Egyptian Journal of Aquatic Biology & Fisheries
Zoology Department, Faculty of Science,
Ain Shams University, Cairo, Egypt.
ISSN 1110 – 6131
Vol. 29(5): 2217 – 2239 (2025)
www.ejabf.journals.ekb.eg

Spatial Patterns of Reef Fishes Relative to Coral Reef Conditions in Morowali Marine Protected Area, Indonesia

Ana Faricha[1*], Subhan[2], Fione Yukita Yalindua[1], Ayuningtyas Indrawati[1], Moh Arif Latjuba[3], Fonni Helmince[4], Sahril Syam[2]

[1]Research Center for Biota Systems, National Research and Innovation Agency (BRIN), Cibinong, Indonesia
[2] Department of Marine Science, Faculty of Fishery and Marine Science, Halu Oleo University, Kendari, Indonesia
[3] Department of Marine Affairs and Fisheries, Central Sulawesi Province, Palu, Indonesia
[4] Fisheries Port and Coastal–Small Islands Conservation Technical Unit, Region VII Morowali, Indonesia

[*]Corresponding Author: anaf001@brin.go.id

ARTICLE INFO

Article History:
Received: July 10, 2025
Accepted: Sep. 15, 2025
Online: Oct. 10, 2025

Keywords:
Betadiversity,
Conservation,
Fish community,
Species distribution

ABSTRACT

The global environmental crisis has led to biodiversity loss and degradation of marine ecosystems. In response, conserving biodiversity and marine resources through the establishment of marine protected areas (MPAs) is recognized as one of the most effective tools to address environmental pressures. However, the effectiveness of Indonesia's MPA management remains weak, therefore, better coordination, monitoring, and improved governance are needed to achieve conservation goals. This study aimed to assess how variations in coral reef condition influence reef fishes in terms of diversity, structure, distribution, and biomass at Morowali MPA, Central Sulawesi, to enhance the effective management. The results reveal that the fish assemblages in Morowali MPA are characterized by high species richness and strong spatial structuring driven by species turnover. Families of Acanthuridae, Chaetodontidae, Labridae, Pomacentridae, Serranidae, and Siganidae form the most commonly reef fishes found in Morowali MPA, beyond that the small fish were dominant and larger species were herbivorous and carnivorous groups. Fish diversity and abundance might be driven by variation in benthic substrates. Moreover, the patterns of species dominance illustrate interplay between reef geomorphology, seasonal oceanographic processes, and life-history traits in shaping community structure.

INTRODUCTION

Marine protected areas (MPAs) are designated zones of the marine environment managed to safeguard ecological functions and sustainability of ecosystems and resources **(Kriegl *et al*., 2021)**. In Indonesia, the establishment of MPAs is considered ecologically appropriate because marine environments have suffered degradation affected from overfishing, destructive activities and climate change **(Amkieltiela *et al*., 2022; Estradivari *et al*., 2022)**. Conservation issues have become a strategic priority, and the government emphasizes effective management to secure both ecological and socio-economic benefits **(Estradivari *et al*., 2022)**. Indonesia's national MPA policy led by the Ministry of Marine Affairs and Fisheries (MMAF), aligns with the global commitments such as Aichi Target 11 and SDG 14, with a target of 32.5 million ha under protection by 2030 **(Meilana *et al*., 2023)**. Clear goals for MPAs are necessary to guide management, monitoring, and research activities. However, the complexity of marine ecosystems means that ecological responses to MPA establishment vary across regions and are difficult to predict, influenced by factors such as habitat distribution, connectivity, wave exposure, depth, historical resource extraction, regulatory frameworks, and compliance levels **(Edgar *et al*., 2007)**.

Since the 2000s, MPA criteria have been standardized worldwide, with progress in ecosystem-based approaches, climate change mitigation, and expansion beyond national waters, yet oceans remain highly affected by human activities **(Maestro *et al*., 2019)**. The sustainability and effectiveness of MPA depend on fishing pressure, anthropogenic threats, and climate change **(Hilborn, 2018; Moutopoulos *et al*., 2021)**. Ecotourism can directly and indirectly support sustainability, highlighting the vital role of community involvement in achieving long-term conservation **(Rahman *et al*., 2022)**. By 2020, Indonesia's MPA network had reached 23.9 million hectares, but management effectiveness remains limited, requiring stronger oversight and policy actions to align with post-2020 biodiversity goals **(Meilana *et al*., 2023)**. The MPA faces growing pressures, requiring stronger management, integration with fisheries and tourism, and resilient strategies to ensure long-term sustainability **(Tranter *et al*., 2022)**. Expansion of MPAs should be balanced with improved management, coordination, resources, and monitoring, while addressing gaps in representation and governance to meet future conservation targets **(Amkieltiela *et al*., 2022)**.

Indonesia's coral reef, part of Coral Triangle, represents a global hotspot of marine biodiversity **(Moore & Ndobe, 2008)**. They provide critical ecosystem services, including coastal protection, ecological processes, fisheries support, and socio-economic benefits **(Hoegh-Guldberg *et al*., 2017)**. Reef fish diversity and abundance are strongly influenced by coral cover and structural complexity, with numerous studies showing a positive relationship between coral reefs and reef fish **(Komyakova *et al*., 2013; Arias-Godínez *et al*., 2021; Sebastian *et al*., 2024)**. Reef fishes play key ecological roles in maintaining reef functioning and structuring. However, fish assemblage patterns can shift due to natural or human disturbances **(Thilakarathne *et al*., 2024)**. Increase in the number and extension of MPAs is therefore one of the most effective conservation instruments, particularly in the coastal and small islands such as Central Sulawesi regions **(Maestro *et al*., 2019)**. Central Sulawesi, consists of terrestrial and marine areas, with its marine territory hosting some of the most extensive coral reefs in Indonesia **(Moore & Ndobe, 2008)**.

Nevertheless, coral reefs in Central Sulawesi face widespread degradation, destructive fishing, sedimentation, mining, tourism, ship groundings, and other human activities **(Tranter *et al*., 2022; Tosepu *et al*., 2025)**. Although coastal ecosystems show some capacity for recovery after stress, community structures are often altered **(Touza *et al*., 2021)**. To address these challenges, regular biophysical monitoring is conducted to track ecological trends and assess the impacts of climate change and anthropogenic threats **(Hadi *et al*., 2018)**. In addition to data on fish diversity and abundance, fish biomass is a fundamental parameter for evaluating the status of aquatic ecosystems **(Robinson *et al*., 2016)**. Biomass not only reflects ecosystem health but also indicates disturbances such as overfishing, pollution, and climate change **(Duffy *et al*., 2016)**. Moreover, biomass data are essential for establishing sustainable fisheries management strategies, determining catch quotas, and supporting the economic well-being of communities dependent on marine resources **(McClanahan *et al*., 2016; Robinson *et al*., 2016)**. In addition, fish biomass provides insights into trophic interactions and community structure, offering a broader understanding of ecosystem dynamics under environmental change **(Russ *et al*., 2021)**. Coral reefs, which are ecologically and economically valuable, have mostly been studied in association with reef fish. Knowledge of this interaction between benthic substrate percent cover at reef ecosystems and fish families remains limited in Central Sulawesi, particularly in Morowali marine protected area. To address this gap, the Department of Marine Affairs and Fisheries, Central Sulawesi Province provides data to assess trends in coral reefs ecology and impact of environmental changes, if any, through reef health monitoring. Therefore, this study aimed to assess the relation of coral reef and reef fish, especially on spatial distribution of reef fishes and variation on fish diversity, species composition, and also trends in fish biomass at selected sites in the Morowali MPA, Central Sulawesi.

