BIODIVERSITAS
Volume 27, Number 3, March 2026
Pages: 12

ISSN: 1412-033X
E-ISSN: 2085-4722
https://doi.org/10.13057/biodiv/d270333

Coral resilience in marginal reefs of South Sulawesi, Indonesia

FUNTY SEPTIYAWATI POLAPA[1,3,5], CHAIR RANI[1,2,♥], JAMALUDDIN JOMPA[1,2], SUHARTO[4]

[1]Doctoral Program in Fisheries Science, Faculty of Marine Science and Fisheries, Universitas Hasanuddin. Jl. Perintis Kemerdekaan Km. 10, Makassar 90245, South Sulawesi, Indonesia

[2]Department of Marine Science, Faculty of Marine Science and Fisheries, Universitas Hasanuddin. Jl. Perintis Kemerdekaan Km. 10, Makassar 90245, South Sulawesi, Indonesia. Tel.: +62-41-586025, ♥email: erickch_rani@yahoo.com

[3]Department of Marine Science, Faculty of Science and Technology, Universitas Muhammadiyah Palopo. Jl. Jendral Sudirman Km. 1, Palopo 91923, South Sulawesi, Indonesia

[4]Department of Fisheries Science, Faculty of Marine Science and Fisheries, Universitas Hasanuddin. Jl. Perintis Kemerdekaan Km. 10, Makassar 90245, South Sulawesi, Indonesia

[5]Aksi Konservasi Celebica Fondation. Perumahan Lo'Tauro No. A4, Palopo 91925, South Sulawesi, Indonesia

Manuscript received: 27 September 2025. Revision accepted: 30 March 2026.

Abstract. *Polapa FS, Rani C, Jompa J, Suharto. 2026. Coral resilience in marginal reefs of South Sulawesi, Indonesia. Biodiversitas 27 (3): d270333. https://doi.org/10.13057/biodiv/d270333*. Coral reefs face escalating global and local threats, yet data on coral resilience to inform rehabilitation strategies remain limited, especially in marginal environments. We compared coral community structure and water quality between marginal and reference reefs in South Sulawesi, Indonesia, to identify stress-adapted genera with restoration potential. Generic diversity was comparable between marginal (16.3±7.5 genera) and reference sites (17.5±3.5 genera), but reference reefs exhibited 2.6× higher coral abundance. Coral abundance showed a strong negative correlation with water quality (r = -0.82). Non-metric multidimensional scaling revealed clear community segregation between reef types, with reef type explaining 37.6% of the variation in composition. Using performance ratios (marginal/reference abundance), we identified *Turbinaria* (exclusive to marginal sites), *Platygyra* (ratio = 4.60), *Dipsastraea* (4.00), and *Galaxea* (3.13) as genera with exceptional adaptive potential under marginal conditions. Despite a lower performance ratio (0.26), *Porites* maintained the highest absolute abundance across all sites, highlighting its ecological importance. Our findings provide science-based criteria for coral species selection in restoration programs. We recommend a combined strategy, prioritizing high-performance-ratio genera (*Turbinaria*, *Platygyra*, *Dipsastraea*, *Galaxea*) for their adaptive advantages while including ecologically dominant, stress-tolerant taxa like *Porites* to enhance restoration success. This recommendation is specifically targeted for reefs experiencing moderate water quality degradation (STORET scores 12-18) and elevated sedimentation as documented at our nearshore marginal sites in South Sulawesi. This targeted approach leverages marginal reefs as reservoirs of stress-adapted genotypes, offering a practical strategy for enhancing reef recovery in rapidly changing tropical seascapes. Our study underscores the conservation value of marginal reefs and provides actionable insights for reef restoration in Indonesia and similar regions facing cumulative environmental pressures.

Keywords: Coral reef, marginal, performance ratio, rehabilitation, resilience

INTRODUCTION

Coral reefs are among the most biologically diverse and economically vital ecosystems on Earth, providing essential services such as coastal protection, fisheries support, and tourism revenue (Phelan et al. 2020; Jury et al. 2024). However, these ecosystems are increasingly threatened by both global climate change, including rising sea temperatures, ocean acidification, and frequent extreme weather events and local anthropogenic impacts (Wei et al. 2022) such as water pollution, sedimentation, and overfishing (Pendleton et al. 2016; Johnson et al. 2022). The synergistic effects of these stressors have led to widespread coral bleaching, mortality, and loss of reef structure worldwide, necessitating urgent conservation and restoration interventions.

In this context, the concept of "marginal reefs" has gained prominence in coral reef science. These are reef systems that persist under sub-optimal environmental conditions—such as turbid coastal waters, upwelling zones, and habitats with high temperature variability—which differ markedly from the clear, oligotrophic waters typically associated with robust coral growth (Yates et al. 2014; Camp et al. 2018; Figueroa-Pico et al. 2020). Functioning as natural laboratories, marginal reefs offer critical insights into coral adaptation, acclimatization, and resilience mechanisms. Corals thriving in these environments may harbor unique physiological and genetic traits that could inform conservation strategies in an era of rapid environmental change (Kavousi and Keppel 2017; Nelson et al. 2022).

Despite their ecological significance, the mechanisms underlying coral success in marginal environments remain inadequately understood, particularly in highly biodiverse yet threatened regions such as Indonesia (Burt et al. 2020; Gantt et al. 2024a). Distinguishing genuinely stress-adapted coral populations from those not merely persisting but potentially thriving under sub-optimal conditions requires rigorous comparative analysis between marginal and more favorable reference environments (Good and Bahr 2021; Briski et al. 2025). To facilitate such comparisons, we adopt the following operational definitions: (i) stress-resistant genera refer to coral genera that maintain higher

relative abundance in marginal versus reference conditions, (ii) stress-adapted populations are those demonstrating measurable physiological or ecological advantages in sub-optimal settings, (iii) marginal reefs are sites characterized by significant anthropogenic influence and/or degraded water quality, and (4) reference reefs are sites with minimal human disturbance and good water quality, representing regional ecological baselines.

Indonesia lies at the heart of the Coral Triangle, the global epicenter of marine biodiversity, and hosts some of the world's most diverse coral reef ecosystems (Veron 2013). Recent studies have documented the persistence of coral reefs under marginal conditions in this region, including in Bone Bay where thriving reefs with hard coral cover from 43% to 63% are found in oligotrophic to eutrophic waters (Irwan et al. 2024). However, these marginal reefs face escalating pressures from anthropogenic activities such as overfishing and nickel mining, resulting in variable live coral cover (Hasim et al. 2025). In the Spermonde Archipelago, coral reef islands are undergoing morphological changes due to sea-level rise and ecosystem degradation, with significant shoreline erosion observed on eastern margins (Sengupta et al. 2025), yet these reef complexes demonstrate capacity to keep pace with rising sea levels (Hynes et al. 2025). Such findings underscore the urgency of understanding coral resilience in marginal environments to inform targeted rehabilitation strategies, particularly as conservation frameworks increasingly incorporate passive and active restoration approaches (Kusumo et al. 2025).

This study focuses on community-level patterns and uses performance ratios calculated as the relative abundance of coral genera in marginal versus reference sites as a practical ecological indicator of resilience. Physiological mechanisms are inferred from established literature rather than directly measured. This study aims to compare coral community structure between marginal and reference reefs in South Sulawesi, evaluate the relationship between water quality parameters and coral abundance/diversity, and identify stress-resistant coral genera with demonstrated potential for use in rehabilitation programs. By highlighting locally adapted, resilient taxa, this work seeks to provide targeted, science-based recommendations for coral reef restoration in rapidly changing environments. The findings are intended to directly inform coral rehabilitation planning and species selection for marginal reef environments in Indonesia and similar tropical regions facing multifaceted environmental pressures.

MATERIALS AND METHODS

Study area

This research was conducted from August 4 to 25, 2025, as part of a planned field campaign under the BIMA Fundamental Basic Research scheme (2025 funding cycle). Surveys were carried out across five reef sites in South Sulawesi, Indonesia, representing three marginal and two reference environments (Figure 1).

