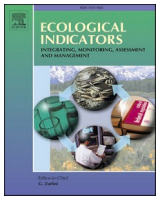
Ecological Indicators 189 (2026) 115096

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Integrating physicochemical and microbial indicators to assess small-scale nutrient pollution in the Lease Islands, Indonesia

Agustin Capriati [a,b,c,*], Stephanie J. Martinez [b,c], Thomas Kemenes van Uden [d], Marcel T.J. van der Meer [e], Purwanto [f], Ingrid A. van de Leemput [a,1], Leontine E. Becking [b,c,1]

[a] Aquatic Ecology and Water Quality Management, Wageningen University and Research, 6708PB, the Netherlands
[b] Aquaculture Biology and Fisheries Ecology, Wageningen University and Research, 6808WD, the Netherlands
[c] Marine Evolution and Ecology Group, Naturalis Biodiversity Center, 2333CR, the Netherlands
[d] Wageningen Marine Research, Ankerpark 27, 1781 AG, Den Helder, the Netherlands
[e] NIOZ Royal Netherlands Institute for Sea Research, Texel 1790AB, the Netherlands
[f] Coral Triangle Center, Jalan Bet Ngandang II No.88-89, Bali 80228, Indonesia

1. Introduction

Coral reef ecosystems are in decline globally due to global and local stressors (Burke et al., 2011). Global stressors, such as increasing sea surface temperature, drive mass coral bleaching events (Hughes et al., 2018; Kubicek et al., 2019). Local stressors, such as nutrient enrichment or pollution, degrade reefs at regional and site-specific scales (Fabricius, 2005). Nutrient enrichment in the water column promotes the growth of fast-growing algae and microbes (Lapointe et al., 2004; Teichberg et al., 2018), which can outcompete corals for space and resources, thereby hindering their survival. Such processes are increasingly linked to the global phenomenon of reef microbialization, in which energy flow is redirected toward microbial pathways under nutrient-enriched conditions (Haas et al., 2016). The increased of nutrient conditions often includes elevated concentrations of ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), and phosphate (PO_4^{3-}), which are widely recognized as indicators of degraded water quality in reef ecosystems (Fabricius, 2005). By amplifying physiological stress, nutrient enrichment not only drives local degradation but also reduces reefs' resilience to global stressors (Silbiger et al., 2018).

Nutrient pollution is one of the major local drivers of coral decline globally (Andrello et al., 2022) and has emerged as a pressing and escalating concern across the Indonesian archipelago, which hosts approximately 16% of the world's coral reefs (Burke et al., 2011). Recent assessments indicate that 82% of reef sites across 22 locations in Indonesia exceed national regulatory limits for dissolved inorganic nutrients (Adyasari et al., 2021). Indonesia's uniform national standard (0.158 μM for phosphate, PP No.22/2021) falls within the range of thresholds established for the Great Barrier Reef, Australia (phosphate thresholds of 0.1–0.2 μM)(Bell, 1991, 1992). However, recorded phosphate concentrations in Indonesian coastal waters span four orders of magnitude (0.001 to 18.95 μM) (Edward and Kusnadi, 2023; Maslukah et al., 2019), reflecting strong local heterogeneity in nutrient exposure. This wide range suggests that a single national standard may be insufficient to capture local variability and that site-specific monitoring is necessary to characterize nutrient stress in Indonesian reef systems.

Most reef water quality assessments have historically focused on broad, kilometer-scale spatial gradients, e.g. (Damar et al., 2019; Fong et al., 2020), with comparatively little attention to the smaller scale of the land–sea interface (1–75 m). Consequently, nutrient dynamics within this proximal nearshore zone remain poorly characterized. This spatial mismatch is particularly important in Indonesia, where the inherent patchiness of reef near-coastal environments, combined with highly localized anthropogenic inputs, can trigger sharp variations in water quality over short distances (Fabricius, 2011; Fabricius et al., 2013; Ford et al., 2017). Understanding nutrient dynamics across these land-sea gradients thus provides a more nuanced understanding of localized nutrient loading.

