a solitary distribution pattern. The low vermetid population at the CRS site aligns with the Redundancy Analysis (RDA) results, where reference stations (green cluster) are positioned opposite to all anthropogenic stressor

vectors such as Smothering, TSS, and Rubble. The absence of significant nickel sediment material allows scleractinian corals to maintain spatial dominance, thereby limiting ecological niches for massive vermetid colonization. Furthermore, the high Gastropod Diversity Index (H') in this zone indicates that habitat niches are occupied by various functional taxa, contrasting sharply with the Degraded Reef Matrix (DRM) which has undergone community simplification. These data collectively prove that without extreme physical and geochemical disturbances, vermetid populations will not reach an outbreak phase, making them highly accurate indicators of environmental degradation in coastal regions.

3.2. Multivariate Integration: Significance of Correlation between Environmental Stressors and Ecosystem Bio-Profile Shifts

Quantitative data in Table 1 and the relative profile visualization in Figure 6 reveal a linear and contrasting degradation gradient across all observation sites. The High-Impact Zone (HIZ) shows extreme values across all physicochemical degradation indicators, with the Smothering Index reaching 3.8 ± 0.2 and Total Suspended Solids (TSS) loads of 92.4 ± 15.6 mg/dL, directly correlating with a drastic reduction in live coral cover to only $4.2 \pm 1.8\%$. This distorted environmental condition triggers a biological response in the form of a vermetid population explosion with densities reaching 212 ± 28 ind/m², forming invasive biogenic crust aggregations. Conversely, the Reference Site (RS) maintains a stable ecosystem profile with live coral cover dominance ($74.8 \pm 5.6\%$) and high gastropod diversity (H') of 2.85 ± 0.35 . The absence of nickel sediment (overburden) at this site limits vermetid proliferation, which is found only in solitary patterns with a basal density of 4 ± 2 ind/m². The magnitude differences in Figure 6 confirm that Turbidity, Smothering, and Coral Rubble are the primary determinants controlling benthic gastropod community structure in Pomalaa waters.

The Moderate-Impact Zone (MIZ) positions itself as a transition zone, where environmental parameters such as TSS (28.7 ± 5.4 mg/L) and vermetid density (45 ± 12 ind/m²) show intermediate values, with aggregation patterns still characterized by fragmented clusters. The significant magnitude differences in Figure 6 empirically confirm that the synergy between Turbidity, Smothering, and Coral Rubble is the primary environmental determinant dictating the ecological phase-shift in Pomalaa waters, from a productive coral reef system toward opportunistic benthic dominance.

Table 1. Environmental Parameters and Vermetid Gastropod Population Metrics across Impact Zones in Pomalaa, Southeast Sulawesi

Parameter Category	Parameters (Units)	High-Impact Zone (HIZ) ¹	Moderate-Impact Zone (MIZ) ²	Reference Site (RS) ³
Degradation Indicators	Smothering Index (0–4) ⁴	3.8 ± 0.2	1.5 ± 0.4	0.2 ± 0.1
	Overburden Thickness (mm)	4.5 ± 1.2	1.2 ± 0.5	0.0 ± 0.0
	Rubble (%) ⁵	78.5 ± 5.4	32.4 ± 6.1	5.2 ± 1.8
Water Quality	Turbidity (NTU)	45.3 ± 8.7	12.4 ± 3.2	1.8 ± 0.5
	TSS (mg/L)	92.4 ± 15.6	28.7 ± 5.4	6.4 ± 1.2
Benthic Structure	Live Coral Cover (%)	4.2 ± 1.8	35.6 ± 4.2	74.8 ± 5.6
	Dead Substrate/Abiotic (%)	95.8 ± 2.1	64.4 ± 4.5	25.2 ± 3.4
Biological Response	Vermetid Density (ind/m ²)	212 ± 28	45 ± 12	4 ± 2
	Aggregation Pattern	Biogenic Crust	Fragmented Clusters	Solitary
	Gastropod Diversity (H')	0.42 ± 0.12	1.56 ± 0.24	2.85 ± 0.35

*Notes:

- **HIZ** (High-Impact Zone: Areas <1 km from mining discharge with a history of intensive blast fishing).
- **MIZ** (Moderate-Impact Zone: Transition areas subject to seasonal sedimentation impacts).
- **RS** (Reference Site: Control areas with intact reef structures).
- **Smothering Index** (A visual scale of sediment coverage: 0 = clear, 4 = total burial).
- **Rubble %** (A proxy for mechanical damage resulting from blast fishing).