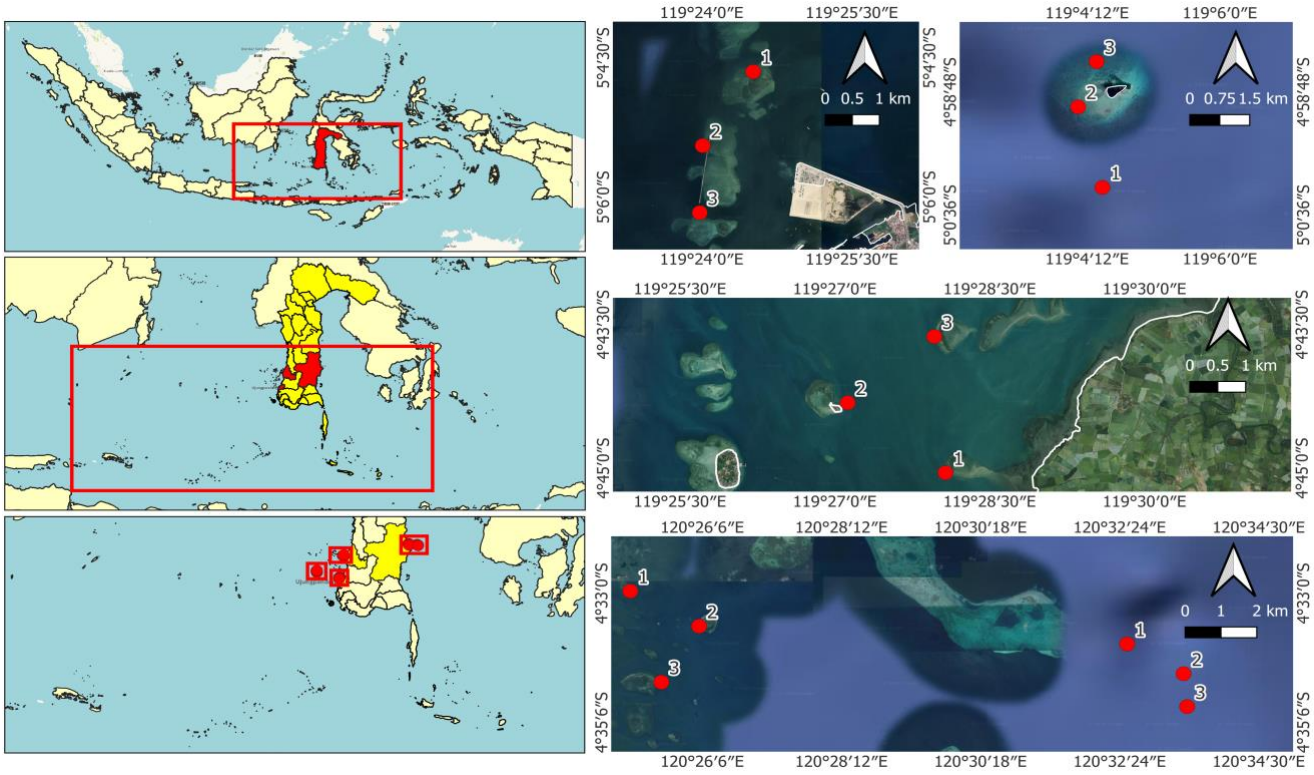

Figure 1. The five sampling sites in the waters of South Sulawesi, Indonesia

Table 1. Geographic coordinates of sampling stations at each of the five sampling sites (marginal and reference reefs)

Station	Latitude	Longitude	Site	Information
1	-5.077458	119.4086	Makassar	Urban nearshore reefs close to Makassar city center, high population
2	-5.090741	119.4002	Makassar	density, adjacent to port activities
3	-5.102762	119.3997	Makassar	
1	-4.750769	119.4679	Pangkep	Pangkep Regency nearshore reefs, influenced by river discharge from
2	-4.738591	119.4521	Pangkep	agricultural hinterland, aquaculture activities nearby
3	-4.727071	119.4661	Pangkep	
1	-5.003224	119.0735	Makassar Reference	Offshore island with clear waters, minimal anthropogenic influence, serves
2	-4.98359	119.068	Makassar Reference	as regional (Makassar Strait) reference for good water quality
3	-4.972565	119.0722	Makassar Reference	
1	-4.549348	120.4169	Bone	Located in a semi-enclosed bay, influenced by terrestrial input from
2	-4.558872	120.4342	Bone	multiple small rivers, moderate turbidity
3	-4.574047	120.4247	Bone	
1	-4.563696	120.5419	Bone Reference	Offshore site with strong water circulation, minimal terrestrial influence,
2	-4.571771	120.5561	Bone Reference	regional (Bone Bay) reference for good water quality
3	-4.580704	120.557	Bone Reference	

The three marginal sites were located in Bone (BN), Makassar (MKS), and Pangkep (PKP), characterized by proximity to potential pollution sources such as urban runoff, river discharge, and port activities. The two reference sites (Makassar Reference and Bone Reference) were situated in areas with minimal direct anthropogenic influence. All surveys were performed at a consistent depth range of 3-5 m to avoid confounding effects of depth on coral community structure. Each site comprised three replicate sampling stations (15 stations total), with geographic coordinates provided in Table 1.

Coral community assessment

Coral community composition was assessed using the Line Intercept Transect (LIT) method following established protocols for tropical marine resource surveys (English et al. 1998; Hill and Wilkinson 2004). This method has been widely validated for coral reef monitoring and is recognized as a standard approach for characterizing benthic (UNEP 1993; Facon et al. 2016). At each station, three 50-m replicate transects were deployed parallel to the reef slope at 5-m intervals. All scleractinian hard coral colonies whose growth form intersected the transect line were identified to genus level and recorded. Representative photographs of each genus observed are given in Figure 2. Each colony was counted only once, regardless of how many times it intersected the line (Smithsonian Institution 2021). No size threshold was applied; all colonies, including, were included. Colony count (rather than percent cover) was used as the primary abundance metric. Recent studies have demonstrated that colony-based (demographic) data provide better resolution of taxon-specific change in coral communities compared to percent cover estimates alone (Miller et al. 2016). Colony counts are more sensitive to change in population density and are appropriate for comparing relative performance across sites (Urbina-Barreto et al. 2021), though this metric does not directly reflect structural contribution.

Water quality analysis

Water quality data were obtained from a concurrent study conducted during the same sampling period (Rathnakumari 2025). For transparency, a brief methodological summary is provided here. Surface water samples were collected in triplicate at each station using clean, acid-washed Niskin bottles. Turbidity was measured in situ using a calibrated portable turbidimeter. For laboratory analysis, water for nutrient (nitrate, phosphate) and TSS analysis was filtered (0.45 μm) and preserved on ice. Nitrate and phosphate concentrations were determined using standard colorimetric methods (APHA 2017) with a spectrophotometer. Dissolved oxygen, pH, and salinity were measured using calibrated multi-parameter probes. Parameters included turbidity, Total Suspended Solids (TSS), salinity, Dissolved Oxygen (DO), nitrate, phosphate, pH, and temperature. Samples were collected at 1 m depth during morning hours (08:00-10:00) and analyzed within 48 hours at the Water Productivity and Quality Laboratory, Universitas Hasanuddin, Makassar.

Water quality classification followed the Indonesian STORET index, which is based on Decree of the State Minister of Environment No. 115/2003 (Kepmen LH No. 115/2003) and Government Regulation No. 22/2021 (PP No. 22/2021). The method compares water quality data against water quality standards (based on water class) with a scoring system based on US Environmental Protection Agency (EPA) guidelines and refers to US-EPA standards. The STORET scoring system was applied, with higher absolute scores indicating poorer water quality. For clarity in interpretation, absolute values are presented throughout the manuscript. Sites with STORET scores of 0-10 were classified as reference sites (good water quality), while scores of 11-30 indicated sites with marginal conditions (moderate water quality).

