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Research Article



# Morphological Plasticity as a Response to Environmental Heterogeneity: A Comparative Study of *Porites lobata* in the Spermonde Archipelago and Bone Gulf, Indonesia

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## ABSTRACT

Phenotypic plasticity enables reef-building corals to respond to environmental variability through modification of morphological characters. This study analyzed the morphological plasticity of *Porites lobata* from three locations in South Sulawesi, Indonesia: the Spermonde Archipelago (n = 30), Bone Gulf (n = 12), and Taka/Bone Control (n = 6). Morphometric analysis of 21 numerical skeletal characters using Welch's independent-samples t-test revealed 7 characters that differed significantly between Spermonde and Bone ($p<0.05$), in a bidirectional pattern: four characters were larger in Bone (maximum columella diameter +42.6%; minimum lateral palus diameter +55.5%; lateral septa spacing +18.8%; palus count +12.2%), while three were larger in Spermonde (ventral palus spacing +38.6%; dorsal palus spacing +37.5%; fossa width +17.7%). Taka exhibited the largest corallite dimensions among all sites (29.8% larger than Bone; $p<0.001$). Of the seven water quality parameters tested, only temperature ($p = 0.017$) and nitrate ($p = 0.026$) differed significantly between Spermonde and Bone. Nitrate was negatively correlated with columella diameter ($r = -0.999$), and dissolved oxygen was positively correlated with palus count ($r = 0.983$). These findings indicate that *P. lobata* expresses two functionally distinct plasticity strategies across sites. In Bone Gulf, lower nitrate and higher dissolved oxygen supported more complex corallite architecture, consistent with more efficient skeletal calcification. In Spermonde, a more open architecture reflected in wider palus and fossa spacing appears to facilitate passive sediment clearance and enhance heterotrophic feeding capacity, offsetting reduced autotrophic productivity under multi-stressor conditions.

## 1. Introduction

Coral reefs are among the most biologically diverse and economically valuable ecosystems on Earth, providing essential services including coastal protection, fisheries production, and tourism revenue that support the livelihoods of millions of people worldwide (Wang *et al.* 2024). These ecosystems have evolved over thousands of years to thrive under specific environmental conditions, yet now face unprecedented threats from climate change, ocean acidification, and local anthropogenic pressures (Wernberg *et al.* 2023). The accelerating pace of environmental change has triggered widespread coral bleaching and mass mortality events, raising urgent questions about the capacity of coral species to persist under future climate scenarios (Putnam 2021). In this context, understanding the mechanisms enabling corals to acclimatize and adapt to changing conditions has become a central focus of reef science and conservation (Drury *et al.* 2022).

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Phenotypic plasticity, the ability of a single genotype to produce different phenotypes in response to environmental conditions has emerged as a key mechanism enabling coral populations to persist in the face of environmental fluctuations (Gomez-Campo *et al.* 2023). This plasticity can manifest across a range of traits, including morphological, physiological, and behavioral characteristics, functioning as a buffer against environmental change while genetic adaptation evolves over longer timeframes (Gomez-Campo *et al.* 2023; Gantt *et al.* 2024). For sessile organisms such as corals that cannot relocate to more favorable environments, phenotypic plasticity is the primary means of responding to local environmental heterogeneity (Castillo *et al.* 2024). The capacity for plastic responses may be especially critical for reef-building corals, which must maintain a delicate symbiosis with photosynthetic dinoflagellates while constructing massive calcium carbonate structures under variable conditions (Hoadley *et al.* 2021).

The genus *Porites* is among the most ecologically important and geographically widespread coral genera throughout the Indo-Pacific region, playing a fundamental role in reef framework construction and ecosystem function (Veron 2000). Within this genus, *Porites lobata* exhibits remarkable morphological variability across its broad geographic range, forming what taxonomists have long described as a species complex that presents persistent challenges to systematic classification (Forsman *et al.* 2015). This morphological variability has historically generated considerable taxonomic confusion, with numerous species and subspecies described that may represent phenotypic variants of a single plastic species (Jacob & Legrand 2021). The capacity of this species to exhibit substantial intraspecific variation along environmental gradients indicates considerable phenotypic plasticity, making it an ideal model organism for investigating environmental influences on coral morphology (Drury *et al.* 2022).

Indonesian coral reefs, situated at the center of marine biodiversity known as the Coral Triangle, host the world's richest scleractinian fauna and are among the most threatened yet least-studied reef systems in the global conservation agenda (Bongaerts *et al.* 2021). The Spermonde Archipelago and Bone Gulf represent two contrasting reef systems in Indonesia that experience distinct oceanographic conditions, water quality parameters, and anthropogenic influences. The Spermonde Archipelago, located in the Makassar Strait off the coast of South Sulawesi, experiences complex hydrodynamic patterns influenced by seasonal monsoon currents and receives substantial terrestrial inputs from the adjacent city of Makassar (Faizal 2023). These conditions result in higher nutrient loads, increased turbidity, and greater temperature fluctuations compared to oceanic environments. In contrast, Bone Gulf, which opens to the Flores Sea, exhibits more typical oceanic conditions with generally clearer waters, more stable temperatures, and a distinct light regime (Irwan *et al.* 2024a). These environmental differences create a natural laboratory for investigating how *P. lobata* varies morphologically along environmental gradients (Forsman *et al.* 2009; Tisthammer & Richmond 2018). However, intraspecific variation at the regional scale, particularly as a response to local environmental heterogeneity, remains relatively understudied despite its importance for understanding coral adaptive capacity (Kenkel & Matz 2016). Furthermore, although molecular studies have revealed extensive cryptic diversity within the genus Porites (Forsman *et al.* 2020), the extent to which environmental factors shape morphological variation within recognized species such as *P. lobata* remains incompletely understood. Quantifying this variation and identifying its environmental correlates is essential for predicting how coral populations may respond to ongoing environmental change (Forsman *et al.* 2015; Sempere-Valverde *et al.* 2024).

