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Spatial and depth patterns of reef fish assemblages in Pulau Tenggol, Malaysia and their links to benthic composition

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Abstract. *Syafruddin R, Qamarina MFN, Safuan CDM, Yusuf Y, Afiq-Firdaus AM, Bachok Z. 2026. Spatial and depth patterns of reef fish assemblages in Pulau Tenggol, Malaysia and their links to benthic composition. Biodiversitas 27 (1): d270148. https://doi.org/10.13057/biodiv/d270148.* A total of 142 reef fish species (71 genera, 33 families) were recorded at Pulau Tenggol in the South China Sea, Peninsular Malaysia, based on surveys conducted in May 2024 across five stations and three depth strata (5, 10, and 15 m), yielding 12 station-depth transects. Fish assemblages were surveyed using belt transects, while major benthic categories and Hard coral growth-forms composition were quantified using Coral Video Transects and analyzed with Coral Point Count with Excel extensions (CPCe). Fish indices, including fish density, species richness, Shannon diversity, Simpson diversity, and Pielou's evenness, showed no significant differences among stations or depths (Kruskal-Wallis test, $p>0.05$), whereas species composition differed significantly across both spatial and depth gradients (PERMANOVA, $p>0.05$). Major benthic categories and hard coral growth-forms did not differ significantly with depth ($p>0.05$) but showed significant variation among stations ($p>0.05$). Mantel tests indicated that fish assemblage structure was significantly associated with hard coral growth-forms ($p\leq 0.05$), while no significant correlation was detected with major benthic categories ($p>0.05$). Fish density was positively correlated with *Acropora staghorn*/branching growth-forms (ρ: 0.783, p: 0.004, FDR: 0.047; partial ρ: 0.769, p: 0.006, FDR: 0.073) and negatively correlated with encrusting corals (ρ: -0.790, p: 0.004, FDR: 0.047; partial ρ: -0.775, p: 0.005, FDR: 0.073). Healthy hard coral cover was strongly associated with obligate corallivores (ρ: 0.757, p: 0.004, FDR: 0.015; partial ρ: 0.716, p: 0.013, FDR: 0.017) and Chaetodontidae (ρ: 0.669, p: 0.017, FDR: 0.035; partial ρ: 0.616, p: 0.044, FDR: 0.027). Overall, coral health and growth-form complexity were stronger predictors of reef fish assemblage structure than major benthic categories.

Keywords: Coral growth forms, corallivore, density, PERMANOVA, South China Sea

INTRODUCTION

The structural complexity and diversity of coral reef substrates are vital for creating habitats that support a wide variety of marine fish species (Ménard et al. 2012; Richardson et al. 2017; Oren et al. 2023). Fish depend on these complex environments for shelter, foraging, and reproduction, with many species adapting their behaviors and ecological niches to the diverse features offered by the reef (Helder et al. 2022). Within coral reef ecosystems, reef fish occupy distinct ecological niches that are primarily defined by their trophic-functional groups, which are determined by their feeding behaviors (Triki and Bshary 2019).

Herbivorous fish play a crucial role in suppressing algal growth, and high herbivore abundance helps maintain low algal cover, supporting overall reef resilience (Tebbett et al. 2018; Randazzo-Eisemann et al. 2024). At the same time herbivores may associate with different non-coral substrate types, such as rock, rubble, and dead coral as grazing surfaces (Robinson et al. 2020). Carnivorous fish function as key predators, regulating population dynamics by preying on smaller fish and invertebrates, thereby promoting ecosystem stability (Mihalitsis et al. 2021, 2022). Corallivores, particularly those belonging to Chaetodontidae, exhibit a strong dependence on hard corals due to their specialized diet of coral polyps (Putra et al. 2024). This dietary reliance makes them highly sensitive to coral health, leading to their frequent use as indicator species in reef health assessments (Iskandar et al. 2020). Coral reef ecosystems include various benthic elements in addition to hard corals, each supporting different fish groups (Aulia et al. 2021). Classifying reef fish by their functional groups provides a robust framework for understanding their ecological roles and interactions with benthic assemblages (Sheppard et al. 2023).

While many studies use major benthic categories or total coral cover to link fish and habitats, coral growth forms often better predict overall fish assemblages because they capture fine-scale structural complexity that broad categories or total coral cover overlook (Komyakova et al. 2013; Coker et al. 2017; Darling et al. 2017; Oren et al. 2023). Thus, comparing major benthic categories to growth-form complexity shows stronger links between habitats and overall fish abundances or fish composition patterns (Richardson et al. 2017; Ferreira et al. 2025). The structure of reef fish communities is shaped by multiple environmental factors, including spatial and depth factors, as different species exhibit distinct depth preferences based on their ecological requirements (Pereira et al. 2018). Factors such as light availability, prey abundance, and the presence of suitable shelter play crucial roles in determining these depth-associated patterns; as a result, fish assemblages vary across depth gradients (Jankowski et al. 2015; Heyns-Veale et al. 2016; Smallhorn-West et al. 2017).

The east coast of Peninsular Malaysia, especially Terengganu, is home to several ecologically rich islands popular with tourists, among which Pulau Tenggol stands out for its relatively healthier reefs compared to other marine parks such as Pulau Redang, Pulau Perhentian, and Pulau Kapas (Tan et al. 2020). Surveys conducted in 2020 reported live coral cover at around 37.83%, indicating that Tenggol's reefs are in better condition than nearby sites but still require ecological attention (Lee et al. 2020). However, most existing assessments have focused on benthic condition, leaving gaps in knowledge about reef fish communities, particularly how they vary across depth gradients and interact with benthic habitats.

This study seeks to address that gap by examining the structure and composition of fish assemblages at Pulau Tenggol in relation to benthic features. We hypothesize that fish assemblage structure, particularly species composition, differs significantly among the three surveyed depth zones (5 m, 10 m, and 15 m), with shifts in dominant species across depths. We further hypothesize that corallivorous fish will be positively associated with areas of high healthy hard coral cover. In contrast, an herbivore fish will be positively associated with non-coral substrates, specifically rock, rubble, dead coral, and dead coral with algae.

MATERIALS AND METHODS

Study area

Pulau Tenggol, located off the east coast of Peninsular Malaysia in the state of Terengganu, is less popular as a general tourist destination compared to Pulau Redang and Pulau Perhentian. However, it is widely recognized among SCUBA divers for its exceptional marine biodiversity. The island lies approximately 30 km from the mainland town of Dungun, with primary access via Dungun Jetty, and forms part of the Terengganu Marine Parks, a designated marine protected area encompassing 591.37 km² that underscores its ecological significance and conservation importance (Safuan et al. 2022). The reefs around Pulau Tenggol are characterized by fringing reef structure. Visibility exceeding 10 m during each survey and low to moderate currents within slack tide throughout the sampling period.

Ecological surveys for this study were conducted at five designated dive sites around Pulau Tenggol across three depths (5, 10, and 15 m) with one transect established at each station and depth combination (Figure 1). However, not all stations contained all three depth strata due to local reef morphology. The 5 m depth could not be surveyed at Coral Garden and The Edge because of a steep reef slope. In comparison, the 15 m depth was excluded at Gua Rajawali because the substrate consisted primarily of unconsolidated sand with no coral reef habitat (Table 1). These depth exclusions resulted in a total sample size of (*n*: 12) transects, comprising five transects at 10 m, four transects at 15 m, and three transects at 5 m (Table 1).

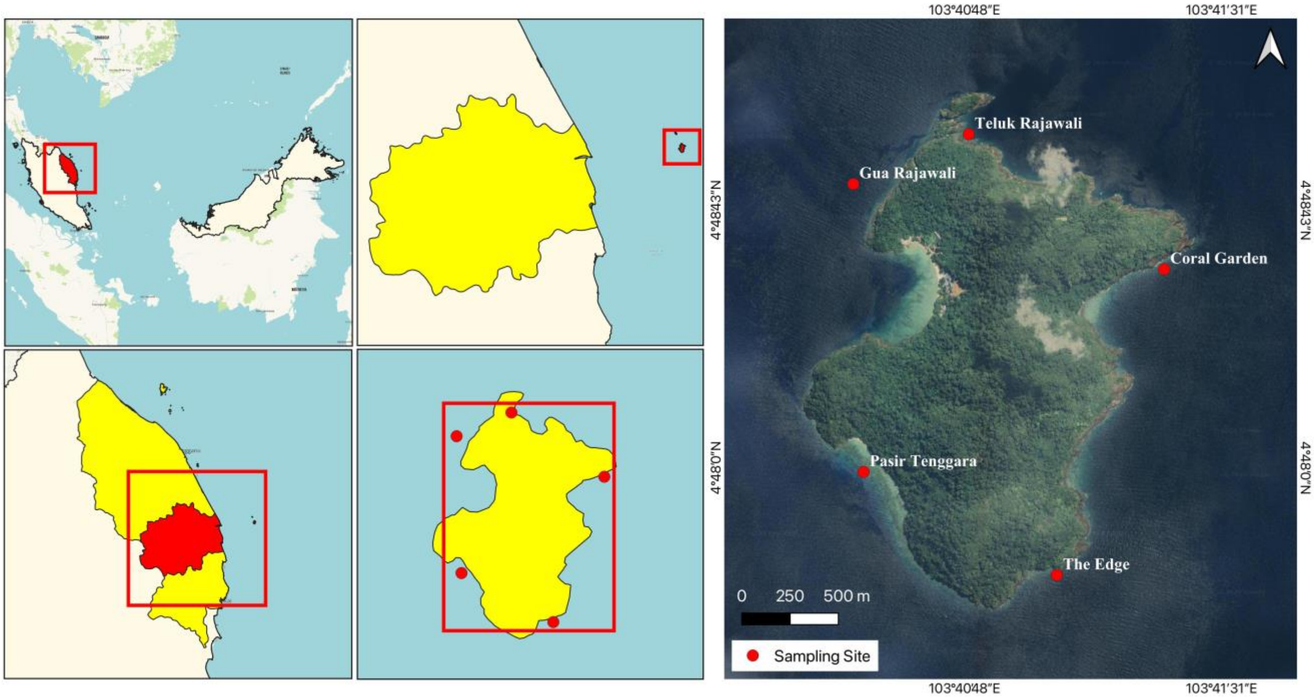

Figure 1. Map showing the location of Pulau Tenggol, Malaysia, and sites where coral reef fish surveys and benthic surveys were conducted

Table 1. List of sampling stations and the coordinates with the surveyed depth of each station at Pulau Tenggol

Station	Entry coordinate	Depth		
		5m	10m	15m
Station 1 (Coral Garden)	4.809251, 103.689327		✓	✓
Station 2 (Teluk Rajawali)	4.815542, 103.680202	✓	✓	✓
Station 3 (The Edge)	4.795009, 103.684318		✓	✓
Station 4 (Pasir Tenggara)	4.7998086, 103.6752984	✓	✓	✓
Station 5 (Gua Rajawali)	4.813223, 103.67482	✓	✓	

Note: ✓: Depth that was survey

Field survey

Surveys were undertaken in May 2024 at Pulau Tenggol across all stations and depths, except for those excluded as specified in Table 1. Two primary components were conducted: a reef fish survey and a benthic survey, both carried out via SCUBA. The reef fish survey employed a belt transect technique, with fish enumerated in situ by the same trained observer to minimize observer bias, at a constant speed of approximately 5 m min^{-1}. Fish were identified underwater and subsequently verified post-dive using the “Field Guide to Tropical Reef Fishes of the Indo-Pacific” book by Allen et al. (2020) and FishBase (Froese and Pauly 2024), with uncertain taxa grouped at the genus level. At each station and depth combination, a 100 m transect line was established and subdivided into four 20 m segments, separated by 5 m gaps. Each belt transect measured 5 m in width, 5 m in height, and 20 m in length per segment, resulting in a survey volume of 500 m^3 per segment. Coral Video Transect (CVT) recordings were conducted along the same segment with four video segments per transect by a trained scientific diver using an Olympus TG-6 camera in underwater wide mode (25 mm equivalent focal length). The diver also maintained a steady swimming speed of approximately 5 m min^{-1} while maintaining a consistent height of ~0.5 m above the reef surface to ensure a stable field-of-view. Illumination was provided by an underwater torchlight directed toward the benthos to enhance color accuracy and visibility under variable ambient light conditions. This setup ensured consistent video quality suitable for extracting benthic cover and habitat-structure information (Safuan et al. 2015).

