

Spatial variation in coral reef condition and reef fish assemblages along a proximity to Jakarta Bay, Indonesia

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Abstract. *Siringoringo RM, Bengen DG, Nurjaya IW, Subhan B, Giyanto, Putra RD, Abrar M, Sari NWP, Aji LP. 2025. Spatial variation in coral reef condition and reef fish assemblages along a proximity to Jakarta Bay, Indonesia. Biodiversitas 26: 5919-5930.* The coral reef ecosystems of the Seribu Islands, Indonesia, exhibit complex ecological interactions between benthic assemblages and reef fish communities under the combined influence of local anthropogenic pressures and regional environmental stressors. This study examined benthic composition and reef fish functional structure across 14 sites along a spatial gradient from Jakarta Bay, Seribu Islands, to the outer islands. Benthic cover was assessed using the Underwater Photo Transect (UPT) method, and reef fish assemblages were quantified through Underwater Visual Census (UVC). Analyses revealed that distance from Jakarta Bay had a weak and inconsistent influence on benthic composition, with a low explanatory power for variations in hard coral cover (R^2 : 0.023, p : 0.6). In contrast, corallivorous fish abundance increased significantly with distance from the bay (R^2 : 0.30, p : 0.043), indicating a more pronounced spatial response among higher trophic groups. Cluster analyses identified three distinct ecological assemblages aligned with the nearshore-offshore gradient, reflecting subtle yet detectable shifts in community structure. These findings suggest that while benthic recovery remains constrained by persistent sedimentation and nutrient enrichment, reef fish assemblages particularly corallivores retain spatial sensitivity to urban influence. The emerging ecological differentiation across the archipelago underscores that the Seribu Islands function as a transitional system shaped by both urban proximity and broader ecological processes. Effective management should therefore integrate local mitigation of land-based stressors with broader seascape-scale strategies to enhance reef resilience in urban-influenced marine ecosystems.

Keywords: Abundance, coral reef resilience, functional groups, spatial gradient, urban impact

INTRODUCTION

Coastal megacities increasingly impose multi-stressor regimes on adjacent coral reefs, combining chronic nutrient enrichment, sediment inputs, contaminants, and intense resource use (Dsikowitzky et al. 2016; Hewitt et al. 2016; Gotama et al. 2024). The Jakarta Bay-Seribu Islands, Indonesia, system exemplifies this problem: an ~80 km inshore-offshore reef chain extending from Jakarta Bay into the Java Sea (Draisma et al. 2018). Along this axis, reef communities exhibit pronounced turnover, yet key causal pathways and interacting drivers remain only partly resolved (Baum et al. 2015; Cleary 2017; Polónia et al. 2019). Gradient studies show that coral diversity and composition decline toward nearshore, disturbed settings influenced by terrestrial and urban inputs (Heery et al. 2018). Long-term assessments spanning 1985-2011 reported substantial declines and compositional shifts on Jakarta-area reefs, underscoring the cumulative effects of chronic urban stressors and disturbance history (Cleary et

al. 2014). Trait-based analyses further indicate that coral species with particular life-history and morphological attributes are filtered by local environmental conditions, suggesting deterministic community assembly along the gradient rather than purely stochastic turnover.

Among quantified drivers, pollution-related variables have emerged as dominant correlates of benthic structure (Aji et al. 2024; Wright et al. 2025). In a cross-archipelago analysis, sedimentation rate, dissolved nutrients, and chlorophyll-a collectively explained >80% of the variation in benthic community composition, indicating that water quality can overwhelm simple distance-to-shore relationships in structuring benthos (Baum et al. 2015). Beyond the inner bay, however, reef condition does not follow a monotonic decline with distance: reefs form a spatial patchwork of differential degradation linked to localized anthropogenic pressures and site-level processes (Baum et al. 2015). This patchiness is mirrored in cross-taxa community variation along the gradient (Cleary et al. 2016). Reef fish assemblages also change markedly in diversity, trophic

structure, and composition across the Jakarta Bay-Seribu Islands complex, with clear shifts along environmental and anthropogenic pressure gradients (Polónia et al. 2019). Together with the benthic findings, these patterns suggest bidirectional benthic-fish linkages mediated by habitat quality and environmental stress, although formal causal pathways have yet to be tested using integrated datasets (Hoeksema et al. 2019; Polónia et al. 2019).

Despite numerous studies documenting coral cover and reef fish assemblages in the region, most investigations have been conducted in isolation, focusing either on benthic or fish communities without explicitly integrating their ecological interdependencies (Madduppa et al. 2016; Anzani et al. 2019; Puspasari et al. 2025). Madduppa et al. (2013) showed that reef fish biodiversity and trophic composition across 33 sites vary from nearshore to offshore zones, forming distinct community clusters that reflect gradients in anthropogenic pressure and habitat condition. Komala et al. (2024) reported that live hard coral cover averaged 32.51%, classifying Seribu reefs as moderately degraded, with 53 genera from 15 families and medium coral diversity that highlight the need for restoration, continuous monitoring, and habitat protection. However, few studies have explicitly addressed ecosystem-level interactions, particularly feedbacks between coral health and fish community structure that underpin reef resilience. This fragmented approach limits predictive capacity, weakens the ecological foundation of reef health assessments, and constrains the development of evidence-based conservation strategies.

This study addresses this gap by integrating benthic cover and functional reef fish assemblages across 14 sites in the Seribu Islands, incorporating spatial proximity to Jakarta Bay and pressure gradients to provide a holistic

assessment of reef ecosystem condition in an urban-impacted seascape. Building on evidence that chronic inputs of sediment, nutrients, and other pollutants from Jakarta Bay mediate benthic responses to urban proximity (Baum et al. 2015; Hewitt et al. 2016), we treat spatial proximity as a key determinant of coral reef condition and resilience, influencing coral cover, life-form composition, and functional fish assemblages, and amplifying vulnerability to disturbances. We therefore posited that coral reef condition and reef fish assemblages in the Seribu Islands deteriorate with increasing proximity to Jakarta Bay, where coastal pollution and sedimentation impose stronger ecological stress on nearshore reef systems. However, the mechanisms linking spatial gradients, coral condition, and fish assemblage structure remain poorly understood. By disentangling these relationships across a Jakarta Bay gradient, this study aims to clarify coupled benthic-fish dynamics, provide insights into reef resilience, and inform management priorities in urbanized seascapes.

MATERIALS AND METHODS

Study area

The study was conducted in the Kepulauan Seribu Marine National Park, situated in the Java Sea approximately 34-76 km north of Jakarta, Indonesia, during November 2021 (Figure 1). This spatial range allows the study to capture variations in reef condition, coral cover, and fish assemblages along a gradient of human impact, thereby enabling a more comprehensive understanding of how proximity to urban and industrial stressors influences reef ecosystem health.