This study addresses these knowledge gaps through morphometric analysis of *P. lobata* from the environmentally contrasting Spermonde Archipelago and Bone Gulf, measuring 26 skeletal characters to quantify morphological variation and assess evidence for phenotypic plasticity. Specifically, we (1) characterized and compared corallite morphology across populations using an extensive suite of skeletal traits including corallite dimensions, septal arrangement, and columella structure; (2) confirmed species identification through morphometric analysis cross-referenced against established diagnostic characters; (3) evaluated patterns of morphological variation in relation to environmental differences between sites, with attention to traits likely representing adaptive responses to local conditions; and (4) discuss the implications of these findings for coral resilience and conservation management under rapid environmental change.

## 2. Materials and Methods

### 2.1. Study Sites and Sampling Design

This study was conducted at two contrasting reef systems in Indonesia: the Spermonde Archipelago (5°01'S, 119°23'E) and Bone Gulf (4°30'S, 120°20'E). The Spermonde Archipelago, located in the Makassar Strait off the coast of South Sulawesi, comprises approximately 120 islands with fringing reefs influenced by complex hydrodynamic patterns, seasonal monsoon currents, and substantial terrestrial inputs from the adjacent city of Makassar (Faizal 2023). This results in higher nutrient loads, elevated turbidity, and greater temperature fluctuations compared to oceanic environments. In contrast, Bone Gulf, which opens to the Flores Sea, exhibits more typical oceanic conditions with generally clearer waters, more stable temperatures, and a distinct light regime, making these two systems a useful comparative framework for examining how skeletal morphology tracks local environmental conditions (Irwan *et al.* 2024a).

Sampling was conducted during the dry season (June–August 2025) to minimize the influence of extreme seasonal fluctuations, such as increased turbidity and rainfall associated with the monsoon season, which are more pronounced in the Spermonde Archipelago. This approach enabled a more equitable baseline comparison between sites, while site-specific environmental differences such as temperature gradients and local hydrodynamics remained apparent and constituted the core focus of this study. A stratified random sampling design was employed, with sampling locations selected to represent environmental gradients within each region. At each site, three replicate stations were established, with a minimum distance of 1 km between stations to ensure spatial independence.

From each station, five *Porites lobata* colonies that appeared healthy with a massive growth form were selected randomly (Figure 1). The total sample size was 48 specimens, comprising 30 colonies from the Spermonde Archipelago (codes pkp and mks), 12 colonies from Bone Gulf (code bn), and 6 colonies from Taka/Bone Control (code bk). This sample size imbalance reflects logistical constraints in Bone Gulf, where colonies meeting the strict selection criteria (healthy, massive growth form, depth 3–10 m, no visible signs of stress) were less frequently encountered within the designated sampling transects. Although this imbalance may affect the statistical power of comparisons, Welch's independent-samples t-test was employed, which remains valid for unequal sample sizes and heterogeneous variances. Additionally, effect sizes (Cohen's d) were calculated to ensure that biological relevance was assessed beyond statistical significance alone.

All collections were made from depths of 3–10 m to control for depth-related morphological variation. Colonies showing signs of bleaching, disease, or recent physical damage were excluded to ensure that measured skeletal morphology reflected normal growth conditions and was not confounded by acute physiological stress, reduced calcification rates, or post-stress skeletal alterations (e.g., bioerosion, algal overgrowth).

Each colony was photographed in situ with a scale reference. To standardize sampling and minimize within-colony morphological variation, fragments approximately 5 × 5 cm were collected from the outermost living margin (apical zone) of each colony using a hammer and chisel. This region was selected to represent actively growing corallite structure while avoiding basal areas that may exhibit different growth patterns or partial mortality. Care was taken to obtain complete corallite structures for morphological analysis.

### 2.2. Sample Preparation and Microscopy

In the laboratory, coral samples were carefully processed to prepare skeletal structures for morphometric analysis. The protocol followed established methods for coral skeleton preparation (Kruszyński *et al.* 2007) with modifications. Tissue removal was accomplished through a combination of mechanical cleaning and chemical treatment. Samples were first immersed in 5.23% sodium hypochlorite (NaOCl) for 24 hours to dissolve organic material, then thoroughly rinsed with distilled water.

Cleaned skeletons were air-dried for 48 hours at room temperature and stored in individually labeled sealed containers to prevent physical cross-contamination (e.g., mixing of skeletal fragments between specimens) and to ensure accurate specimen identification throughout the analysis. Morphometric analysis was conducted using an Infitek stereoscopic microscope (MSC-ST830) equipped with a calibrated ocular micrometer and an integrated digital camera system.

Prior to measurement, the microscope was calibrated using a stage micrometer, and measurement accuracy was verified at ±0.01 mm. All observations