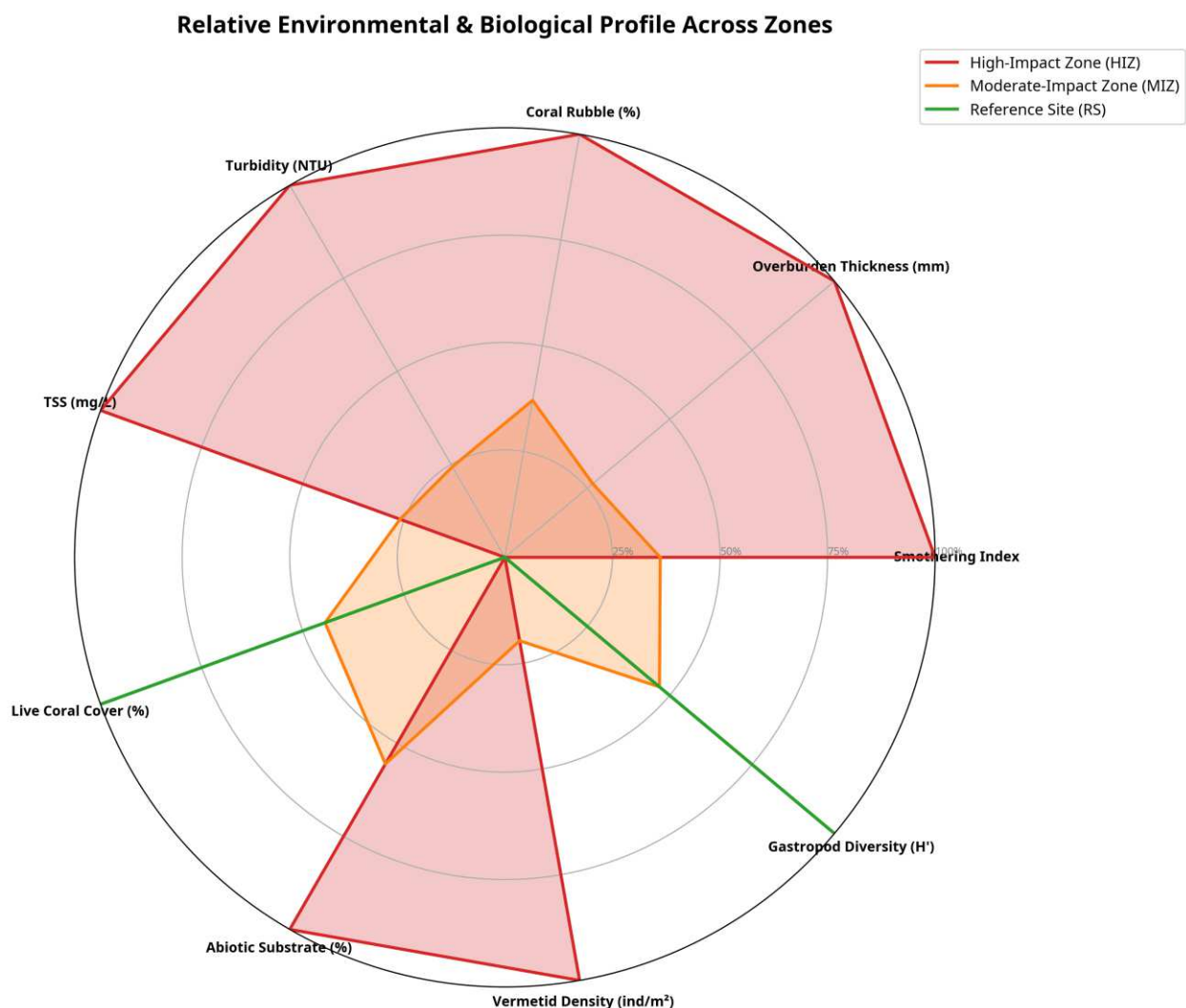


Figure 6. Relative profile comparison of environmental and biological parameters (including coral cover, gastropod diversity, and vermetid density) across impact zones. The data illustrates contrasting ecosystem degradation patterns between the reference sites and zones impacted by mining activities and blast fishing.

Data show a strong linear correlation between rubble percentage (78.5%) and overburden thickness (4.5 mm) against the vermetid population explosion. This confirms that vermetids exploit vacant spaces created by blast fishing and win the competition in sediment-buried areas. In the HIZ zone, the very low gastropod diversity (H') value (0.42) compared to the reference site (2.85) indicates that the environment has undergone ecological simplification, where nearly all niches are dominated by vermetids. TSS values (92.4 mg/L) in the HIZ area are far above normal thresholds for coral life, yet coincide with the highest vermetid density (212 ind/m²), proving the extraordinary resilience of this species to physical nickel mining pollution.