Nutrient inputs fluctuate across space and time, occurring as both short-term peaks and longer-term enrichment (Anthony et al., 2015). Direct measurements of water-column nutrients are effective for capturing short-term enrichment events, but their ability to represent overall nutrient exposure is limited by strong spatial and temporal variability. Effective monitoring, therefore, requires a multi-tiered approach that combines water-column measurements with biological indicators that integrate nutrient signals over longer timescales and

* Corresponding author at: Department of Aquatic Ecology and Water Quality Management, Environmental Sciences, Wageningen University & Research, Droevendaalsesteeg 3a, 6700AA Wageningen, the Netherlands.
E-mail address: agustin.capriati@wur.nl (A. Capriati).
[1] Share senior authorship

https://doi.org/10.1016/j.ecolind.2026.115096
Received 10 January 2026; Received in revised form 12 June 2026; Accepted 16 June 2026
Available online 28 June 2026

across spatial gradients.

Bioindicators that integrate signals over time and space can provide more consistent estimates of nutrient loading. Stable isotope analysis of macroalgae, for instance, has been proposed as a complementary tool for understanding nutrient dynamics in complex reef ecosystems (Skinner et al., 2022). Stable isotopes integrate ambient nutrient conditions over timescales of weeks to several months, depending on species, tissue type, and growth rate (Costanzo et al., 2001; Fernandes et al., 2012; Barr et al., 2013; Gorman et al., 2017; Bailes and Gröcke, 2020). Time-averaged signals from isotope analysis also allow discrimination among nitrogen sources, such as sewage and fertilizer (Gartner et al., 2002; Cohen and Fong, 2005). Stable nitrogen isotope ($\delta^{15}N$) signatures of natural sources typically range between 0‰ and 4‰, while nitrogen derived from fertilizer or sewage generally ranges between >4‰ and 38‰ (Gartner et al., 2002; Dailer et al., 2010). Macroalgae such as *Halimeda* and *Padina* are widely applied as bioindicators of nitrogen sources because they assimilate nitrogen with minimal isotopic fractionation (Gartner et al., 2002; Cohen and Fong, 2005). When paired with direct physicochemical measurements, macroalgae $\delta^{15}N$ analysis serves as a powerful tool for mapping nutrient sources (Salo and Salovius-Laurén, 2022; Skinner et al., 2022).

Another potential biological indicator of nutrient enrichment and reef decline is the community composition within benthic cyanobacterial mats (BCMs). BCMs respond rapidly to changes in nutrient availability, and their abundance is often associated with reef degradation (Brocke et al., 2018; Ford et al., 2018; Reverter et al., 2020). BCMs alter reef biogeochemistry by increasing nitrogen fixation, releasing large amounts of dissolved organic carbon, and producing toxic compounds (Brocke et al., 2015a; Brocke et al., 2018; Chagas et al., 2024). These changes suppress coral recruitment, promote coral disease, and shift microbial community structure (Bourne et al., 2008; Zaneveld et al., 2016; de Bakker et al., 2017; Glasl et al., 2017; Puyana et al., 2019). Experimental and observational studies further indicate that the BCM community composition is highly sensitive to organic matter loading, climate change, and herbivore decline (Zaneveld et al., 2016; Ford et al., 2018).

To date, there are a limited number of molecular studies that have evaluated the species composition of BCMs (Brocke et al., 2018; Cissell and McCoy, 2021; Ford et al., 2021; Biessy et al., 2021; Ribeiro et al., 2022; Stuij et al., 2023). BCMs community structure is typically dominated by filamentous genera such as *Oscillatoria* and *Lyngbya* (Brocke et al., 2018; Cissell et al., 2022). One study from the Caribbean and one study from Thailand have shown that cyanobacteria often constitute less than half of the total mat community, with significant representation from *Proteobacteria, Bacteroidetes,* and *Planctomycetes* (Cissell et al., 2022; Stuij et al., 2023). Despite increasing insights from molecular analyses, the spatial variation in microbial communities of BCMs remains poorly studied, particularly in relation to nutrient pollution (Ford et al., 2021).