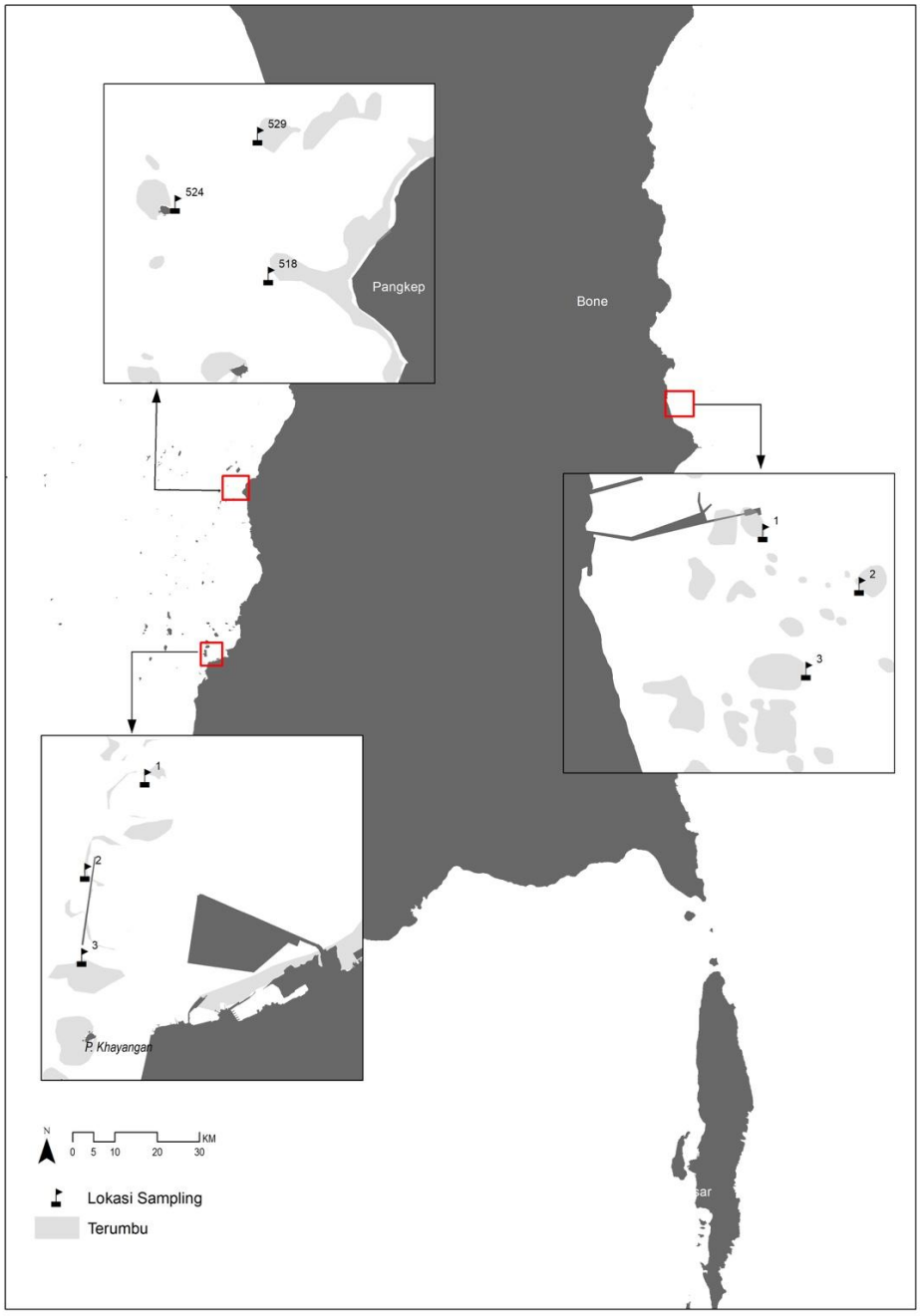


Figure 1. Map of sampling locations

were conducted at a standard magnification of 20× for corallite measurements and 50× for finer septal and palus structures, with lighting conditions maintained consistently throughout the analysis.

For each specimen, three representative corallites were selected from the central area of the fragment to avoid edge effects. Selection criteria required that corallites be undamaged, fully developed, and representative of the overall colony morphology. Each corallite was oriented by identifying the dorsoventral axis based on the position of directive septa (dorsal and ventral septa) and palus arrangement following standard taxonomic references for Porites (Veron 2013). These anatomical landmarks enabled consistent alignment of the roughly circular corallites on the microscope stage, ensuring repeatable measurement geometry across all samples.

## 2.3. Morphometric Characterization

A comprehensive set of 26 morphological characters was measured from three representative corallites taken from the central area of each skeletal sample, following the corallite character suite exactly as defined by (Tisthammer & Richmond 2018). This suite encompasses corallite dimensions, septal arrangement, columella structure, and descriptive traits, which have been validated for morphometric analysis in *Porites lobata*. Table 1 reproduces these characters, their types, and descriptions as used in the present study.

To assess intra-observer measurement error, all 26 characters were measured three times on the same three representative corallites per specimen by a single observer. The mean value of three replicate measurements for each character was then calculated and used for subsequent analyses. This approach allowed us to quantify measurement precision independently of within-colony biological variation. Intra-observer measurement error, calculated as the coefficient of variation for replicate measurements, was less than 3% for all continuous variables, indicating high measurement consistency.

Our morphometric approach, focusing on detailed skeletal architecture, builds upon the growing recognition that quantitative trait-based frameworks are essential for understanding coral biology and ecology beyond simple growth form categories (Forsman *et al.* 2015).

## 2.4. Species Identification Protocol

Species identification followed a rigorous multi-step protocol combining qualitative assessment and quantitative verification. Initial field identification was based on overall colony morphology, including: (1) massive or dome-shaped growth form; (2) compact, relatively smooth surface texture; and (3) corallite arrangement characterized by small, circular calices (0.8–1.3 mm diameter) evenly distributed across the colony surface, forming a regular, non-linear pattern characteristic of *Porites lobata* (Veron 2013). This preliminary assessment was subsequently confirmed through detailed morphometric analysis. Laboratory confirmation employed the taxonomic keys and diagnostic characters established by Veron (2013) (Figure 2).

It should be noted that identification in this study was entirely morphology-based without molecular

Table 1. Corallite characters of Porites specimens measured for morphometric analysis