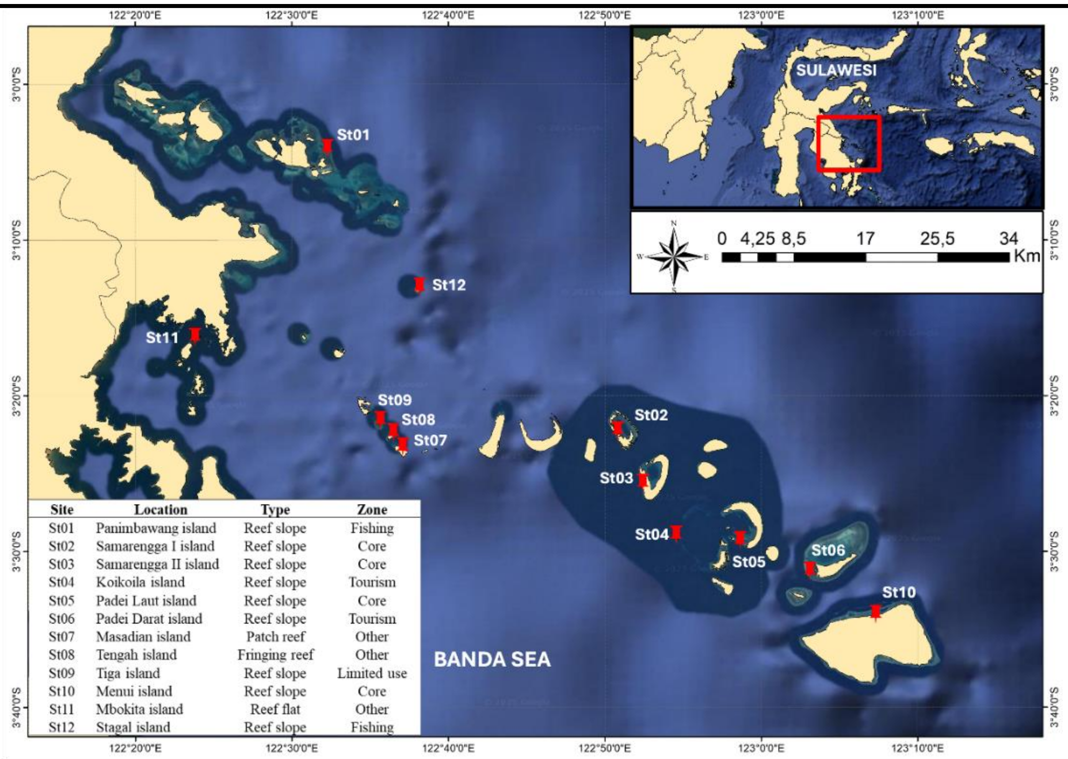
MATERIALS AND METHODS

1. Study sites

This study was conducted in October 2024 at Morowali Marine Protected Area (MPA) and focused on coral reefs at depths of 5- 7m. A total of 12 study sites were selected and distributed in the Regency of Morowali and North Morowali, Central Sulawesi, Indonesia (Fig. 1). The majority of study sites were represented by substrate sand. Almost all sites were located on inhabited islands, with the exception of two uninhabited islands, namely Koikoila Island (St04) and Stagal Island (St12). Most locations were characterized by reef slope types, with the exception of St07, St08, and St11 which were documented by patch, fringing and reef flat, respectively (Fig. 1).

2. Data collections

The method used for data collection of benthic substrates was underwater photo transect method (UPT), and underwater visual census method (UVC) was used to obtain the fish data **(Hill & Wilkinson, 2004)**. A 50m of line transect was placed on parallel positions to the shoreline, with an additional 5m on each side of line to cover an observation area of 500m^2 for fish data. All fish encountered were documented and identified supported by a coral reef fish identification guidebook of **Kuiter and Tonozuka (2001)**. The number of individuals was recorded to determine species abundance and fish occurrence across study sites, and the fish biomass was calculated by using length estimation of fish (cm). The fish biomass measurement was evaluated using formula of the length weight relationship, $W= a \times L^b$, where W is the weight of fish (g), L is the total length (cm), while a and b are constants for a particular fish referring to FishBase.org **(Froese & Pauly, 2024)**. Moreover, benthic substrate percentage was obtained using 44 × 58cm quadrat transect to frame the photo and helped as a border for photo data analyzing using CPCe software **(Kohler & Gill, 2006)**. Photos were taken along the line transect with quadrat transects placed to the left of the line transect at odd meters and to the right at even meters to obtain a representative of benthic substrates. A total of 30 random points was selected for each photo data and identified the category of these benthic substrates, meanwhile there about 1500 random points from 50 photos for each line transect (study site). According to **Giyanto (2012)**, the benthic substrate was grouped into category of life coral including acropora (AC) and non-acropora (NAC), dead coral (DC), dead coral with algae (DCA), soft coral (SC), sponge (SP), fleshy seaweed (FS), other fauna (OT), rubble (R), sand (S), silt (SI), and rock (RK). The data collection was conducted along the same line transect for both data of fish and benthic substrates.



Site	Location	Type	Zone
St01	Panimbawang island	Reef slope	Fishing
St02	Samarengga I island	Reef slope	Core
St03	Samarengga II island	Reef slope	Core
St04	Koikoila island	Reef slope	Tourism
St05	Padei Laut island	Reef slope	Core
St06	Padei Darat island	Reef slope	Tourism
St07	Masadian island	Patch reef	Other
St08	Tengah island	Fringing reef	Other
St09	Tiga island	Reef slope	Limited use
St10	Menui island	Reef slope	Core
St11	Mbokita island	Reef flat	Other
St12	Stagal island	Reef slope	Fishing

Fig. 1. Location of study sites across Morowali MPA, Central Sulawesi, Indonesia

3. Data analysis

The adequacy of species documented was examined using species accumulation curve. Fish body size estimations were categorized into 4 groups (≤ 10 cm, 11- 20 cm, 21- 30 cm, and 31- 40 cm), likewise trophic groups were classified into 9 functional groups (carnivore, herbivore, omnivore, detrivore, invertivore, planktivore, zooplanktivorous, obligate corallivore, and facultative corallivore) based on data from FishBase.org. The dataset was used to assess fish biomass, size distribution, beta-diversity, trophic structure, and relative abundances among 12 study sites. Reef fish community structure in Morowali MPA was examined using cluster analysis based on Bray-Curtis dissimilarity matrices derived from presence and absence data using ggdendro package. Compositional dissimilarity among sites was assessed to evaluate spatial variation by combining abundance and incidence-based approaches. Bray-Curtis dissimilarity was calculated from log-transformed abundance data to reduce the influence of dominant species while preserving sensitivity to both species absence and relative abundance **(Bray & Curtis, 1957; Clarke *et al*., 2006)**. Sørensen dissimilarity was partitioned into turnover (species replacement) and nestedness-resultant components (species loss or gain without replacement) using the beta.pair function (betapart package), allowing identification of beta diversity drivers **(Baselga, 2010; Baselga & Orme, 2012)**. Benthic substrates composition was visualized using the ggplot2 package, and following the assessment of normality distributions, Pearson's correlation (r) was conducted to analyze the relationships between fish species richness and hard coral cover, as well as fish biomass and hard coral cover using vegan package. Non-metric multidimensional scaling (nMDS) was employed to visualize distribution patterns of the 10 dominant fish taxa and benthic substrates using vegan package, wherein the plot could reflect the variation of dominant reef fish in Morowali MPA might driver by benthic substrate percent cover. All analyses were performed in R 4.5.1 version, with visualizations using ggplot2 package **(Wickham, 2016)**, and dissimilarity matrices were visualized using heatmaps through pheatmap package **(Kolde, 2025)**.

RESULTS

1. Community structure and diversity of reef fishes

This study recorded a total of 206 species which belong to 35 families of reef fish. The species accumulation curve presented approaching an asymptote (Fig. 3B), indicating that sampling effort (n = 12 study sites) was nearly sufficient to record most species. The study site of Padei Laut Island (St05) has the highest number of species (87 taxa), followed by Samarengga I (St02) island (69 taxa), with the high contribution from families Chaetodontidae and Acanthuridae, respectively. However, the study sites of Samarengga II Island (St03) and Mbokita Island (St11) reported the lowest number of species (36 taxa in each). Furthermore, the family of reef fish with the highest number of species was Pomacentridae, while there were 16 families that reported the lowest number of species with only 1 species recorded (Table 1). The most widespread reef fish in Morowali MPA was for the families Acanthuridae, Chaetodontidae, Labridae, Pomacentridae, Serranidae, and Siganidae being present at all study sites.

The finding across study sites in the Morowali MPA reveal a fascinating tapestry of reef fish diversity, pairwise Sørensen dissimilarity βsor was high overall, indicating marked among-site heterogeneity in species composition. The lowest dissimilarity occurred between St02 and St03 (βsor = 0.358), whereas the highest was between St07 and St04 (βsor = 0.868), with most other station pairs exceeding 0.65 (e.g., St01-St02 = 0.782, St08-St10 = 0.824, St06-St08 = 0.833, Fig. 2). Partitioning of beta diversity showed that dissimilarity was predominantly driven by species turnover (βsim) rather than nestedness (βsne) for most comparisons, this means that differences in reef fish species between study sites are largely due to the replacement of one species by another, rather than variations in the number of species present. Several pairs were near “pure turnover,” with negligible nestedness (e.g., St04-St10 βsor = 0.679, βsne = 0; St07- St08 βsne = 0; St07-St11 βsne = 0). High-dissimilarity pairs such as St08-St06 (βsor = 0.833, βsne = 0.018) and St10-St08 (βsor = 0.824, βsne = 0.035) were likewise dominated by species replacement. In contrast, a smaller subset of comparisons exhibited elevated nestedness, suggesting richness or occupancy differences. The clearest case was St02-St03, where βsne = 0.277 for exceeded βsim = 0.081, and additional examples included

St03-St05 (βsne = 0.232) and St05-St09 (βsne = 0.218, Fig. 2). Overall, study sites such as St07 and St08 were compositionally distinctive from many others due to high turnover, while St02 and St03 formed a comparatively similar pair with nestedness-driven differences.