Data analysis

Density (DEN) of fish was calculated as the number of individuals per 500 m^3 (ind/500 m^3) based on abundance data. All reef fish were identified to species level and assigned to trophic categories. Trophic groups followed an adjusted version of Pratchett et al. (2011) comprising carnivores (CV), invertivores (IV), herbivores (HV), planktivores (PV), omnivores (OV), obligate corallivores (OCLV), and facultative corallivores (FCLV) (Table 2). Classification of corallivorous species was further informed by Cole et al. (2008), with species described as specialist coral feeders assigned as obligate and those feeding on coral only occasionally assigned as facultative, except for Scaridae, which were retained in herbivorous categories because their occasional coral biting reflects grazing behavior rather than true corallivore (Charendoff et al. 2023; Tebbett et al. 2024). Additional species-level dietary information was obtained from FishBase (Froese and Pauly 2024), which provided verified diet records used to assign functional groups (Ladds et al. 2018). Other fish indices, species richness (SR), Shannon diversity (H), Simpson diversity (D), and Pielou’s evenness (J), were calculated following standard ecological procedures (Wu et al. 2025).

Coral Video Transect (CVT) footage from each segment was processed by extracting 50 still images per video at systematic intervals using Video Image Master software. Each transect consisted of four CVT segments, resulting in 200 still images per transect. All images were analyzed in Coral Point Count with Excel extensions (CPCe) using a 5×10 stratified random grid (50 points per image). This produced a total of 2,500 points per segment and 10,000 points per transect, with the minimum measurable increment in percent cover set at 0.01%, reflecting the discrete nature of CPCe point-count data. Points were classified into major benthic categories, comprising biotic and abiotic components. Biotic components included healthy hard coral (HHC), soft coral (SC), bleached hard coral (BC), algae (ALG), and other invertebrates (OI); abiotic components included dead coral (DC), dead coral with algae (DCA), rubble (RB), rock (RCK), and sand (SD). Minor categories further subdivided all hard corals (HC) into growth forms following Safuan et al. (2022). Point classifications were first averaged within each segment and then pooled across the four segments to obtain transect-level benthic cover estimates. All image annotation was conducted by the same trained annotator.

Statistical analysis

All statistical analyses were conducted in RStudio. Fish indices were averaged at the transect level, and all univariate hypothesis tests were conducted using transect-level data. Due to the unbalanced sampling design (only one transect per station and depth combination; *n*: 12), univariate comparisons among stations and depths were treated as exploratory and interpreted with caution due to limited statistical power. Differences in univariate metrics across depths were assessed using Kruskal-Wallis tests with the effect size. Relationships between univariate fish indices and benthic components were examined using Spearman correlations, with partial Spearman correlations applied to account for depth effects using the stats and ppcor packages. Multiple correlations were corrected for false discovery rate (FDR) using the Benjamini-Hochberg procedure to account for potential Type I errors.

Table 2. Functional group categories of coral reef fishes

Trophic group	Definition	References
Carnivore (CV)	Consume other animals (excluding IV and CLV)	(Putra 2023)
Invertivore (IV)	Exclusively consume small invertebrates (excluding CLV)	(Chen et al. 2022b)
Obligate Corallivore (OCLV)	Exclusively consume Hard coral polyps	(Cole et al. 2008; Putra et al. 2024)
Facultative Corallivore (FCLV)	Consume Hard coral polyps with other alternative diets	(Cole et al. 2008; Putra et al. 2024)
Herbivore (HV)	Exclusively targeted and consume plant-based materials	(Tebbett et al. 2024)
Planktivore (PV)	Exclusively consume plankton	(Siqueira et al. 2021)
Omnivore (OV)	Consume plant-based materials and other animals	(Chong-Seng et al. 2012)

For multivariate analyses, species abundance data were log-transformed log (x+1) and Bray-Curtis dissimilarity matrices were constructed in vegan. Segment-level data were used for exploratory non-metric multidimensional scaling (nMDS) to visualize fine-scale patterns in raw species composition across stations and depths. In contrast, fish and benthic composition data were aggregated at the transect level for Permutational Multivariate Analysis of Variance (PERMANOVA), Permutational Analysis of Multivariate Dispersions (PERMDISP), Canonical Analysis of Principal Coordinates (CAP), Similarity Percentages (SIMPER), and Mantel test.

Differences in fish species composition among stations and depths were tested using PERMANOVA (adonis2), applying partial (Type III) sums of squares to accommodate the unbalanced design and 999 permutations to assess statistical significance. Homogeneity of multivariate dispersion was examined using PERMDISP (betadisper) prior to interpretation of PERMANOVA results. CAP was then used to visualize group separation constrained by the tested factors, and SIMPER analysis was conducted to explore and visualize the taxa contributing most to observed between-group dissimilarities. Species-level significance in SIMPER was evaluated using a one-sided permutation test (999 permutations) against a null distribution generated by randomizing group labels; species with p>0.05 were considered significant, and only those cumulatively explaining the first 70% of Bray-Curtis dissimilarity were retained.

To further evaluate how fish assemblage structure relates to benthic composition, Mantel and partial Mantel tests were performed using transect-level Bray-Curtis dissimilarity matrices to explore the correlation of fish assemblage with major benthic categories, composition and HC growth form composition, as the partial Mantel framework allows depth to be controlled explicitly. Together, they provide an exploratory, non-parametric assessment of variation in major benthic categories and HC growth forms corresponded to differences in fish assemblage composition. Complementary Spearman and partial Spearman correlations with FDR correction, also accounting for depth, highlighted more targeted relationships between OCLV, FCLV, and Chaetodontidae with Hard Coral, and between HV and Scaridae with Algae and possible grazing substrate (RCK, RB, DC, DCA).

RESULTS AND DISCUSSION

Coral reef fish biodiversity

This study recorded a total of 33 families, 71 genera, and 142 species of coral reef fish at Pulau Tenggol, including several species observed outside the survey area; however, a total of 28 families, 63 genera and 93 species were identified in the surveyed area, with each species classified according to its trophic group. The total biodiversity, including several species observed outside the surveyed transects, which were documented and added to the inventory of biodiversity list and their IUCN Red List statuses were assessed. However, only transect-derived dataset was used for data analysis and statistical analyses for each figure and table. Bar graphs illustrated the SR of each family and trophic group, while the heatmap was generated using log(x+1) transformed DEN data to stabilise variance and reduce the influence of high abundance species, thereby improving interpretability while preserving underlying distributional patterns to enhance the detection of among-group differences (Clarke and Green 1988; Májeková et al. 2016; Dees et al. 2025) (Figures 2 and 3). Among the surveyed families, Pomacentridae exhibited the highest SR, with 26 species, followed by Labridae (19 species) and Scaridae (18 species).

In terms of overall mean family DEN, Pomacentridae demonstrated the highest mean DEN (87.520 ind/500 m^3), followed by Scaridae (11.959 ind/500 m^3) and Labridae (6.833 ind/500 m^3). A total of 10 species of Chaetodontidae were recorded, reflecting a moderate level of SR within this family. For trophic composition, HV represented the most species-rich trophic group (29 species), followed by OV (27 species) and CV (26 species), with OV exhibiting the highest total mean trophic group DEN (69.167 ind/500 m^3), followed by PV (23.9 ind/500 m^3) and HV (13.688 ind/500 m^3). Both OV and PV were dominated by Pomacentridae, 17 and 6 species respectively, with five species from this family accounting for the highest overall mean densities observed: *Amblyglyphidodon leucogaster* (19 ind/500 m^3), *Chromis viridis* (17.02 ind/500 m^3), *Pomacentrus alexanderae* (11.229 ind/500 m^3), *Neoglyphidodon nigroris* (9.917 ind/500 m^3), and *Pomacentrus moluccensis* (8.042 ind/500 m^3). Family Caesionidae contributed four PV species (3.854 ind/500 m^3).

Herbivorous fishes, predominantly from Scaridae (18 species; 11.958 ind/500 m^3) and Siganidae (5 species; 0.938 ind/500 m^3), were observed either in small aggregations (Scaridae) or pairs (Siganidae). CV exhibited lower mean densities (3.5625 ind/500 m^3) despite their relatively high SR (26 species). Large predatory fish such as Epinephelidae (groupers; 2 species, 0.729 ind/500 m^3) and Lutjanidae (snappers; 3 species, 0.703 ind/500 m^3) were present, while invertivores displayed moderate mean densities (6.083 ind/500 m^3) with 18 species, including *Thalassoma lunare*, which was frequently observed in small groups. OCLV were represented mainly by Chaetodontidae (3 species; 1.708 ind/500 m^3), with additional species from Labridae such as *Labrichthys unilineatus* (0.417 ind/500 m^3) and *Diproctacanthus xanthurus* (0.125 ind/500 m^3). FCLV were mostly dominated by Chaetodontidae (6 species; 0.479 ind/500 m^3), with additional representatives from Tetraodontidae (*Arothron nigropunctatus*, 0.0417 ind/500 m^3; *Arothron stellatus*, 0.0208 ind/500 m^3), Balistidae (*Balistapus undulatus*, 0.104 ind/500 m^3; *Balistoides viridescens*, 0.0208 ind/500 m^3), and Monocanthidae (*Cantherhines dumerilii*, 0.083 ind/500 m^3).

The dominance of Pomacentridae observed in this study is consistent with patterns reported from other Southeast Asian reefs and nearby Bidong Island (Fahlevy et al. 2018; Afiq-Firdaus et al. 2023). The high abundance of Scaridae aligns with the extremely low algal cover recorded at Pulau Tenggol, reflecting their key role as herbivorous grazers in maintaining reef condition (Wilson et al. 2021). Although Labridae exhibited the second-highest SR, they ranked third in mean DEN, likely due to predominantly solitary foraging behavior among most species, in contrast to the group-feeding behavior of Scaridae (Fulton and Bellwood, 2002; Michael et al. 2013; Guerra et al. 2023). The moderate SR of Chaetodontidae further suggests relatively healthy coral reef conditions, as this family is often associated with live coral availability (Putra et al. 2024).

Across trophic groups, OV were dominated by Pomacentridae with generally flexible feeding strategies, although several taxa (e.g., *Neopomacentrus* spp., and *Chromis* spp.) primarily consumed plankton (Leray et al. 2019; Chen et al. 2022a). PV exhibited high densities but comparatively low SR, driven by dominance of schooling taxa such as *Chromis* spp. and fusiliers. HV were mainly represented by Scaridae and Siganidae, foraging in schools and pairs, respectively (Mirbach and Brandl 2016; Mou-Tham et al. 2018). In contrast, CV and IV displayed relatively high SR but lower densities, reflecting solitary hunting strategies typical of these functional groups, particularly among wrasses, where risk-sensitive foraging reduces competition but increases variability in feeding success (Unsworth and Cullen-Unsworth 2012; Casey et al. 2017; Bogdan et al. 2020). OCLV and FCLV were the least abundant groups, largely dominated by Chaetodontidae, consistent with their specialized coral-polyp feeding strategies and limited trophic flexibility (Baird et al. 2025). Collectively, these patterns highlight a functionally diverse assemblage structured along a classic trophic pyramid, supporting ecosystem resilience through complementary roles across trophic levels (Valdivia et al. 2017; Favoretto et al. 2020; Seguin et al. 2022).