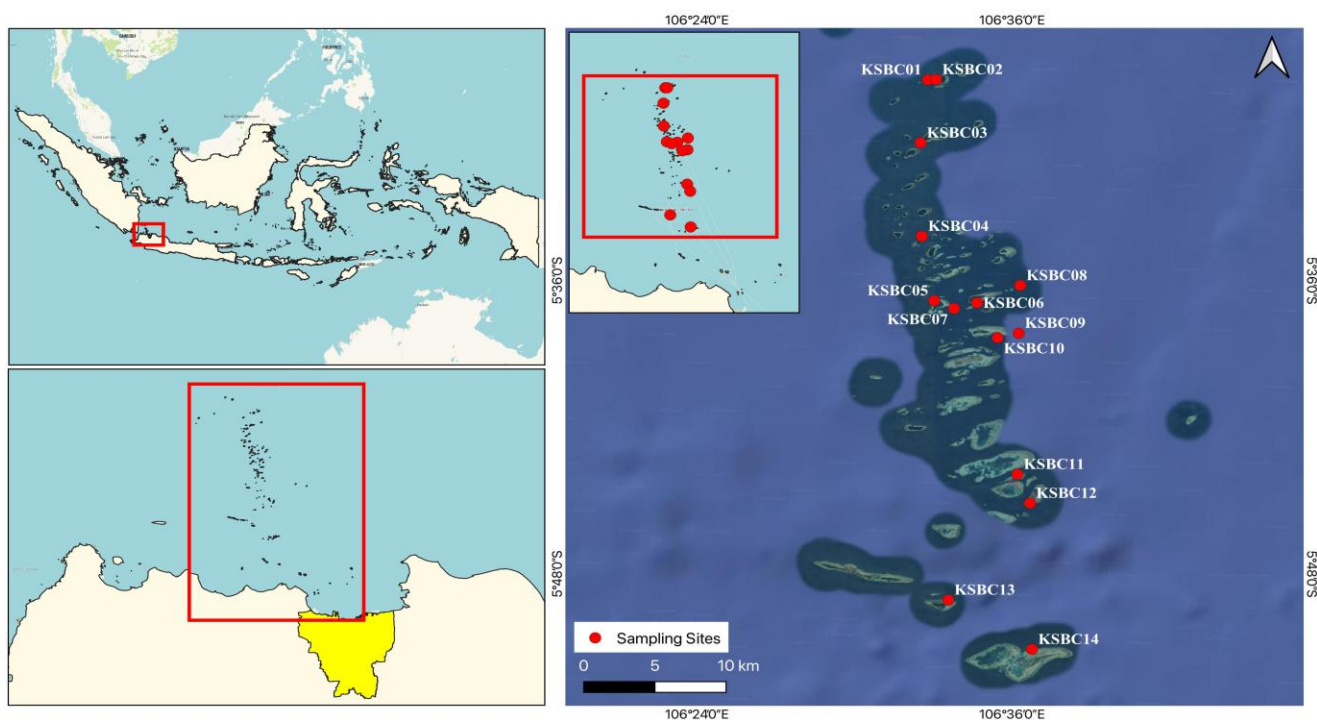


Figure 1. Study locations fourteen reef sites within the Kepulauan Seribu Marine National Park, Java Sea, surveyed along an inshore-offshore gradient at varying distances from Jakarta Bay, Indonesia. KSBC01-14: Study sites (see Table 1)

Fourteen reef sites were selected along an inshore-offshore gradient, representing varying degrees of distance from Jakarta Bay with anthropogenic influence and ecological conditions (Table 1). Geographical coordinates ranged from 5°27'47.52"S to 5°51'04.68"S latitude and from 106°32'31.20"E to 106°36'45.72"E longitude. These islands are characterized by fringing reefs with varying benthic structures, supporting diverse coral reef fish assemblages. The spatial arrangement of the sites captures a gradient of ecological variability influenced by proximity to the mainland, water quality, and local human activities, thereby providing a representative framework for assessing benthic and fish community dynamics across the Seribu Islands.

Underwater assessment of coral benthic communities

Quantitative assessments of coral benthic communities were conducted using the Underwater Photo Transect (UPT) protocol, a standardized method for long-term coral reef monitoring (Giyanto et al. 2017, et al. 2023; Hadi et al. 2020a, b). Underwater Photo Transects (UPT) were conducted by capturing a series of 50 photographic frames at depths ranging from 5 to 7 meters to quantitatively document benthic substrate composition and coral cover. At each sampling station, a 50-m transect line was deployed parallel to the reef crest along representative reef habitat with fixed quadrat frame measuring 58×44 cm, corresponding to a sampling area of approximately 2,500 cm² per frame.

The resulting a total of 50 photographs imagery was analyzed for each sampling station using Coral Point Count with Excel extensions (CPCe) (Siringoringo et al. 2021; Giyanto et al. 2023). For each photographic frame, 30 randomly distributed points were automatically generated, and the benthic category underlying each point was identified and recorded. This sampling design has been widely recognized as an efficient and statistically robust approach for accurately quantifying benthic cover categories and assessing coral biotic diversity within reef ecosystems. Categories encompassed major biotic components (e.g., scleractinian corals, octocorals, macroalgae, sponges) as well as abiotic substrates (e.g., rubble, sand, consolidated reef matrix) (Siringoringo et al. 2021; Giyanto et al. 2023). To safeguard temporal comparability and minimize sampling bias, permanent reference markers were installed at each site, enabling repeated surveys at identical locations across years. This design ensured methodological reproducibility and robust quantification of benthic composition, thereby providing a reliable basis for detecting ecological change and evaluating long-term reef trajectories.

In situ inclusion of reef fish for assemblage assessment

Coral reef fish biodiversity was quantified using the Underwater Visual Census (UVC) technique (Putra et al. 2020a, b, et al. 2022; Sari et al. 2021) with standardized belt transect protocol established by the Reef Health Monitoring Program (RHMP) (Giyanto et al. 2023). A

globally recognized method for assessing reef fish assemblages. UVC is widely applied in long-term reef monitoring programs due to its reliability in estimating species composition, abundance, and biomass, as well as its utility in supporting ecosystem-based management and conservation planning. At each station, a transect measuring 70 m in length and 5 m in width was deployed, with observations extending 2.5 m on either side of the transect line, yielding a total survey area of 350 m² per transect (Putra et al. 2018, et al. 2020a, b, et al. 2022). The UVC for fish transect surveys were conducted by systematically sweeping designated areas to record all observed fish species along transect area. During each transect, data were collected on species identity, abundance, and estimated length and weight of individuals to characterize the structure and composition of reef fish communities. This design ensured consistency across sites and facilitated comparability with other regional and global reef assessments. All censuses were performed by trained and certified scientific divers who maintained a controlled and consistent swimming pace to minimize fish disturbance and maximize detection accuracy. Within each transect, all reef-associated fishes were visually identified to the lowest feasible taxonomic level and enumerated. Particular emphasis was placed on quantifying reef fish functional groups, including corallivores (Chaetodontidae), herbivores (Acanthuridae, Scaridae, and Siganidae), and carnivores (Haemulidae, Lethrinidae, Lutjanidae, and Serranidae), with species-specific counts recorded to assess their relative abundance and diversity.