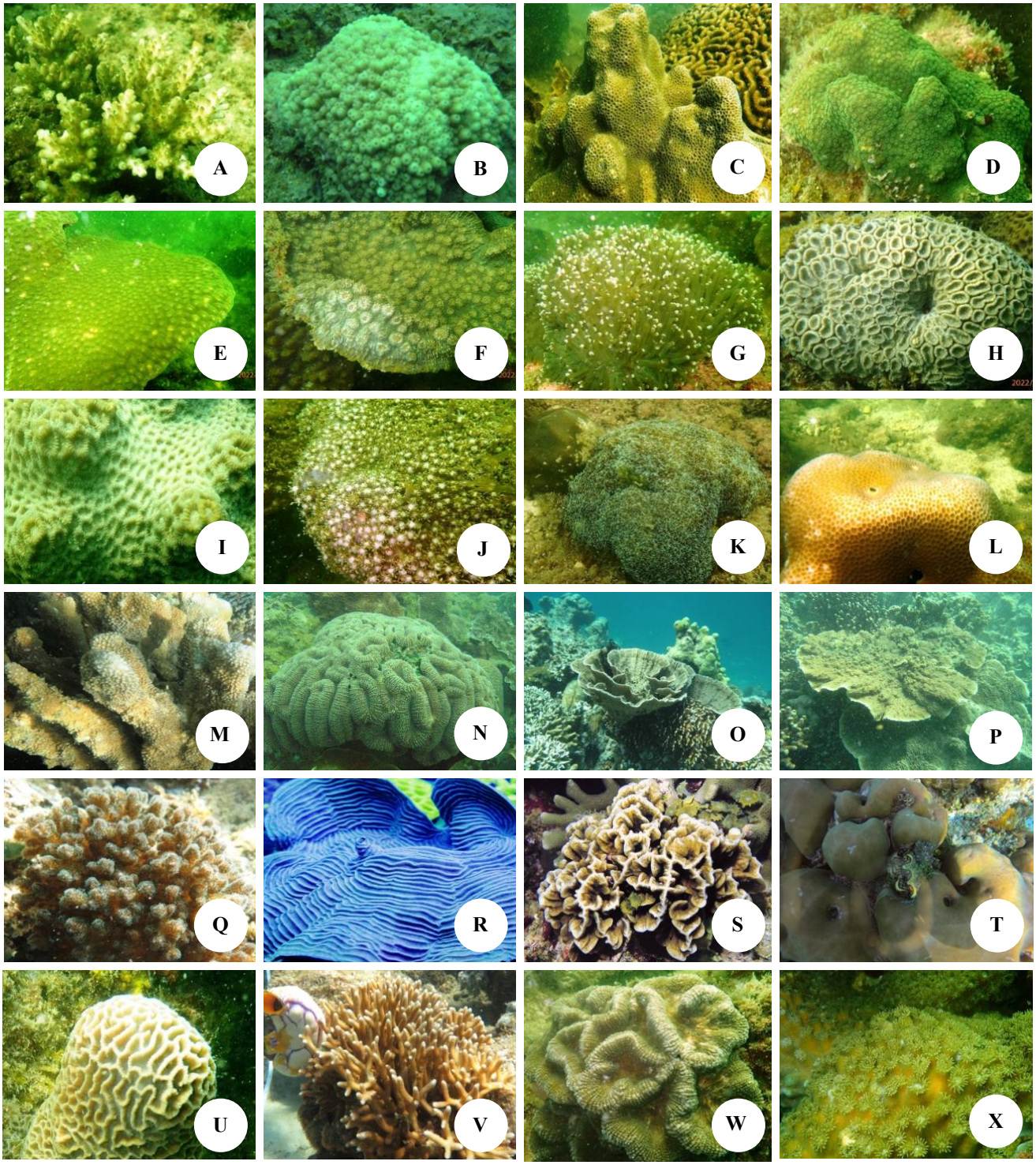

Figure 2. A. *Acropora*, B. *Astreopora*, C. *Coeloseris*, D. *Cyphastrea*, E. *Dipsastraea*, F. *Echinopora*, G. *Euphyllia*, H. *Dipsastrea*, I. *Favites*, J. *Goniopora*, K. *Galaxea*, L. *Goniastrea*, M. *Isopora*, N. *Lobophyllia*, O. *Montipora*, P. *Merulina*, Q. *Pocillopora*, R. *Pachyseris*, S. *Pavona*, T. *Porites*, U. *Platygyra*, V. *Seriatopora*, W. *Symphillia*, X. *Turbinaria*

Data analysis

Multivariate community analysis

Permutational Multivariate Analysis of Variance (PERMANOVA) was performed using the adonis2 function in the vegan package (Oksanen et al. 2022) with the model: community ~ reef type. To account for the nested structure of our design (stations within sites), permutations were restricted within each 'site' using the strata argument. The analysis was based on Bray-Curtis dissimilarities calculated from square-root-transformed abundance data, using 9999

permutations to obtain p-values. The assumption of homogeneity of multivariate dispersions between reef types was formally tested using the PERMDISP procedure (Lawrence et al. 2025). Results confirmed that dispersion did not differ significantly between reef types ($F = 1.245$, $p = 0.312$), validating the PERMANOVA results.

Performance ratio assessment

Genus-specific resilience was quantified using the Performance Ratio (PR):

$$PR = \frac{\text{Mean colony count in marginal sites}}{\text{Mean colony count in reference sites}}$$

Genera with zero abundance in either reef type were excluded from ratio calculation to avoid division by zero or extreme inflation of ratios. This metric identifies genera with PR>1.0 as potentially advantaged in marginal conditions. We note that ratios derived from small sample sizes (n = 2 reference sites) should be interpreted cautiously, and results are presented as ecological indicators rather than definitive measures of adaptation.

Correlation analysis

Pearson correlation was used to examine relationships between water quality scores and coral abundance/diversity. Given the limited sample size (n = 5 sites), correlations are interpreted as descriptive trends rather than strong inferential statistics. All analyses were conducted in R 4.2.3 (R Core Team 2022).

RESULTS AND DISCUSSION

Water quality

A summary of key water quality parameter data for each site is provided in Table 2. The data are presented as mean±Standard Deviation (SD).

Coral community composition

The genus-level coral community composition across the five study sites is summarized in Table 2. After verification and consolidation of genus entries (*Platygyra* counts were merged), the highest generic richness was observed at the Pangkep marginal reef (23 genera), compared to 18 and 14 genera at the Bone and Makassar reference sites, respectively. *Porites* was the most abundant genus overall, representing 36.3% of total colonies recorded (184 colonies). However, cumulative *Porites* abundance was higher in reference sites (126 colonies) than in marginal sites (60 colonies). It should be noted that all analyses were conducted at the genus level; species-level diversity may exhibit different patterns. The prevalence of stress-tolerant genera like *Porites* in marginal environments aligns with findings from other marginal reef systems in Southeast Asia, where these genera demonstrate persistence under sub-optimal conditions (Burt et al. 2020; Gantt et al. 2024b).

Several genera exhibited site-specific distribution patterns. The genera *Lobophyllia*, *Platygyra* and *Paraclavarina* were exclusively found at the Pangkep marginal site, while *Astreopora* and *Isopora* were only found at the Makassar Reference site. This suggests possible environmental filtering and niche specialization across the environmental gradient. Similar patterns of site-specificity in marginal environments have been reported for certain genera in turbid reef systems of Singapore and Jakarta Bay, where distinctive species assemblages developed in response to local environmental stressors (Laverick et al. 2020; Smith et al. 2020; Doropoulos et al. 2022). Cumulatively, the marginal sites hosted 25 of the 26 documented genera, while 23 genera were found at reference sites. While the absence of a genus from the sampling transects does not prove absence from the sites, this marginal deficit of only 2 genera (as opposed to a deficit of 5 genera for reference reefs) highlights the capacity of marginal environments to maintain high generic diversity despite sub-optimal water quality conditions. These findings reinforce the evidence that marginal reefs can serve as important reservoirs of coral biodiversity in Indonesia, as previously demonstrated in studies from the Persian Gulf and eastern Pacific upwelling-affected reefs (Guinotte et al. 2003; Galand et al. 2023; Jury et al. 2024), where diverse coral communities persist under environmental extremes.

Coral community patterns

Our surveys revealed distinct patterns in coral community structure between marginal and reference reefs in South Sulawesi. While reference sites supported significantly higher coral abundance (mean = 160 colonies/site) compared to marginal sites (mean = 62.3 colonies/site), generic diversity remained remarkably similar between the two environments. Marginal sites hosted 16.3±7.5 genera, compared to 17.5±3.5 genera at reference sites. This pattern of maintaining high diversity despite reduced abundance aligns with findings from other marginal reef systems, such as the turbid reefs of Singapore, where high species richness persists despite lower coral cover (Guest et al. 2016), and sediment-impacted reefs where diversity remains relatively stable even as overall abundance declines (Mellin et al. 2019).