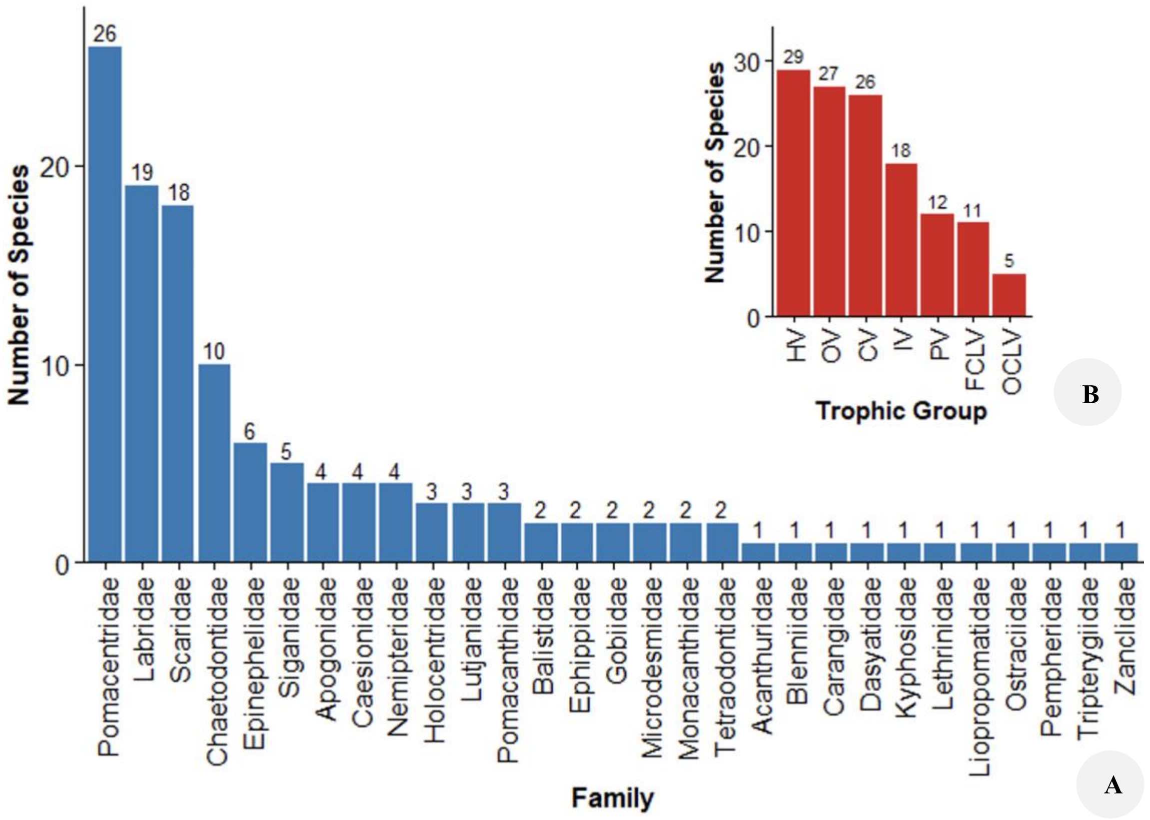

Figure 2. A. Bar chart showing species richness by family. B. Bar chart showing species richness by trophic group (Note: CV: Carnivore, IV: Invertivore, PV: Planktivore, OV: Omnivore, HV: Herbivore, OCLV: Obligate corallivore, FCLV: Facultative corallivore)

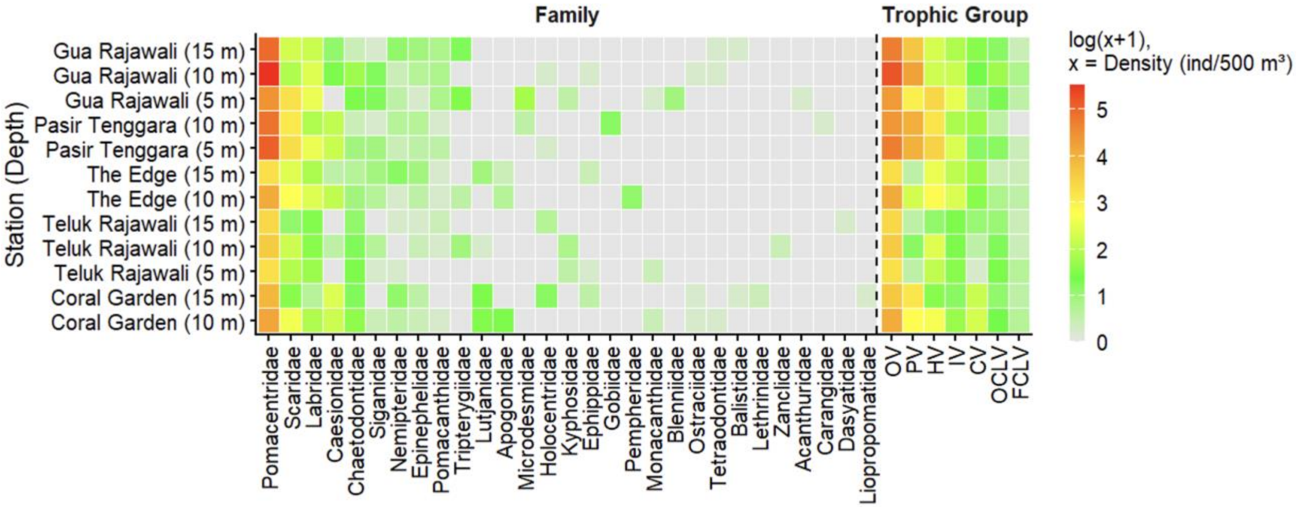

Figure 3. Heatmaps depicting the log(x+1) transform of mean density for fish families and trophic groups across each survey area (Note: CV: Carnivore, IV: Invertivore, PV: Planktivore, OV: Omnivore, HV: Herbivore, OCLV: Obligate corallivore, FCLV: Facultative corallivore, ind: individual)

Benthic cover

HHC generally dominated the major benthic category composition across transects around Tenggol Island, with a mean cover of approximately 32.30% per transect (Figure 4). The highest HHC cover was recorded at Teluk Rajawali (5 m) with 52.96%, followed by Gua Rajawali (5 m) (45.02%) and Teluk Rajawali (10 m) (44.09%). In contrast, lower HHC cover was observed at The Edge (15 m) (8.17%) and The Edge (10 m) (12.45%), where RB and SC contributed relatively higher proportions to the major benthic category composition (Figure 4). SC cover ranged from 1.60-33.10% across transects (mean: 15.0%), while RB ranged from 5.70-51.40%, indicating substantial spatial variability in these components (Figure 4). BC cover was consistently low across all transects, ranging from 0-8.16% (mean: 0.8%), with the highest BC recorded at Pasir Tenggara (5 m) at 8.16%. Algal cover was extremely low across all transects, with the highest measured value being 0.11%. No large macroalgae were recorded anywhere in the survey area, a pattern consistent with strong herbivory and sustained grazing pressure that suppresses macroalgal development on many well-grazed coral reefs (Sarkar et al. 2020).

The HC growth forms included several *Acropora* spp. such as staghorn/branching (ASTAG), tabulate (ATB), bottlebrush (ABO), bushy (ABU), corymbose (ACO), and digitate (ADG) types. These were followed by non-*Acropora* categories, which featured encrusting (EN), platy (PL), massive (MS), branching (BR), sub-massive (SUBMS), free-living (FREE), columnar (COL), and tabulate (TB) forms. Spatial contrasts among stations showed variable levels of community differentiation (Table 3). The highest Bray-Curtis dissimilarities were recorded between Teluk Rajawali and Pasir Tenggara (0.698), as well as between Coral Garden and Pasir Tenggara (0.682). Conversely, relatively low Bray-Curtis dissimilarity values were observed between Pasir Tenggara and Gua Rajawali (0.436), Teluk Rajawali and Gua Rajawali (0.445), and Teluk Rajawali and Coral Garden (0.452). These patterns are reflected in the specific growth form dominance observed across various stations and depths.

Teluk Rajawali and Coral Garden exhibited the highest mean EN coverage among the surveyed sites, at 25.17% and 27.69%, respectively. At Coral Garden, EN growth form coverage measured 15.68% at the 10 m depth and increased to 39.70% at 15 m. Teluk Rajawali maintained high EN levels across the vertical profile, with 27.11% at 5 m and 19.61% at 10 m, reaching a maximum of 28.80% at 15 m. The low dissimilarity values between Pasir Tenggara and Gua Rajawali coincided with a high prevalence of ASTAG at both stations. At Pasir Tenggara, ASTAG coverage was 27.30% at 5 m and 19.54% at 10 m. Gua Rajawali displayed variations in dominant growth forms across depths; PL was the most prevalent category at 5 m (20.49%), while ASTAG coverage measured 18.16% at 10 m and 26.44% at 15 m. The Edge recorded the lowest overall coral cover across all transects. At this station, ASTAG coverage was 5.49% at 10 m, while at 15 m, MS (3.62%) and EN (2.90%) were the most frequent growth forms. Other notable growth form occurrences included ATB at Teluk Rajawali (7.22% at 5 m) and PL at Gua Rajawali (14.17% at 10 m).

Reef fish indices

Boxplots (Figure 5), summarizing data using medians and interquartile ranges (IQRs), illustrate transect-level variation in DEN, SR, H, D, and J in across stations and depths. DEN ranged from 38 to 278 individuals/500 m³ per transect, with the lowest value recorded at Teluk Rajawali (15 m) and the highest at Gua Rajawali (10 m). SR varied between 11 and 28 species, with the lowest count recorded at Teluk Rajawali (15 m) and the highest at Pasir Tenggara (5 m). H, D and J ranged from 1.89 to 2.56, 0.77 to 0.89, 0.68 to 0.87, respectively. Across most stations, SR, H, and D generally declined with increasing depth. At Coral Garden, median SR decreased from 21.5 species at 10 m to

13.5 species at 15 m, with the interquartile range (IQR) narrowing from 9.0 to 4.5, while median H declined from 2.57 to 2.02 and variability decreased (from an IQR of 0.45 to 0.10). Teluk Rajawali deviated from this pattern, with SR peaking at 10 m (median: 17.5 species). Evenness (J) remained relatively stable across stations and depths, with consistently narrow IQRs (<0.12). In contrast, DEN showed stronger site-specific variation, reaching its highest median at Gua Rajawali (10 m; 261.5 individuals/500 m³) and declining with depth at Pasir Tenggara from 204.0 ind/500 m³ (5 m) to 140.5 ind/500 m³ (10 m).

Based on Table 4, statistical analysis revealed no significant value detected between station and depth in DEN, SR, H, D, J, HHC (all FDR $p > 0.05$). However, the magnitude of the differences varied; The DEN showed the highest degree of variation (H-Statistic: 9.372) with a large effect size (0.767), and HHC followed closely (H-statistic: 8.628, effect size: 0.661). These moderate-to-large effect sizes suggest that while not statistically significant, likely due to high variance or limited sample size, yet there are observable differences in DEN and HHC between stations. In contrast, other fish indices showed much less variation; SR and J displayed small effect sizes (0.262 and 0.249, respectively), while H and D indices were nearly identical across stations (effect sizes>0.1).

The influence of depth was even less pronounced than that of Station, with all adjusted p-values exceeding 0.59. The H-statistics for depth were uniformly lower, ranging from a maximum of 3.296 for SR to a minimum of 0.138 for J. The effect sizes for all depth-related indices were small (ranging from -0.093 to 0.174), indicating that depth had no detectable impact on the community structure or coral health in this study. Notably, J returned an FDR p: 0.933, signifying almost total uniformity in species distribution across the depth gradients.