Table 1. Distribution of reef fish species across study sites

Family	**Total species**	**Number of species each site**											
		St01	**St02**	**St03**	**St04**	**St05**	**St06**	**St07**	**St08**	**St09**	**St10**	**St11**	**St12**
Acanthuridae	14	3	11	7	3	4	5	3	2	4	7	2	4
Apogonidae	2	2						1	1				1
Aulostomidae	1		1	1	1	1			1			1	1
Balistidae	7	1	3	1	2	3	1	2		1	3		
Blenniidae	1	1	1										
Caesionidae	3		1	1	1	2	2		2	2	1	1	
Carangidae	2		1	2	1								
Centriscidae	1	1						1					
Chaetodontidae	21	1	8	5	4	15	7	3	3	6	9	2	5
Cirrhitidae	1		1								1		
Dasyatidae	1		1										
Echeneididae	1	1											
Ephippidae	1						1						
Haemulidae	3	2						1			1		
Holocentridae	7	1	2	1		4	1			2	2		
Labridae	27	7	7	3	11	13	5	5	7	12	6	6	9
Lethrinidae	1	1			1	1	1						
Lutjanidae	9		1	1	2	2	2	2			3		
Monacanthidae	1											1	
Mullidae	5	1	2	1	5	4			2	1	2		
Nemipteridae	7	3	1	1	2	3		1	3	1		1	2
Ostraciidae	2		1			1							
Pempheridae	1		1										
Plotosidae	1											1	
Pomacanthidae	5		1		1	2	2	1			2		
Pomacentridae	40	9	8	5	5	13	8	9	10	8	7	10	15
Priacanthidae	1		1										
Scaridae	18	6	6	4	10	9	5	5	1		5	5	5
Scombridae	1						1	1					
Scorpaenidae	1										1		
Serranidae	11	1	5	2	1	2	3	3	3	1	1	1	3
Siganidae	4	1	2	1	1	4	2	1	2	1	1	3	2
Synodontidae	1				1	1						1	1
Tetraodontidae	3	1	2			2							1
Zanclidae	1		1		1	1	1	1		1	1	1	1

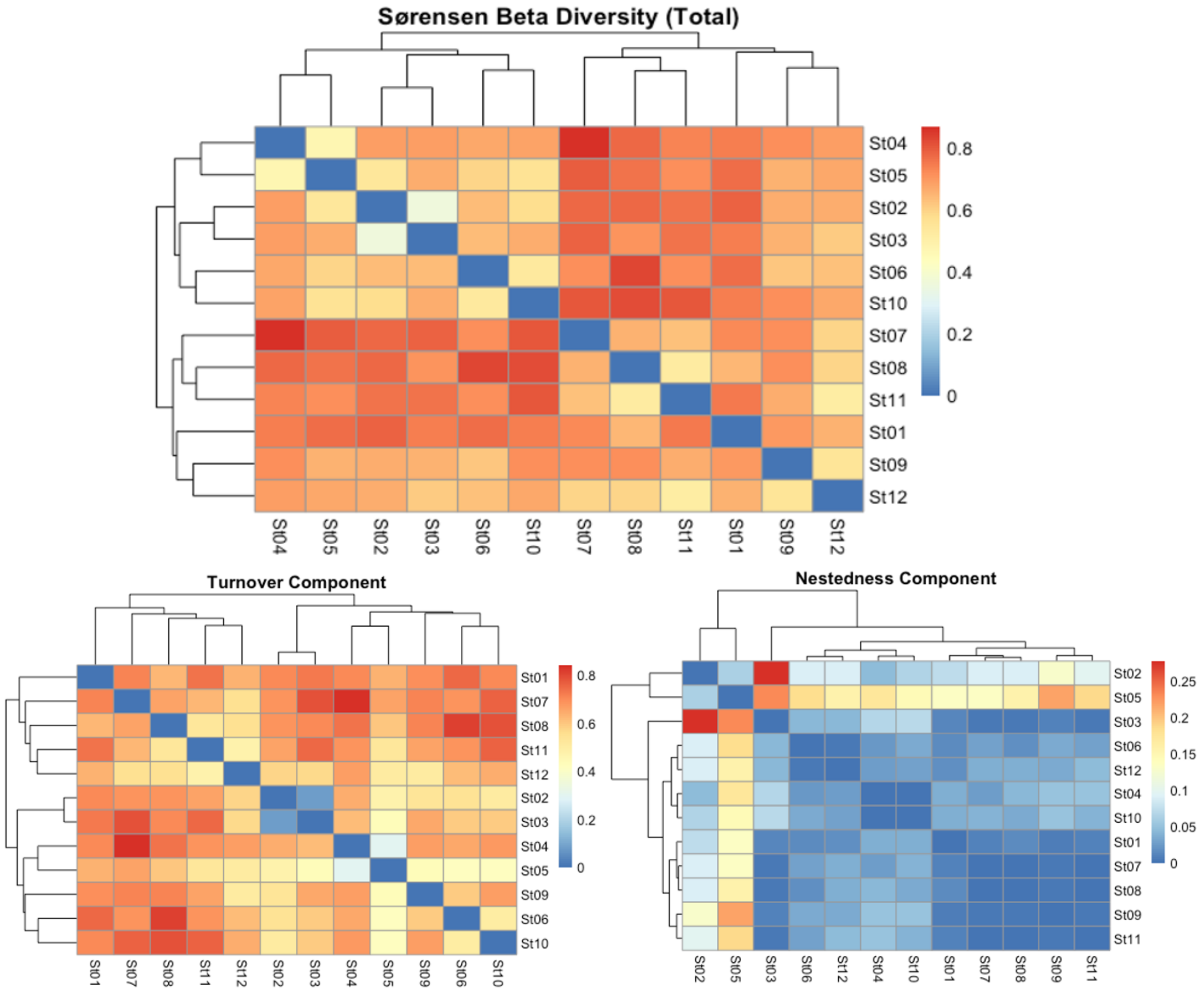


Fig. 2. Total betadiversity (Sorensen), turnover and nestedness components of reef fishes at Morowali MPA

These patterns in beta diversity of reef fish at Morowali MPA are also aligned with community structure. The reef fish composition at family level showing a high abundance was that recorded for Balistidae, Pomacentridae, Caesionidae, Carangidae, Acanthuridae, Chaetodontidae, Labridae, Scombridae, Serranidae, Mullidae, Scaridae, Siganidae, and Plotosidae (Fig. 3A). In terms of family composition, there are 4 study sites with the similar community structure of reef fish with the highest abundance as Family Balistidae, St02, St03, St04 and St05 were located in close geographical proximity (Fig. 1). Interestingly, the other study sites which also distributed in adjacent areas and shared a similar family composition but different from the previous group were Padei Darat Island (St06) and Menui Island (St10) (Fig. 3A). However, Tiga Island (St09) showed a unique fish composition, which is the only study site with different fish abundance, dominated by the family Labridae and followed by Caesionidae, Pomacentridae, and Acanthuridae. This result of community structure based on relative abundances of reef fish was also consistent with the clustering analysis of species composition that showed dissimilarity between study sites was high, about 75% (Fig. 3C). The group of study sites with the low dissimilarity (< 50%) was Samarengga I (St02), Samarengga II (St03), Koikoila (St04), and Padei Laut (St05), wherein family Balistidae was the highest abundance at those study sites. However, the other study sites revealed the dissimilarity of reef fish species composition was high with the most abundance was family Pomacentridae, likewise the most dissimilarity between study sites was St01 and St09 (Panimbawang and Tiga island), about 75% with high abundance of Pomacentridae and Labridae, respectively.