Table 1. Summary of water quality parameters (mean±SD) per site during the study period (August 2025)

Parameter	Makassar	Pangkep	Makassar Reference	Bone	Bone Reference
pH	8.1±0.06	8.2±0.16	8.6±0.04	8.1±0.05	8.2±0.06
Salinity (ppt)	31.1±0.5	31.2±0.37	31.8±0.8	31.3±0.2	30.7±0.06
Temperature (°C)	31±0.6	27.4±0.71	30.37±0.1	28.28±0.3	30.07±0.5
Dissolved Oxygen (mg/L)	5.8±0.2	5.5±0.5	6.7±0.1	5.9±0.4	5.02±0.1
Nitrate (mg/L)	0.03±0.01	0.03±0.03	0.04±0.002	0.02±0.009	0.02±0.002
Phosphate(mg/L)	0.005±0.002	0.007±0.001	0.005±0.0008	0.008±0.01	0.005±0.001

PERMANOVA confirmed significant differences in community composition between marginal and reference reefs ($F = 6.02$, $p = 0.001$), with reef type explaining 37.6% of the observed variation (Figure 3). This segregation in community structure is consistent with environmental filtering processes documented in other marginal environments worldwide. For instance, in the extreme temperature environments of the Persian Gulf, distinct coral assemblages develop that differ significantly from adjacent, more favorable sites (Burt et al. 2020), while in eastern Pacific upwelling-affected reefs, unique community compositions emerge in response to chronic environmental stress (Glynn et al. 2016). The explanatory power of reef type in our study (37.6%) appears stronger than values reported in some other marginal systems, such as the Florida Reef Tract (28% explained by environmental stress; Lirman et al. 2018), though direct comparisons should be made cautiously given differences in study design and environmental contexts.

The observed decoupling of abundance and diversity patterns—where coral populations are substantially reduced and there may be a shift in the taxa present but generic richness remains largely intact—may have implications for reef resilience. A similar phenomenon has been documented in other Southeast Asian marginal reefs, including at sites in the Java Sea (Cleary et al. 2019) and the Philippines (Torres et al. 2021), where diverse coral communities persist despite chronic environmental challenges. However, the observational nature of our study design limits definitive conclusions about causal mechanisms or long-term resilience outcomes.

Water quality and coral abundance relationship

Water quality assessment revealed a clear distinction between marginal and reference sites (Table 3). Marginal sites had moderate water quality status with STORET scores ranging from 12 to 18 (mean = 14.7±3.1), while reference sites maintained good water quality with scores of 4. Coral abundance showed a parallel gradient, with reference sites supporting 2.6× higher colony counts than marginal sites (Table 3). The Pangkep marginal site had the poorest water quality (STORET score = 18) but the highest coral abundance among marginal sites (90 colonies), while Bone had both moderate water quality (score = 14) and the lowest coral abundance (36 colonies). The 10.7-point difference in mean water quality scores between marginal and reference categories indicates a substantial environmental gradient across our study sites.

Water quality scores had a strong negative correlation with coral abundance ($r = -0.82$, $p<0.05$), where poorer water quality (higher STORET scores) corresponded with reduced coral population density. However, the relationship between water quality and generic diversity was weaker ($r = -0.45$, $p>0.05$), suggesting that generic diversity may be less affected by water quality stress than population abundance (Figure 4). The progressive decline in coral abundance from reference sites (mean = 160 colonies) to marginal sites (mean = 62.3 colonies) aligns with this water quality gradient. This pattern is consistent with findings from other marginal reef systems in Southeast Asia, where water quality parameters influence coral community structure while taxonomic diversity exhibits greater resistance to environmental stress (Cvitanovic et al. 2024). The observed relationship between water quality degradation and coral abundance mirrors patterns documented in other anthropogenically influenced reef systems, such as urban reefs in Singapore (Lai et al. 2014) and sediment-impacted reefs in the Java Sea (Tanzil et al. 2019).

Table 3. Water quality STORET scores and classification for the five sampling sites. Marginal sites exhibited moderate water quality (scores 12-18), while reference sites showed good water quality (score 4)

Site	STORET score	Water quality classification	Coral abundance	Reef type
Makassar	12	Moderate	61	Marginal
Pangkep	18	Moderate	90	Marginal
Bone	14	Moderate	36	Marginal
Makassar Reference	4	Good	133	Reference
Bone Reference	4	Good	186	Reference

Note: STORET classification follows Indonesian Government Regulation No. 22/2021. Coral abundance = Total colonies recorded across three 50-m transects. Generic diversity expressed as mean number of genera per transect±standard deviation

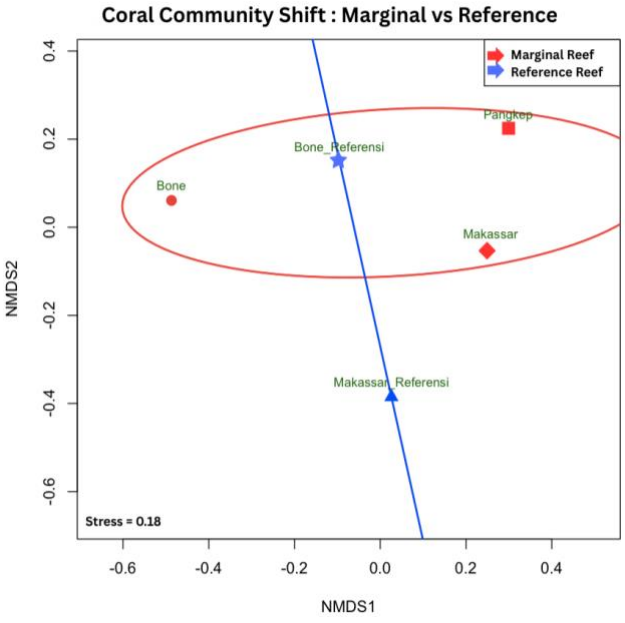

Figure 3. Non-Metric Multidimensional Scaling (NMDS) ordination of coral community composition based on genus-level abundance data (stress = 0.18). Points represent sampling stations: red/orange hues = marginal sites (Bone, Makassar, Pangkep), blue/purple hues = reference sites (Bone Reference, Makassar Reference). Although convex hulls are not displayed, clear separation is evident along NMDS1. PERMANOVA confirmed significant community separation by reef type (pseudo-$F = 6.02$, $df = 1$, $p = 0.001$, $R^2 = 0.376$)

Despite the strong relationship with abundance, water quality stress showed a weaker effect on generic diversity, with marginal sites maintaining 93% of the generic richness found in reference sites (see Table 4 for site-specific data). This preservation of diversity under environmental stress has been observed in other marginal systems, including turbid reefs (Muller-Karanassos et al. 2021) and thermally variable reefs (Burt et al. 2020), suggesting a common pattern of diversity resilience in sub-optimal environments. However, the correlational nature of these relationships warrants caution in inferring direct causal mechanisms. Furthermore, this pattern was observed at the generic diversity level, and the conservation of taxonomic diversity may be less evident at the species level, where the reduced number of individuals of a given genus may belong to fewer species within the genus.

Identification of resilient genera and community composition shifts (performance ratio)

The performance ratio analysis (Figure 5) revealed a spectrum of ecological responses among coral genera across the marginal-reference gradient. Notably, *Turbinaria* was found exclusively in marginal sites (indicating effectively infinite PR), followed by *Platygyra* (PR = 4.60), *Dipsastraea* (PR = 4.00), and *Galaxea* (PR = 3.13)—all demonstrating performance ratios >3.0 and suggesting strong potential adaptation to sub-optimal conditions. These genera not only persisted but demonstrated enhanced performance in marginal environments relative to reference sites, indicating possible local adaptation to conditions characterized by moderate water quality (Aeby et al. 2020). Importantly, restoration planning must consider both adaptive potential (PR) and existing ecological dominance. Despite its modest PR (0.26), *Porites* warrants special attention as it maintained the highest absolute abundance across all sites (184 colonies total, 36.3% of all recorded colonies) and substantial populations in marginal environments (51 colonies). This pattern mirrors observations from other marginal reef systems where *Porites* demonstrates context-dependent resilience—maintaining ecological dominance despite environmental stress (Lee et al. 2021).

The performance of *Platygyra* and *Galaxea* in marginal conditions corresponds with findings from other turbid reef systems in Southeast Asia, where these genera exhibit comparable stress tolerance patterns (Zweifler et al. 2021; Doropoulos et al. 2022). These genera not only persisted but demonstrated enhanced performance in marginal environments relative to reference sites, indicating possible local adaptation to sub-optimal conditions.