Most molecular studies on BCMs have been conducted in Curaçao, the Caribbean (Brocke et al., 2018), French Polynesia, the central Pacific (Villeneuve et al., 2012), Thailand, Southeast Asia (Stuij et al., 2023), Moorea, Nuku Hiva, Tongatapu, Vava'u, Rarotonga, and Aitutaki in the South Pacific Islands (Biessy et al., 2021). In contrast, no BCM molecular study has been conducted in Indonesian reef ecosystems, despite visual surveys suggesting that BCMs can dominate benthic cover on some Indonesian reefs (Aji et al., 2024). Hence, the microbial community composition of these mats remains uncharacterized. This knowledge gap is particularly important given that Indonesia's coral reefs are among the world's most biodiverse (Burke et al., 2011).

To map the variation in nutrient pollution on reef ecosystems, we conducted an integrated assessment of physicochemical water quality, stable isotope signatures ($\delta^{15}N$) in macroalgae, and the microbial community composition of BCMs across contrasting site types of anthropogenic influence (*Non-populated, Populated,* and *River Mouth* sites) in the Lease Islands, Indonesia. We tested three hypotheses: (1) physicochemical characteristics and dissolved inorganic nutrient concentrations follow a decline along 1–75 m land-sea gradient (from the coast toward the ocean), (2) sites near *Populated Areas* and *River Mouths* would have higher nutrient levels, distinct isotopic signatures $\delta^{15}N$, and distinct microbial composition than waters at *Non-Populated Sites*, and (3) the abundance and microbial composition of BCMs correlate with dissolved inorganic nutrient levels, with a higher prevalence of pathogenic taxa in nutrient rich sites. We integrated direct measurements with biological responses to capture spatial patterns of nutrient stress.

2. Materials and methods

2.1. Study area

Field surveys were conducted in the Lease Islands, Maluku, Indonesia (3°38′43.27”S, 128°26′1.94″E). The Lease Islands comprises four islands: Saparua, Haruku, Nusa Laut, and Molana. Covering approximately 359 km^2, with a total population of 63,517 and is classified as a densely populated small island cluster (USAID SEA Project, 2018). The most populous island is Saparua, located in the middle of the Lease Islands, followed by Haruku and Nusa Laut, while Molana Island remains uninhabited (Fig. 1). Sampling sites were selected to include a range of anthropogenic conditions, including areas near *Non-Populated, Populated,* and *River Mouth* sites. In this study, a *Populated Area* is defined as coastal regions where human populations are concentrated and located near the ocean. While a *Non-Populated* area refers to coastal zones with little to no permanent human settlement nearby, a *River Mouth* refers to the area where a river flows into the ocean. Twelve sampling sites were selected across the Lease Islands, based on the spatial distribution of administrative villages and their varying degrees of coastal proximity (Table S.1).

2.2. Water quality parameters and inorganic nutrients

To capture the spatial variability and land-sea gradients in nutrient concentrations and water physical characteristics, a survey was conducted across 12 sampling sites. At each site, water was measured and collected at distances of 1, 5, 10, 25, 50, and 75 m from the coastline, at approximately 50 cm below the surface. Not all distances could be sampled due to shallow water, exposure to the reef crest, or limited boat access. Sampling was conducted at the beginning of the wet season (April–May 2022) in the Maluku region (BMKG, 2022). This period was intentionally selected to maximize the likelihood of detecting land-based nutrient runoff, as higher rainfall increases terrestrial inputs. To minimize variability associated with tidal dynamics, all sites were sampled within a consistent tidal window. Water quality parameters, including dissolved oxygen, temperature, pH, and salinity, were measured in situ using WTW Multiline and Hanna Instruments HI98190 probes. Chlorophyll *a*, depth, and turbidity were recorded using a CTD sensor (Alec Electronics Co. Ltd., ASTD0687) at the same distance intervals, spanning from the surface to the seafloor. Vertical profiles were examined, and no significant variation was observed within the water column (Fig. S1). Therefore, for general water quality assessment, only surface-layer data (~50 cm) were used for further analysis. For analyses related to BCMs, average physicochemical and inorganic nutrient concentrations from shore to the diving sites were used to characterize site-level water-column environmental conditions associated with BCM habitats.