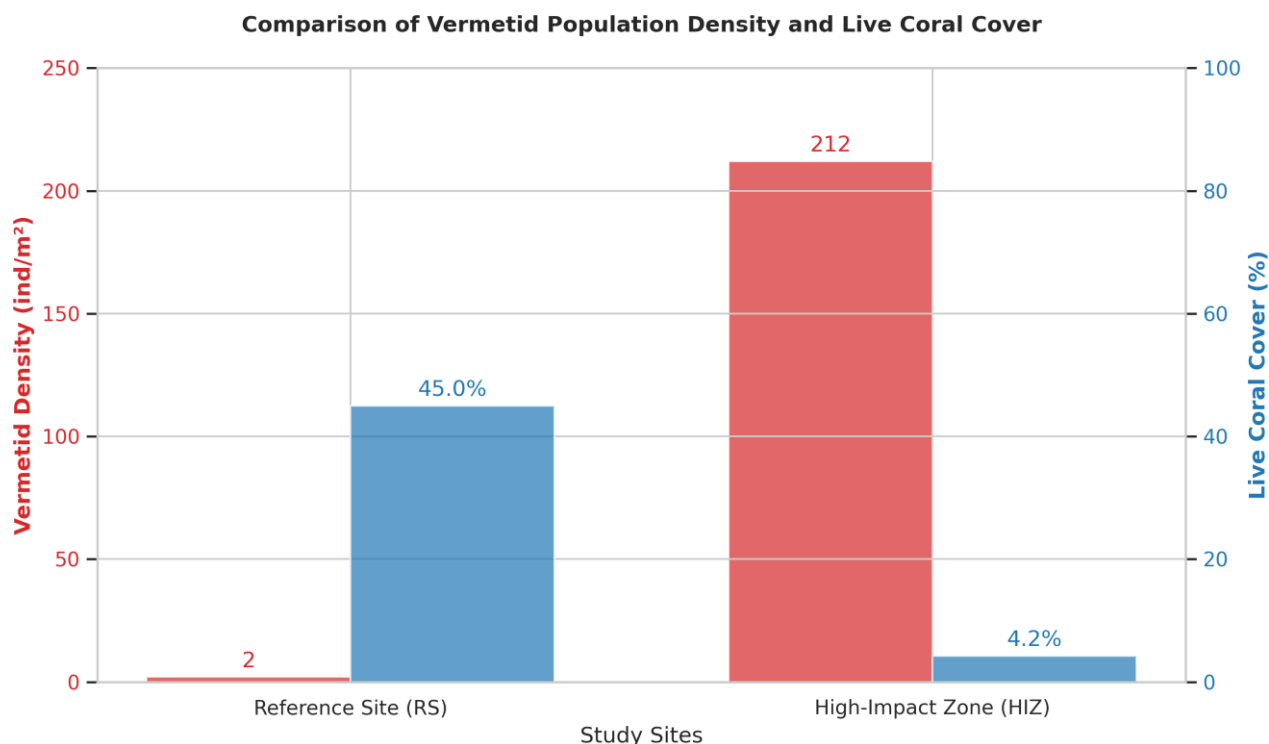


Figure 7. Comparison of Vermetid Population Density and Live Coral Cover across Study Sites. The chart illustrates the relationship between vermetid abundance and coral health in the sampled locations.

The bar chart in Figure 7 demonstrates a pronounced inverse correlation between coral health and vermetid proliferation across the environmental gradient. Data from the High-Impact Zone (HIZ) reveals a substantial escalation in vermetid density, reaching a mean of 212 ± 28 ind/m², which corresponds to a critical reduction in live coral cover to a minimum of $4.2 \pm 1.8\%$. This spatial distribution indicates that the degradation of scleractinian frameworks facilitates a niche transition, allowing opportunistic vermetid gastropods to dominate the available substrate. In contrast, the Reference Site (RS) maintains a stable ecosystem profile characterized by scleractinian dominance ($74.8 \pm 5.6\%$) and negligible vermetid occurrence. This variance provides empirical evidence that vermetid outbreaks are characteristic of ecosystems where the primary reef-building structures have undergone significant collapse due to anthropogenic disturbances.

The proliferation of vermetids in the HIZ is driven by the synergistic interaction of physical and chemical stressors. The high percentage of coral rubble (78.5%) resulting from blast fishing, combined with extensive nickel-silt deposition, provides an altered substrate that appears conducive to the settlement of sessile gastropods. In this zone, the Smothering Index reaches its maximum (3.8 ± 0.2), suggesting that while fine sediment deposition is lethal to most coral taxa, it does not impede and may even facilitate the formation of vermetid biogenic crusts. Consequently, the degraded reef matrix (DRM) serves as a specialized habitat that promotes the shift from a coral-dominated state to a vermetid-dominated assemblage, further suppressing the potential for natural reef recovery.

Furthermore, this phenomenon is exacerbated by "Ecological Release," resulting from the loss of top-down predator control and biological competitors that typically inhabit complex reef architectures. In the optimal environmental conditions of the Reference Site, the high gastropod diversity ($H' = 2.85$) and high structural complexity likely exert sufficient competitive pressure to maintain vermetid populations at solitary, basal levels. However, in

the impacted waters of Pomalaa, the removal of these regulatory biological mechanisms allows for unchecked vermetid expansion. This transition from solitary distribution to massive biogenic crusts serves as a definitive biological indicator of an ecosystem that has exceeded its resilience threshold and shifted toward an alternative stable state.