Across all tests, the failure to reach the significance threshold (α: 0.05) means that the 95% Confidence Intervals for these fish indices and HHC encompass zero. This indicates that the observed differences in H-statistics and effect sizes cannot be distinguished from random sampling noise with 95% certainty. The large effect sizes for DEN and HHC with different stations suggest potential areas for closer examination. Based on Table 5, the descriptive patterns still reveal clear ecological contrasts across the reef. Pasir Tenggara shows the highest median DEN at 190.250 ind/500 m³ (IQR: 22.000), followed closely by Gua Rajawali at 172.000 ind/500 m³ (IQR: 69.125), whereas Teluk Rajawali records the lowest DEN at 40.5 ind/500 m³ (IQR: 8.375). SR mirrors this pattern, with Pasir Tenggara reaching 23.500 species (IQR: 4.000) and the shallow 5 m depth layer showing 23.250 species (IQR: 7.750), compared to the lower SR at Teluk Rajawali 12.000 species (IQR: 3.000).

Table 3. Average Bray-Curtis dissimilarity of hard coral growth form composition across depths and stations

Category	Contrast	Average dissimilarity
Depth	10 m-15 m	0.529
	10 m-5 m	0.428
	15 m-5 m	0.586
Station	Coral Garden-Teluk Rajawali	0.452
	Coral Garden-The Edge	0.498
	Coral Garden-Pasir Tenggara	0.682
	Coral Garden-Gua Rajawali	0.566
	Teluk Rajawali-The Edge	0.504
	Teluk Rajawali-Pasir Tenggara	0.698
	Teluk Rajawali-Gua Rajawali	0.445
	The Edge-Pasir Tenggara	0.641
	The Edge-Gua Rajawali	0.493
	Pasir Tenggara-Gua Rajawali	0.436

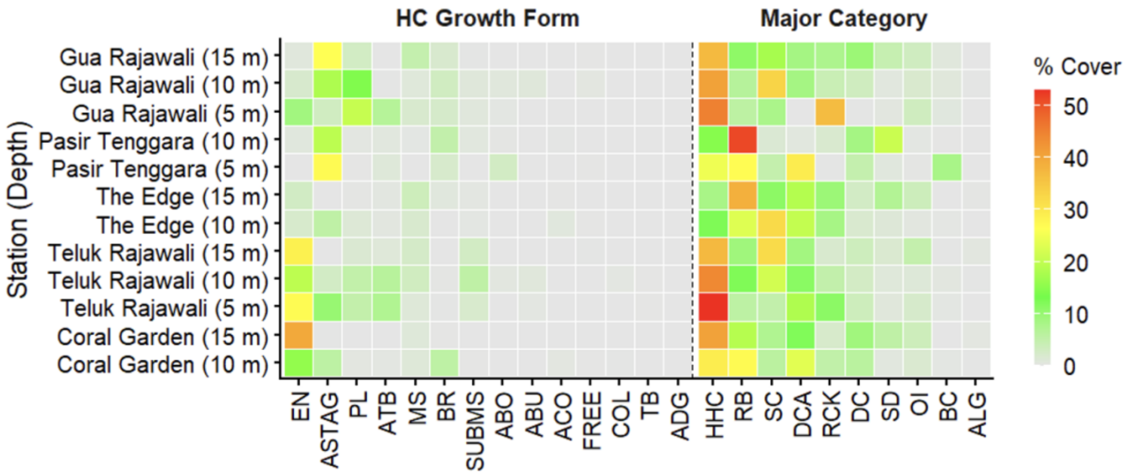

Figure 4. Major benthic component (% cover) across transects at different stations and depths (HC: Hard Coral, SC: Soft Coral, BC: Bleached Coral, ALG: Algae, OI: Other Invertebrates, DC: Dead Coral, DCA: Dead Coral with Algae, RCK: Rock, RB: Rubble, SD: Sand; ASTAG: *Acropora* staghorn/branching, ATB: *Acropora* tabulate, ABO: *Acropora* bottlebrush, ABU: *Acropora* bushy, ACO: *Acropora* corymbose, ADG: *Acropora* digitate; EN: Encrusting, PL: Platy, MS: Massive, BR: Branching, SUBMS: Sub-massive, FREE: Free-living, COL: Columnar, TB: Tabulate)

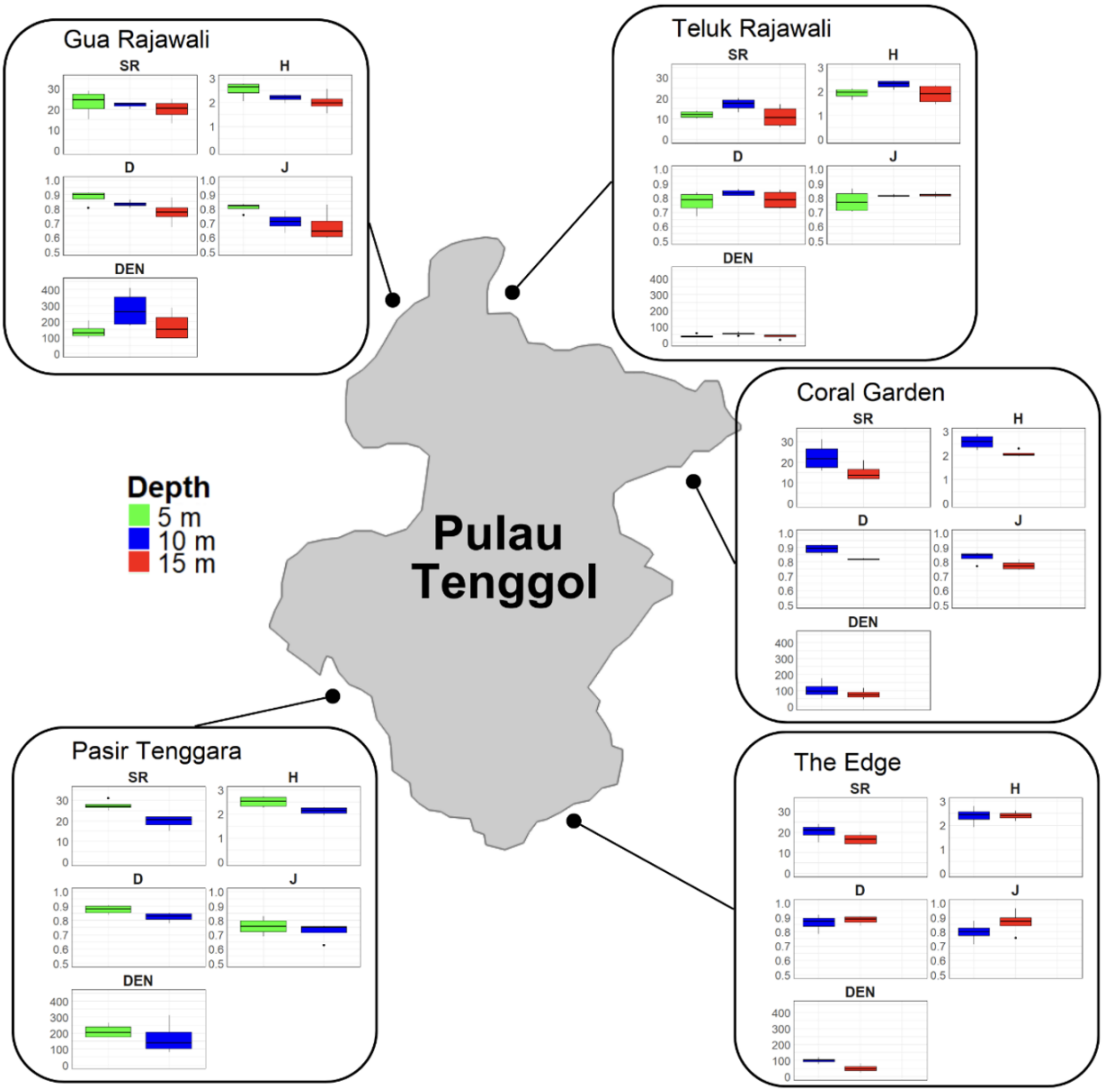

Figure 5. Fish indices across stations and depths. (Note: SR: Species Richness, H: Shannon's Index, D: Simpson's Index, J: Pielou's Index, DEN: Density)

Other fish indices remain relatively consistent across stations, though slight differences are visible. The Edge exhibits the highest H at 2.401 (IQR: 0.005), while Teluk Rajawali shows a lower value of 1.917 (0.205). J ranges from 0.788 (IQR: 0.032) at Teluk Rajawali to 0.871 (0.010) at The Edge, and Simpson's dominance (D) varies modestly, with values such as 0.71 (IQR: 0.065) at Gua Rajawali and 0.831 (IQR: 0.034) at The Edge.

HHC also displays strong spatial variation, from 10.31% (IQR: 2.140) at The Edge to 44.090% (IQR: 7.805) at Teluk Rajawali, with the shallow 5 m depth layer showing relatively high cover at 45.02% (14.072). Depth-related trends show that DEN declines from 139.250% (IQR: 85.875) at 5 m to 62.875% (IQR: 52.75) at 15 m, accompanied by decreases in SR, H, D. Overall, these descriptive values highlight meaningful spatial and depth-related variation in community structure and habitat characteristics, even though none of these differences reach statistical significance within the current sampling scope.

Reef fish composition distribution

The non-metric multidimensional scaling (nMDS) ordination, based on Bray-Curtis dissimilarity, was used to visualize patterns in fish species composition across stations and depths (Figure 6). Although the nMDS provided an effective exploratory overview of community structure, the stress value (0.248) indicates that the two-dimensional configuration should be interpreted cautiously. These fine-scale ordination patterns illustrate how variability in species abundances can obscure broader spatial structure, a phenomenon widely noted in reef fish studies where microhabitat differences strongly influence local assemblages (MacNeil et al. 2009; Smale et al. 2010; Kendall et al. 2011; Barton et al. 2013; Podani et al. 2013). To formally evaluate these patterns, transect level aggregation was applied for PERMANOVA alongside CAP analysis.

The PERMANOVA of reef fish species, major benthic category composition, and HC growth form composition revealed clear spatial structuring (Table 6). PERMANOVA results showed that Station was a major determinant of community composition for reef fishes (R^2: 0.492, p: 0.001), major benthic categories (R^2: 0.628, p: 0.003), and HC growth forms (R^2: 0.674, p: 0.001). Depth also exerted a significant influence on fish assemblages (R^2: 0.205, p: 0.010), whereas its effects on major benthic categories, and HC growth form composition were not statistically significant ($p>0.05$). To verify that these patterns were not driven by differences in within-group variability, multivariate homogeneity of dispersions (PERMDISP) was evaluated in parallel with the PERMANOVA. All PERMDISP tests were non-significant for both Station ($p\geq0.544$) and Depth ($p\geq0.121$), indicating relatively homogeneous dispersion among groups. This absence of dispersion effects supports the interpretation that the observed community differences arise from shifts in group centroids rather than differences in within-group variance.

The results demonstrate a contrast between univariate and multivariate descriptions of the community. In univariate terms, several stations exhibited overlapping median values and IQRs for biodiversity indices (SR, H, D, and J), suggesting a degree of uniformity in bulk community indices across certain depths. However, similar values (SR, H, D, and J) do not imply identical communities. Multivariate analyses were more sensitive to shifts in species identities and their relative abundances, revealing significant compositional differences driven by station-specific factors and, for fish assemblages, depth-related turnover rather than by changes in total SR or J.

These compositional shifts are consistent with the patterns observed in the nMDS and CAP ordinations, where samples clustered according to depth and spatial position, reflecting differences in species assemblages rather than broad structural indices. Such dynamics show stable SR but varying species identities, which are well documented in complex reef systems (Zintzen et al. 2012; Pereira et al. 2018; Bayley et al. 2019; Fukunaga et al. 2020; Spyksma et al. 2022). The multivariate patterns observed here align with depth-linked habitat transitions and horizontal environmental heterogeneity characteristic of Indo-Pacific reefs (Jankowski et al. 2015; Scott et al. 2022; Richardson et al. 2023).