To measure dissolved inorganic nutrient concentrations, including ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), and phosphate (PO_4^{3-}), surface water samples were collected at each distance using a 2.5-l KAHLSICO water sampler. To preserve the sample and minimize contamination, 6 mL of seawater was immediately filtered in the field using sterile Acrodisc Supor PF 0.8/0.2 μm filters. Filtrates were collected in clean, sterile high-density polyethylene (HDPE) bottles, which had been triple-rinsed with seawater from the KAHLSICO

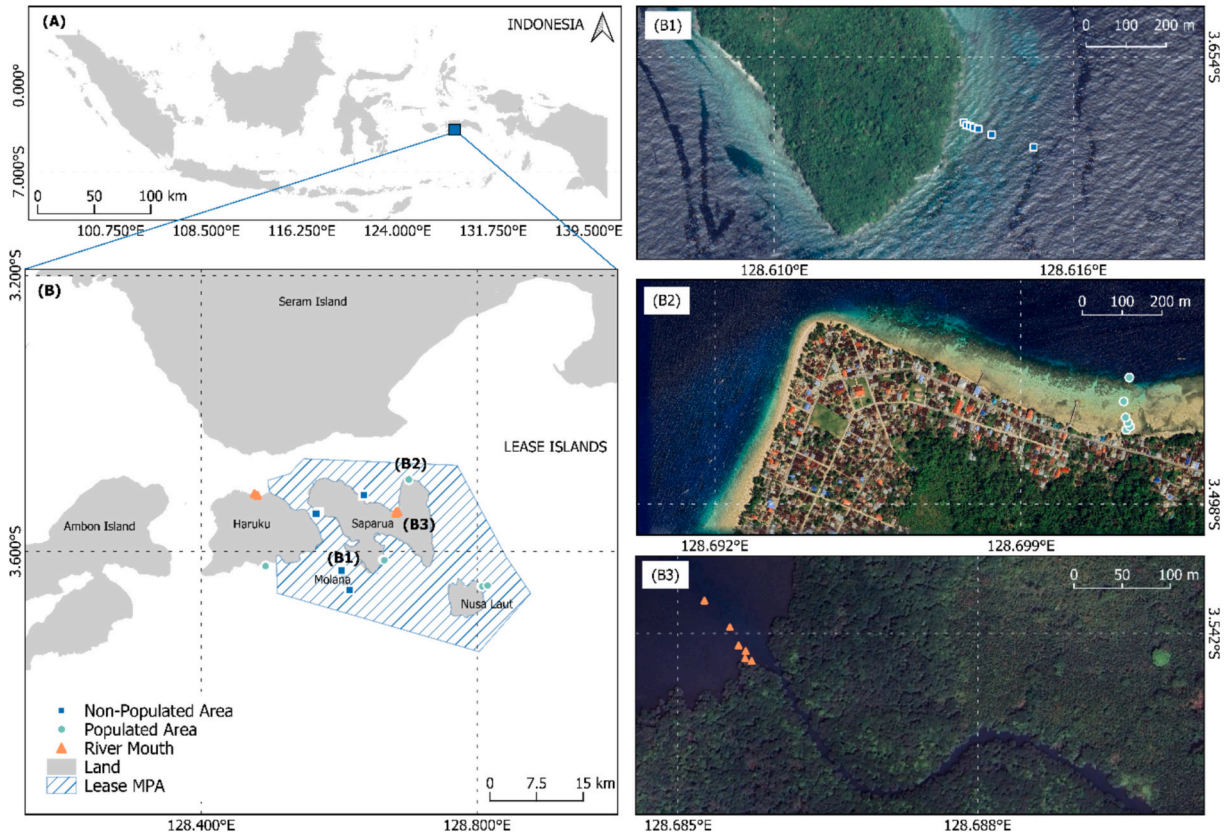


Fig. 1. Sampling sites within the study area and their location within Indonesia. (A) Location of the Lease Islands, Maluku, within Indonesia, indicated by the blue rectangle; (B) Locations of the twelve sampling sites within Lease Islands classified by site type: non-populated (green squares), populated (red circles), and river mouth (orange triangles). Note that several sites are closely clustered and may not be individually distinguishable at this scale. The Lease Marine Protected Area (MPA), established in 2021, is outlined by the hatched blue area. B1-B3 are example aerial views of (B1) a non-populated site, (B2) a populated site, and (B3) a river mouth site (B1-B3: retrieved from Google Earth, 2025).