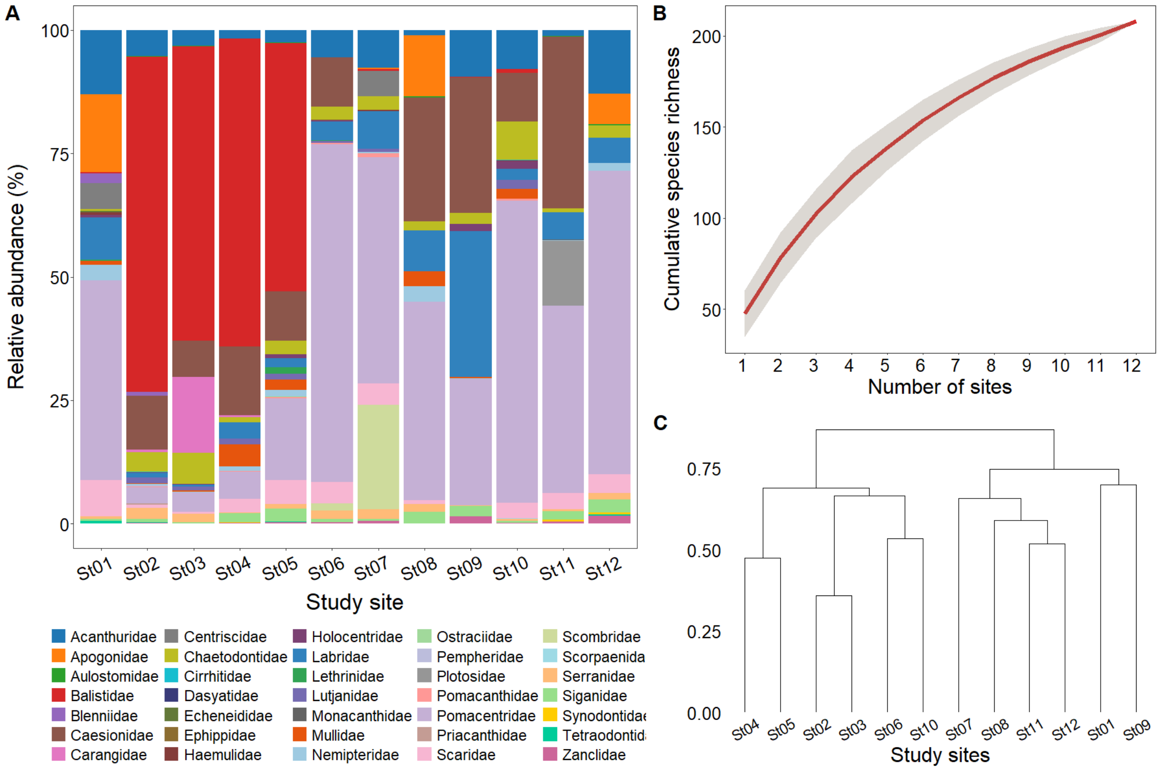


Fig. 3. (A) Relative abundance of reef fish families across study sites; (B) Species accumulation curve of reef fishes in Morowali MPA; (C) Cluster analysis chart of fish species composition across study sites based on present-absence data

2. Spatial variation of fish and size distribution

Fish biomass was reported high at study sites St02 to St05, despite being dominated by small size individuals (Fig. 4A-B), these indicated the dominance of a few taxa of fish. Study site St02 documented fish families such as Balistidae, Caesionidae, and Carangidae contributed most to biomass, particularly *Odonus niger*, *Pterocaesio tile*, and *Elagatis bipinnulata*. The abundance of these fishes reached high, although *E. bipinnulata* (Carangidae) was less abundant, its large body size contributes substantially to the overall fish biomass. The fish domination that contributed to the high biomass at St03 was recorded for *O. niger*, *Caranx ignobilis*, and *P. tile*, while at St04 was *O. niger* and *P. tile*; however, St05 only documented *O.niger* which was dominant within high biomass. *Odonus niger* prefers steep reef drop-offs areas such as Samarengga (St02 and St03), Koikoila (St04), and Padei Islands (St05), wherein the density was 736 to 1791 individuals per 500m². These dominant fish have characteristics as schooling behavior, which aggregate to enhance foraging efficiency and reduce predation risk.

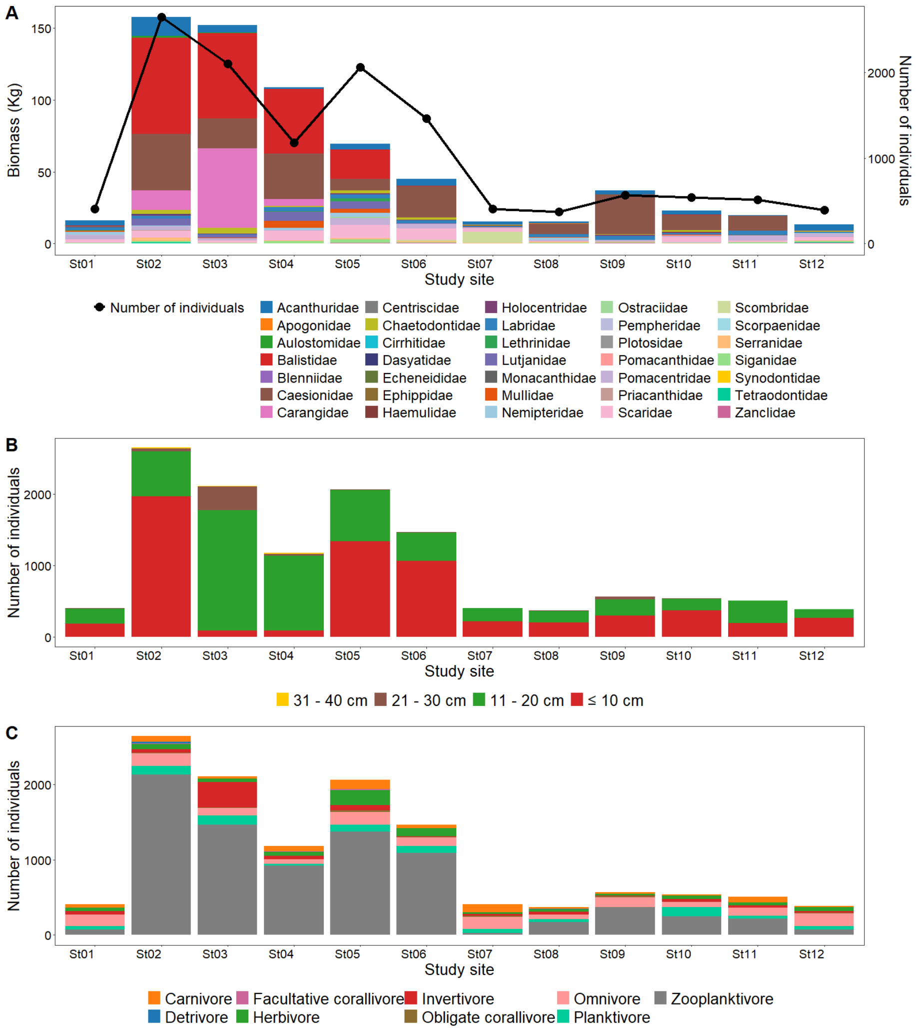


Fig. 4. Distribution of reef fishes across 12 study sites in Morowali MPA based on (A) Biomass of fish each family and number of individuals; (B) Number of individuals in each size class of reef fishes; and (C) Trophic group distribution of reef fish across study sites

Among the 12 study sites in Morowali MPA, 5 study sites were reported to exhibit relatively higher fish abundances, dominated by small size (< 20cm), possibly indicating successful recruitment or past fishing pressure. Based on Morowali MPA zones, these sites (St02, St03, St04, St05, and St06) are not take zones (Fig. 1), and the fish communities were dominated by zooplanktivorous trophic group (Fig. 4C), suggesting abundance of zooplankton which might be driven by the southeast monsoon event in this region. The high number of small fish sizes within zooplanktivorous trophic groups may reflect ecological processes such as plankton fluctuations, high turnover rates of diversity, and trophic specialization. Moreover, the high abundance of *O. niger* is likely linked to decline in seawater temperatures during the southeast monsoon (June – August) in Banda Sea. This season encourages upwelling processes, which can enrich nutrients and provide food resources, coupled with environmental conditions could be suitable to stimulate fish spawning activities. During sampling, *O. niger* was mostly documented in juvenile stages with relatively uniform size under 15cm. At 3 study sites (St02, St05, and St06), over 65% of the fish ranged ≤ 10cm, with some individuals reaching up to 40cm at St02. Additionally, most fish at St03 and St04 ranged between 11 - 20cm (≥ 80%) (Fig. 4B). Small fish (≤ 10cm) were generally from Balistidae, Pomacentridae, and Labridae families, while the larger sized (21-40 cm) was composed by target fish groups such as trevallies (Carangidae), snapper (Lutjanidae), fusilier (Caesionidae), and parrotfish (Scaridae).

3. Relationship between benthic substrate and reef fish

The benthic compositions showed a variation percent cover, while the most benthic substrates (> 20%) among study sites were non-acropora (NAC) and followed by dead coral (DC). The benthic substrates of NAC and DC were reported with the high percent coverages at 7 and 3 study sites, respectively (Fig. 5A). Moreover, a benthic substrate with high percent cover documented only at one study site was soft coral (27.1%) at St04, fleshy seaweed (22.1%) at St11, sand (21.1%) at St01, and rubble (25.8%) at St07. The study site of St05, St06, St08, and St12 which was dominated by NAC, likewise, St04 by DC (22.1%), and St09 by DCA (26.9%). Furthermore, Pearson correlation analysis showed that there was no correlation between hard coral percent cover including AC and NAC with species richness of reef fish (r = 0.16, *P* = 0.62), nor between hard coral percent cover and fish biomass (r = 0.049, *P* =0.88) (Fig. 5B-C). The Non-metric Multidimensional Scaling (nMDS) ordination plot presented the variation of 10 highest abundance reef fish at Morowali MPA, wherein suggesting ecological associations with the benthic percent cover, stress = 0.079 (Fig. 6). Fish families such as Chaetodontidae, Labridae, Siganidae, and Serranidae are strongly associated with AC, NAC, FS and DC, respectively. The vector orientation of sand (S) and rubble(R) are linked to Scaridae and Acanthuridae, and also Pomacentridae.