Data analysis

Data obtained from the Coral Point Count with Excel extensions analyses (CPCe 4.1) were first tabulated in Microsoft Excel and subsequently processed using the R statistical environment (R Core Team, 5.4.1) (Giyanto et al. 2017, et al. 2023). To examine spatial variability in coral cover and reef fish assemblages across the study sites, multiple multivariate statistical approaches were applied. Hierarchical heatmap analyses, based on benthic community categories and functional groups of reef fishes, were employed to visualize compositional similarities and differences among the 14 island stations. These analyses revealed distinct clustering patterns that corresponded with spatial gradients relative to the proximity of Jakarta Bay. To further assess the influence of distance from Jakarta Bay on benthic and fish community structure, hierarchical clustering with multiscale bootstrap resampling was performed using the *pvc* package in R (R Core Team, 5.4.1).

Dendrograms were constructed based on Euclidean distance matrices, separately for benthic cover categories and for functional groups of reef fishes (corallivores, herbivores, and carnivores). Bootstrap Probability (BP) values and Approximately Unbiased (AU) confidence values were calculated to evaluate the robustness of cluster formation.

Table 1. Study locations fourteen reef sites were surveyed along gradient relative to Jakarta Bay, Indonesia

Location	Station ID	Latitude (S)	Longitude (E)	Distance (km) Jakarta Bay	Description
Peteloran Barat Island	KSBC01	5°27'47.52"S	106°32'47.76"E	76.24	Located in Core Zone II, about 200 m east of the island, the site features a sandy substrate, coastal vegetation, high rugosity, and large coral colonies.
Penjaliran Barat Island	KSBC02	5°27'46.80"S	106°33'06.84"E	76.05	Located in Core Zone II, uninhabited, with coastal mangroves; transect 150 m offshore. The site hosts large, diverse coral colonies, dominant soft corals, and coral growth to 15 m depth.
Sebaru Besar Island	KSBC03	5°30'21.96"S	106°32'31.20"E	72.02	Located in the National Park Protection Zone, the site is uninhabited with ongoing resort development, sparse mangroves, low coral cover, high rubble, unstable sandy and Dead Corals with Algal overgrowth (DCA) substrate, and macroalgae <i>Padina</i> sp.
Melinjo Island	KSBC04	5°34'11.28"S	106°32'34.08"E	65.53	Located in the Tourism Utilization Zone, the uninhabited island features a narrow, coconut-lined coast, sparse mangroves, a rubble-sand substrate prone to slumping, and <i>Acropora</i> -dominated coral cover.
Genteng Besar Island	KSBC05	5°36'49.32"S	106°33'02.16"E	60.77	Located in the Tourism Utilization Zone, the uninhabited island with a private resort has partial mangrove cover, dead corals overgrown by algae, abundant <i>Padina</i> sp., and coral colonies affected by white band disease.
Bira Besar Island	KSBC06	5°36'54.36"S	106°34'40.44"E	59.32	Located in Core Zone III, the uninhabited island with mangrove-fringed shores and a nearby jetty with dominated by large <i>Acropora brueggemanni</i> and foliose <i>Montipora</i> spp.
Kayuangi Genteng Island	KSBC07	5°37'08.40"S	106°33'47.52"E	59.62	Located in the Tourism Utilization Zone, the small private resort island has sandy shores with seawalls, and reefs dominated by tabulate and branching <i>Acropora</i> extending to 20 m depth.
Belanda Island	KSBC08	5°36'11.88"S	106°36'19.08"E	59.35	Located in Core Zone III, the uninhabited island exposes its reef at low tide, featuring high rugosity, diverse coral assemblages, and economically valuable taxa such as <i>Goniopora</i> and <i>Euphyllia</i> .
Pamagaran Island (East)	KSBC09	5°38'09.24"S	106°36'15.48"E	56.02	Located in the Settlement Zone, the site has an extensive reef located far from shore, with a DCA, rubble, and sand substrate. Macroalgae, particularly <i>Padina</i> spp., <i>Sargassum</i> spp., and <i>Halimeda</i> spp., are abundant along the transect.
Pamagaran Island (South)	KSBC10	5°38'20.04"S	106°35'27.24"E	56.31	Located in the Settlement Zone, the area hosts private villas, with mangroves and coastal vegetation along the shore. The seafloor consists of rubble and DCA, with macroalgae <i>Padina</i> spp. commonly present.
Karya Island	KSBC11	5°43'55.20"S	106°36'12.60"E	46.39	Located in the Settlement Zone, the small inhabited island hosts government housing, with the reef flat reinforced by perforated concrete barriers. The substrate consists of rubble, sand, and DCA, with macroalgae <i>Padina</i> spp. present.
Pramuka Island	KSBC12	5°45'06.12"S	106°36'41.04"E	44.04	Located in the Settlement Zone, the inhabited island shows intensive land use, with perforated concrete barriers on the reef and a DCA and rubble substrate.
Payung Island	KSBC13	5°49'03.72"S	106°33'34.56"E	41.18	Located in the Settlement Zone, coastal mangroves border reefs with live corals and dominant DCA, where dead corals are overgrown by <i>Padina</i> spp. and <i>Halimeda</i> spp.
Pari Island	KSBC14	5°51'04.68"S	106°36'45.72"E	34.59	Located in the Settlement Zone, the inhabited island supports intense tourism activity, with mangroves near the reef and a seafloor composed of live corals and DCA.

In addition, regression-based analyses were conducted to quantify the relationship between distance from Jakarta Bay and benthic community composition, with particular

focus on the proportional cover of key categories including Hard Corals (HC), Dead Corals (DC), Dead Corals with Algal overgrowth (DCA), Sponges (S), and Fleishy

Seaweed (FS). Parallel analyses were performed for reef fish functional groups to determine whether distance influenced the relative abundance of corallivores (Chaetodontidae), herbivores (Acanthuridae, Scaridae, and Siganidae), and carnivores (Haemulidae, Lethrinidae, Lutjanidae, and Serranidae). Prior to regression assumption linearity, independence and normality of residuals were assessed using Shapiro-Wilk test. All statistical tests were evaluated at a significance threshold of α : 0.05. Finally, Principal Component Analysis (PCA) was applied to integrate benthic composition and reef fish functional group data into a multivariate ordination framework. All variables were standardized and evaluated using Bartlett test. The resulting PCA biplots provided a holistic view of site-level variation, enabling visualization of the relative contributions of individual benthic and fish parameters to the overall patterns of community structure across the 14 monitoring stations.