| Character | Type | Description |
|---|---|---|
| Corallite diameter (length) | N | Length parallel to the dorsoventral axis |
| Corallite diameter (width) | N | Length perpendicular to the dorsoventral axis |
| Corallite spacing | N | Mean linear distance between the nearest and farthest neighboring corallite centers |
| Dorsal septum length | N | Linear distance from the dorsal septum tip to the inner theca edge |
| Ventral septum length | N | Linear distance from the ventral septum tip to the inner theca edge |
| Lateral septum length | N | Mean of four linear distances from lateral septum tips to the inner theca edge |
| Columella diameter | N | Mean of maximum and minimum columella diameters |
| Ventral palus diameter | N | Mean diameter of ventral pali |
| Lateral palus diameter | N | Mean of maximum and minimum lateral palus diameters |
| Dorsal palus diameter | N | Dorsal palus diameter |
| Fossa length | N | Distance measured across the corallite center from the median ventral palus to the dorsal palus |
| Fossa width | N | Mean distance measured across the corallite center from a lateral palus to the diagonal lateral palus |
| Lateral septa spacing | N | Mean distance measured across the corallite center from a lateral palus to the diagonal lateral palus |
| Ventral septa spacing | N | Mean distance between ventral septa at the theca edge |
| Ventral palus spacing | N | Mean distance between ventral pali |
| Dorsal palus spacing | N | Mean distance from the dorsal palus to the adjacent lateral palus |
| Lateral septum thickness | N | Mean cross-distance of lateral septa at mid-length |
| Dorsal septum thickness | N | Cross-distance of the dorsal septum at mid-length |
| Ventral septum thickness | N | Mean cross-distance of ventral septa at mid-length |
| Palus count | D | Number of pali per corallite |
| Lateral palus height | D | Degree of lateral palus prominence (1 = not prominent, 2 = slightly prominent, 3 = moderately prominent, 4 = highly prominent) |
| Triplet form | D | 1 = separate, 2 = fused, 3 = trident |
| Wall height | D | Palus height relative to wall: 1 = Wall high, palus tips well below wall; 2 = Wall slightly higher than pali; 3 = Pali level with wall |
| Corallite shape | D | 3 = round, 4 = rhomboid/square/rectangular, 5 = pentagonal, 6 = hexagonal |
| Columella shape | D | 0 = not visible/absent, 1 = rod-shaped, 2 = compressed |

This table reproduces the corallite character suite from Tisthammer & Richmond (2018) without modification

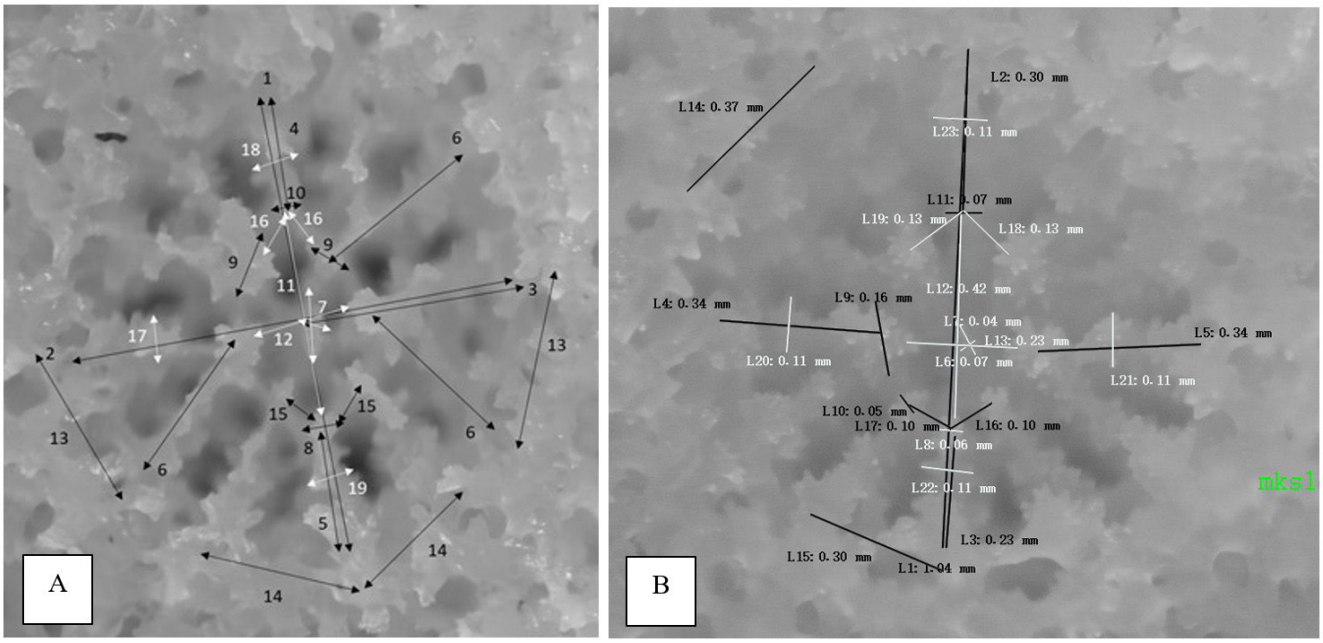


Figure 2. (A) Example diagram of *P. lobata* corallite measurement locations as listed in Table 1, (B) example diagram of *P. lobata* corallite measurements.

validation. Given the well-documented complexity of the *P. lobata* species complex (Forsman *et al.* 2020), the possibility of cryptic taxa cannot be entirely excluded and represents a limitation of this study that should be addressed through molecular validation in future research.

### 2.5. Environmental Characterization and Water Quality Data

To provide environmental context for the observed morphological variation, water quality parameter data from both study sites were compiled and analyzed. These data encompass in situ measurements of six key parameters: pH, salinity, temperature, dissolved oxygen, nitrate, and phosphate. Measurements were conducted concurrently with the coral sampling period of this study, using calibrated standard instruments. Water quality data were collected directly by the same research team, at locations and depths identical to those used for coral sampling, thereby providing a representation of environmental conditions directly relevant to the growth of Porites lobata colonies analyzed. Environmental parameters measured in situ using a Hanna water quality meter (15 sampling points per observation site) included salinity, temperature, dissolved oxygen (DO), pH, and turbidity. Water samples were collected using Niskin bottles. Samples were placed in labeled dark sterile bottles, fixed with Lugol's solution, and kept cold in an ice-filled cooler during transport to the Laboratory of the Faculty of Marine Science and Fisheries, Hasanuddin University, Makassar. Phosphate and nitrate concentrations were determined using a spectrophotometer.

### 2.6. Data Analysis

The analytical approach was conducted in sequential steps as described below.

#### 2.6.1. Site Grouping

Specimens were grouped by sample code into three sites: the Spermonde Archipelago (codes pkp and mks, n = 30), Bone Gulf (code bn, n = 12), and Taka/Bone Control (code bk, n = 6). This grouping was essential to ensure that comparative analyses were performed on appropriate units. Taka was separated from Bone Gulf as it represents an ecologically distinct control site within the same system.