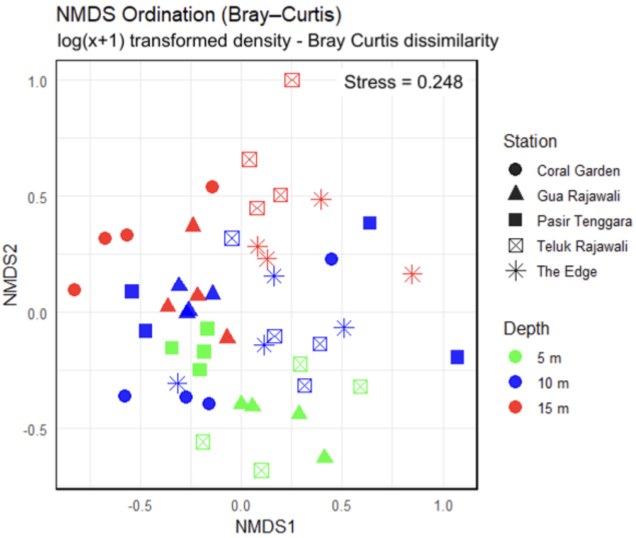

Figure 6. Non-metric multidimensional scaling (nMDS) ordination segment level based on between-site Bray-Curtis similarities derived from log(x+1), transformed coral reef fish species density. The plot illustrates patterns in community composition across stations and depths at Pulau Tenggol

Table 4. Kruskal-Wallis test of fish indices between station and depth with false discovery rate testing and effect size

Factor	Fish indices and HHC	df	H-statistic	Kruskal Wallis p-value	FDR p-value	Effect size
Station	Total Fish Density (DEN)	4	9.372	0.052	0.572	0.767
	Species Richness (SR)	4	6.567	0.161	0.590	0.262
	Shannon's Diversity Index (H)	4	3.436	0.488	0.620	-0.081
	Simpson's Diversity Index (D)	4	3.679	0.451	0.620	-0.046
	Pielou's Evennes Index (J)	4	5.744	0.219	0.590	0.249
	Healthy Hard Coral Cover (HHC)	4	8.628	0.071	0.572	0.661
Depth	Total Fish Density (DEN)	2	1.465	0.481	0.620	-0.059
	Species Richness (SR)	2	3.296	0.192	0.590	0.174
	Shannon's Diversity Index (H)	2	2.337	0.311	0.590	0.037
	Simpson's Diversity Index (D)	2	1.164	0.559	0.620	-0.093
	Pielou's Evennes Index (J)	2	0.138	0.933	0.933	-0.093
	Healthy Hard Coral Cover (HHC)	2	1.938	0.379	0.596	-0.007

Note: Df: degrees of freedom, FDR: False discovery rate (Benjamini-Hochberg) test

Table 5. Median values and interquartile ranges (IQR) of fish indices and hard coral cover across different sampling stations and depth gradients

Factor	Median (IQR)					
	DEN	**SR**	**H**	**D**	**J**	**HHC**
Station						
Coral Garden	90.125 (14.375)	18.75 (3.75)	2.316 (0.246)	0.853 (0.035)	0.803 (0.029)	35.025 (5.635)
Gua Rajawali	172 (69.125)	22 (1.75)	2.191 (0.257)	0.833 (0.052)	0.71 (0.065)	40.816 (3.947)
Pasir Tenggara	190.25 (22)	23.5 (4)	2.322 (0.189)	0.849 (0.026)	0.74 (0.018)	19.748 (5.068)
Teluk Rajawali	40.5 (8.375)	12 (3)	1.917 (0.205)	0.788 (0.032)	0.814 (0.022)	44.09 (7.805)
The Edge	74.25 (24.25)	18.375 (1.875)	2.401 (0.005)	0.871 (0.01)	0.831 (0.034)	10.31 (2.14)
Depth						
5 m	139.25 (85.875)	23.25 (7.75)	2.511 (0.304)	0.875 (0.055)	0.775 (0.025)	45.02 (14.072)
10 m	104.5 (69.75)	20.25 (2.5)	2.295 (0.205)	0.835 (0.029)	0.797 (0.091)	29.39 (26.136)
15 m	62.875 (52.75)	15.75 (3.312)	2.041 (0.174)	0.803 (0.049)	0.797 (0.081)	37.238 (8.29)

Note: IQR: interquartile ranges, SR: Species Richness, H: Shannon's Index, D: Simpson's Index, J: Pielou's Index

Table 6. PERMANOVA and PERMDISP results in differences in coral reef fish species vs major benthic categories vs categories vs and hard coral growth form composition across stations and depths with FDR testing. Significant levels are denoted as *($p \leq 0.05$), **($p \leq 0.01$), and ***($p \leq 0.001$)

Matrix	Statistic	Factor	Df	Sum of square	R^2	F	p-value	FDR p-value	Perm
Fish species log (x+1) transformed	PERMANOVA	Station	4	0.911	0.492	2.273	***0.001	**0.003	999
		Depth	2	0.379	0.205	1.891	**0.010	*0.015	999
	PERMDISP	Station	4	0.015		0.655	0.642		999
		Depth	2	0.001		0.137	0.874		999
Major benthic category composition	PERMANOVA	Station	4	0.608	0.628	3.705	**0.003	**0.006	999
		Depth	2	0.157	0.163	1.919	0.123	0.148	999
	PERMDISP	Station	4	0.025		0.834	0.544		999
		Depth	2	0.013		0.232	0.798		999
HC growth form composition	PERMANOVA	Station	4	1.708	0.674	5.252	***0.001	**0.003	999
		Depth	2	0.263	0.104	1.619	0.206	0.206	999
	PERMDISP	Station	4	0.616		0.014	0.700		999
		Depth	2	0.887		0.005	0.121		999

Note: Df: degrees of freedom, R^2: proportion of variation in community composition explained by each factor, F: pseudo-F statistic, perm: number of permutations used, p-value: permutation-based significance level

CAP ordination at the transect level, constrained by station and depth, was conducted (Figure 7). The station-constrained CAP analysis (Figure 7A) showed that CAP1 and CAP2 explained 39.40% and 17.30% of the total variation, respectively, with station-level patterns forming distinct clusters. Coral Garden and The Edge displayed tight ellipses, indicating consistent fish assemblages, while Teluk Rajawali showed greater variability. Based on Figure 8, SIMPER analysis revealed the greatest dissimilarity between Coral Garden and Teluk Rajawali (0.674), followed by Teluk Rajawali and Pasir Tenggara (0.625). High dissimilarity also occurred between Coral Garden and The Edge (0.597) and Coral Garden and Pasir Tenggara (0.596), identifying Coral Garden as the most distinct station based on average dissimilarity. Moderate dissimilarities were observed among other station pairs, while the lowest was found between Pasir Tenggara and Gua Rajawali (0.457), indicating these stations were the most similar.

The CAP constrained by depth (Figure 7B) revealed even stronger structuring, with CAP1 and CAP2 explaining 18.90% and 4.8% of the total variation, respectively. Note that when looking at variation fitted to the model, CAP1 accounted for 79.80% and CAP2 for 20.20%. Depth-related patterns were sharply defined: 5 m and 15 m samples formed well-separated ellipses along CAP1, whereas 10 m samples occupied an intermediate position with partial overlap with 15 m, indicating a transitional assemblage between shallow and deeper habitats. SIMPER analysis corroborated these depth contrasts, with the highest average dissimilarity observed between 15 m and 5 m (0.634), followed by 10 m vs 15 m (0.545) and 10 m vs 5 m (0.541) (Figure 8).

Constrained ordinations clarified spatial structuring by highlighting station-level differences linked to habitat heterogeneity. Stations with consistent HC growth forms supported more cohesive fish assemblages, whereas heterogeneous sites exhibited greater within-station variability. This aligns with evidence that fine-scale coral morphology strongly influences fish community differentiation (Komyakova et al. 2013; Darling et al. 2017; Komyakova et al. 2018). The correspondence between fish dissimilarities and hard-coral growth forms underscores the importance of structural complexity in shaping species composition, even when broader benthic categories appear similar. Despite the lack of significant differences in major benthic categories across depths, depth-related patterns reflected ecological sorting along light and habitat gradients, with species distributions aligning with known preferences for shallow, high-light coral habitats or deeper, lower-light environments (Carpenter et al. 2022; Scott et al. 2022). Transitional zones at mid-depths are characteristic of reefs where species adapted to contrasting conditions overlap (Williams et al. 2010; Richardson et al. 2023). These depth-linked shifts highlight the role of vertical habitat complexity in structuring reef communities.

Based on Figure 8, SIMPER analysis corroborated the CAP patterns by identifying species that contributed most to compositional dissimilarity among stations and depths. DEN of *A. leucogaster* and *P. alexanderae* were higher at 15 m than at 5 m, whereas *P. moluccensis* DEN was higher at 5 m. At the station-level, *Chromis ternatensis* DEN was higher at Pasir Tenggara compared with Coral Garden, Teluk Rajawali, and Gua Rajawali, while *C. viridis* exhibited higher DEN at Pasir Tenggara and Gua Rajawali than at Teluk Rajawali. Conversely, *T. lunare* DEN was higher at Teluk Rajawali than at Gua Rajawali. Collectively, these results demonstrated pronounced depth and station specific structuring of reef fish assemblages across Coral Garden, Teluk Rajawali, The Edge, Pasir Tenggara, and Gua Rajawali. The greatest number of significantly different species was observed between 15 m and 5 m, while among stations, Coral Garden versus Teluk Rajawali and Teluk Rajawali versus Pasir Tenggara exhibited the highest number of significant species as detected by one-sided permutation testing.

Dominant species in the SIMPER output showed possible associations with ecological traits such as light dependence, foraging strategies, and microhabitat specialization (Dwirama et al. 2018; Fahlevy et al. 2018; Fukunaga et al. 2020; Carpenter et al. 2022). Higher ASTAG in Pasir Tenggara and Gua Rajawali may provide suitable habitat for *Chromis* spp. (González-Rivero et al. 2017). Such species often act as ecological anchors or foundation taxa, influencing community structure and serving as indicators of reef condition (Burns et al. 2015; Pinnegar 2018; Putra et al. 2024). Overall, the assemblage patterns reflect the interplay of habitat heterogeneity, depth-related environmental gradients, and species-specific ecological traits. These interacting factors reinforce the importance of both vertical and horizontal habitat complexity in maintaining reef fish diversity and functional structure.

Relationship between reef fish and benthic component

Mantel tests showed no significant correlations between major benthic categories and fish community structure at any taxonomic level (simple $p>0.05$; FDR $p>0.05$). Partial Mantel tests controlling for depth produced similar non-significant outcomes (partial $p>0.05$; FDR $p>0.05$) (Table 7). In contrast, HC growth form composition showed significant correlations with fish assemblages across all taxonomic levels (Table 7). At the species level, simple Mantel tests indicated a positive correlation (*r*: 0.383, *p*: 0.003, FDR *p*: 0.014), and the relationship remained significant after controlling for depth (partial *r:* 0.387, p: 0.002, FDR *p*: 0.014). At the family level, correlations were also significant in both simple (*r*: 0.362, p: 0.006, FDR: 0.014) and partial tests (*r:* 0.359, *p*: 0.007, FDR *p*: 0.015). Trophic groups showed similar patterns, with significant correlations in simple (*r*: 0.398, *p*: 0.005, FDR *p*: 0.014) and partial analyses (*r*: 0.396, *p*: 0.005, FDR *p*: 0.015).