RESULTS AND DISCUSSION

Benthic community response to distance from Jakarta Bay

Across the 14 island stations and a distance gradient of ≈ 35 -75 km from Jakarta Bay, fitted trendlines show

uniformly weak relationships between distance and benthic cover categories and none reach statistical significance at α : 0.05 (Figure 2). Specifically, Dead Coral exhibited almost no explained variance (R^2 : 0.0015, p : 0.89) with cover ≈ 0 -6% and a near-flat to slightly negative slope; Dead Coral with Algae was similarly weak (R^2 : 0.028, p : 0.57) with percent cover clustered ≈ 28 -46% and a modest negative trend. Fleishy Seaweed showed a small positive trend (R^2 : 0.045, p : 0.47) with values spanning ≈ 0 -23% and a visible high point near 22%; Hard Coral declined marginally with distance (R^2 : 0.023, p : 0.60) across a range of ≈ 10 -65% cover. Soft Coral produced the largest, though still non-significant, effect (R^2 : 0.21, p : 0.10), indicating a modest positive association with distance but not meeting conventional significance; observed soft coral cover was low (≈ 0 -2.2%). Sponges showed a weak positive association (R^2 : 0.06, p : 0.40) with most values $< 5\%$ and one outlier $\approx 13\%$. Each panel displays a fitted trend line with a shaded confidence band and annotated R^2 and p -values; collectively these results indicate that distance from Jakarta Bay explains little of the variance in benthic community cover across the sampled islands.

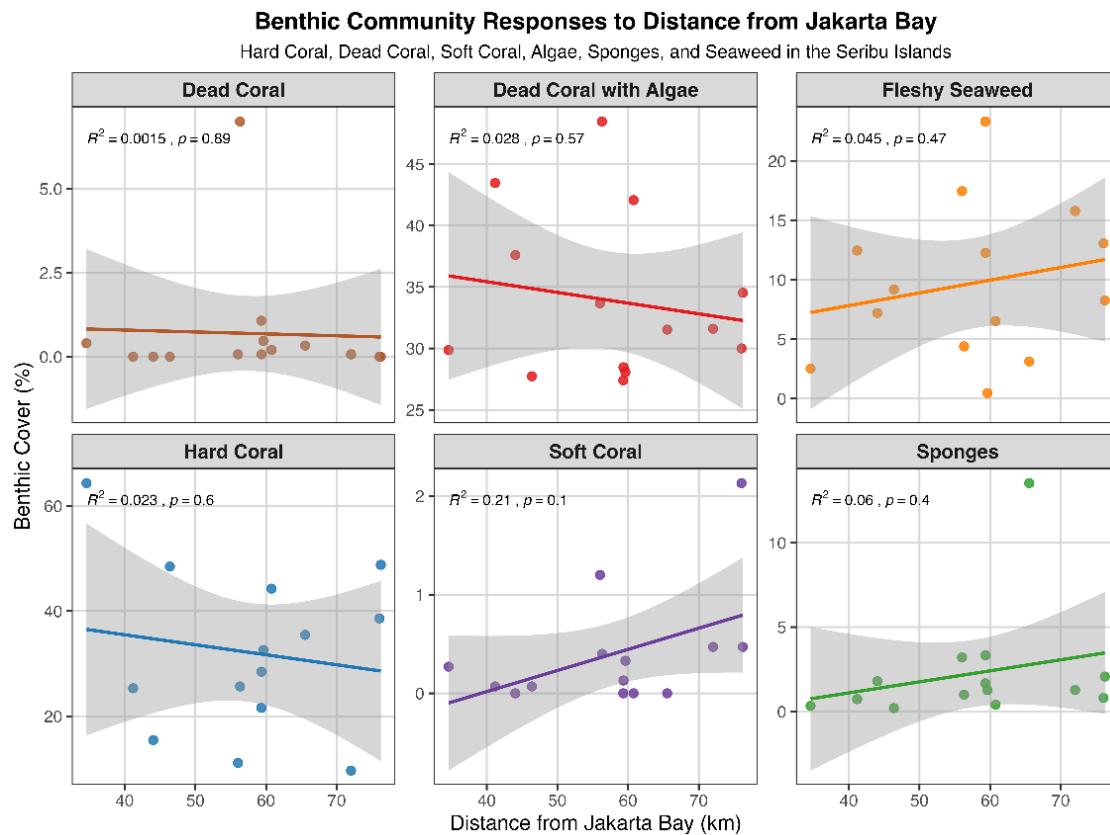


Figure 2. Benthic community response (%) to distance from Jakarta Bay (km) across 14 reef sites in the Seribu Islands, Indonesia. The figure illustrates variations in the proportional cover of key benthic categories including Hard Corals (HC), Dead Corals (DC), Dead Corals with Algal overgrowth (DCA), Soft Coral (SC), Sponges (S), and Fleishy Seaweeds (FS). The site locations are arranged along a spatial gradient from nearest to farthest from Jakarta Bay to highlight the influence of urban proximity on benthic composition

Functional group reef fish response to distance from Jakarta Bay

Across the 14 island stations and a distance gradient of ≈ 35 -75 km from Jakarta Bay, fitted linear models show contrasting and statistically resolvable responses among fish functional groups (Figure 3). Carnivore abundance exhibited a significant negative relationship with distance (range ≈ 400 -1,500 individu/ha, R^2 : 0.31, p : 0.04). Corallivore abundance increased significantly with distance (range ≈ 750 -2,100 individu/ha, R^2 : 0.30, p : 0.043), with several outer stations reaching $>2,000$ ind/ha. Herbivore abundance showed high variability and a weak, non-significant negative trend (range $\approx 1,100$ -6,500 ind/ha, R^2 : 0.086, p : 0.31). Each panel presents the fitted trend line with a 95% confidence band and annotated R^2 and p -values; only the carnivore and corallivore models met conventional statistical significance ($p < 0.05$).

Hierarchical heatmaps on benthic community categories and reef fish functional groups

The hierarchical heatmaps based on benthic community categories and reef fish functional groups revealed clear but distinct clustering patterns among the 14 island stations driven by proximity to Jakarta Bay (Figure 4). Within the benthic community matrix, notable variations in the relative composition of Dead Coral Algae (DCA) and Hard Coral (HC) were observed among sites. Pari Island exhibited the highest proportion of live coral cover, characterized by 29.87% DCA and 64.33% HC, corresponding to a good coral condition classification. In contrast, Genteng Besar Island (DCA: 42.07%, HC: 44.27%) and Peteloran Barat Island (DCA: 34.53%, HC: 48.50%) both displayed moderate coral condition categories. These patterns indicate spatial heterogeneity in benthic community structure, reflecting differential ecological conditions and reef resilience among the surveyed islands. Soft coral and dead coral cover remained consistently low across nearly all sites. Fleshy seaweed and sponge cover displayed intermediate variability, with localized increases at several mid-cluster stations. The benthic dendrogram grouped these islands into distinct clusters according to their substrate composition. In contrast, the fish functional group matrix showed that herbivorous fishes were most abundant at Pramuka Island (Abundance: 6514 (Ind./ha), Bira Besar Island (Abundance: 4800 (Ind./ha), Payung Island (Abundance: 4800 (Ind./ha), and Peteloran Barat Island (Abundance: 4285 (Ind./ha), while carnivores were generally scarce across the Seribu Islands. Corallivores exhibited low-to-moderate abundances without clear concentration at specific sites. The fish dendrogram separated herbivore-dominated islands from those with lower herbivore abundance, forming cluster structures distinct from the benthic assemblages. Overall, the analysis highlighted site-specific contrasts in benthic cover and functional reef fish abundances, with robust clustering apparent in both community matrices though with differing island associations.