#### 2.6.2. Descriptive Statistics

For each numerical morphometric character and each water quality parameter, the mean ($\bar{x}$), standard deviation (SD), standard error (SE = SD/$\sqrt{n}$), and range (minimum and maximum values) were calculated, stratified by site.

### 2.6.3. Assumption Testing

Data distribution normality was tested using the Shapiro-Wilk test for each variable per site group. Homogeneity of variances between groups was tested using the F-test (Levene's test). The results of these tests determined the selection of appropriate comparative tests in subsequent steps.

### 2.6.4. Morphometric Comparative Analysis

Comparisons of 21 numerical morphometric characters were conducted using Welch's independent-samples t-test (Welch's independent-samples t-test) across three comparison pairs: (1) Spermonde vs. Bone Gulf, (2) Bone Gulf vs. Taka, and (3) Spermonde vs. Taka. Welch's test was selected because it does not assume homogeneity of variances between groups, remaining valid even when Levene's test indicated significant heteroscedasticity. Negative t-values indicate the second group is larger; positive t-values indicate the first group is larger.

For each character showing a significant difference ($p<0.05$), effect size was calculated using Cohen's d, following the formula $d = (\bar{X}_2 - \bar{X}_1) / \text{spooled}$, where $\text{spooled} = \sqrt{[(s^2_1 + s^2_2) / 2]}$. Interpretation criteria: $|d| < 0.2$ = small effect; $0.2 \leq |d| < 0.5$ = medium effect; $0.5 \leq |d| < 0.8$ = large effect; $|d| \geq 0.8$ = very large effect (Cohen 1988). Based on the pattern of p-values and direction of differences, morphometric characters were classified into three categories: Group A (Bone larger, significant), Group B (Spermonde larger, significant), and Group C (not significantly different).

### 2.6.5. Water Quality Comparative Analysis

Seven water quality parameters (pH, salinity, temperature, dissolved oxygen/DO, nitrate, phosphate, and TSS) were compared between Spermonde (n = 28 sampling points) and Bone (n = 14 sampling points) using Welch's independent-samples t-test at a significance level of $\alpha = 0.05$. A similar comparison was conducted between Bone (n = 14) and Taka (n = 2 stations); these results are considered indicative given the very small sample size of Taka.

### 2.6.6. Correlation Analysis

To explore relationships between environmental conditions and corallite morphology, Pearson correlation analysis was conducted between mean water quality parameters and mean morphometric characters per sub-site (Pangkep, Makassar, and Bone; n = 3). Sub-site means were used as the unit of analysis because water quality data and morphological data were collected at the same spatial scale. Correlation coefficients (r) were interpreted as follows: $|r| \geq 0.9$ = very strong; $0.7 \leq |r| < 0.9$ = strong; $0.4 \leq |r| < 0.7$ = moderate; $|r| < 0.4$ = weak. Given the very small number of analytical units (n = 3), correlation p-values are indicative and results should be interpreted with caution.

All statistical tests used a significance level of $\alpha = 0.05$. No Bonferroni correction was applied for multiple comparisons given the exploratory nature of this analysis; instead, Cohen's d was used to assess biological relevance beyond statistical significance alone.

## 3. Results

### 3.1. General Overview of Corallite Morphometry

Morphometric analysis of 48 specimens collected from three sites — the Spermonde Archipelago (n = 30: Pangkep 18, Makassar 12), Bone Gulf (n = 12, code bn), and Taka/Bone Control (n = 6, code bk) — confirmed that all specimens belong to the species Porites lobata. The overall mean corallite diameter (length) was 0.987±0.145 mm (range: 0.80–1.40 mm), corallite diameter (width) was 0.977±0.125 mm (range: 0.70–1.30 mm), and the mean palus count was 6.77±1.06 per corallite (range: 5–8). All values fell within the diagnostic range for *P. lobata* 0.8–1.3 mm for corallite diameter and 5–8 for palus count. All specimens also exhibited a synapticulothecal wall structure, compact columella, and septal arrangement characteristic of this species.

Of the 21 numerical characters tested, 7 (33.3%) showed significant differences between Spermonde (n = 30) and Bone Gulf (n = 12), as presented in Table 2. The pattern of differences was bidirectional: four characters were larger in the Bone Gulf population (Group A), three characters were larger in the Spermonde population (Group B), and 14 characters did not differ significantly (Group C).

### 3.2. Morphometric Comparison Among Three Character Groups

Group A: Bone larger (4 characters). Maximum columella diameter was 42.6% larger in Bone (0.176±0.048 mm vs 0.123±0.056 mm; $t = -3.074$; $p = 0.005$; $d = 1.015$). Minimum lateral palus diameter was 55.5% larger in Bone (0.104±0.026 mm vs 0.067±0.023

Table 2. Results of morphometric analysis and Welch's t-test for 21 skeletal characters of *Porites lobata* from the Spermonde Archipelago (n=30) and Bone Gulf (n=12), grouped by pattern of difference