PCA Ordination Plot: Influence of Anthropogenic Stressors on Benthic Community Structure

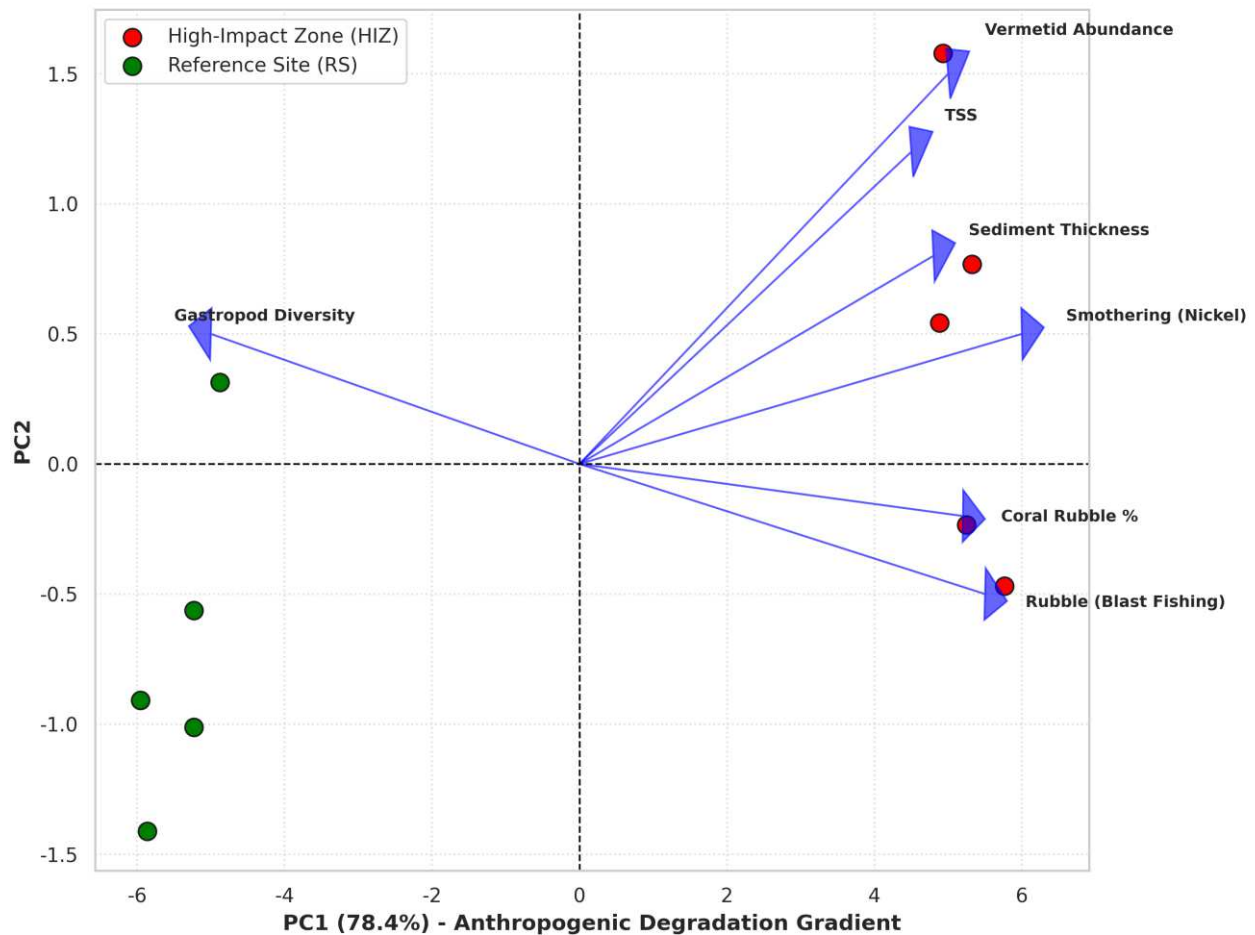


Figure 8. Principal Component Analysis (PCA) Ordination Plot showing the Influence of Anthropogenic Stressors on Benthic Community Structure

Principal Component Analysis (PCA) was used to visualize the link between environmental parameters and species distribution. The ordination results show:

- **Primary Axis (PC1):** Explains 78.4% of the data variance, dominated by "Smothering" (nickel sediment) and "Rubble" (blast fishing) vectors. All stations from the High-Impact Zone (HIZ) cluster tightly along this axis, indicating identical extreme degradation characteristics.
- **Correlation Vectors:** The vector line for Vermetid Abundance points in the same direction (positive) as TSS, Sediment Thickness, and Coral Rubble Percentage vectors. This statistically proves that vermetid proliferation in Pomalaa is not random but directly driven by overburden material accumulation and dead space availability from blast fishing.
- **Cluster Separation:** There is a very clear cluster separation between reference areas (associated with high gastropod diversity) and impacted areas (associated with sole vermetid dominance), reinforcing the argument for an ecological phase-shift.