Cluster analysis-pvclust dendrogram from 14 reef stations

The pvclust dendrogram based on benthic cover and functional reef fish composition (Euclidean distance, Ward.D2) resolved the 14 reef stations into three principal clusters (α : 0.95) (Figure 5). Cluster 1 grouped Peteloran Barat (KSBC01), Penjaliran Barat (KSBC02), and Sebaru Besar (KSBC03), supported at AU: 82, although the Penjaliran Barat-Sebaru Besar pair showed weaker stability (AU: 49). Cluster 2 comprised Pamagaran South (KSBC10), Melinjo (KSBC04), Genteng Besar (KSBC05), and Kayuangi Genteng (KSBC07), with the Genteng Besar-Kayuangi Genteng pair exhibiting the strongest support across the dendrogram (AU: 97). Cluster 3 encompassed two subgroups: Bira Besar (KSBC06), Belanda (KSBC08), Payung (KSBC13), and Pamagaran East (KSBC09); and Karya (KSBC11), Pramuka (KSBC12), and Pari (KSBC14). Within this cluster, the Bira Besar-Belanda pair was strongly supported (AU: 94), whereas other nodes demonstrated moderate stability (AU: 63-83). At a higher level, Clusters 2 and 3 merged with AU: 81, forming a broad separation from Cluster 1. Overall, the analysis identified two highly stable associations ($AU \geq 94$) and several moderately supported groupings (AU : 72-83), reflecting distinct but uneven clustering patterns in benthic cover and functional reef fish assemblages across the island stations.

The Principal Component Analysis (PCA) of benthic cover categories and reef fish functional groups

The Principal Component Analysis (PCA) of benthic cover categories and reef fish functional groups resolved two primary axes that jointly explained 46.4% of the total variance in community structure (Dim1: 24.1%, Dim2: 22.3%) (Figure 6). Loadings indicated strong positive associations of hard coral and carnivores with Dim1, whereas dead coral and dead algae loaded negatively on the same axis. Along Dim2, fleshy seaweed and soft coral exhibited positive scores, while dead coral and dead algae were aligned negatively. The vectors for herbivores and corallivores projected toward the upper right and upper center of the ordination space, respectively, with herbivores aligning positively on both axes and corallivores primarily on Dim2. Site distributions showed distinct spatial segregation: Pari Island was positioned at the extreme positive end of Dim1 ($\approx +2.5$, -2.2), closely aligned with the carnivore and hard coral vectors, while Pamagaran Island (South) was located at the extreme negative end of both axes (≈ -3.5 , -2.8), adjacent to dead coral and dead algae. Stations including Bira Besar Island, Penjaliran Barat Island, and Sebaru Besar Island plotted in the upper-left quadrant (positive Dim2, negative Dim1), coinciding with fleshy seaweed and soft coral vectors. In contrast, Belanda Island and Pramuka Island were positioned in the upper-right quadrant (positive scores on both axes), aligning with the herbivore vector. Remaining sites, such as Melinjo Island, Genteng Besar Island, and Karya Island, occupied intermediate positions closer to the sponge and hard coral loadings. Point colors representing distance from Jakarta Bay (ranging from ≈ 35 km to >70 km) were

distributed across the ordination space, with no single axis dominated by distance alone. Arrow lengths reflected the relative strength of loadings, with hard coral and carnivore

exhibiting the strongest projections on Dim1, and fleshy seaweed and soft coral contributing most strongly to Dim2.

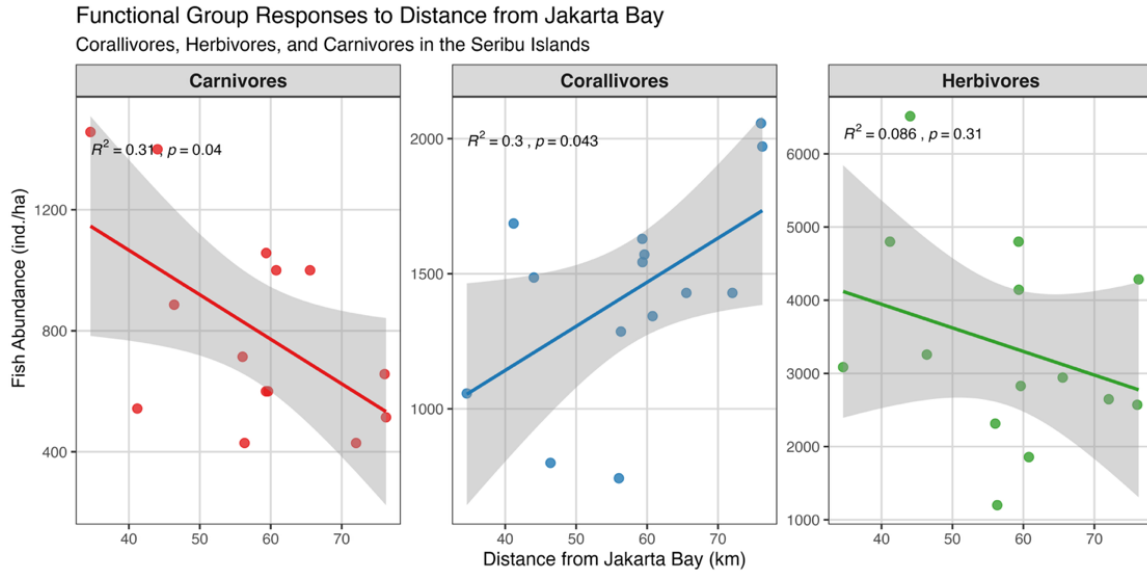


Figure 3. Functional group reef fish response (Ind./ha) to distance from Jakarta Bay (km) across 14 reef sites in the Seribu Islands, Indonesia. Benthic community response (%) to distance from Jakarta Bay (km) across 14 reef sites in the Seribu Islands. The figure illustrates variations in the Functional group reef fish abundance of key benthic categories including carnivores (Haemulidae, Lethrinidae, Lutjanidae, Serranidae), herbivore (Acanthuridae, Scaridae, and Siganidae), and corralivore (Chaetodontidae)