| Character (mm) | Site | Mean ± SD | Range | t | p | Sig. |
|---|---|---|---|---|---|---|
| A. Bone > Spermonde — 4 characters significant (p<0.05) | | | | | | |
| Columella diameter (max) | Spermonde | 0.123±0.056 | 0.018–0.300 | -3.074 | 0.005 | ** |
| | Bone | 0.176±0.048 | 0.110–0.250 | | | |
| Lateral palus diameter (min) | Spermonde | 0.067±0.023 | 0.030–0.130 | -4.320 | <0.001 | *** |
| | Bone | 0.104±0.026 | 0.050–0.140 | | | |
| Lateral septa spacing | Spermonde | 0.257±0.047 | 0.130–0.370 | -2.967 | 0.008 | ** |
| | Bone | 0.305±0.048 | 0.220–0.400 | | | |
| Palus count | Spermonde | 6.53±1.11 | 5–8 | -2.648 | 0.013 | * |
| | Bone | 7.33±0.78 | 6–8 | | | |
| B. Spermonde > Bone — 3 characters significant (p<0.05) | | | | | | |
| Fossa width | Spermonde | 0.279±0.058 | 0.200–0.440 | 3.029 | 0.005 | ** |
| | Bone | 0.230±0.043 | 0.180–0.310 | | | |
| Ventral palus spacing | Spermonde | 0.157±0.037 | 0.100–0.260 | 7.250 | <0.001 | *** |
| | Bone | 0.097±0.017 | 0.080–0.140 | | | |
| Dorsal palus spacing | Spermonde | 0.149±0.027 | 0.100–0.200 | 5.669 | <0.001 | *** |
| | Bone | 0.093±0.030 | 0.050–0.150 | | | |
| C. Not significantly different — 14 characters (p>0.05) | | | | | | |
| Corallite diameter (length) | Spermonde | 0.944±0.097 | 0.800–1.180 | -0.475 | 0.641 | ns |
| | Bone | 0.963±0.127 | 0.800–1.220 | | | |
| Corallite diameter (width) | Spermonde | 0.952±0.111 | 0.700–1.200 | 0.052 | 0.959 | ns |
| | Bone | 0.950±0.086 | 0.800–1.120 | | | |
| Dorsal septum length | Spermonde | 0.255±0.042 | 0.160–0.340 | -0.206 | 0.840 | ns |
| | Bone | 0.258±0.056 | 0.170–0.340 | | | |
| Ventral septum length | Spermonde | 0.265±0.052 | 0.150–0.420 | 1.180 | 0.255 | ns |
| | Bone | 0.239±0.068 | 0.130–0.360 | | | |
| Lateral septum length | Spermonde | 0.283±0.038 | 0.200–0.360 | -0.832 | 0.414 | ns |
| | Bone | 0.293±0.034 | 0.240–0.360 | | | |
| Columella diameter (min) | Spermonde | 0.058±0.016 | 0.020–0.090 | -1.943 | 0.070 | ns |
| | Bone | 0.072±0.022 | 0.030–0.100 | | | |
| Ventral palus diameter | Spermonde | 0.110±0.053 | 0.050–0.260 | 1.432 | 0.164 | ns |
| | Bone | 0.088±0.040 | 0.040–0.200 | | | |
| Lateral palus diameter (max) | Spermonde | 0.155±0.044 | 0.040–0.240 | -2.001 | 0.059 | ns |
| | Bone | 0.186±0.045 | 0.140–0.260 | | | |
| Dorsal palus diameter | Spermonde | 0.091±0.038 | 0.040–0.230 | 1.758 | 0.090 | ns |
| | Bone | 0.073±0.028 | 0.040–0.120 | | | |
| Fossa length | Spermonde | 0.365±0.083 | 0.230–0.600 | -1.148 | 0.269 | ns |
| | Bone | 0.409±0.122 | 0.240–0.660 | | | |
| Ventral septa spacing | Spermonde | 0.259±0.037 | 0.190–0.370 | -1.884 | 0.075 | ns |
| | Bone | 0.284±0.041 | 0.220–0.360 | | | |
| Lateral septum thickness | Spermonde | 0.101±0.033 | 0.060–0.200 | -0.038 | 0.970 | ns |
| | Bone | 0.102±0.023 | 0.060–0.140 | | | |
| Dorsal septum thickness | Spermonde | 0.100±0.034 | 0.050–0.200 | -0.696 | 0.493 | ns |
| | Bone | 0.108±0.028 | 0.060–0.160 | | | |
| Ventral septum thickness | Spermonde | 0.098±0.041 | 0.040–0.220 | -0.514 | 0.610 | ns |
| | Bone | 0.103±0.022 | 0.060–0.140 | | | |

Sig.: *** p<0.001, ** p<0.01, * p<0.05, ns: not significant. Negative t: Bone > Spermonde, positive t: Spermonde > Bone

mm; t = −4.320; p<0.001; d = 1.518). representing the largest effect size in this dataset. Lateral septa spacing was 18.8% larger in Bone (0.305±0.048 mm vs 0.257±0.047 mm; t = −2.967; p = 0.008; d = 1.021). Palus count 12.2% higher in Bone (7.33±0.78 vs 6.53±1.11; t = −2.648; p = 0.013; d = 0.837).

Group B: Spermonde larger (3 characters). Ventral palus spacing was 38.6% larger in Spermonde (0.157±0.037 mm vs 0.097±0.017 mm; t = 7.250; p<0.001; d = −2.109). representing the second largest effect size in this dataset. Dorsal palus spacing was 37.5% larger in Spermonde (0.149±0.027 mm vs

0.093±0.030 mm; t = 5.669; p<0.001; d = −1.974). Fossa width 17.7% larger in Spermonde (0.279±0.058 mm vs 0.230±0.043 mm; t = 3.029; p = 0.005; d = −0.967).

Group C: Not significantly different (14 characters). Fourteen characters showed no significant difference between the two populations (p>0.05), including both corallite diameter dimensions, all septum lengths (dorsal, ventral, lateral), minimum columella diameter, ventral and dorsal palus diameters, fossa length, ventral septa spacing, and all septum thicknesses. Although some characters showed numerically substantial differences, such as maximum lateral palus diameter (+19.6%) and ventral septa spacing (+9.9%), high within-group variance resulted in p-values that did not reach the significance threshold.

### 3.3. T-test: Bone Gulf vs. Taka (Bone Control)

Comparison between Bone Gulf (bn, n = 12) and Taka/Bone Control (bk, n = 6) yielded 8 significantly different characters. Taka exhibited larger values for seven characters: corallite diameter length (+29.8%; t = −5.085; p<0.001; d = 2.461), corallite diameter width (+22.1%; t = −3.908; p = 0.005; d = 2.047), ventral septum length (+51.2%; t = −3.418; p = 0.007), ventral septa spacing (+27.3%; t = −3.557; p = 0.006), lateral septum length (+24.4%; t = −3.058; p = 0.018), dorsal septum length (+17.4%; t = −2.731; p = 0.018), and fossa width (+15.9%; t = −2.806; p = 0.015). Conversely, minimum columella diameter was larger in Bone (−23.3%; t = 2.170; p = 0.045). The very large effect sizes for corallite diameter characters (d = 2.461 and d = 2.047) indicate that the differences between Bone and Taka are biologically highly meaningful, although interpretation should be made cautiously given the small Taka sample size (n = 6).