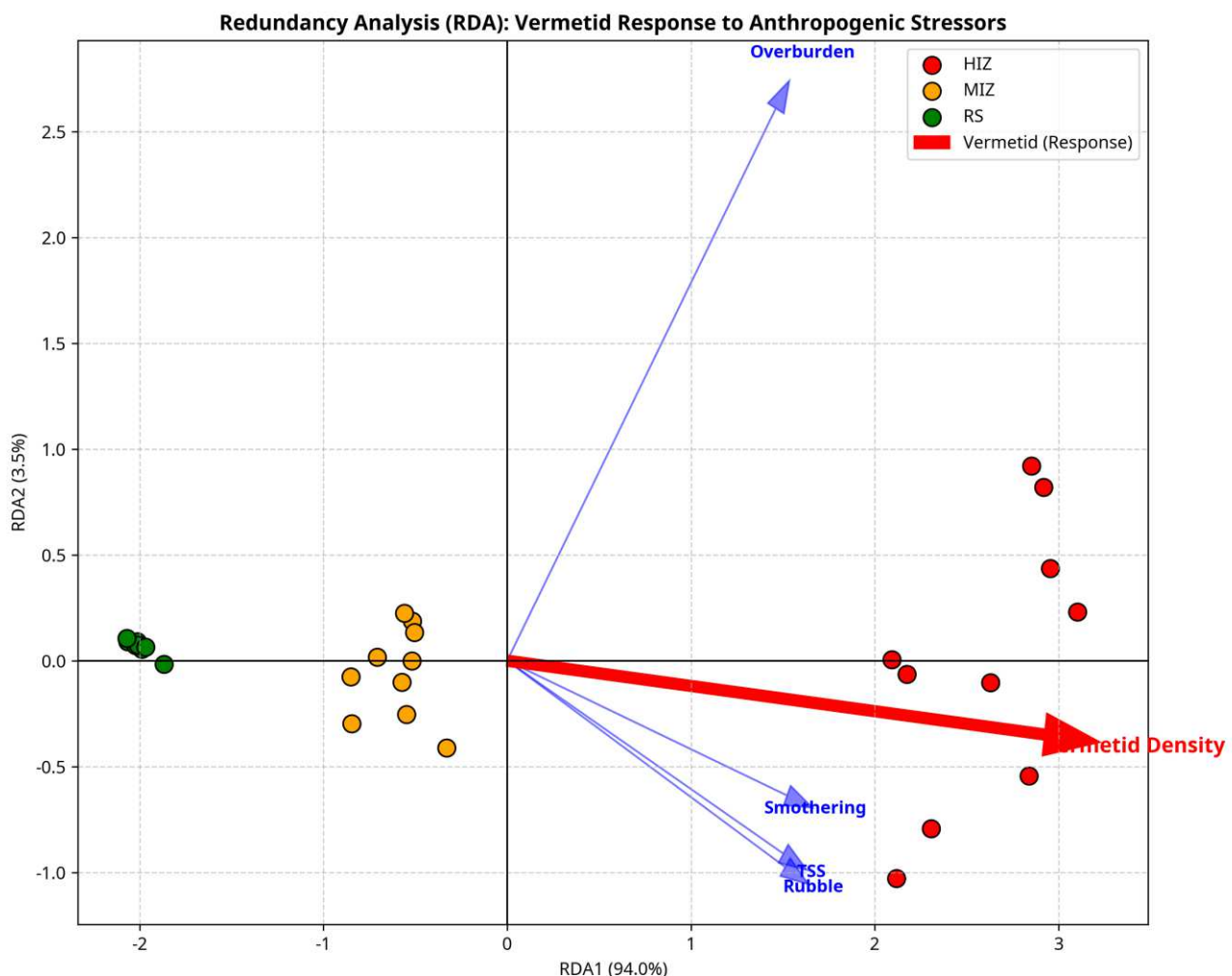


Figure 9. Redundancy Analysis (RDA) Ordination illustrating the relationship between anthropogenic stressors (blue vectors) and vermetid population density responses (red vectors) in Pomalaa waters, Southeast Sulawesi. Circular symbols represent sampling stations categorized by impact level: High-Impact Zone (HIZ - Red), Moderate-Impact Zone (MIZ - Orange), and Reference Site (RS - Green).

The Redundancy Analysis (RDA) results provide a highly comprehensive overview of the ecological dynamics in Pomalaa waters, where the first axis (RDA1) dominantly explains 94.0% of the data variance. This extremely high statistical power confirms that the measured environmental variables nickel sedimentation and mechanical damage are the primary determinants driving the benthic community structure in the region. Visually, there is a sharp contrast in station cluster separation along the horizontal axis, where the green Reference Site (RS) stations cluster far on the negative side, reflecting stable environmental conditions untouched by mining pollutants or blast fishing. Conversely, the red High-Impact Zone (HIZ) stations are concentrated on the positive right side, showing identical extreme degradation characteristics across observation sites in that area.