Table 4. Coral colonies recorded (genus and abundance) at the sampling sites (three marginal reefs and two reference reefs) in South Sulawesi, Indonesia

Coral family	Coral genus	Marginal reef site			Reference site	
		Bone	Makassar	Pangkep	Makassar	Bone
Acroporidae	*Acropora*	0	0	2	2	0
Acroporidae	*Astreopora*	0	0	0	0	1
Agariciidae	*Coeloseris*	0	0	1	6	0
Merulinidae	*Cyphastrea*	0	0	7	3	9
Merulinidae	*Dipsastraea*	0	8	4	0	2
Lobophylliidae	*Echinopora*	1	0	1	2	0
Euphylliidae	*Euphyllia*	2	0	1	1	0
Merulinidae	*Dipsastrea*	0	1	1	4	0
Merulinidae	*Favites*	0	2	3	1	13
Poritidae	*Goniopora*	8	2	1	12	2
Euphylliidae	*Galaxea*	0	3	11	2	1
Merulinidae	*Goniastrea*	0	1	3	0	0
Acroporidae	*Isopora*	0	0	0	0	8
Lobophylliidae	*Lobophyllia*	0	0	3	0	0
Acroporidae	*Montipora*	3	3	1	15	37
Merulinidae	*Merulina*	0	1	2	1	0
Pocilloporidae	*Pocillopora*	0	2	0	6	8
Agariciidae	*Pachyseris*	4	0	0	3	0
Agariciidae	*Pavona*	2	1	5	15	4
Poritidae	*Porites*	14	16	21	47	86
Merulinidae	*Platygyra*	0	6	8	1	2
Clavariidae	*Paraclavarina*	0	0	2	0	0
Pocilloporidae	*Stylophora*	0	0	2	0	3
Pocilloporidae	*Seriatopora*	1	7	0	4	8
Lobophylliidae	*Symphillia*	0	3	3	1	0
Dendrophylliidae	*Turbinaria*	0	4	3	0	0
Total number of colony colonies		35	60	85	126	184
Total number of genera		8	15	22	18	14
Total number of families		6	8	9	7	6

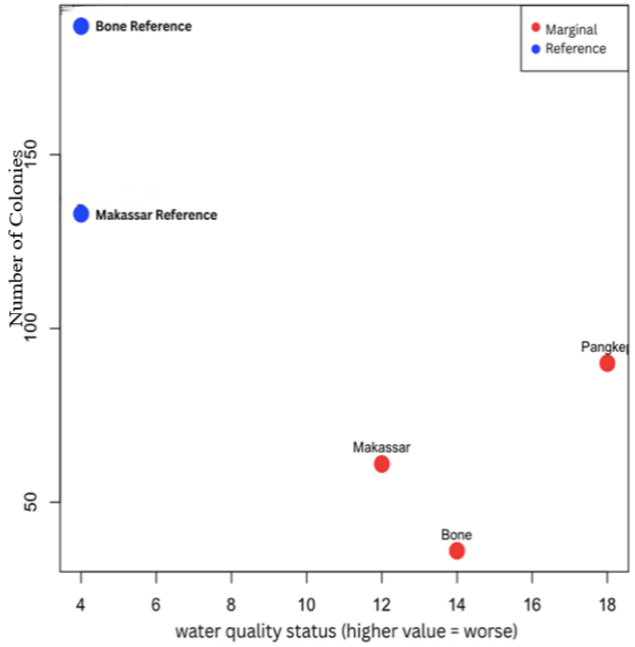

Figure 4. Plot of coral abundance (number of colonies) versus water quality (STORET scores) for marginal and reference reefs in South Sulawesi, Indonesia

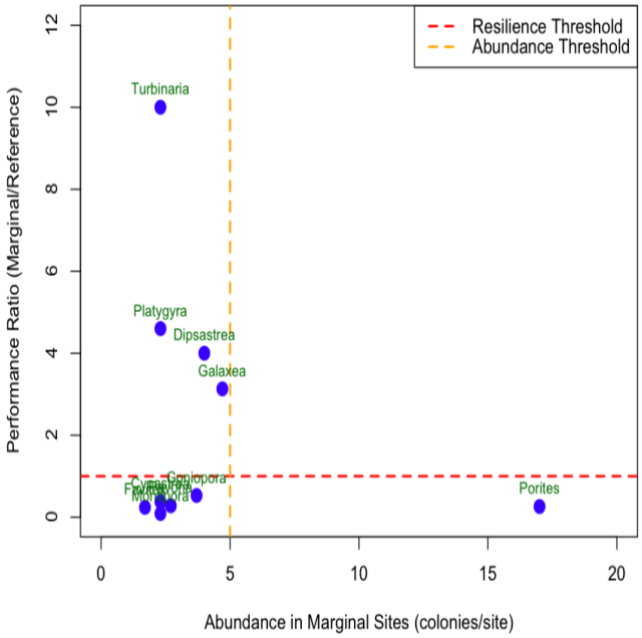

Figure 5. Performance ratios (marginal/reference abundance) for coral genera with PR>1.0

The differential performance among genera highlights the multidimensional nature of coral resilience. While *Porites* showed reduced relative performance (PR = 0.26), its maintained high absolute abundance in marginal sites underscores its ecological importance and practical value for restoration. This pattern aligns with observations from other Southeast Asian marginal reefs where *Porites* maintains structural dominance despite environmental stress (Lee et al. 2021). The contrast between high-PR genera (*Turbinaria*, *Platygyra*, *Dipsastraea*, *Galaxea*) and high-abundance genera (*Porites*) suggests complementary roles in marginal reef ecosystems: The former may represent specialized adaptations to local stressors, while the latter provides ecological continuity and structural complexity.

Non-Metric Multidimensional Scaling (NMDS) revealed clear separation between marginal and reference reef communities along the primary axis (Figure 3), confirming distinct community assemblages between the two reef types. Marginal sites were characterized by higher representation of resilient genera, including *Platygyra*, *Dipsastraea*, *Galaxea*, and *Turbinaria*, which formed a defined cluster associated with moderate water quality conditions. This community composition resembles patterns observed in other marginal systems, such as the sediment-impacted reefs of Jakarta Bay (Cleary et al. 2019) and turbid reefs of Western Australia (Zweifler et al. 2021), where stress-tolerant taxa dominate under suboptimal conditions.

Conversely, reference sites showed greater abundance of typically sensitive genera, including *Pocillopora*, *Montipora*, *Seriatopora*, and, which are predominantly found under optimal water quality conditions. The sensitivity of these genera to environmental stress has been consistently documented across multiple reef systems, including the Caribbean (Lirman et al. 2018) and the Great Barrier Reef (Hughes et al. 2025), confirming their utility as indicators of reef health.

The stress value of 0.18 for the NMDS solution indicates a good representation of the community patterns in two-dimensional space, with reef type explaining 37.6% of the observed variation in community composition (PERMANOVA: $F = 6.02$, $p = 0.001$). This explanatory power is comparable to, though somewhat higher than, values reported from other marginal reef studies in the region (e.g., 29% in the Java Sea (Cleary et al. 2019), 32% in Philippine marginal reefs (Torres et al. 2021)), suggesting relatively strong environmental filtering in South Sulawesi reef systems.

However, the interpretation of our findings must consider sampling design limitations. As the representation of 'reef type' (marginal vs. reference) was not fully balanced across locations (e.g., Pangkep had only marginal representation), it is possible that regional differences in biogeography or unmeasured disturbance sources also contributed to the observed coral community patterns. Therefore, claims of specific adaptation to marginal conditions require future confirmation through studies with stronger spatial replication and a paired design between marginal and reference sites within the same region.

This clear segregation underscores the role of environmental filtering in structuring coral assemblages, where marginal conditions select for stress-adapted (resilient) taxa, while reference conditions support more sensitive taxa that are competitively superior in the conditions to which they are adapted. The identification of taxa resilient to local stressors can be valuable when selecting suitable candidates for targeted rehabilitation programs in degraded

reef environments, following examples from other regions where stress-adapted corals have been utilized in restoration efforts (Burt et al. 2020; Defilippo et al. 2022).