### 3.4. Water Quality

Water quality data were collected from four locations: Pangkep (n = 14), Makassar (n = 14), Bone (n = 14), and Taka (n = 2 stations), as presented in Table 3. Welch's t-test between Spermonde (n = 28) and Bone (n = 14) showed that of the seven parameters tested, only two differed significantly. Temperature was higher in Spermonde (29.24±1.92°C vs. 28.29±0.39°C; t = 2.521; p = 0.017), with temperature variability in Spermonde nearly five times greater due to the contrast between Makassar (31.04°C) and Pangkep (27.44°C). Nitrate was also higher in Spermonde (0.032±0.012 mg/L vs. 0.024 ± 0.010 mg/L; t = 2.332; p = 0.026). The remaining five parameters — pH, salinity, DO, phosphate, and TSS — did not differ significantly between the two sites, although TSS approached significance (p = 0.061).

## 4. Discussion

### 4.1. Bidirectional Morphological Plasticity as a Response to Environmental Gradients

Seven of 21 skeletal characters showed significant differences between Spermonde and Bone, with opposing directional patterns between the two character groups. The four Group A characters that were larger in Bone reflect the development of more complex corallite architecture: larger columella diameter (d = 1.015), larger minimum lateral palus diameter (d = 1.518), greater lateral septa spacing (d = 1.021), and higher palus count (d = 0.837). This is consistent with the more physiologically favorable conditions at Bone: lower, more stable temperatures (28.29±0.39°C), the highest DO (5.85 mg/L), and lower nitrate (0.024 mg/L) that support zooxanthellae productivity and more efficient calcification (Ross *et al.* 2022; Kahng *et al.* 2024). The

Table 3. Mean water quality parameters per site (Mean ± SD). Asterisks indicate significant differences relative to Bone on Welch's t-test: *** p<0.001, ** p<0.01, * p<0.05

| Parameter | Pangkep (n = 14) | Makassar (n = 14) | Bone (n = 14) | Taka (n = 14) |
|---|---|---|---|---|
| (Mean ± SD) | Spermonde | Spermonde | Bone gulf | Bone control |
| Temperature (°C) | 27.44±0.74 | 31.04±0.30 | 28.29±0.39* | 29.79±0.30 |
| pH | 8.22±0.17 | 8.15±0.06 | 8.16±0.05 | 8.23±0.07 |
| Salinity (ppt) | 31.24±0.39 | 31.16±0.52 | 31.36±0.24 | 30.73±0.04*** |
| DO (mg/L) | 5.43±0.52 | 5.79±0.38 | 5.85±0.36 | 5.07±0.15** |
| Nitrate (mg/L) | 0.030±0.008 | 0.035±0.015 | 0.024±0.010* | 0.026±0.004 |
| Phosphate (mg/L) | 0.007±0.002 | 0.006±0.002 | 0.009±0.013 | 0.005±0.001 |
| TSS (mg/L) | 2.39±0.39 | 3.25±0.46 | 3.14±0.45 | 2.65±0.15 |

very strong positive correlation between DO and palus count (r = 0.983) reinforces this interpretation.

The larger columella diameter in Bone (+42.6%) can be specifically linked to higher calcification efficiency as a response to more stable water conditions. Irwan *et al.* (2024b) documented that along the trophic status gradient in Bone Gulf waters, nitrate concentrations ranged from 0.014–0.025 ppm across oligotrophic to eutrophic zones, with turbidity approaching zero in waters farther from the coast. These conditions are consistent with the water quality data from our study (Bone nitrate = 0.024 mg/L; TSS = 3.14 mg/L), placing the Bone sampling site within the mesotrophic range under clearer and chemically more stable conditions. Under low-nitrate conditions, competition for nitrogen allocation between soft tissue growth and calcium carbonate deposition can be minimized, thereby supporting the formation of larger and more complex central skeletal structures including the columella (Todd 2008; Houlbrèque & Ferrier-Pagès 2009). The near-perfect negative correlation between nitrate and maximum columella diameter (r = −0.999; p = 0.031) in our data provides direct empirical support for this mechanism.

Conversely, the three Group B characters that were larger in Spermonde ventral palus spacing (d = −2.109), dorsal palus spacing (d = −1.974), and fossa width (d = −0.967) represent the most functionally meaningful findings. Proportionally wider palus and fossa spacing relative to the smaller corallite size indicates a more open internal architecture, which may enhance heterotrophic feeding efficiency to compensate for reduced photosynthesis due to elevated temperatures and terrestrial influence in Spermonde (Todd 2008; Morgan *et al.* 2017).

Irwan *et al.* (2024b) noted that the marginal waters of the Spermonde Archipelago experience substantially greater environmental stress than Bone Gulf, with hard coral cover below 15% and algal dominance a condition reflecting chronic accumulation of multi-factor stress from terrestrial inputs. This contrasts markedly with Bone Gulf, where hard coral cover reaches 59.08–63.63% even in eutrophic to mesotrophic waters. The more open internal architecture in Spermonde as reflected in wider palus spacing can be interpreted as a dual adaptive response: first, facilitating passive sediment clearance through wider inter-palus channels, since in higher-turbidity environments a more open corallite structure can passively prevent particle accumulation on the polyp surface (Anthony & Larcombe 2000 cited in Irwan *et al.* 2024b); and second, enhancing heterotrophic capture capacity to compensate for reduced autotrophic productivity under multi-stressor conditions (Anthony & Fabricius 2000; Houlbrèque & Ferrier-Pagès 2009). The positive correlation of nitrate with ventral palus spacing (r = 0.836) is consistent with the hypothesis that greater terrestrial influence drives the development of heterotrophic strategies reflected in corallite micro-morphological architecture.