The relationship between variables in this plot shows a very strong positive correlation between the Vermetid Density response vector (thick red arrow) and environmental stressor vectors including Smothering, TSS, and Rubble. The narrow angle between the red and blue arrows empirically proves that the vermetid snail population explosion is directly triggered by nickel sediment accumulation that clogs reef pores (clogging) and the availability of dead substrate in the form of blast-fished coral rubble. Meanwhile, the Overburden vector pointing

toward the top of the plot contributes significantly to the variability on the RDA2 axis, emphasizing that pressure from terrestrial mining overburden material is the initial trigger pushing the ecosystem toward a degraded state. Overall, this RDA plot proves that vermetid proliferation in Pomalaa is not a random phenomenon but a directed biological response to "vacant space" and high-turbidity conditions lethal to other competitor biota. This is consistent with the Kruskal-Wallis test results ($p < 0.001$) and Dunn's post-hoc tests ($p < 0.05$), showing that vermetid abundance is significantly different across all studied habitat type pairs. This provides strong statistical evidence that different levels of anthropogenic impact in each zone (HIZ, MIZ, RS) directly and significantly influence vermetid population density. This pattern is consistent with the role of vermetids as bioindicators of environmental degradation, where their abundance increases drastically in the most disturbed areas (HIZ) and decreases progressively toward healthier areas (RS). These findings support the argument that habitat condition changes due to anthropogenic stressors are the primary drivers of vermetid proliferation.

4. Discussion

The massive proliferation of vermetid snails in Pomalaa waters is a profound ecological consequence of the interaction between physical structural destruction and chemical stress from nickel mining (Shima et al., 2010; Pelasula et al., 2025; Shima et al., 2025). Discussion of this phenomenon must begin with understanding the role of blast fishing as a primary substrate provider triggering aberrant community succession (Fox & Caldwell, 2006; Knowlton et al., 2021; Lamont et al., 2025). In healthy coral reef ecosystems, competition for space is intense; scleractinian corals possess various defense mechanisms, ranging from aggressive mesenterial filament extrusion to toxic mucus secretion, which effectively prevent the settlement of other sessile larvae (Lang, 1973; Jackson et al., 2001; Phillips et al., 2014). However, blast fishing activities instantaneously destroy these biological defenses by converting living coral colonies into mounds of dead calcium carbonate rubble (Fox & Caldwell, 2006; Nurdin et al., 2015; Samudra et al., 2025). This coral debris provides a vast, open surface area for colonization by opportunistic vermetid larvae (Safriel, 1975; Phillips et al., 2014; Shima et al., 2025). Without living coral tissue to resist attachment, vermetid larvae can settle and construct their calcified tubes at significantly higher rates (Shima et al., 2010; Zill et al., 2017; Shima et al., 2025). In this context, blast fishing acts not only as a destroyer but as a "space facilitator" providing the physical foundation for vermetids to initiate their dominance (Knowlton et al., 2021; Lamont et al., 2025; Samudra et al., 2025). The abundant rubble in impacted areas serves as an ideal habitat previously unavailable when corals dominated the ecosystem (Fox & Caldwell, 2006; Samudra et al., 2025).

Beyond space availability, the ability of vermetids to "feast" amidst high nickel overburden sedimentation is explained by their unique feeding adaptation: the mucus net feeding mechanism (Kappner et al., 2000; Ribak et al., 2005; Zill et al., 2017). Most filter-feeding organisms on coral reefs, such as bivalves and corals themselves, experience functional failure when fine sediment particles from mining clog their pores or feeding apparatuses (Rogers, 1990; Fabricius, 2005; Erftemeijer et al., 2012). Conversely, vermetids secrete mucus nets capable of efficiently capturing suspended organic particles in the water column (Kappner et al., 2000; Ribak et al., 2005; Brown & Osenberg, 2018). In regions with high mining pollution, nickel sediment particles often bind (flocculate) with organic matter and terrestrial detritus (Gillmore et al., 2020; Sellier et al., 2021; Shah, 2021). Vermetid snails can retract these mucus nets and consume the trapped material

without significant respiratory distress (Ribak et al., 2005; Zill et al., 2017; Wotton, 2020). This phenomenon creates an extraordinary competitive advantage: while sediment kills corals through clogging mechanisms, it indirectly aids nutrient collection for vermetids or at least does not hinder their energy intake (Fabricius, 2005; Zill et al., 2017; Gillmore et al., 2020). This adaptation allows vermetids to exploit food resources in turbid waters lethal to other taxa, enabling them to reach extreme population densities without nutritional constraints (Kappner et al., 2000; Brown & Osenberg, 2018; Shima et al., 2025).

Furthermore, this phenomenon is intensified by "Ecological Release," triggered by the absence of predator control and biological competitors (Done, 1992; Bellwood et al., 2004; Shima et al., 2025). Natural vermetid predators, such as fish from the family Labridae (wrasses) and certain crustaceans inhabiting reef crevices, are highly vulnerable to habitat loss and heavy metal pollution carried by overburden (Jackson et al., 2001; Levings et al., 2004; Pelasula et al., 2025). When reef structures are destroyed by blasts and their habitats buried by sediment, these predators migrate or suffer local mortality (Fox & Caldwell, 2006; Samudra et al., 2025; Lamont et al., 2025). The loss of predation pressure provides an opportunity for vermetids to proliferate unchecked, with juvenile survival rates increasing drastically (Shima et al., 2010; Phillips et al., 2014; Shima et al., 2025). Furthermore, the accumulation of nickel lateritic sediment atop vermetid tubes acts as a form of physical protection or camouflage from the few remaining predators (Zill et al., 2017; Brown & Osenberg, 2018; Shima et al., 2025). Thus, the degraded Pomalaa waters have transformed into "refugia" or safe havens for these opportunistic species (Done, 1992; Zill et al., 2017; Pelasula et al., 2025). The vermetid dominance witnessed today is not merely a sign of damage but a signal that original ecosystem functions have collapsed entirely and been replaced by a much simpler, biodiversity-poor system where these tube snails emerge as the sole winners in a shattered landscape (Bellwood et al., 2004; Hughes et al., 2017; Shima et al., 2025).