Ecological mechanisms and resilience patterns

Our study revealed ecological trade-offs in coral reef communities across environmental gradients in South Sulawesi, demonstrating how environmental filtering shapes distinct community assemblages while maintaining functional diversity. The significant reduction in coral abundance (2.6× lower) at marginal sites, despite preserved generic diversity (93% of reference site richness), aligns with ecological theory suggesting that diversity can persist through species replacement even as overall abundance declines under environmental stress (Riegl et al. 2017; Stewart et al. 2021). This pattern is evident in our study system, where the community segregation observed in the NMDS analysis (37.6% explained by reef type) exceeds values reported from other Southeast Asian marginal systems, including Singapore's turbid reefs (28% (Guest et al. 2016) and Java Sea sediment-impacted reefs (32%, (Cleary et al. 2019), suggesting strong selective pressures in South Sulawesi marginal environments.

The performance of genera such as *Platygyra* (PR = 4.60), *Dipsastraea* (PR = 4.00), and *Galaxea* (PR = 3.13) under marginal conditions may reflect physiological adaptations to suboptimal water quality. *Platygyra*'s massive growth form and sediment rejection capabilities (Chang et al. 2024), *Dipsastraea* 's heterotrophic plasticity (Wang et al. 2024) and *Galaxea*'s competitive abilities in fluctuating environments (Yu et al. 2024), provide potential explanations for their resilience at these sites. Conversely, the reduced performance of typically robust genera such as *Porites* (ratio = 0.26) highlights the context-dependent nature of coral resilience, where tolerance to thermal stress may not confer advantages under sedimentation and nutrient enrichment—a pattern observed in other urbanized reef systems (Lee et al. 2021). These genus-specific responses underscore that coral resilience is multidimensional and stressor-specific, requiring nuanced understanding for conservation planning.

The maintenance of high generic diversity in marginal reefs, despite reduced abundance, positions these environments as important reservoirs of genetic diversity and potential sources of climate-resilient genotypes. This finding challenges traditional conservation paradigms that prioritize reefs with high coral cover, and supports the growing recognition of marginal reef ecosystems' conservation value (Camp et al. 2018). The diverse coral communities persisting in South Sulawesi's marginal conditions may represent important evolutionary incubators for developing climate resilience, similar to patterns observed in other environmentally extreme reef systems such as the Persian Gulf (Burt et al. 2020) and turbid reefs in Palau (Muller-Karanassos et al. 2021).

Conservation implications and management recommendations

The identification of coral genera with varying resilience patterns provides a nuanced, science-based foundation for developing targeted rehabilitation strategies in South Sulawesi and similar degraded environments. Our analysis supports a two-tiered restoration approach based on complementary ecological attributes:

High-performance-ratio genera

Turbinaria (exclusively present in marginal sites), *Platygyra* (PR = 4.60), *Dipsastraea* (PR = 4.00), and *Galaxea* (PR = 3.13) demonstrate exceptional relative success in marginal conditions, likely reflecting specialized adaptations to sediment-rich, nutrient-influenced environments. *Platygyra*'s remarkable performance probably reflects sediment management capabilities, while *Dipsastraea*'s success suggests heterotrophic plasticity under reduced light conditions.

Ecologically dominant stress-tolerant genera

Despite its modest PR (0.26), *Porites* represents a practical restoration candidate due to its high absolute abundance (36.3% of all colonies), proven stress tolerance in other systems, and existing established populations in marginal sites. Its inclusion ensures ecological continuity and structural function while higher-PR genera established.

Rather than relying solely on traditionally dominant species or exclusively on high-PR taxa, we recommend a combined strategy: prioritizing propagation of high-PR genera to leverage their adaptive advantages, while strategically including ecologically dominant, stress-tolerant genera like *Porites* to enhance initial establishment success and ecosystem function. This approach aligns with emerging examples from other regions, including the use of sediment-tolerant corals in Singapore's turbid reef restoration (Guest et al. 2016) and mixed-species approaches in Great Barrier Reef rehabilitation (Matz et al. 2020). *Platygyra*'s remarkable performance likely reflects specialized sediment management capabilities, with its massive growth form and documented mucus production providing critical advantages in high-turbidity conditions (TSS: 15-22 mg/L) where sedimentation excludes more sensitive taxa. *Dipsastraea*'s success suggests heterotrophic plasticity, allowing for maintained energy acquisition through particle feeding when photosynthetic efficiency declines under reduced light penetration. *Galaxea*'s competitive superiority in spatially heterogeneous environments may stem from aggressive mesenterial filaments that provide advantages in the disturbance-prone habitats characteristic of marginal reefs. Rather than relying primarily on traditionally dominant species from pristine reefs, our results suggest prioritizing these locally adapted resilient genera that have demonstrated specific stressor-specific performance. This approach aligns with emerging examples from other regions, including the use of sediment-tolerant corals in Singapore's turbid reef restoration (Guest et al. 2016) and thermally resilient corals in Great Barrier Reef rehabilitation (Matz et al. 2020). The stressor-specific adaptations of *Platygyra*, *Dipsastraea*, and *Galaxea* make them promising candidates for propagation in degraded areas with similar environmental challenges.

Finally, the resilience patterns we observed, while robust within our sampling framework, should be interpreted with

due consideration of the study's limited temporal scope. Our August 2025 surveys captured community dynamics during seasonal conditions of relatively low environmental stress in South Sulawesi. Future investigations across multiple seasons would clarify whether the performance advantages of genera like *Platygyra* and *Dipsastraea* persist under different environmental regimes, particularly during and after periods of increased rainfall and terrestrial influence.

Limitation and future direction

Several limitations should be addressed in future research. The small sample size (n = 5 sites) and single-season sampling (August 2025) limit the generalizability of our findings; multi-season and inter-annual studies are needed to capture temporal variability in coral performance under marginal conditions. Additionally, our genus-level analysis may mask species-specific responses, and the inferred adaptive mechanisms require confirmation through physiological measurements, reciprocal transplant experiments, and genomic analyses. Future studies should also investigate the underlying drivers of resilience, including symbiont associations, reproductive biology, and recruitment dynamics of high-performance genera. Finally, long-term monitoring (>3-5 years) of restoration plots incorporating the recommended two-tier strategy (high-PR genera combined with ecologically dominant taxa) is essential to validate the effectiveness of this approach under field conditions. As climate change and local stressors continue to impact coral reefs, the patterns observed in South Sulawesi's marginal reefs highlight the value of understanding nature's existing responses to environmental challenges, with implications for reef restoration across the Coral Triangle and similar marginal environments globally.

In conclusion, this study documented coral community shifts and identified genera with varying resilience patterns in South Sulawesi's marginal reefs, providing insights for reef conservation strategies. Three key findings emerge, all verified against corrected community data. First, marginal reefs support significantly lower coral abundance (2.6× reduction) compared to reference sites, yet maintain comparable generic diversity (16.3 vs 17.5 genera), demonstrating their capacity to preserve biodiversity under sub-optimal conditions. Second, water quality STORET scores had a strong negative relationship with coral abundance (r = -0.82) but a weaker effect on diversity, indicating differential responses to environmental stress. Third, we identified coral genera with complementary resilience signatures: *Turbinaria*, *Platygyra*, *Dipsastraea*, and *Galaxea* showed exceptional performance ratios (>3.0 or exclusive marginal presence), indicating strong potential adaptation to marginal conditions, while *Porites* maintained high absolute abundance despite moderate PR (0.26), highlighting its ecological dominance and practical restoration value. The clear community segregation between marginal and reference reefs (37.6% explained by reef type) indicates environmental filtering shapes coral assemblages, while the persistence of diverse genera in marginal environments suggests these systems may act as reservoirs of stress-associated taxa and potentially stress-adapted genotypes. Our findings suggest that marginal reefs could contribute to climate resilience, pending verification by genetic and long-term studies. For rehabilitation practitioners, our results refine existing restoration approaches by demonstrating how performance ratios provide an empirical, site-specific metric for identifying candidate genera beyond simply selecting locally common or traditionally hardy taxa, thus extending traditional restoration paradigms.

ACKNOWLEDGEMENTS

We acknowledge the field team (Randy and Arham) for their assistance with data collection and thank all contributors who supported the successful completion of this research. This research is a mandatory output of the Directorate of Research, Technology, and Community Service grant, Ministry of Higher Education, Science, and Technology, Indonesia, under the BIMA Fundamental Basic Research scheme with the main contract number 069/C3/DT.05.00/PL/2025 and the derivative contract number 02209/UN4.22/PT.01.03/2025.

REFERENCES

Aeby GS, Howells E, Work T, Abrego D, Williams GJ, Wedding LM, Caldwell JM, Moritsch M, Burt JA. 2020. Localized outbreaks of coral disease on Arabian reefs are linked to extreme temperatures and environmental stressors. Coral Reefs 39: 829-846. https://doi.org/10.1007/s00338-020-01928-4.