The patterns observed indicate fish assemblages, particularly Chaetodontidae and Siganidae. The distribution of Chaetodontidae revealed a positive association with AC indicating that fish tends to occur as attributed by acropora percent cover (Fig. 6). Chaetodontidae are known as bio-indicator for coral health where the fish majority have a feeding habit corallivore by consuming coral polyps. The high species richness of Chaetodontidae is documented at St05, and the lowest was at St01 (Table 1). The only species that found at St01 was *Chaetodon lunulatus* with obligate corallivore feeding habits, while benthic substrate in this study sites was dominated by percent cover of NAC, S, and R (22.2%, 21.1%, and 18.6%, respectively), however, domination of benthic substrates at St05 was NAC, DCA, and DC (28.3%, 16.1%, and 14.9%, respectively). Meanwhile, the highest number of individuals was recorded at St03 and St02 although their species richness was low (133 Ind, 5 species; and 104 Ind, 8 species, respectively), suggesting that structural complexity of Chaetodontidae may favor abundance of particular taxa, such as *Hemitaurichthys polylepis*, which is documented in schooling formation at reef slopes and has attributes as planktivore. This align with those study sites which is reef slope types, wherein the benthic substrate was dominated by DC, AC, and DCA (22.1%, 21.3%, and 19.9%) and (22.1%, 18.2%, and 17.0%) at St03 and St02, respectively. Furthermore, Siganidae revealed 4 species documented across study sites and has relations to fleshy seaweed (Fig. 6). *Siganus canaliculatus* recorded exclusively at St04 and St05, and reported a high number of individuals in which the fish exhibits schooling behavior, however FS percent cover was 4.5% and 0% for St04 and St05, respectively. The species of Siganidae with widespread distribution was *Siganus vulpinus* (except at St04 and St10), moreover, *Siganus doliatus* and *Siganus puellus* were recorded at 4 and 5 study sites, respectively. These findings highlight that fish diversity and abundance are not determined by a single benthic substrate, but rather by the complementary roles by variation of benthic substrate compositions.

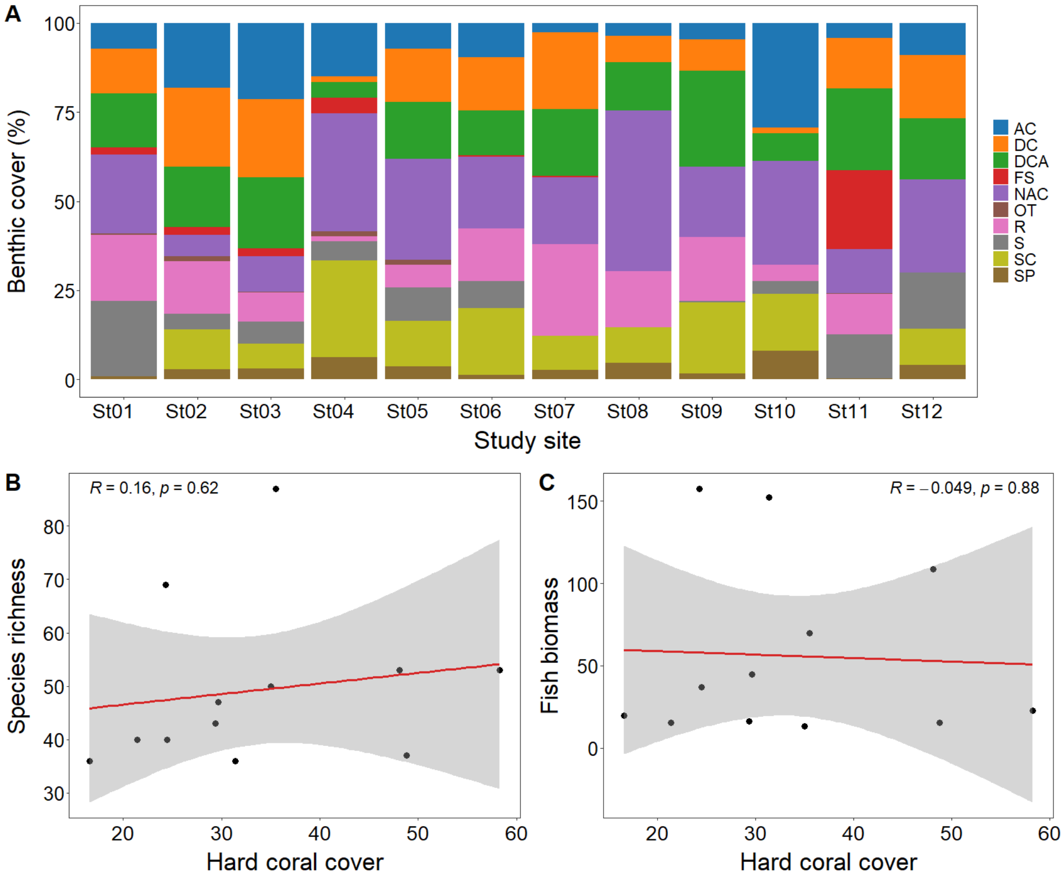


Fig. 5. Benthic substrate composition among study sites (A), and Pearson correlations among benthic substrate of hard coral, including acropora (AC) and non-acropora (NAC), and reef fish species richness (B) and fish biomass (C)

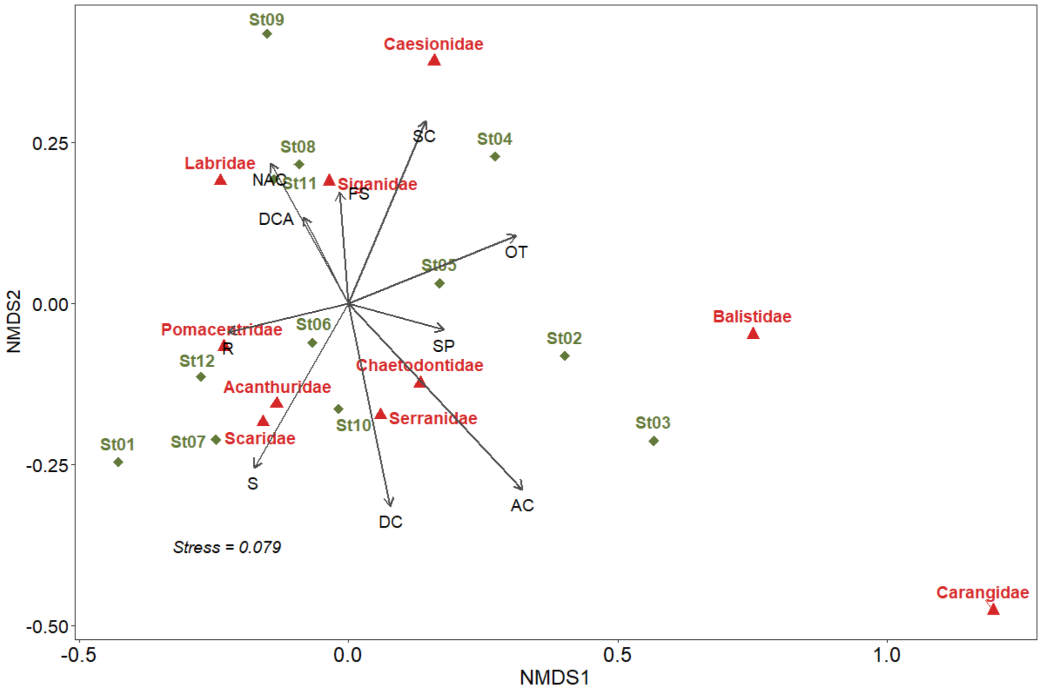


Fig. 6. Non-metric multidimensional scaling based on Bray Curtis, distance among benthic substrate and 10 reef fishes most abundant in study areas

DISCUSSION

High species turnover (βsor) among study sites indicate strong spatial structuring of reef fish assemblages, with site differences driven by species presence of rather than abundance variations. This pattern aligns with habitat mosaic and environmental gradients (depth, current exposure, and benthic complexity) that promote species replacement rather than gains or losses of species **(Edgar *et al.*, 2014; Medina *et al.*, 2021)**. Near-zero βsne in many pairs (e.g., St04 – St10, St07 – St08, St07 – St11) suggest sites harbor distinct species groups, highlighting the importance of diverse habitat representation in conservation planning. Elevated nestedness in pairs such as St02 – St03 and St03-St05) likely reflect richness gradients or partial faunal subsets, potentially influenced from environmental factors (turbidity, marginal reef condition, or depth-limited assemblages). Localized disturbance or fishing pressure might selectively impact on sensitive taxa, while variations in sampling effort or environmental conditions could influence species detectability. Distinguishing between these factors requires comprehensive site metadata and standardized sampling protocols.