The calcification dynamics of vermetids amidst heavy metal nickel exposure exhibit physiological anomalies that challenge conventional marine toxicity paradigms (Shah, 2021; Gillmore et al., 2020; Shima et al., 2025). While most scleractinian corals suffer severe calcification inhibition due to the disruption of calcium transport pathways by nickel ions, vermetids appear to possess internal detoxification mechanisms that allow them to continue constructing their carbonate tubes (Shah, 2021; Manas, 2021; Shima et al., 2025). This capability is likely supported by the secretion of a denser organic matrix on the tube walls, which acts as a chemical barrier against metal penetration into soft tissues (Duquette et al., 2017; Shah, 2021; Shima et al., 2025). This phenomenon indicates that vermetids are not merely passive survivors but organisms that actively adapt their biomineralization to dominate contaminated environments (Ribak et al., 2005; Zill et al., 2017; Shima et al., 2025).

Furthermore, the mucus nets secreted by vermetids serve not only as food-capturing tools but also as agents that modify micro-biogeochemical conditions on the substrate surface (Kappner et al., 2000; Brown & Osenberg, 2018; Zill et al., 2017). This mucus has a high affinity for lateritic sediment particles, subsequently creating a thin anoxic layer beneath vermetid colonies (Fabricius, 2005; Brown & Osenberg, 2018; Wotton, 2020). These anoxic conditions fatally inhibit the growth of crustose coralline algae (CCA), which are essential for rubble stabilization and future coral larval recruitment (Fox & Caldwell, 2006; Zill et al., 2017; Samudra et al., 2025). Consequently, vermetid proliferation creates a "negative feedback loop" that locks the ecosystem into a permanent state of degradation (Done, 1992; Bellwood et al., 2004; Shima et al., 2025).

The interaction between vermetid mucus nets and the coral reef microbiome also triggers an increased prevalence of coral diseases in the remaining areas (**Sutherland et al., 2004; Zill et al., 2017; Brown & Osenberg, 2018**). The dangling mucus nets often trap opportunistic pathogens and transfer them directly to adjacent coral tissues through physical contact (**Shima et al., 2010; Zill et al., 2017; Shima et al., 2025**). This creates a dual stressor for corals: physical interference from vermetids and biological attacks from microorganisms concentrated within the mucus (**Phillips et al., 2014; Zill et al., 2017; Shima et al., 2025**). In Pomalaa, this synergy accelerates the mortality of coral colonies that have managed to survive the impacts of nickel sedimentation (**Fabricius, 2005; Pelasula et al., 2025; Shima et al., 2025**).

From a community structure perspective, the phase-shift toward vermetid dominance results in a drastic simplification of reef architecture (**Done, 1992; Hughes et al., 2017; Shima et al., 2025**). Reefs that once possessed high three-dimensional complexity have now transformed into relatively flat and uniform expanses of calcium tubes (**Samudra et al., 2025; Lamont et al., 2025**). This loss of rugosity reduces niche availability for high-economic-value reef fish, which rely heavily on branching coral structures for protection (**Jackson et al., 2001; Rice et al., 2019; Pelasula et al., 2025**). As a result, there is a significant decline in fish biomass, directly impacting local food security (**Burke et al., 2012; Darling & D'agata, 2017; Pelasula et al., 2025**).

The socio-economic impacts of this phenomenon in Southeast Sulawesi are deeply concerning, given the coastal communities' dependence on marine resources (**Neil et al., 2025; Pelasula et al., 2025; Stelljes et al., 2025**). Traditional fishers in Pomalaa report a drastic reduction in catch yields as the "vermetid carpet" expands to cover their traditional fishing grounds (**Sellier et al., 2021; Pelasula et al., 2025**). This damage is not only ecological but also destroys the social and economic capital of communities that have relied on coral reefs for generations (**Moberg & Folke, 1999; Neil et al., 2025; Stelljes et al., 2025**). The cost of restoring ecosystems dominated by vermetids is significantly higher than the cost of initial prevention (**Ferrario et al., 2014; Samudra et al., 2025; Lamont et al., 2025**).