APHA [American Public Health Association]. 2017. Standard Methods for the Examination of Water and Wastewater (23rd ed.). APHA Press, Washington DC.

Briski E, Langrehr L, Kotronaki SG, Sidow A, Reyes CGM, Geropoulos A, Steffen G, Theurich N, Dickey JWE, Hütt JC, Haubrock PJ, Soto I, Kouba A, Cuthbert RN. 2025. Urban environments promote adaptation to multiple stressors. Ecol Lett 28 (2): e70074. https://doi.org/10.1111/ele.70074.

Burt JA, Camp EF, Enochs IC, Johansen JL, Morgan KM, Riegl B, Hoey AS. 2020. Insights from extreme coral reefs in a changing world. Coral Reefs 39: 495-507. https://doi.org/10.1007/s00338-020-01966-y.

Camp EF, Schoepf V, Mumby PJ, Hardtke LA, Rodolfo-Metalpa R, Smith DJ, Suggett DJ. 2018. The future of coral reefs subject to rapid climate change: Lessons from natural extreme environments. Front Mar Sci 5: 4. https://doi.org/10.3389/fmars.2018.00004.

Chang TKT, Cheung BCT, Leong JCH, Ricardo GF, Chan JTC, Fang JKH, Mumby PJ, Chui APY. 2024. Suspended sediment and reduced salinity decrease development success of early stages of *Acropora tumida* and *Platygyra carnosa* in a turbid coral habitat, Hong Kong. Mar Pollut Bull 209 (Pt B): 117255. https://doi.org/10.1016/j.marpolbul.2024.117255.

Cleary DFR, Polónia ARM, Huang YM, Putchakarn S, Gomes NCM, De Voogd NJ. 2019. A comparison of prokaryote communities inhabiting sponges, bacterial mats, sediment and seawater in Southeast Asian coral reefs. FEMS Microbiol Ecol 95 (12): fiz169. https://doi.org/10.1093/femsec/fiz169.

Cvitanovic C, Acedera M-AM, Samonte PC et al. 2024. Roadmap for improving coral reef restoration practices in Southeast Asia. Ecol Manag Restor 25 (3): 160-167. https://doi.org/10.1111/emr.12615.

Defilippo LB, McManus LC, Schindler DE, Pinsky ML, Colton MA, Fox HE, Tekwa EW, Palumbi SR, Essington TE, Webster MM. 2022. Assessing the potential for demographic restoration and assisted evolution to build climate resilience in coral reefs. Ecol Appl 32 (7): e2650. https://doi.org/10.1002/eap.2650.

Doropoulos C, Gómez-Lemos LA, Salee K, Mclaughlin MJ, Tebben J, Van Koningsveld M, Feng M, Babcock RC. 2022. Limitations to coral recovery along an environmental stress gradient. Ecol Appl 32 (3): e2558. https://doi.org/10.1002/eap.2558.

English S, Wilkinson C, Baker V. 1998. Survey Manual for Tropical Marine Resources. 2nd eds. Australian Institute of Marine Science, Queensland.

Facon M, Pinault M, Obura D, Pioch S, Pothin K, Bigot L, Garnier R, Quod J-P. 2016. A comparative study of the accuracy and effectiveness of line and point intercept transect methods for coral reef monitoring in the southwestern Indian Ocean islands. Ecol Indic 60: 1045-1055. https://doi.org/10.1016/j.ecolind.2015.09.005.

Figueroa-Pico J, Tortosa FS, Carpio AJ. 2020. Coral fracture by derelict fishing gear affects the sustainability of the marginal reefs of Ecuador. Coral Reefs 39: 819-827. https://doi.org/10.1007/s00338-020-01926-6.

Galand PE, Ruscheweyh H-J, Salazar G et al. 2023. Diversity of the Pacific Ocean coral reef microbiome. Nat Commun 14: 3039. https://doi.org/10.1038/s41467-023-38500-x.

Gantt SE, Keister EF, Jerry SE, Tindal RF, Manfroy AA, Merck DE, Muller EM, Kemp DW. 2024b. Physiological and symbiotic flexibility of reef-building corals to new habitats: Insights from clonal colony transplants. J Appl Ecol 62 (2): 207-219. https://doi.org/10.1111/1365-2664.14836.

Gantt SE, Kemp KM, Colin PL, Hoadley KD, Lajeunesse TC, Warner ME, Kemp DW. 2024a. Influence of reef habitat on coral microbial associations. Environ Microbiol Rep 16 (6): e70051. https://doi.org/10.1111/1758-2229.70051.

Glynn PW, Mones AB, Podestá GP, Colbert A, Colgan MW. 2016. El niño-southern oscillation: Effects on Eastern Pacific coral reefs and associated biota. In: Glynn PW, Manzello DP, Enochs IC (eds). Coral Reefs of the Eastern Tropical Pacific. Coral Reefs of the World. Springer, Dordrecht. https://doi.org/10.1007/978-94-017-7499-4_8.

Good AM, Bahr KD. 2021. The coral conservation crisis: Interacting local and global stressors reduce reef resiliency and create challenges for conservation solutions. SN Appl Sci 3: 312. https://doi.org/10.1007/s42452-021-04319-8.

Guest JR, Tun K, Low J, Vergés A, Marzinelli EM, Campbell AH, Bauman AG, Feary DA, Chou LM, Steinberg PD. 2016. 27 years of benthic and coral community dynamics on turbid, highly urbanised reefs off Singapore. Sci Rep 6: 36260. https://doi.org/10.1038/srep36260.

Guinotte JM, Buddemeier RW, Kleypas JA. 2003. Future coral reef habitat marginality: Temporal and spatial effects of climate change in the Pacific basin. Coral Reefs 22: 551-558. https://doi.org/10.1007/s00338-003-0331-4.

Hasim H, Umar W, Moka WJC, Sampe F, Rani C, Polapa FS. 2025. Condition of coral reef cover in the regional marine conservation area plan, Bone Bay, South Sulawesi, Indonesia. BIO Web Conf 185: 02003. https://doi.org/10.1051/bioconf/202518502003.

Hill J, Wilkinson C. 2004. Methods for Ecological Monitoring of Coral Reefs. Version 1. Australian Institute of Marine Science, Queensland.

Hughes JM, Johnson DD, Ochwada-Doyle FA, Murphy JJ, Taylor MD, Fowler AM. 2025. Variable post-capture condition estimated by visual assessment for key recreational species discarded in a nearshore marine charter fishery off eastern Australia. Fish Res 285: 107372. https://doi.org/10.1016/j.fishres.2025.107372.

Hynes MG, Masdar H, Parenden D, de Voogd NJ, Stuut J-BW, Jompa J, Webster JM, Renema W. 2025. Impact of Holocene relative sea-level changes on patch reef-island development in the Spermonde Archipelago, South Sulawesi, Indonesia. Holocene 35 (5): 556-570. https://doi.org/10.1177/09596836251313628.

Irwan, Rani C, Jompa J, Kadir NN. 2024. Coral reef condition at different trophic status in marginal waters of Bone Bay, South Sulawesi, Indonesia. IOP Conf Ser: Earth Environ Sci 1410: 012006. https://doi.org/10.1088/1755-1315/1410/1/012006.

Johnson JV, Dick JTA, Pincheira-Donoso D. 2022. Marine protected areas do not buffer corals from bleaching under global warming. BMC Ecol Evol 22: 58. https://doi.org/10.1186/s12862-022-02011-y.

Jury CP, Bahr KD, Cros A, Dobson KL, Freel EB, Graham AT, McLachlan RH, Nelson CE, Price JT, De Souza MR, Shizuru L, Smith CM, Sparagon WJ, Squair CA, Timmers MA, Vicente J, Webb MK, Yamase NH, Grottoli AG, Toonen RJ. 2024. Experimental coral reef communities transform yet persist under mitigated future ocean warming and acidification. Proc Natl Acad Sci 121 (45): e2407112121. https://doi.org/10.1073/pnas.2407112121.

Kavousi J, Keppel G. 2017. Clarifying the concept of climate change refugia for coral reefs. ICES J Mar Sci 75 (1): 43-49. https://doi.org/10.1093/icesjms/fsx124.