Reef fish assemblage structuring at Morowali MPA is likely influenced by habitat heterogeneity and topography, with secondary effects from human pressure and spatial proximity. This aligns with previous studies showing habitat and topography as key predictors of fish abundance, biomass, and species richness **(García-Charton *et al.*,**

2004; Darling *et al*., 2017; Fukunaga *et al*., 2023; Bellwood & Tebbett, 2024). The dominance of *Odonus niger* at sites St02 – St05 referring steep slopes, reflect environmental sorting mechanisms driven by topography and current/exposure regimes. This case of fish–habitat coupling around Samarengga, Koikoila, and Padei supports previous findings of strong fish–habitat coupling and schooling behavior **(Wong *et al*., 2018; Pimentel *et al*., 2022)**. Topographic features like steep slopes, crevices, and variable substrate create microhabitats that support higher diversity and specialized behaviors in reef fishes. Complex topography increases available shelter, food resources, and refugia, which are critical for both resident and transient species.

The high abundance of *O. niger* is likely influenced by seasonal oceanographic processes, particularly the southeast monsoon (June-August) in the Banda Sea. This period induces seawater cooling and increased vertical mixing, enhancing upwelling and nutrient enrichment **(Wyrtki, 1961; Gordon & Fine, 1996; Pusparini *et al*., 2017)**, which boost planktonic productivity and food availability, those could promote fish aggregations and spawning **(Thiaw *et al*., 2017; Kesaulya *et al*., 2023)**. The prevalence of juvenile *O. niger* (<15cm) suggests that the area may serve as a recruitment ground, with over 65% of individuals under 10cm at St02, St05 and St06. in contrast, St03 and St04 had predominantly medium-sized individuals (11– 20cm; ≥80%), indicating possible ontogenetic habitat partitioning. Small-bodied size classes (≤ 10cm) were mainly composed of Balistidae, Pomacentridae, and Labridae, groups typically associated with high site fidelity and habitat dependency. Larger-bodied fishes (21- 40cm) included ecologically and economically important target taxa such as Carangidae, Lutjanidae, Caesionidae and Scaridae. This ontogenetic and taxonomic partitioning highlights the role of reef structural heterogeneity in supporting both juvenile nursery grounds and adult foraging habitats **(Darling *et al*., 2017)**. Seasonal oceanographic variability, particularly monsoon-driven upwelling, interacts with reef geomorphology to shape fish community dynamics, productivity, and recruitment **(Wong-Ala *et al*., 2018; Eisele *et al*., 2021)**.

A second cluster of adjacent sites (e.g., Padei Darat, St06; Menui, St10) displayed similar family-level composition, while Tiga Island (St09) was unique, dominated by Labridae, followed by Caesionidae, Pomacentridae, and Acanthuridae. High dissimilarity (~75%) and a small subset of low-dissimilarity sites (Samarengga I, II, Koikoila, Padei Laut; <50%), with Balistidae dominance suggest differences stem from species replacement across environmental gradient rather than species richness (Figure 3C). High beta diversity often results from species replacement along gradients, particularly in system woth strong environmental factor such as reef structure and water quality **(López-Delgado *et al*., 2020; Camara *et al*., 2023)**. Reef structure patterns in Morowali MPA revealed non-acroporid hard corals (NAC) and dead corals (DC) as dominant substrates, but no significan relationshop was found between coral cover and fish richness or biomass, suggesting more nuanced influences such as habitat complexity, functional groups and life history traits **(Chong-Seng *et al*., 2012; Fukunaga *et al*., 2020; Pombo-Ayora *et al*., 2020)**.

The nMDS ordination revealed ecological linkages, with Chaetodontidae richness tracked closely with Acropora percent cover, highlighting their role as bioindicators of reef health **(Pratchett *et al*., 2008; Graham & Nash, 2013; Fukunaga *et al*., 2020)**. At St05, where Acropora dominated, species richness was highest, while St01 with NAC, sand, and rubble hosted only *Chaetodon lunulatus*, a generalist species. The absence of specialized corallivores at St01 show how coral loss erodes butterflyfish assemblages **(Berumen & Pratchett, 2006; Richardson *et al*., 2018)**. At St02 and St03, despite lower Chaetodontidae richness due to extensive DC, AC, and DCA, planktivorous *Hemitaurichthys Polylepis* aggregated in current-exposed slope habitats **(Cole *et al*., 2008; Agudo-Adriani *et al*., 2019)**. Siganidae, notably *Siganus canaliculatus* exhibited clear associations with fleshy seaweeds (FS), showing that localized food resources can drive fish abundances, regardless of broad-scale benthic cover. Other siganid species (*S. vulpinus*, *S. doliatus*, and *S. puellus*) displayed dietary flexibility and habitat generality, highlighting their role in reef resilience by controlling macoralga **(Hoey *et al*., 2013)**. These findings suggest that fish assemblage structure is shaped by both coral cover and substrate composition, with reef geomorphology contributing to community dynamics **(Wilson *et al*., 2006; Graham & Nash, 2013)**.

Evidence from other Indo-Pacific MPAs supports this interpretation. In Wakatobi, Southeast Sulawesi, reef fish diversity was influenced by live coral cover, reef slopes complexity and exposure gradients, with rubble and dead coral providing shelter for juveniles and crypto benthic fish **(Ahmadia *et al*., 2012)**. In Raja Ampat, West Papua, fish assemblages were strongly associated with habitat mosaics including macroalgae, rubble, sponges and hard corals **(Fidler *et al*., 2021)**. On the Great Barrier Reef, fish community composition remained stable even with coral cover declined, as non-coral substrates like turf algae and rubble supported herbivores and planktivores **(Wilson *et al*., 2006)**. These studies suggest that benthic diversity, rather than coral cover alone, support reef fish resilience across the Indo-Pacific. Therefore management strategies focused solely on maximizing live coral cover may overlook the ecological roles of non-coral substrates such as soft coral, fleshy seaweed and macroalgae. While Acropora remain vitals for obligate corallivores such as Chaetodontidae, other fish families thrive in varied benthic environments, particularly where structural complexity and food availability are maintained. For Morowali MPA, this highlights the need to conserve both live coral and diverse benthic habitat substrates that sustain reef fish assemblage, ensuring ecosystem functions like herbivory, planktivory, and predation to support reef resilience amid environmental change.

CONCLUSION

The reef fish assemblages in Morowali MPA are marked by high species richness (206 species, 35 families) and strong spatial structuring, primarily driven by species turnover rather than nestedness. Sites like Padei Laut (St05) and Samarengga I (St02) exhibited the highest species richness, while Tiga Island (St09) had a unique composition dominated by Labridae, Caesionidae, Pomacentridae, and Acanthuridae. The *Pomacentridae* family was the most species-rich, and widespread families included Acanthuridae, Chaetodontidae, Labridae, Pomacentridae, and Siganidae. Fish biomass was at its highest at St02, St03, St04, and St05, with species like *Odonus niger* and *Pterocaesio tile* dominating, exhibiting schooling behavior and preferring steep reef slopes. The abundance of juvenile *O. niger* might affected by oceanographic links, particularly upwelling during the southeast monsoon. Size distributions showed dominance of smaller fish (≤ 10cm) at several sites, with larger species (21- 40cm) found in herbivorous and carnivorous groups. Benthic substrate composition, with non-acroporid corals (NAC) and dead corals (DC) being dominant, showed no significant relationship with fish species richness or biomass, indicating that benthic complexity, rather than coral cover alone, supports diverse fish communities. The nMDS ordination revealed associations between fish families and specific benthic substrates such as Acropora and macroalgae, underscoring the importance of habitat heterogeneity for sustaining reef fish diversity. These findings highlight the need for conservation strategies that preserve a range of benthic habitats to ensure reef resilience.

ACKNOWLEDGEMENT

The research was funded by the Department of Fisheries and Maritime Affairs of Central Sulawesi Province for Reef Health Monitoring Programs in Coastal and Small islands Conservation Area (KKP3K), Regency of Morowali and North Morowali, and Surrounding Waters. We thank all colleagues and stakeholders who contributed to the field work and data collections.