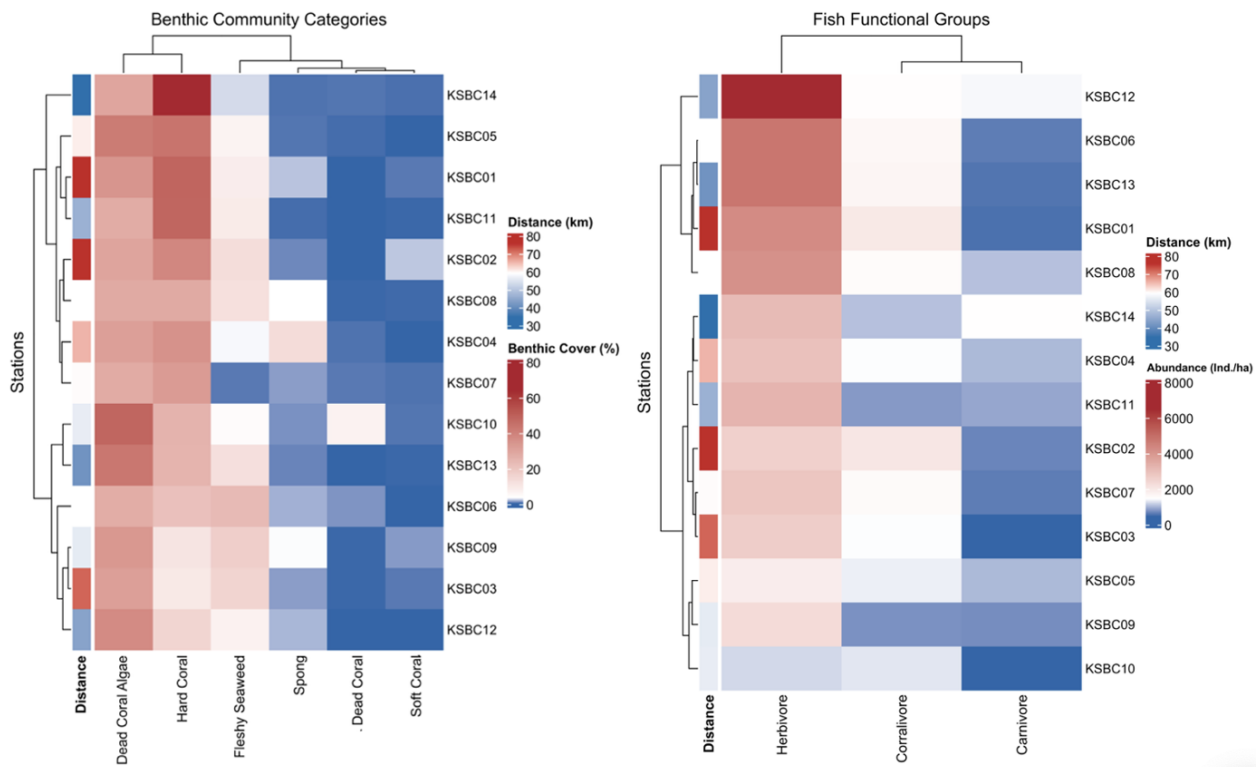


Figure 4. Hierarchical heatmaps display compositional similarity among sites for benthic categories (hard corals, dead corals, dead corals with algal overgrowth, soft coral, sponges, fleshy seaweeds) and reef fish functional groups (corallivores, herbivores, and carnivores)

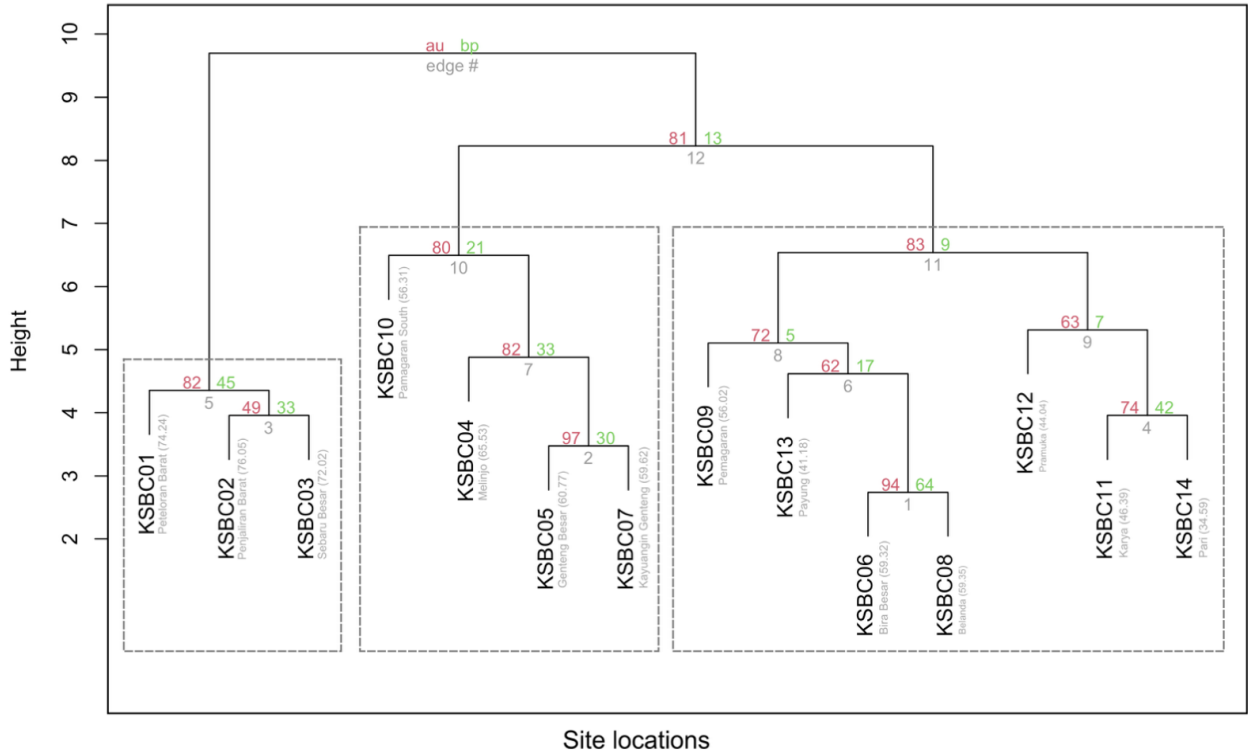


Figure 5. Cluster analysis of benthic and reef fish communities across 14 reef sites using pvclust dendrogram based on Euclidean distance matrices. Approximately Unbiased (AU) and Bootstrap Probability (BP) values are shown at each node, with AU values $\geq 95\%$ indicating strong support for the clusters. This analysis highlights site-specific similarities and differences in community composition, illustrating how proximity to Jakarta Bay structures both benthic and fish assemblages