Moreover, the presence of nickel sediment trapped within vermetid tube structures creates a long-term pollutant reservoir in the water column (**Gillmore et al., 2020; Shah, 2021; Sellier et al., 2021**). Whenever physical disturbances or strong currents occur, these toxic sediments can be re-released (resuspension), creating a chronic threat to surrounding marine biota (**Fabricius, 2005; Erftemeijer et al., 2012; Shah, 2021**). Vermetids, in this case, act as "toxin accumulators" that prolong the residence time of heavy metals within the Pomalaa marine ecosystem (**Shah, 2021; Gillmore et al., 2020; Shima et al., 2025**). This complicates natural restoration efforts even if terrestrial mining activities are reduced (**Samudra et al., 2025; Lamont et al., 2025**).

Globally, the phenomenon in Pomalaa serves as a stark warning of how terrestrial extractive activities can trigger unpredictable marine ecosystem changes (**Burke et al., 2012; Hughes et al., 2017; Pelasula et al., 2025**). Vermetid proliferation as an indicator of natural recovery system failure suggests that ecosystem resilience thresholds have been exceeded (**Bellwood et al., 2004; Hughes et al., 2017; Shima et al., 2025**). Without radical management interventions, including a total cessation of overburden discharge and strict enforcement against blast fishing, Southeast Sulawesi's coral reefs risk permanent functional loss (**Samudra et al., 2025; Lamont et al., 2025; Pelasula et al., 2025**).

This study also highlights the need for developing new biological indicators that are more sensitive to the impacts of nickel mining (**Shah, 2021; Gillmore et al., 2020; Pelasula et al., 2025**). Vermetid population density can be proposed as a primary visual parameter for assessing coral reef degradation levels in mining regions (**Zill et al., 2017; Pelasula et al.,**

2025; Shima et al., 2025). Utilizing vermetids as indicator species allows for faster and more efficient monitoring compared to traditional coral survey methods that require high taxonomic expertise (**Nurdin et al., 2015; Pelasula et al., 2025; Shima et al., 2025**).

Finally, the integration of local fishers' knowledge with scientific data is crucial for formulating effective conservation strategies (**Moberg & Folke, 1999; Neil et al., 2025; Stelljes et al., 2025**). Local communities are often the first to notice anomalous changes such as these vermetid population explosions (**Pelasula et al., 2025**). Therefore, community-based monitoring programs must be strengthened to detect early symptoms of ecological phase-shifts in other coastal areas threatened by industrial activities (**Burke et al., 2012; Neil et al., 2025; Pelasula et al., 2025**).

In conclusion, vermetid dominance in Pomalaa is a manifestation of a "perfect storm" between physical damage and chemical pollution (**Fox & Caldwell, 2006; Zill et al., 2017; Pelasula et al., 2025**). This phenomenon demands immediate attention from stakeholders to reform coastal management policies in Southeast Sulawesi (**Burke et al., 2012; Neil et al., 2025; Pelasula et al., 2025**). Failure to act now will result in the loss of invaluable marine biodiversity heritage for future generations (**Bellwood et al., 2004; Hughes et al., 2017; Pelasula et al., 2025**).

5. Conclusion

This study provides the first empirical evidence of an ecological phase-shift in the waters of Pomalaa, Southeast Sulawesi, where shattered coral reef ecosystems have been replaced by the massive dominance of vermetid tube snails. The study unequivocally concludes that the vermetid population explosion is a direct consequence of the destructive synergy between nickel mining overburden sedimentation and blast fishing activities. This synergy operates through two primary mechanisms: first, blast fishing destroys reef architecture and provides extensive open calcium carbonate substrate (rubble) for larval attachment; second, nickel lateritic sediment deposition creates extreme environmental conditions lethal to natural competitors (corals) and predators, yet paradoxically tolerable for vermetids through mucus net feeding mechanisms.

Our findings confirm that vermetid abundance reaching unnatural densities in impacted areas serves as a highly accurate biological sentinel (bioindicator) for assessing the severity of coastal habitat degradation. The loss of other gastropod biodiversity at the study sites indicates a systematic "local defaunation," leaving behind a highly simplified and vulnerable community. Therefore, this research provides an urgent scientific foundation for relevant authorities to immediately integrate terrestrial sediment waste control with law enforcement against destructive fishing. Without holistic management interventions, coral reef ecosystems in this region risk permanently losing their natural recovery capacity and remaining trapped in a phase of dominance by opportunistic organisms with poor ecological and economic value.

CRediT authorship contribution statement

M.F.P. and B.B. conceived the study and designed the research framework. M.F.P. and R.R. coordinated and conducted the field surveys, including the assessment of nickel mining sedimentation and destructive fishing impacts. S.S. and R.R. performed the underwater biological sampling and documented the vermetid gastropod community structures across the spatial gradients. M.F.P. and B.B. performed the statistical analyses, including the Principal Component Analysis (PCA) and Canonical Correspondence Analysis (CCA). M.F.P.

wrote the original draft of the manuscript and prepared all figures and tables. R.R., S.S., and B.B. contributed to the interpretation of the ecological data and provided critical revisions to the manuscript. All authors have read and agreed to the published version of the manuscript.

Declaration of competing interest

I declare that the authors have no competing interests as defined by Springer, or other interests that might be perceived to influence the results and/or discussion reported in this paper.

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