REFERENCES

Ahmadia, G.N.; Pezold, F.L. and Smith, D.J. (2012). Cryptobenthic fish biodiversity and microhabitat use in healthy and degraded coral reefs in SE Sulawesi, Indonesia. *Marine Biodiversity*, *42*(4), 433–442. https://doi.org/10.1007/s12526-012-0118-3

Amkieltiela; Handayani, C.N.; Andradi-Brown, D.A.; Estradivari; Ford, A.K.; Beger, M.; Hakim, A.; Muenzel, D.K.; Carter, E.; Agung, F.; Veverka, L.;

Iqbal, M.; Lazuardi, M.E.; Fauzi, M.N.; Tranter, S.N. and Ahmadia, G.N. (2022). The rapid expansion of Indonesia's marine protected area requires improvement in management effectiveness. *Marine Policy, 146,* 105257. https://doi.org/10.1016/j.marpol.2022.105257

Arias-Godínez, G.; Jiménez, C.; Gamboa, C.; Cortés, J.; Espinoza, M.; Beita-Jiménez, A. and Alvarado, J.J. (2021). The effect of coral reef degradation on the trophic structure of reef fishes from Bahía Culebra, North Pacific coast of Costa Rica. *Journal of Coastal Conservation*, *25*(1), 22. https://doi.org/10.1007/s11852-021-00802-x

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography, 19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A. and Orme, C.D.L. (2012). Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution, 3*(5), 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x

Bellwood, D.R. and Tebbett, S.B. (2024). Habitat trumps biogeography in structuring coral reef fishes. *Coral Reefs, 43*(6), 1599–1609. https://doi.org/10.1007/s00338-024-02556-y

Berumen, M.L. and Pratchett, M.S. (2006). Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs, 25*(4), 647–653. https://doi.org/10.1007/s00338-006-0145-2

Bray, J.R. and Curtis, J.T. (1957). An Ordination of the Upland Forest Communities of Southern Wisconsin. *Ecological Monographs, 27*(4), 325–349. https://doi.org/10.2307/1942268

Camara, E.M.; de Andrade-Tubino, M.F.; Franco, T.P.; Neves, L.M.; dos Santos, L.N.; dos Santos, A.F.G.N. and Araújo, F.G. (2023). Temporal dimensions of taxonomic and functional fish beta diversity: scaling environmental drivers in tropical transitional ecosystems. *Hydrobiologia, 850*(8), 1911–1940. https://doi.org/10.1007/s10750-023-05202-w

Chong-Seng, K.M.; Mannering, T.D.; Pratchett, M.S.; Bellwood, D.R. and Graham, N.A.J. (2012). The Influence of Coral Reef Benthic Condition on Associated Fish Assemblages. *PLOS ONE, 7*(8), e42167. https://doi.org/10.1371/journal.pone.0042167

Clarke, K.R.; Somerfield, P.J. and Chapman, M.G. (2006). On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology, 330*(1), 55–80. https://doi.org/10.1016/j.jembe.2005.12.017

Cole, A.J.; Pratchett, M.S. and Jones, G.P. (2008). Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries, 9*(3), 286–307.

https://doi.org/10.1111/j.1467-2979.2008.00290.x

Darling, E.S.; Graham, N.A.J.; Januchowski-Hartley, F.A.; Nash, K.L.; Pratchett, M.S. and Wilson, S.K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*, *36*(2), 561–575. https://doi.org/10.1007/s00338-017-1539-z

Duffy, J.E.; Lefcheck, J.S.; Stuart-Smith, R.D.; Navarrete, S.A. and Edgar, G.J. (2016). Biodiversity enhances reef fish biomass and resistance to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(22), 6230–6235. https://doi.org/10.1073/pnas.1524465113

Edgar, G.J.; Russ, G.R. and Babcock, R.C. (2007). Marine protected areas. In: *Marine Ecology;* Connell, S.D. and Gillanders, B.M., Eds.; Oxford University Press, pp. 533–557.

Edgar, G.J.; Stuart-Smith, R.D.; Willis, T.J.; Kininmonth, S.; Baker, S.C.; Banks, S.; Barrett, N.S.; Becerro, M.A.; Bernard, A.T.F.; Berkhout, J.; Buxton, C.D.; Campbell, S.J.; Cooper, A.T.; Davey, M.; Edgar, S.C.; Försterra, G.; Galván, D.E.; Irigoyen, A.J.; Kushner, D.J. and Thomson, R.J. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature*, *506*(7487), 216–220. https://doi.org/10.1038/nature13022

Eisele, M.H.; Madrigal-Mora, S. and Espinoza, M. (2021). Drivers of reef fish assemblages in an upwelling region from the Eastern Tropical Pacific Ocean. *Journal of Fish Biology*, *98*(4), 1074–1090. https://doi.org/10.1111/jfb.14639

Estradivari; Agung, M.F.; Adhuri, D.S.; Ferse, S.C.A.; Sualia, I.; Andradi-Brown, D.A.; Campbell, S.J.; Iqbal, M.; Jonas, H.D.; Lazuardi, M.E.; Nanlohy, H.; Pakiding, F.; Pusparini, N.K.S.; Ramadhana, H.C.; Ruchimat, T.; Santiadji, I.W.V.; Timisela, N.R.; Veverka, L. and Ahmadia, G.N. (2022). Marine conservation beyond MPAs: Towards the recognition of other effective area-based conservation measures (OECMs) in Indonesia. *Marine Policy*, *137*, 104939. https://doi.org/10.1016/j.marpol.2021.104939

Fidler, R.Y.; Andradi-Brown, D.A.; Awaludinnoer; Pada, D.; Purwanto; Hidayat, N.I.; Ahmadia, G.N. and Harborne, A.R. (2021). The importance of biophysical context in understanding marine protected area outcomes for coral reef fish populations. *Coral Reefs*, *40*(3), 791–805. https://doi.org/10.1007/s00338-021-02085-y

Froese, R. and Pauly, D. (2024). *FishBase*. World Wide Web Electronic Publication. www.fishbase.org

Fukunaga, A.; Asner, G.P.; Grady, B.W. and Vaughn, N.R. (2023). Fish assemblage structure, diversity and controls on reefs of South Kona, Hawaiʻi Island. *PLOS ONE*, *18*(7), e0287790. https://doi.org/10.1371/journal.pone.0287790

Fukunaga, A.; Kosaki, R.K.; Pascoe, K.H. and Burns, J.H.R. (2020). Fish assemblage structure in the northwestern hawaiian islands is associated with the architectural complexity of coral-reef habitats. *Diversity*, *12*(11), 430. https://doi.org/10.3390/d12110430

García-Charton, J.A.; Pérez-Ruzafa, Á.; Sánchez-Jerez, P.; Bayle-Sempere, J.T.; Reñones, O. and Moreno, D. (2004). Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. *Marine Biology*, *144*(1), 161–182. https://doi.org/10.1007/s00227-003-1170-0

Giyanto. (2012). Penilaian kondisi terumbu karang dengan metode transek foto bawah air. *Oseanologi Limnologi Di Indonesia*, *38*(3), 377–390.

Gordon, A.L. and Fine, R.A. (1996). Pathways of water between the Pacific and Indian oceans in the Indonesian seas. *Nature*, *379*(6561), 146–149. https://doi.org/10.1038/379146a0

Graham, N.A.J. and Nash, K.L. (2013). The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, *32*(2), 315–326. https://doi.org/10.1007/s00338-012-0984-y

Gudo-Adriani, E.A.; Cappelletto, J.; Cavada-Blanco, F. and Cróquer, A. (2019). Structural Complexity and Benthic Cover Explain Reef-Scale Variability of Fish Assemblages in Los Roques National Park, Venezuela. *Frontiers in Marine Science*, *6*, 690. https://doi.org/10.3389/fmars.2019.00690

Hadi, T.A.; Tuti, Y.; Hadiyanto; Abrar, M.; Suharti, S.R.; Suharsono and Gardiner, N.M. (2018). The dynamics of coral reef benthic and reef fish communities in Batam and Natuna Islands, Indonesia. *Biodiversity*, *19*(1–2), 81–94. https://doi.org/10.1080/14888386.2018.1473797

Hilborn, R. (2018). Are MPAs effective? *ICES Journal of Marine Science*, *75*(3), 1160–1162. https://doi.org/10.1093/icesjms/fsx068

Hill, J. and Wilkinson, C. (2004). *Methods for Ecological Monitoring of Coral Reefs*. Australian Institute of Marine Science.

Hoegh-Guldberg, O.; Poloczanska, E.S.; Skirving, W. and Dove, S. (2017). Coral reef ecosystems under climate change and ocean acidification. *Frontiers in Marine Science*, *4*, 158. https://doi.org/10.3389/fmars.2017.00158

Hoey, A.S.; Brandl, S.J. and Bellwood, D.R. (2013). Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: Implications for ecosystem function. *Coral Reefs*, *32*(4), 973–984. https://doi.org/10.1007/s00338-013-1043-z

Kesaulya, I.; Haumahu, S.; Triyulianti, I.; Widiaratih, R.; Oktavianto, E.A.; Rugebregt, M.J.; Kalambo, Y.L. and Fadhilah, A. (2023). Phytoplankton abundance and diversity in the Northern Banda Sea. *IOP Conference Series: Earth and Environmental Science*, *1207*(1), 012031. https://doi.org/10.1088/1755-1315/1207/1/012031

Kohler, K.E. and Gill, S.M. (2006). Coral Point Count with Excel extensions (CPCe): A

Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences, 32*(9), 1259–1269. https://doi.org/10.1016/j.cageo.2005.11.009

Kolde, R. (2025). *pheatmap: Pretty Heatmaps*. R package version 1.0.12. https://github.com/raivokolde/pheatmap

Komyakova, V.; Munday, P.L. and Jones, G.P. (2013). Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. *PLOS ONE, 8*(12), e83178. https://doi.org/10.1371/journal.pone.0083178

Kriegl, M.; Elías Ilosvay, X.E.; von Dorrien, C. and Oesterwind, D. (2021). Marine Protected Areas: At the Crossroads of Nature Conservation and Fisheries Management. *Frontiers in Marine Science, 8,* 676264. https://doi.org/10.3389/fmars.2021.676264

Kuiter, R.H. and Tonozuka, T. (2001). *Pictoral Guide to Indonesian Reef Fishes - Part 3*. Zoonetics.