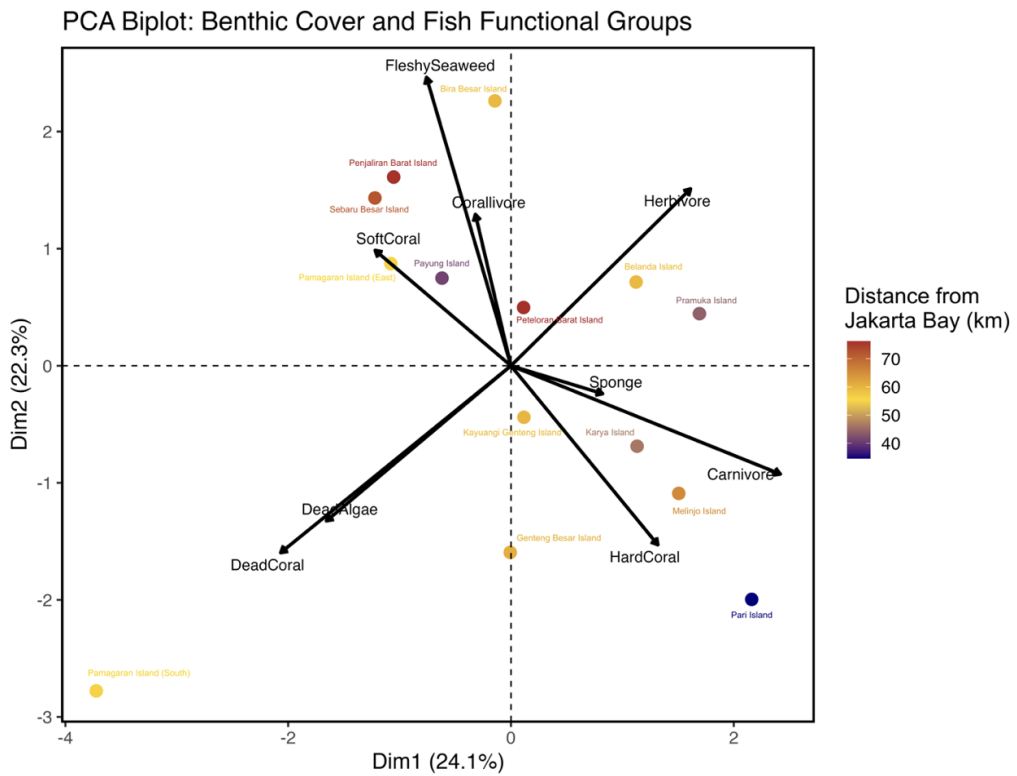


Figure 6. Principal Component Analysis (PCA) of benthic cover categories and reef fish functional groups across 14 location reef sites in the Seribu Islands, Indonesia. The PCA integrates proportional cover of benthic categories (hard corals, dead corals, dead corals with algal, sponges, soft coral, fleshy seaweeds) with relative abundance of reef fish functional groups (corallivores, herbivores, and carnivores) to visualize multivariate patterns of community structure

Discussion

Our results show substantial spatial variability in benthic composition across the Seribu Islands, particularly in hard coral cover, with several stations dominated by Dead Coral with Algae (DCA) (Figure 4). This pattern reflects the complex influence of local environmental conditions, geomorphology, and depth gradients on benthic community structure (Fahlevy et al. 2019). Consistent with previous observations, living hard corals accounted for only 32.5% of the substrate at Bira Island (Komala et al. 2024), whereas Pramuka Island exhibited high dominance of *Acropora* submassive (72.4% of total coral cover) (Permana et al. 2020), illustrating heterogeneous reef conditions and site-specific resilience. DCA also emerged as a prominent benthic component at multiple stations, with coverage ranging from 20.5 ha at Pamagaran Island (Batubara et al. 2023) to 37.1% at Seureudong Island (Najmi et al. 2023), and 30.3% at Kelapa Island (Fahlevy et al. 2019). These findings indicate that elevated DCA cover is pervasive throughout the Seribu Islands, serving as a consistent indicator of reef degradation influenced not only by anthropogenic pressures near Jakarta Bay but also by environmental variability at more remote northern sites. DCA represents areas of historical coral mortality, where previously living corals have gradually been overgrown by algae. Within the benthic cover assessment, DCA reflects past coral loss; however, these areas continue to function as important substrates for other benthic organisms, including coral recruits, thereby contributing to ongoing ecosystem processes.

Benthic community gradients along the distance

Our results highlight that the proximity of Jakarta Bay exerts only a weak and inconsistent influence on benthic cover composition across the Seribu Islands (Figure 2). Regression analyses revealed that the relationship between distance from Jakarta Bay and the variability in hard coral cover was weakly negative, with an extremely low coefficient of determination (R^2 : 0.023, p : 0.6). This suggests that areas located farther from Jakarta Bay paradoxically exhibited lower hard coral cover compared to sites closer to the bay. A similar trend was observed for Dead Coral with Algae (DCA), where the proportion of DCA also showed a negative but negligible relationship with distance (R^2 : 0.028, p : 0.57). These findings indicate that proximity to Jakarta Bay alone cannot sufficiently explain spatial patterns in benthic composition across the Seribu Islands. Instead, multiple local and regional factors likely drive the observed variability. Previous studies have shown that water quality parameters such as nutrient concentrations, turbidity, and sedimentation rates are known to strongly influence coral vitality and algal proliferation (Fauzanabri et al. 2021). Likewise, direct anthropogenic stressors including pollution, coastal development, tourism pressure, and destructive fishing practices substantially shape benthic assemblages, frequently favoring DCA dominance over live coral cover (Hermansyah et al. 2020). For example, blast fishing not only causes extensive coral mortality but also creates degraded substrates that are rapidly colonized by algae

(Hermansyah et al. 2020). Nonetheless, our results still suggest a subtle effect of Jakarta Bay, as sites closer to the bay exhibited slightly higher DCA cover than more distant islands. This pattern is consistent with the hypothesis that nutrient loading from sewage discharge and agricultural runoff in nearshore waters promotes algal blooms, suppresses coral recruitment, and ultimately accelerates the transition towards DCA-dominated reef states (Cindewiyani et al. 2019; Johnson et al. 2019; Hermansyah et al. 2020).