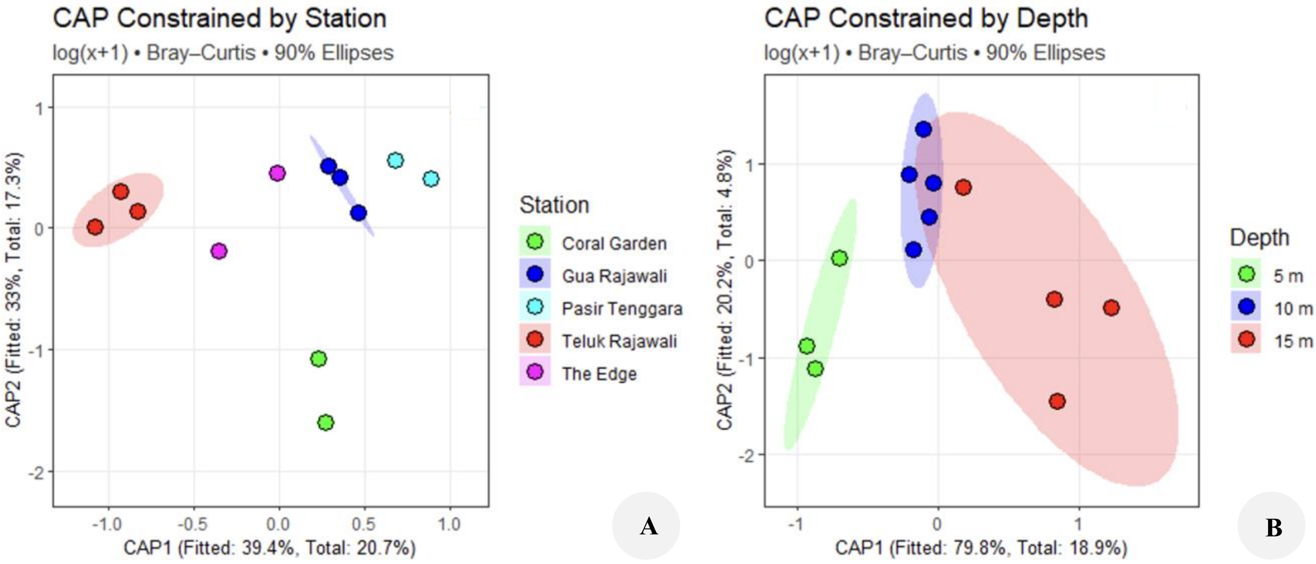

Figure 7. CAP ordination of reef fish species assemblages based on Bray-Curtis dissimilarity of log(x+1) densities. A. Constrained by station-level with 90 % ellipses, B. Constrained by depth-level with 90 % ellipses

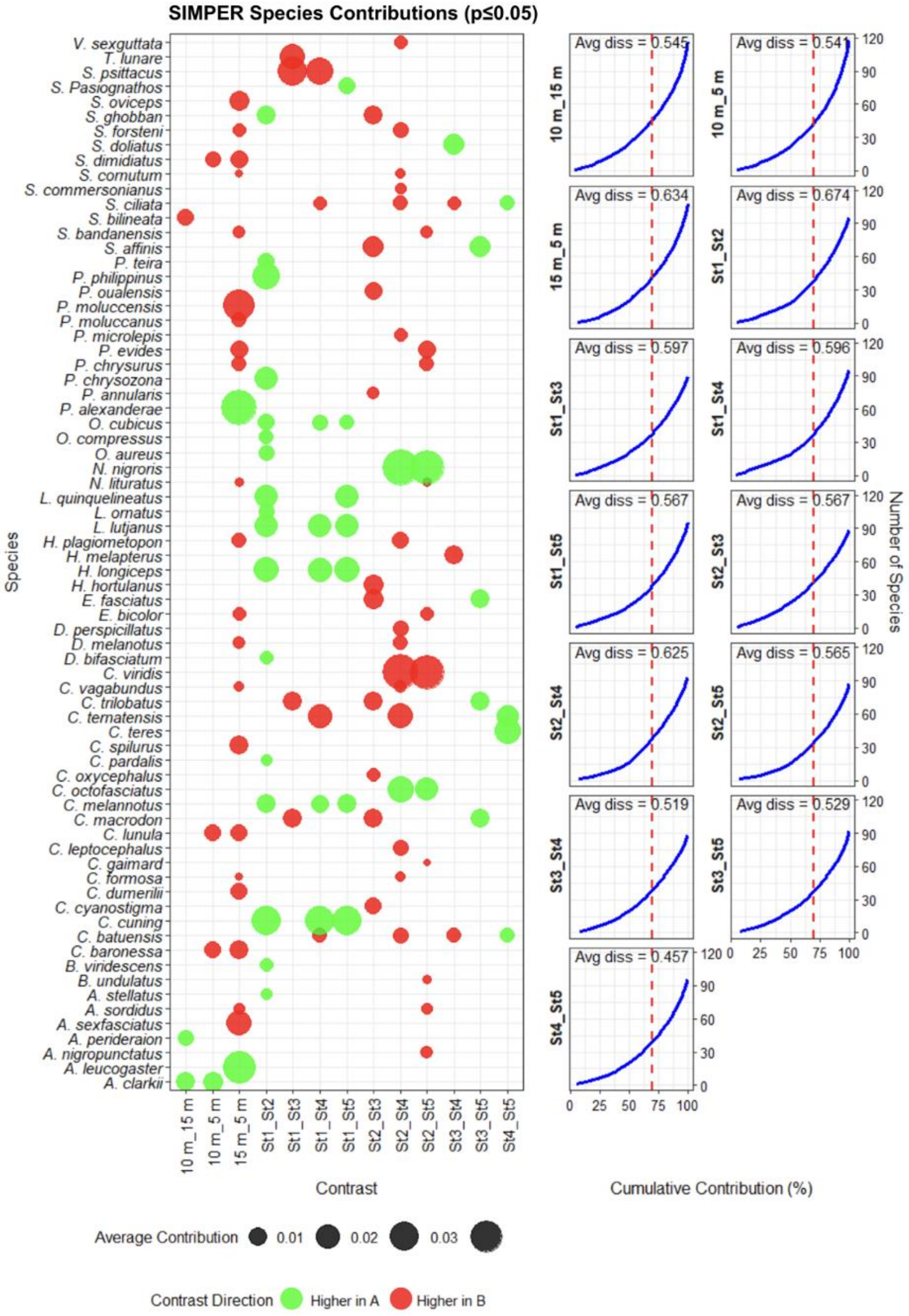

Figure 8. Similarity percentage analysis (SIMPER) of reef fish assemblages. The bubble plot (left) Displays only species that contributed significantly to among-group dissimilarities (p≤0.05), based on one-sided permutation tests. Bubble size represents each species' average contribution to dissimilarity, while bubble color indicates the direction of the difference (higher density in factor A or factor B). The cumulative contribution curves (right) show the ranked contributions of all species within each contrast. A vertical dashed line marks the 70% cumulative contribution threshold, below which species are considered the dominant contributors to assemblage differences. (Note: Avg diss: Average dissimilarity values (Avg diss) are shown for each contrast. (Note: St1: Coral Garden, St2: Teluk Rajawali, St3: The Edge, St4: Pasir Tenggara, St5: Gua Rajawali)

These correlations were moderate in magnitude (r: 0.359-0.398), suggesting ecologically relevant associations rather than stochastic noise. The Mantel patterns indicate that major benthic categories provide less sensitive association value with fish community organization compared to the HC growth form composition (Komyakova et al. 2013; Darling et al. 2017). Moreover, different HC architectures provide shelter, foraging substrates, and are associated with fish assemblages (Darling et al. 2017; Richardson et al. 2017). Thus, specific coral growth forms were key drivers of reef fish structure, even amid depth variation (Rogers et al. 2014; Hall and Kingsford 2021). Furthermore, HC growth form composition exhibited a strong association with fish assemblages across taxonomic and functional levels, even after accounting for depth (Komyakova et al. 2013; Fukunaga et al. 2020). Because Mantel tests are best interpreted as exploratory assessments of matrix concordance, these results were considered alongside complementary Spearman and partial Spearman correlations, which showed the same directional patterns and reinforced the robustness of the observed associations.

Based on Figure 9, Spearman and partial Spearman correlation analyses incorporating depth as a covariate yielded no significant correlations for relationships between overall fish community indices and major benthic categories after FDR correction (all FDR p>0.05). DEN showed two simple correlations that met the FDR threshold, although these did not remain significant in the partial analyses. DEN was positively correlated with *Acropora* staghorn/branching cover (ASTAG; ρ: 0.783, p: 0.003, FDR p: 0.047), but the depth-controlled partial correlation, despite being similar in magnitude (partial ρ: 0.796, p: 0.003), did not meet the FDR criterion (FDR p: 0.073). A similar pattern occurred for encrusting coral (EN): the simple correlation was strong and FDR-significant (ρ: -0.790, p: 0.002, FDR p: 0.047), whereas the partial correlation did not remain significant after correction (partial ρ: -0.787, p: 0.004, FDR p: 0.073). These results suggest that DEN-benthos associations were detectable in simple correlations but were not statistically robust once depth and multiple-comparison adjustments were considered. This aligns with the fact that ASTAG offers greater structural complexity, while EN provides minimal to no structure for fish habitat (Williams et al. 2010; Fukunaga et al. 2020; Ferreira et al. 2025).

HC was positively associated with positive associations with Chaetodontidae and obligate corallivores (OCLV), although the strength and statistical support varied. The Chaetodontidae-HC simple correlation (ρ: 0.592, p: 0.043) did not pass FDR correction (FDR p: 0.064), while the OCLV-HC correlation remained significant (ρ: 0.750, p: 0.005, FDR p: 0.015). After accounting for depth, the Chaetodontidae-HC association increased slightly (partial ρ: 0.650, p: 0.031) and met the FDR threshold (FDR p: 0.046), whereas the OCLV-HC partial correlation remained strong and FDR-significant (partial ρ: 0.772, p: 0.005, FDR p: 0.017). The substitution of HHC for total HC yielded stronger and consistently significant correlations for both groups (Chaetodontidae: ρ: 0.669, p: 0.017, FDR p: 0.035; partial ρ: 0.715, p: 0.014, FDR p: 0.027; OCLV ρ: 0.757, p: 0.004, FDR p: 0.015; partial ρ: 0.768, p: 0.006, FDR p: 0.017). No significant relationships were detected between bleached coral cover and either Chaetodontidae or OCLV, nor between facultative corallivores (FCLV) and HC or HHC (all FDR p>0.05).

In terms of corallivore fish species, OCLV showed stronger partial correlations with healthy hard coral and total HC than the Chaetodontidae family overall (Komyakova et al. 2013; Nanami 2023). In contrast, FCLV showed no links to HHC, BC, or total HC. Consequently, OCLV's reliance on healthy coral may be a potential bioindicator of live coral cover and reef health (Richardson et al. 2017; Plass-Johnson et al. 2018; Loong et al. 2025). Shifts in herbivore dynamics offer additional context for understanding benthic patterns. For HV, the negative association with algal cover observed in the correlations was modulated by depth, suggesting this pattern is consistent with the possibility that depth-related habitat structure shapes the degree to which herbivores respond to algal growth (Loong et al. 2025). However, the present dataset does not allow for causal inference, particularly as no significant values were maintained after FDR correction.