This bidirectional pattern more complex corallites in Bone, more open internal space in Spermonde indicates that *P. lobata* modifies the proportions of skeletal components specifically according to its functional environmental requirements, rather than simply scaling proportionally, as predicted by adaptive phenotypic plasticity theory (Forsman *et al.* 2015; Chevin & Hoffmann 2017).

### 4.2. The Role of Water Quality in Shaping Skeletal Architecture

Of the seven water quality parameters tested, only temperature and nitrate differed significantly between Spermonde and Bone, indicating that it is not the number of differing parameters but their specific combination that is ecologically relevant. Temperature variability in Spermonde was nearly five times greater (SD = 1.92°C vs. 0.39°C in Bone), reflecting the extreme contrast between Makassar (31.04°C) and Pangkep (27.44°C), and represents a source of chronic physiological stress more impactful than differences in mean values alone. The negative correlation between temperature and columella diameter (r = −0.739) is consistent with the disruption of calcification enzymes at elevated temperatures (Ross *et al.* 2022). The higher nitrate in Spermonde (0.032 vs. 0.024 mg/L), although still very low in absolute terms, showed a near-perfect negative correlation with columella diameter (r = −0.999; p = 0.031), which can be explained through nitrogen allocation competition between soft tissue growth and calcification (Todd 2008).

Consistent with this interpretation, Irwan *et al.* (2024b) found a counter-intuitive yet ecologically meaningful pattern in Bone Gulf: hard coral cover was actually higher in eutrophic (59.08%) and mesotrophic (63.63%) waters than in oligotrophic zones (43.15%), indicating that corals in Bone's marginal waters possess substantial adaptive capacity to varying trophic conditions. This reinforces the interpretation that the morphological differences we documented do

not simply reflect "good vs. bad conditions," but rather represent functional phenotypic plasticity at both sites. Environmental parameters correlated with hard coral cover in Bone include temperature, chlorophyll-a, TSS, pH, phosphate, nitrate, and turbidity (Irwan *et al.* 2024b). Collectively, these factors define the environmental space within which *P. lobata* expresses the morphological modifications we measured.

Taka exhibited the largest corallite dimensions among all sites, with corallite diameter 29.8% larger than Bone and 32.4% larger than Spermonde ($p<0.001$; $d = 2.461$), despite water conditions that were not consistently superior to those of Bone. The significant salinity difference between Bone and Taka (31.36 vs. 30.73 ppt; $p<0.001$) and the very strong positive correlation between salinity and columella diameter ($r = 0.992$) indicate that specific local oceanographic conditions at Taka contribute to supporting larger corallite growth. However, the mechanism explaining why Taka has the largest corallites requires further investigation with more comprehensive environmental parameter measurements. Overall, these findings underscore that water quality conditions influence corallite morphology through complex multi-parameter interactions rather than through a single factor (Zawada *et al.* 2019).

### 4.3. Implications for Species Identification, Resilience, and Conservation

The fourteen Group C characters that did not differ significantly between populations including all septum thicknesses, minimum columella diameter, and ventral and dorsal palus diameters confirm the identity of all 48 specimens as *P. lobata*. The stability of these characters among populations living under markedly different environmental conditions suggests that they represent evolutionarily conserved diagnostic traits that are not susceptible to plastic modification (Tisthammer & Richmond 2018). The combination of conservative diagnostic characters and plastically modified ones reflects a strategy of phenotypic response partitioning: modification occurs in specific functional characters while taxonomic identity is maintained consistent with theoretical predictions for phenotypic plasticity in variable environments (Sommer 2020).

From a conservation perspective, the three populations in this study are not interchangeable, each serves a different but equally important management purpose. The Spermonde population, persisting under fluctuating high temperatures and strong terrestrial influence, represents genotypes adapted to marginal conditions and constitutes an important candidate for resilience-based conservation programs. The Taka population, with the largest corallites and relatively more controlled water conditions, has the potential to serve as a superior propagule source for coral reef restoration. The Bone population represents an important reference condition for monitoring morphological change resulting from environmental degradation. It should be noted that this study cannot separate the contributions of phenotypic plasticity from local genetic adaptation. Reciprocal transplantation experiments and SNP-based genomic analyses are needed to quantify the relative contribution of these two mechanisms (Baums 2008; Kenkel & Matz 2016), and to determine whether the documented morphological variation is reversible or genetically fixed.

In conclusion, this study generated findings relevant to all four stated objectives. First, morphometric analysis of 21 skeletal characters revealed 7 characters that differed significantly between Spermonde ($n = 30$) and Bone ($n = 12$), with a bidirectional pattern: four characters were larger in Bone and three were larger in Spermonde. Second, the identification of all 48 specimens as *P. lobata* was confirmed by 14 characters that did not differ significantly between populations, reflecting evolutionarily conserved diagnostic traits beyond the reach of phenotypic plasticity. Third, correlations between morphological patterns and water quality gradients, particularly temperature ($p = 0.017$), nitrate ($p = 0.026$), the nitrate–columella relationship ($r = -0.999$), and DO–palus count ($r = 0.983$) indicate that the observed morphological variation is consistent with a plastic response to environmental heterogeneity. Mechanistically, the larger columella diameter in Bone reflects more efficient skeletal calcification under low-nitrate and high-DO conditions, while the wider palus spacing in Spermonde indicates adaptation to a more open internal architecture as a dual response to sedimentation pressure and greater heterotrophic demand in marginal waters. Fourth, the three populations have distinct yet complementary conservation implications: Spermonde as a source of genotypes adapted to marginal conditions, Taka as a candidate propagule source for restoration, and Bone as an ecological reference condition. Overall, these findings reinforce that *P. lobata* expresses coherent, environment-specific phenotypic plasticity adjusting skeletal architecture in functionally meaningful ways rather than responding uniformly to stress, with

important implications for coral reef conservation and management strategies in Indonesia.

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