Spatial response of reef fish assemblages

With respect to the functional composition of reef fish (corallivores, herbivores, and carnivores), our findings revealed a clearer relationship with proximity to Jakarta Bay than that observed for benthic cover (Figure 3). Specifically, we detected a significant positive correlation between the abundance of corallivorous fishes and distance from Jakarta Bay (R^2 : 0.30, p : 0.043), indicating that sites located farther from the bay supported a greater representation of this functional group. In contrast, both herbivorous and carnivorous fishes exhibited weak negative correlations with distance, suggesting that their distributions are influenced by factors beyond simple proximity. Herbivorous fishes are pivotal in coral reef ecosystems, as they regulate algal growth, facilitate coral recruitment, recycle nutrients, and enhance reef resilience, thereby sustaining coral health, diversity, and ecological balance. Carnivorous fishes are essential in coral reef ecosystems by regulating prey populations, maintaining trophic balance, and indirectly supporting coral health through the control of herbivore and invertebrate populations that can otherwise disrupt reef structure. Compared with the findings of (Polónia et al. 2019), which demonstrated that the total abundance of corallivorous (Chaetodontidae) and herbivorous fish groups (Acanthuridae and Scaridae) exhibited a non-linear distribution pattern relative to their proximity to Jakarta Bay, the present results reveal a similar spatial heterogeneity. Such spatial variability aligns with broader ecological principles, suggesting that reef fish assemblages are influenced by the complex interplay of habitat characteristics, benthic composition, and management interventions (Polónia et al. 2019). These patterns underscore the complex interplay of environmental and anthropogenic drivers that regulate reef ecosystem structure. While distance from Jakarta Bay appears to exert some influence, particularly on corallivore assemblages, our analysis suggests that other stressors may play more dominant roles in shaping fish community composition across the Seribu Islands. Variations in water quality, localized anthropogenic pressures (e.g., tourism, pollution, destructive fishing), and the effectiveness of reef management regimes likely contribute substantially to the observed heterogeneity. Moreover, sedimentation processes represent an important factor influencing both benthic and fish communities in Seribu Islands. Seasonal inputs of terrigenous sediments, as well as resuspension of sand in shallow reef flats, have been shown to reduce coral abundance and hinder recruitment success (Madduppa et al.

2013; Cindewiyani et al. 2019). Such sediment-driven degradation may partially explain why reefs located farther from Jakarta Bay do not necessarily exhibit improved ecological conditions, as other stressors can offset the benefits of greater distance from urban centers. Taken together, these results highlight that spatial variation in functional fish groups and benthic cover within the Seribu Islands cannot be attributed to distance from Jakarta Bay alone. Instead, they reflect a multi-scalar interplay of water quality, sediment dynamics, and anthropogenic stressors, underscoring the need for integrated management approaches that consider both local and regional drivers of reef ecosystem change.

Ecological decoupling

Our study provides significant and unexpected insights into coral-fish dynamics in the Seribu Islands. Regression analyses (Figures 2 and 3) revealed contrasting patterns between coral life forms and fish assemblages. Hard coral cover exhibited a negative linear relationship with distance from Jakarta Bay, while corallivorous fishes, which are strongly dependent on hard coral substrates, displayed a positive linear relationship. Field observations confirmed that reefs closer to Jakarta Bay supported relatively high coral cover, largely dominated by fast-growing *Acropora* species. Although these corals have demonstrated the capacity for rapid recovery under favorable conditions, as documented by several studies across diverse reef systems (Nakamura et al. 2022), and their dominance results in structurally less complex habitats. Such reduced structural heterogeneity may limit their capacity to sustain diverse fish communities, particularly corallivores, despite the apparent abundance of coral cover. This finding challenges the widely held assumption that higher coral cover consistently equates to improved habitat quality and increased fish abundance, a view that has been broadly supported in earlier studies (Rosdianto et al. 2021; Melindo et al. 2025). Moreover, persistent sedimentation and anthropogenic stressors from Jakarta Bay likely destabilize corallivore populations, reducing their abundance even in areas with high coral cover. This mismatch suggests a temporal and functional decoupling between coral recovery and fish population dynamics. While *Acropora* can rebound quickly, fish populations require longer recovery periods due to life-history constraints such as reproduction, larval dispersal, and connectivity across reefs (van Dijk et al. 2024). The relatively high coral cover observed in the Seribu Islands near Jakarta is also supported by the presence of marine protected areas (Kepulauan Seribu National Park). These conservation zones are subject to minimal destructive anthropogenic activities, although intense tourism in the region remains a notable source of disturbance. This context supports our findings, where linear regression analyses revealed that sites closer to Jakarta Bay exhibited higher abundances of both carnivorous and herbivorous fishes (Figure 3). This pattern suggests that these areas are characterized by comparatively low fishing pressure and reduced exploitation, a condition that aligns with previous studies from Fitzpatrick et al. (2015), such circumstances likely

enhance the ecological resilience of reef systems by allowing functional fish groups to persist at higher levels, thereby maintaining critical ecosystem processes. Collectively, these results demonstrate that coral cover alone is not a sufficient indicator of ecosystem resilience. Instead, habitat complexity, species-specific life histories, and chronic environmental stressors must be considered when evaluating reef health. This has direct implications for conservation and management strategies in the Seribu Islands, particularly in balancing coral recovery with the restoration of functional fish communities (Razak et al. 2022).

Management implications

A key outcome of our study is revealed through the multivariate and clustering analyses (Figures 5 and 6). Despite variability in benthic cover and functional fish composition, these analyses consistently identified three distinct clusters of reef sites across the Seribu Islands. The configuration of these clusters closely aligned with proximity to Jakarta Bay, indicating that distance is a fundamental structuring factor, even when individual benthic and fish variables show weak or inconsistent correlations with distance. This pattern suggests that, while benthic and functional fish assemblages respond differently to local and regional stressors, their combined community signatures converge to reveal clear spatial structuring (Hynes et al. 2025). Dendrogram analysis revealed that reef sites nearest to Jakarta Bay are compositionally distinct from those located farther offshore, reflecting differential exposure to environmental and anthropogenic pressures (Figure 5). The emergence of three discrete clusters underscores the integrative value of multivariate approaches for informing management strategies. These clustering patterns provide a robust scientific basis for the formulation of management policies, including the designation of protection zones and delineation of marine management boundaries. By leveraging these clustering outcomes, management priorities can be strategically directed toward areas exhibiting the most vulnerable or ecologically critical conditions, optimizing resource allocation and enhancing the effectiveness of conservation strategies. Overall, this clustering-based approach offers a practical, evidence-driven framework for the sustainable management of coral reef ecosystems. Our findings of this study offer empirical insights that can guide adaptive management strategies and provide scientifically grounded recommendations, thereby contributing to the effective conservation and sustainable management of the reef ecosystem.

In conclusion, this research reveals that coral reef ecosystems in the Seribu Islands exhibit divergent ecological responses to spatial gradients of urban influence. While hard coral cover showed a gradual decline with increasing distance from Jakarta Bay, corallivorous fish assemblages displayed an opposite pattern, with higher abundance at offshore sites. These contrasting trends underscore the complexity of ecological processes shaping reef communities and highlight the need to consider both benthic and fish components when assessing ecosystem

health. This study bridges ecological diagnostics with spatial planning, offering a scalable framework for managing coral reef resilience in rapidly urbanizing coastal regions. Overall, our findings demonstrate that proximity to major urban centers exerts scale-dependent and multidimensional effects on coral reef structure and function, with important implications for conservation planning and management in urbanized seascapes.

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