Among the herbivorous groups, only Scaridae showed an FDR-significant simple Spearman correlation with algal cover (ρ: -0.751, p: 0.005, FDR: 0.049), whereas the HV-ALG correlation did not meet the FDR threshold (ρ: -0.691, p: 0.013, FDR: 0.065). These associations weakened further in the partial analyses (HV: partial ρ: -0.529, p: 0.094; Scaridae: partial ρ: -0.624, p: 0.040), again with no FDR-significant results. Moreover, other herbivore Siganidae show no significant correlation, also after FDR correction. However, algal cover across stations was extremely low and highly compressed in range (0-0.11%)

Among the herbivorous groups, only Scaridae showed an FDR-significant simple Spearman correlation with algal cover (ρ: -0.751, p: 0.005, FDR: 0.049), whereas the broader HV-ALG relationship did not meet the FDR threshold (ρ: -0.691, p: 0.013, FDR: 0.065). However, algal cover across stations was extremely low and highly compressed in range (0-0.11%), meaning that even small absolute differences near zero could generate disproportionately strong correlation coefficients. This limited variance reduces the stability and ecological interpretability of correlations. Consistent with this, the associations weakened in the partial analyses (HV: partial ρ: -0.529, p: 0.094; Scaridae: partial ρ: -0.624, p: 0.040), and no FDR-significant results remained. Other herbivores, such as Siganidae showed no significant correlations before or after FDR correction. Taken together, these patterns suggest that while Scaridae displayed the clearest negative association with algal cover, this relationship should be interpreted cautiously, given the near-absence of algae and the narrow data range. The results, therefore, reflect weak evidence of a functional herbivore-algae signal rather than a robust ecological pattern.

In summary, structural complexity showed more association with the fish assemblages, and indicator species such as those in the Chaetodontidae family and obligate corallivores played significant roles as indicator species (Komyakova et al. 2013; Richardson et al. 2017). Although depth modulated some patterns, ASTAG has high structural complexity supported high DEN, while EN with has low complexity support less DEN (Williams et al. 2010; Fukunaga et al. 2020; Nanami 2023). Therefore, coral degradation threatened reef fish, underscoring the need to protect coral structure (Rogers et al. 2014; Darling et al. 2017).

Table 7. Mantel test results (simple and partial controlling for depth) comparing fish composition at species, family, and trophic group levels (log(x+1) transformed) with major Categories and hard coral growth form. Significant levels are denoted as *p≤0.05, **p≤0.01, and *p≤0.001

Comparison	Simple r	Simple p	Simple p (FDR)	Partial r	Partial p	Partial p (FDR)
Major categories						
Species	0.028	0.421	0.548	0.030	0.425	0.545
Family	0.007	0.456	0.548	0.007	0.454	0.545
Trophic group	-0.080	0.654	0.654	-0.079	0.666	0.666
HC growth form composition						
Species	0.383	**0.003	*0.014	0.387	**0.002	*0.014
Family	0.362	**0.006	*0.014	0.359	**0.007	*0.015
Trophic group	0.398	**0.005	*0.014	0.396	**0.005	*0.015

Noted: HC: Hard Coral, FDR: False discovery rate, r: Mantel correlation coefficient, p: significance value

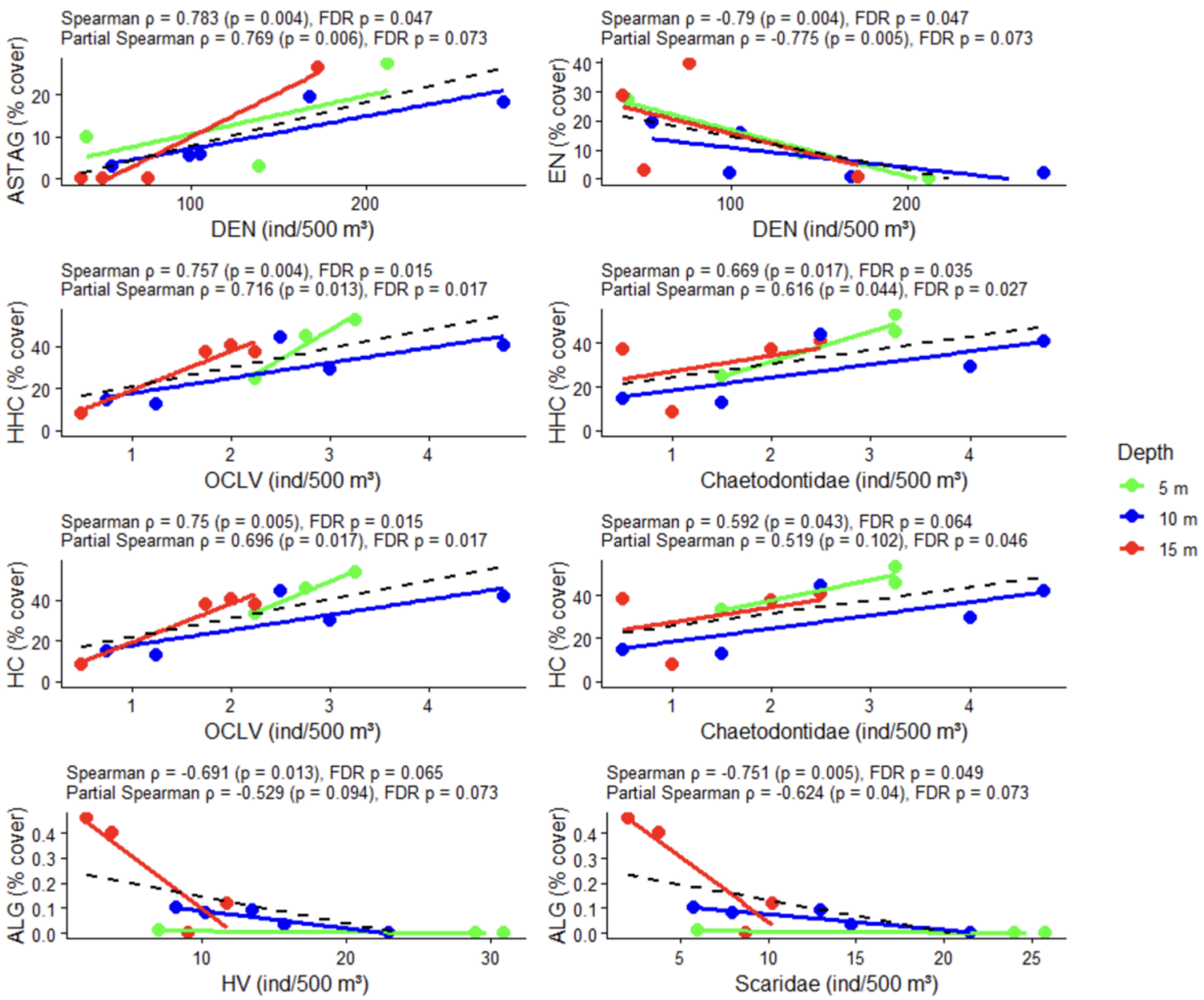

Figure 9. Spearman and Partial Spearman Correlations Between Benthic Cover Types (HC, ALG, RB) and Fish density (OCLV, HV, Scaridae, Chaetodontidae) Across Depths (Note: HHC: Healthy Hard Coral, HC: Overall Hard Coral, ALG: Algae, RB: Rubble, OCLV: Obligate Corallivore, HV: Herbivore)

Conservation status and significance

Based on manual checks of the International Union for Conservation of Nature (IUCN) Red List of Threatened Species of all inventory biodiversity list (IUCN, 2024), most of the recorded species in this study were categorized as Least Concern. However, *Scomberoides commersonnianus* (Talang queenfish) remained unevaluated. The *Chlorurus bowersi* (Bowers parrotfish) is listed as Near Threatened. Additionally, *Carcharhinus melanopterus* (Blacktip reef shark) and *Bolbometopon muricatum* (Bumphead parrotfish) were categorized as Vulnerable.

This study provides important baseline data on the distribution of coral reef fishes in Pulau Tenggol. The higher structural complexity of ASTAG habitats supported greater DEN compared to encrusting EN corals, highlighting the monitoring efforts on these structurally complex reef areas. Coral-dependent Chaetodontidae served as reliable indicators of reef health (Putra et al. 2024), consistent with their role in monitoring live coral cover, while abundant HV regulated algae and supported ecosystem function (Rani et al. 2023). Thus, monitoring OCLV provided management insights as bioindicators of reef health, and further studies on their habitat needs and roles enhanced applications (Loong et al. 2025). In addition, elevated abundances of HV, especially Scaridae, likely regulated algal cover around the island; targeted monitoring and protection were thus crucial for long-term reef sustainability. Specifically, these species, particularly scarids, suppressed macroalgal overgrowth, promoting coral recruitment and resilience (Delevaux et al. 2018).

Limitation and future direction

Several limitations should be considered when interpreting these results. First, although partial correlations and Type III sums of squares helped address unbalanced sampling, the single-period design restricted our ability to evaluate temporal variability in fish assemblages (Caldwell et al. 2016). Second, belt-transect counts remain vulnerable to detection biases, particularly undercounting fast-moving, cryptic, or high DEN species even with single-observer standardization (Coker et al. 2017; Irigoyen et al. 2018; Loong et al. 2025). Third, benthic structure was quantified using 2D metrics, which do not capture the three-dimensional complexity known to influence habitat availability and fish-benthos interactions (González-Rivero et al. 2017; Kornder et al. 2021).

Future work should incorporate replicated, seasonally stratified surveys to capture temporal dynamics in assemblage structure and benthic cover (Heenan et al. 2017), thereby allowing direct tests of seasonal drivers behind patterns such as low algal biomass or shifts in planktivores DEN. Detection biases could be reduced operationally by pairing belt-transects with complementary methods, such as stationary video, stereo-video, or timed-swim surveys, to improve counts of fast-moving and cryptic taxa. Refining trophic classifications through comparative reviews and expert consensus would help reduce uncertainty in guild-level interpretations. Finally, integrating 3D structural metrics (e.g., photogrammetry-derived rugosity, void space, or surface complexity) and finer guild subdivisions where data permit would allow more mechanistic assessments of habitat-fish relationships (Cardoso et al. 2009; Longo et al. 2014; Streit et al. 2015; Suzuki et al. 2018; Zhu et al. 2019). Together, these steps will strengthen ecological inference and improve the accuracy and interpretability of reef monitoring.

In conclusion, reef fish assemblages at Pulau Tenggol exhibit high biodiversity, functional completeness, and subtle but consistent compositional shifts associated with depth-related environmental gradients. Although univariate diversity metrics were relatively insensitive to habitat variation, multivariate and functional analyses revealed ecologically meaningful patterns. The strong correlations between hard coral cover and both OCLV and Chaetodontidae abundance highlight their potential value as bioindicators within this system. Together, these results provide a robust ecological baseline for Pulau Tenggol and support depth-inclusive management strategies aimed at maintaining taxonomic and functional diversity across reef habitats.