Kusumo S, Rahadiya AF, Cahyaningrum YM, Hidayat SA, Ayuningtyas A. 2025. Framework for priority areas in coral reef rehabilitation in conservation zones (case study: KKPD Pasi Gusung Island). BIO Web Conf 188: 03002. https://doi.org/10.1051/bioconf/202518803002.

Lai S, Loke LHL, Hilton MJ, Bouma TJ, Todd PA. 2014. The effects of urbanisation on coastal habitats and the potential for ecological engineering: A Singapore case study. Ocean Coast Manag 103: 78-85. https://doi.org/10.1016/j.ocecoaman.2014.11.006.

Lawrence AK, Heenan A, Williams GJ. 2025. Quantifying spatial gradients in coral reef benthic communities using multivariate dispersion. Royal Soc Open Sci 12 (4): 241254. https://doi.org/10.1098/rsos.241254.

Laverick JH, Tamir R, Eyal G, Loya Y. 2020. A generalized light-driven model of community transitions along coral reef depth gradients. Glob Ecol Biogeogr 29 (9): 1554-1564. https://doi.org/10.1111/geb.13140.

Lee Y-L, Lam SQY, Tay TS, Kikuzawa YP, Tan KS. 2021. Composition and structure of tropical intertidal hard coral communities on natural and man-made habitats. Coral Reefs 40: 685-700. https://doi.org/10.1007/s00338-021-02059-0.

Lirman D, Ault JS, Fourqurean JW, Lorenz JJ. 2018. The coastal marine ecosystem of South Florida, United States. In: Sheppard C (eds). World Seas: An Environmental Evaluation. Volume I: Europe, the Americas and West Africa. Academic Press, Cambridge, USA. https://doi.org/10.1016/B978-0-12-805068-2.00021-8.

Matz MV, Treml EA, Haller BC. 2020. Estimating the potential for coral adaptation to global warming across the Indo-West Pacific. Glob Change Biol 26 (6): 3473-3481. https://doi.org/10.1111/gcb.15060.

Mellin C, Thompson A, Jonker MJ, Emslie MJ. 2019. Cross-shelf variation in coral community response to disturbance on the Great Barrier Reef. Diversity 11 (3): 38. https://doi.org/10.3390/d11030038.

Miller M, Williams DE, Huntington BE, Piniak GA, Vermeij MJA. 2016. Decadal comparison of a diminishing coral community: A study using demographics to advance inferences of community status. PeerJ 4: e1643. https://doi.org/10.7717/peerj.1643.

Muller-Karanassos C, Filous A, Friedlander AM, Cuetos-Bueno J, Gouezo M, Lindfield SJ, Nestor V, Marino LL, Mereb G, Olsudong D, Golbuu Y. 2021. Effects of habitat, fishing, and fisheries management on reef fish populations in Palau. Fish Res 241: 105996. https://doi.org/10.1016/j.fishres.2021.105996.

Nelson CE, Kelly LW, Haas AF. 2022. Microbial interactions with dissolved organic matter are central to coral reef ecosystem function and resilience. Ann Rev Mar Sci 15: 431-460. https://doi.org/10.1146/annurev-marine-042121-080917.

Oksanen J, Simpson GL, Blanchet FG et al. 2022. Vegan community ecology package version 2.6-2 April 2022. The Comprehensive R Archive Network. http://cran.r-project.org.

Pendleton L, Comte A, Langdon C, Ekstrom JA, Cooley SR, Suatoni L, Beck MW, Brander LM, Burke L, Cinner JE, Doherty C, Edwards PET, Gledhill D, Jiang L-Q, van Hooidonk RJ, Teh L, Waldbusser GG, Ritter J. 2016. Coral reefs and people in a high-CO2 world: Where can science make a difference to people? PLoS One 11 (11): e0164699. https://doi.org/10.1371/journal.pone.0164699.

Phelan A, Ruhanen L, Mair J. 2020. Ecosystem services approach for community-based ecotourism: Towards an equitable and sustainable blue economy. J Sustain Tour 28 (10): 1665-1685. https://doi.org/10.1080/09669582.2020.1747475.

R Core Team. 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rathnakumari AR. 2025. Water Quality Analysis. Intl J Sci Res Eng Manag 09 (05): 1-9. https://doi.org/10.55041/ijsrem48481.

Riegl B, Cavalcante G, Bauman AG, Feary DA, Steiner S, Purkis S. 2017. Demographic mechanisms of reef coral species winnowing from communities under increased environmental stress. Front Mar Sci 4: 344. https://doi.org/10.3389/fmars.2017.00344.

Sengupta M, Mann T, Stuhr M, Westphal H. 2025. Reef island morphological change over the past two decades: Spermonde Archipelago, Indonesia. Earth Surf Process Landf 50 (11): e70152. https://doi.org/10.1002/esp.70152.

Smith EG, Gurskaya A, Hume BCC, Voolstra CR, Todd PA, Bauman AG, Burt JA. 2020. Low Symbiodiniaceae diversity in a turbid marginal reef environment. Coral Reefs 39: 545-553. https://doi.org/10.1007/s00338-020-01956-0.

Smithsonian Institution. 2021. MarineGEO Coral Reef Habitat Monitoring Protocol. Smithsonian MarineGEO Network. https://doi.org/10.25573/serc.14717796.

Stewart HA, Kline DI, Chapman LJ, Altieri AH. 2021. Caribbean mangrove forests act as coral refugia by reducing light stress and increasing coral richness. Ecosphere 12 (3): e03413. https://doi.org/10.1002/ecs2.3413.

Tanzil JTI, Sengkeat OSO, Tay SHX, YanXiang OYO, SiewChin CSC, Clews E, Bolton A, Raghavan S, ShieYui LSL. 2019. Tropical marine and brackish ecosystems. In: Tropical Marine and Brackish Ecosystems. CABI. https://doi.org/10.1079/9781786393982.0025.

Torres AF, Valino DAM, Ravago-Gotanco R. 2021. Zooxanthellae diversity and coral-symbiont associations in the Philippine Archipelago: Specificity and adaptability across thermal gradients. Front Mar Sci 8: 731023. https://doi.org/10.3389/fmars.2021.731023.

UNEP [United Nations Environment Programme]. 1993. Monitoring Coral Reefs for Global Change - Reference Methods for Marine Pollution Studies No. 61. United Nations Environment Programme. https://wedocs.unep.org/handle/20.500.11822/31571.

Urbina-Barreto I, Garnier R, Elise S, Pinel R, Dumas P, Mahamadaly V, Facon M, Bureau S, Peignon C, Quod J-P, Dutrieux E, Penin L, Adjeroud M. 2021. Which method for which purpose? A comparison of line intercept transect and underwater photogrammetry methods for coral reef surveys. Front Mar Sci 8: 636902. https://doi.org/10.3389/fmars.2021.636902.

Veron J. 2013. Overview of the taxonomy of zooxanthellate Scleractinia. Zool J Linn Soc 169 (3): 485-508. https://doi.org/10.1111/zoj.12076.

Wang Q, Zhou X, Wang J, Zhang H, Fang H, Cai F, Huang L, Zheng X. 2024. Heterotrophy confers corals with resistance but limits their range expansion: A case of marginal coral communities. Ecosyst Health Sustain 10: 0246. https://doi.org/10.34133/ehs.0246.

Wei Y, Ding D, Gu T, Xu Y, Sun X, Qu K, Sun J, Cui Z. 2022. Ocean acidification and warming significantly affect coastal eutrophication and organic pollution: A case study in the Bohai Sea. Mar Pollut Bull 186: 114380. https://doi.org/10.1016/j.marpolbul.2022.114380.

Yates KK, Rogers CS, Herlan JJ, Brooks GR, Smiley NA, Larson RA. 2014. Diverse coral communities in mangrove habitats suggest a novel refuge from climate change. Biogeosciences 11 (16): 4321-4337. https://doi.org/10.5194/bg-11-4321-2014.

Yu X-L, Liu C-Y, Jiang L, Huang L-T, Luo Y, Zhang P, Zhang Y-Y, Liu S, Huang H. 2024. Local adaptation of trophic strategy determined the tolerance of coral *Galaxea fascicularis* to environmental fluctuations. Sci Total Environ 943: 173694. https://doi.org/10.1016/j.scitotenv.2024.173694.

Zweifler A, O'Leary M, Morgan K, Browne NK. 2021. Turbid coral reefs: Past, present and future-A review. Diversity 13 (6): 251. https://doi.org/10.3390/d13060251.