López-Delgado, E.O.; Winemiller, K.O. and Villa-Navarro, F.A. (2020). Local environmental factors influence beta-diversity patterns of tropical fish assemblages more than spatial factors. *Ecology, 101*(2), e02940. https://doi.org/10.1002/ecy.2940

Maestro, M.; Pérez-Cayeiro, M.L.; Chica-Ruiz, J.A. and Reyes, H. (2019). Marine protected areas in the 21st century: Current situation and trends. *Ocean and Coastal Management*, *171*, 28–36. https://doi.org/10.1016/j.ocecoaman.2019.01.008

McClanahan, T.R.; Maina, J.M.; Graham, N.A.J. and Jones, K.R. (2016). Modeling reef fish biomass, recovery potential, and management priorities in the western Indian Ocean. *PLOS ONE, 11*(5), e0154585. https://doi.org/10.1371/journal.pone.0154585

Medina, M.; Estes, C.; Best, B.; Stallings, C.; Montes, E.; McEachron, L. and Muller-Karger, F. (2021). Reef-Fish Abundance, Biomass, and Biodiversity Inside and Outside No-Take Marine Zones in the Florida Keys National Marine Sanctuary: 1999–2018. *Oceanography, 34*(2), 52–61. https://doi.org/10.5670/oceanog.2021.214

Meilana, L.; Fang, Q.; Susanto, H.A.; Widiastutik, R.; Syaputra, D.E.; Ikhumhen, H.O.; Sholihah, R.; Hakim, A.; Yang, S. and Liu, Z. (2023). How Indonesian marine protected areas (MPAs) are doing: A management performance-based evaluation. *Biological Conservation, 282,* 110033. https://doi.org/10.1016/j.biocon.2023.110033

Moore, A. and Ndobe, S. (2008). Reefs at risk in Central Sulawesi, Indonesia - status and outlook. *Proceedings of the 11th International Coral Reef Symposium*, 840–844.

Moutopoulos, D.K.; Giovos, I.; Kleitou, P.; Kletou, D.; Savva, I.; Cai, L.L. and

Katselis, G. (2021). Multi-disciplinary approach of reported and unreported fisheries in a new established MPA: The case of Cavo Greco, Cyprus. *Regional Studies in Marine Science*, *47*, 101922. https://doi.org/10.1016/j.rsma.2021.101922

Pimentel, C.R.; Pinheiro, H.T.; Giarrizzo, T.; Francini-Filho, R.B.; Reis-Filho, J.A.; Rocha, L.A.; Ferreira, C.E.L.; Barbosa, M.C. and Joyeux, J.C. (2022). Ecological Links between Pelagic and Mesophotic Reef Fishes in an Oceanic Archipelago of the Equatorial Atlantic Ocean. *Diversity*, *14*(4), 273. https://doi.org/10.3390/d14040273

Pratchett, M.S.; Berumen, M.L.; Marnane, M.J.; Eagle, J.V. and Pratchett, D.J. (2008). Habitat associations of juvenile versus adult butterflyfishes. *Coral Reefs*, *27*(3), 541–551. https://doi.org/10.1007/s00338-008-0357-8

Pusparini, N.; Prasetyo, B.; Ambariyanto and Widowati, I. (2017). The Thermocline Layer and Chlorophyll-a Consentration Variability during Southeast Monsson in the Banda Sea. *IOP Conference Series: Earth and Environmental Science*, *55*, 012309. https://doi.org/10.1088/1755-1315/55/1/012309

Rahman, M.K.; Masud, M.M.; Akhtar, R. and Hossain, M.M. (2022). Impact of community participation on sustainable development of marine protected areas: Assessment of ecotourism development. *International Journal of Tourism Research*, *24*(1), 33–43. https://doi.org/10.1002/jtr.2480

Richardson, L.E.; Graham, N.A.J.; Pratchett, M.S.; Eurich, J.G. and Hoey, A.S. (2018). Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Global Change Biology*, *24*(7), 3117–3129. https://doi.org/10.1111/gcb.14119

Robinson, J.P.W.; Williams, I.D.; Edwards, A.M.; McPherson, J.; Yeager, L.; Vigliola, L.; Brainard, R.E. and Baum, J.K. (2016). Fishing degrades size structure of coral reef fish communities. *PeerJ Preprints*, e2118v1. https://doi.org/10.7287/peerj.preprints.2118v1

Russ, G.R.; Rizzari, J.R.; Abesamis, R.A. and Alcala, A.C. (2021). Coral cover a stronger driver of reef fish trophic biomass than fishing. *Ecological Applications*, *31*(1), e02224. https://doi.org/10.1002/eap.2224

Sebastian, P.; Sparks, L.D.; Resolute, P. and Prasetijo, R. (2024). Connecting communities to coral reefs: a socio-ecological perspective on coral restoration programs in a remote marine protected area. *Journal of Coastal Conservation*, *28*(2), 25. https://doi.org/10.1007/s11852-024-01041-6

Thiaw, M.; Auger, P.-A.; Ngom, F.; Brochier, T.; Faye, S.; Diankha, O. and Brehmer, P. (2017). Effect of environmental conditions on the seasonal and inter-annual variability of small pelagic fish abundance off North-West Africa: The case of both Senegalese sardinella. *Fisheries Oceanography*, *26*(5), 583–601. https://doi.org/10.1111/fog.12218

Thilakarathne, E.P.D.N.; Ramawickrama, N.W.; Bandara, T.; Maldeniya, M.U.S.;

Egodauyana, K.P.U.T.; Sewwandi, S.W.R.; Liyanage, N.P.P. and Jayamanne, S.C. (2024). Abundance and diversity of reef fish species and their relationship with corals along the eastern coast of Sri Lanka. *Journal of Coastal Conservation*, *28*(1), 9. https://doi.org/10.1007/s11852-024-01040-7

Tosepu, R.; Resky Apriana, D.; Reva Wardani, I. and Mendila Tappo, L. (2025). The Impact of Clean Water Pollution from Nickel Mining Activities in Kabaena, Southeast Sulawesi. *Journal of Health Science and Pharmacy*, *2*(1), 7–13.

Touza, J.; Lacambra, C.; Kiss, A.; Amboage, R.M.; Sierra, P.; Solan, M.; Godbold, J.A.; Spencer, T. and White, P.C.L. (2021). Coping and Adaptation in Response to Environmental and Climatic Stressors in Caribbean Coastal Communities. *Environmental Management*, *68*(4), 505–521. https://doi.org/10.1007/s00267-021-01500-y

Tranter, S.N.; Estradivari; Ahmadia, G.N.; Andradi-Brown, D.A.; Muenzel, D.; Agung, F.; Amkieltiela; Ford, A.K.; Habibi, A.; Handayani, C.N.; Iqbal, M.; Krueck, N.C.; Lazuardi, M.E.; Muawanah, U.; Papilaya, R.L.; Razak, T.B.; Sapari, A.; Sjahruddin, F.F.; Veverka, L. and Beger, M. (2022). The inclusion of fisheries and tourism in marine protected areas to support conservation in Indonesia. *Marine Policy*, *146*, 105301. https://doi.org/10.1016/j.marpol.2022.105301

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Wilson, S.K.; Graham, N.A.J.; Pratchett, M.S.; Jones, G.P. and Polunin, N.V.C. (2006). Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology*, *12*(11), 2220–2234. https://doi.org/10.1111/j.1365-2486.2006.01252.x

Wong, C.C.; Drazen, J.C.; Callan, C.K. and Korsmeyer, K.E. (2018). Hypoxia tolerance in coral-reef triggerfishes (Balistidae). *Coral Reefs*, *37*(1), 215–225. https://doi.org/10.1007/s00338-017-1649-7

Wong-Ala, J.A.T.K.; Comfort, C.M.; Gove, J.M.; Hixon, M.A.; McManus, M.A.; Powell, B.S.; Whitney, J.L. and Neuheimer, A.B. (2018). How life history characteristics and environmental forcing shape settlement success of coral reef fishes. *Frontiers in Marine Science*, *5*, 65. https://doi.org/10.3389/fmars.2018.00065

Wyrtki, K. (1961). *Physical Oceanography of the Southeast Asian Waters*. NAGA Report Volume 2. The University of California.