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APPENDIX

Table S1. Coral reef fish biodiversity list of Pulau Tenggol (superscript indicates trophic group)

Family/Species	Common name	Family/Species	Common name
Observation in survey area			
Acanthuridae (Surgeonfish)		**Microdesmidae (Wormfishes)**	
Naso lituratus ^{HV}	Orangespine unicornfish	*Ptereleotris microlepis* ^{PV}	Blue gudgeon
Apogonidae (Cardinalfish)		*Ptereleotris evides* ^{PV}	Blackfin dartfish
Cheilodipterus artus ^{CV}	Wolf cardinalfish	**Monacanthidae (Filefishes)**	
Cheilodipterus macrodon ^{CV}	Large toothed cardinalfish	*Cantherhines dumerilii* ^{FCLV}	Whitespotted filefish
Ostorhinchus aureus ^{CV}	Ring-tailed cardinalfish	*Cantherhines pardalis* ^{IV}	Blackbar filefish
Ostorhinchus compressus ^{CV}	Ochre-striped cardinalfish	**Nemipteridae (Breams)**	
Balistidae (Triggerfish)		*Scolopsis affinis* ^{IV}	Peters' monocle bream
Balistapus undulatus ^{FCLV}	Orange-lined triggerfish	*Scolopsis bilineata* ^{CV}	Two-lined monocle bream
Balistoides viridescens ^{FCLV}	Titan Triggerfish	*Scolopsis ciliata* ^{CV}	Saw-jawed monocle bream
Blenniidae (Blenny)		*Scolopsis margaritifera* ^{CV}	Monogrammed monocle brean
Ecsenius bicolor ^{HV}	Bicolor blenny	**Ostraciidae (Boxfish)**	
Caesionidae (Fusilier)		*Ostracion cubicus* ^{OV}	Yellow boxfish
Caesio caerulaurea ^{PV}	Blue and gold fusilier	**Pempheridae (Sweeper)**	
Caesio cuning ^{PV}	Redbelly yellowtail fusilier	*Pempheris oualensis* ^{CV}	Blackspot sweeper
Caesio teres ^{PV}	Yellowfin Fusilier	**Pomacanthidae (Angelfish)**	
Pterocaesio chrysozona ^{PV}	Goldband fusilier	*Chaetodontoplus mesoleucus* ^{OV}	Vermiculated angelfish
Carangidae (Trevally)		*Pomacanthus annularis* ^{OV}	Bluering angelfish
Scomberoides commersonnianus ^{C}	Talang queenfish	*Pomacanthus semicirculatus* ^{OV}	Semicircle angelfish
Chaetodontidae (Butterflyfish)		**Pomacentridae (Damselfish)**	
Chaetodon baronessa ^{OCLV}	Eastern triangular butterflyfish	*Abudefduf sexfasciatus* ^{OV}	Scissortail sergeant
Chaetodon lunula ^{FCLV}	Raccoon butterflyfish	*Abudefduf sordidus* ^{OV}	Blackspot sergeant
Chaetodon lunulatus ^{OCLV}	Oval butterflyfish	*Abudefduf vaigiensis* ^{OV}	Indo-Pacific sergeant
Chaetodon melannotus ^{FCLV}	Blackback butterflyfish	*Amblyglyphidodon aureus* ^{OV}	Golden Damsel
Chaetodon octofasciatus ^{OCLV}	Eightband Butterflyfish	*Amblyglyphidodon curacao* ^{OV}	Staghorn damselfish
Chaetodon oxycephalus ^{FCLV}	Spot-nape butterflyfish	*Amblyglyphidodon leucogaster* ^{OV}	Yellowbelly damselfish
Chaetodon vagabundus ^{FCLV}	Vagabond Butterflyfish	*Amphiprion clarkii* ^{OV}	Clark's Anemonefish
Coradion chrysozonus ^{OV}	Goldengirdled coralfish	*Amphiprion ocellaris* ^{OV}	Ocellaris Clownfish
Heniochus acuminatus ^{FCLV}	Goldengirdled coralfish	*Amphiprion perideraion* ^{OV}	Pink Anemonefish
Heniochus varius ^{FCLV}	Pennant coralfish	*Chromis ternatensis* ^{PV}	Ternate chromis
Dasyatidae (Ray)		*Chromis viridis* ^{PV}	Blue green damselfish
Taeniura lymma ^{CV}	Ribbontail stingray	*Dascyllus reticulatus* ^{OV}	Reticulate dascyllus
Ephippidae (Batfish)		*Dascyllus trimaculatus* ^{OV}	Threespot dascyllus
Platax orbicularis ^{OV}	Orbicular batfish	*Dischistodus melanotus* ^{HV}	Black-vent damsel
Platax teira ^{OV}	Longfin batfish	*Dischistodus perspicillatus* ^{HV}	White damsel
Epinephelidae (Grouper)		*Hemiglyphidodon plagiometopon* ^{HV}	Lagoon damselfish
Cephalopholis boenak ^{CV}	Chocolate hind	*Neoglyphidodon melas* ^{OV}	Bowtie damselfish
Cephalopholis cyanostigma ^{CV}	Bluespotted hind	*Neoglyphidodon nigroris* ^{OV}	Black-and-gold chromis
Cephalopholis formosa ^{CV}	Bluelined hind	*Neopomacentrus cyanomos* ^{PV}	Regal demoiselle
Cephalopholis microprion ^{CV}	Freckled hind	*Neopomacentrus violascens* ^{PV}	Violet demoiselle
Epinephelus fasciatus ^{CV}	Blacktip grouper	*Pomacentrus alexanderae* ^{OV}	Alexander's damsel
Plectropomus leopardus ^{CV}	Leopard coralgrouper	*Pomacentrus chrysurus* ^{OV}	Whitetail damsel
Gobiidae (Goby)		*Pomacentrus coelestis* ^{OV}	Neon damselfish
Cryptocentrus leptocephalus ^{CV}	Pink-speckled shrimpgoby	*Pomacentrus moluccensis* ^{OV}	Lemon damsel
Valenciennea sexguttata ^{CV}	Sixspot goby	*Pomacentrus philippinus* ^{OV}	Philippine damsel
Holocentridae (Soldierfish/Squirrelfish)		*Pycnochromis caudalis* ^{PV}	Blue-axil chromis
Myripristis hexagona ^{IV}	Whitespot soldierfish	**Scaridae (Parrotfish)**	
Sargocentron cornutum ^{CV}	Threespot squirrelfish	*Chlorurus bleekeri* ^{HV}	Bleeker's parrotfish
Sargocentron rubrum ^{CV}	Redcoat	*Chlorurus bowersi* ^{HV}	Bowser's Parrotfish
Kyphosidae (Sea Chubs)		*Chlorurus microrhinos* ^{HV}	Steephead parrots
Kyphosus cinerascens ^{HV}	Blue sea chub	*Chlorurus spilurus* ^{HV}	Daisy parrotfish
Labridae (Wrasses)		*Hipposcarus longiceps* ^{HV}	Pacific longnose parrotfish
Bodianus mesothorax ^{IV}	Splitlevel hogfish	*Scarus chameleon* ^{HV}	Chameleon parrotfish
Cheilinus fasciatus ^{IV}	Redbreasted wrasse	*Scarus dimidiatus* ^{HV}	Yellowbarred parrotfish
Cheilinus trilobatus ^{IV}	Tripletail wrasse	*Scarus forsteni* ^{HV}	Forsten's parrotfish
Coris batuensis ^{IV}	Batu coris	*Scarus frenatus* ^{HV}	Bridled parrotfish
Coris gaimard ^{IV}	African coris	*Scarus ghobban* ^{HV}	Blue-barred parrotfish
Diproctacanthus xanthurus ^{OCLV}	Yellowtail tubelip	*Scarus niger* ^{HV}	Dusky parrotfish

Epibulus insidiator ^{CV}	Sling-jaw wrasse	*Scarus oviceps* ^{HV}	Dark capped parrotfish
Gomphosus varius ^{IV}	Bird wrasse	*Scarus prasiognathos* ^{HV}	Singapore parrotfish
Halichoeres hortulanus ^{IV}	Checkerboard wrasse	*Scarus psittacus* ^{HV}	Common parrotfish
Halichoeres margaritaceus ^{IV}	Pink-belly wrasse	*Scarus quoyi* ^{HV}	Quoy's parrotfish
Halichoeres nigrescens ^{IV}	Bubblefin wrasse	*Scarus rivulatus* ^{HV}	Rivulated parrotfish
Halichoeres prosopeion ^{IV}	Twotone wrasse	*Scarus rubroviolaceus* ^{HV}	Ember parrotfish
Hemigymnus melapterus ^{IV}	Blackeye thicklip	*Scarus spinus* ^{HV}	Greensnout parrotfish
Labrichthys unilineatus ^{OCLV}	Tubelip wrasse	**Siganidae (Rabitfish)**	
Labroides dimidiatus ^{IV}	Bluestreak cleaner wrasse	*Siganus corallinus* ^{HV}	Blue-spotted spinefoot
Oxycheilinus digramma ^{IV}	Yellowspotted wrasse	*Siganus doliatus* ^{HV}	Barred spinefoot
Pseudodax moluccanus ^{OV}	Cheeklined wrasse	*Siganus puellus* ^{HV}	Masked spinefoot
Stethojulis bandanensis ^{IV}	Chiseltooth wrasse	*Siganus virgatus* ^{HV}	Barhead spinefoot
Thalassoma lunare ^{IV}	Moon wrasse	*Siganus vulpinus* ^{HV}	Foxface spinefoot
Lethrinidae (Emperrors)		**Tetraodontidae (Pufferfish)**	
Lethrinus ornatus ^{CV}	Ornated emperor	*Arothron nigropunctatus* ^{FCLV}	Black-spotted Pufferfish
Liopropomatidae (Painted basslets)		*Arothron stellatus* ^{FCLV}	Stellate puffer
Diploprion bifasciatum ^{CV}	Barred soapfish	**Tripterygiidae (Triplefin)**	
Lutjanidae (Snapper)		*Helcogramma striata* ^{PV}	Tropical striped triplefin
Lutjanus decussatus ^{CV}	Checkered snapper	**Zanclidae (Morish idol)**	
Lutjanus lutjanus ^{CV}	Bigeye snapper	*Zanclus cornutus* ^{OV}	Moorish idol
Lutjanus quinquelineatus ^{CV}	Five-lined snapper		
Fish observation outside study area			
Labridae (Wrasses)		**Pomacentridae (Damselfish)**	
Cirrhilabrus cyanopleura ^{PV}	Blueside wrasse	*Amphiprion frenatus* ^{OV}	tomato clownfish
Thalassoma hardwicke ^{IV}	Sixbar wrasse	*Chrysiptera rollandi* ^{OV}	Rolland's demoiselle
Carcharhinidae (Requiem shark)		**Scaridae (Parrotfish)**	
Carcharhinus melanopterus ^{CV}	Blacktip reef shark	*Bolbometopon muricatum* ^{OV}	Green humphead parrotfish
Chaetodontidae (Butterflyfish)		**Scorpaenidae (Scorpionfish)**	
Chaetodon lineolatus ^{FCLV}	Lined butterflyfish	*Scorpaenopsis papuensis* ^{CV}	Papuan scorpionfish
Muraenidae (Moray eel)		**Synodontidae (Lizardfish)**	
Gymnothorax favagineus ^{CV}	Tessellate Moray	*Synodus variegatus* ^{CV}	Variegated lizardfish
Gymnothorax undulatus ^{CV}	Undulated Moray		
Nemipteridae (Breams)			
Scolopsis lineata ^{CV}	Striped monocle bream		
Scolopsis monogramma ^{CV}	Monogrammed monocle bream		

Note: CV: Carnivore, IV: Invertivore, PV: Planktivore, OV: Omnivore, HV: Herbivore, OCLV: Obligate corallivore, FCLV: Facultative corallivore

Table S2. Benthic categories definition

Benthic component	Definition	Primary reference
Hard Coral (HC)	Total Hard Coral Cover including HHC and BC.	English et al. (1997)
Healthy Hard Coral (HHC)	Live hard coral colonies showing natural pigmentation with no signs of disease or bleaching.	Hill and Wilkinson (2004)
Bleached Coral (BC)	Live coral that has expelled its zooxanthellae, appearing white or pale, typically due to thermal stress.	Reef Check (2020)
Dead Coral (DC)	Recently dead coral skeletons: structure is intact and white, with no significant algal colonization.	English et al. (1997)
Dead Coral with Algae (DCA)	Dead coral skeletons covered by a thin layer of filamentous or coralline algae.	Hill and Wilkinson (2004)
Turf Algae (TA)	Multi-specific, low-lying mats of filamentous algae (usually>2 cm in height).	Hill and Wilkinson (2004)
Macroalgae (MA)	Larger, fleshy or calcified algae (e.g., *Sargassum*, *Turbinaria*, *Halimeda*) clearly visible.	English et al. (1997)
Rock (RC)	Hard, consolidated substrate (limestone/volcanic).	Reef Check (2020)
Rubble (RB)	Unconsolidated fragments of dead coral skeletons (typically 0.5 cm-15 cm in diameter).	Hill and Wilkinson (2004)
Growth forms	Morphological classifications (massive, branching, encrusting, etc.) for field identification.	Kelley (2016)