sampling bottle and again with the filtered sample. Then, the filtrates were placed in a Bio-Freeze Bottle System within 8 h of post-collection and stored at −20 °C. Samples remained frozen throughout transport to the Royal Netherlands Institute for Sea Research (NIOZ), where nutrient concentrations were quantified using a gas-segmented continuous flow analyzer, following the protocol described by (Hydes et al., 2010).

2.3. Macroalgae collection and isotopic analysis

To determine the sources of nutrient inputs in each site, stable isotope analysis ($\delta^{15}N$) of macroalgae was conducted. At each of the 12 sites, we aimed to collect three (3) individuals (specimens) per species to represent site-specific variation. The commonly reported macroalgal genera *Padina*, *Halimeda*, and *Dictyota* were along the same 50 m transect used for BCM and water sampling. Specimens were collected by SCUBA diving at depths of 5 m to 10 m to minimize the confounding effects of light on isotopic composition (Umezawa et al., 2002).

After collection, samples were prepared following the methods of Christianen et al. (2017) and Aji et al. (2025) for field conditions in remote areas with limited laboratory facilities. In short, each sample was cleaned of fouling organisms and silt, then dried in aluminum foil envelopes in a rice cooker at ~60 °C for 24–48 h until fully dry. Drying samples after collection is a widely used method that effectively removes moisture, limits microbial and enzymatic activity, and maintains stable nitrogen isotope signatures over months of storage (Silva et al., 2019; Silberberger et al., 2021; Schmid et al., 2022). After initial drying, the samples were stored in a vacuum-sealed dry container with additional silica gel to prevent moisture reabsorption and frozen at −20 °C after fieldwork. Before analysis, samples were thoroughly checked for visible signs of decay or mold and were either re-dried at 60 °C in an oven for 24 h or freeze-dried to remove residual moisture. Then, the samples were transported to NIOZ, ground into a fine powder, and stored in glass vials.

Calcareous *Halimeda* samples were subsampled and decalcified in silver cups with 1 M HCl solution to remove inorganic carbon, then dried in a vacuum oven at 70 °C for 48 h (Tue et al., 2012; Le et al., 2017). Non-calcareous species (*Padina* and *Dictyota*) were not decalcified. The $\delta^{15}N$ values were measured from the original (non-decalcified) samples, whereas the $\delta^{13}C$ values were obtained from decalcified subsamples. Weights ranged from 6 to 7 mg for *Halimeda,* and 1.5 to 2 mg for *Padina* and *Dictyota*. Carbon and nitrogen isotope ratios were measured using stable isotope ratio mass spectrometry, Flash2000 Elemental analyzer connected to a Delta V Advantage Isotope Ratio Mass Spectrometer via a Conflo IV interface. Ratios were expressed in delta (δ) notation relative to international standards (VPDB for carbon, AIR for nitrogen), following the formula $\delta X = [(R\_sample / R\_standard) - 1] \times 1000‰$, where X is ^{13}C or ^{15}N, and R is the ratio of heavy to light isotopes. The ^{13}C and ^{15}N values were reported in per mil (‰) notation relative to Vienna Pee Dee Belemnite and atmospheric nitrogen (AIR) standards, using certified reference materials, acetanilide, urea, and casein for $\delta^{15}N$ and $\delta^{13}C$, and benzoic acid and acetanilide for $\delta^{13}C$ of the decalcified samples.

2.4. BCM sampling and molecular analysis

To investigate the microbial community composition of BCMs, we collected BCM samples at the same 12 sampling sites described above

(2.1 Study Area) at depths of 5–10 m along the transect line (3 × 50 m). At each site, BCMs were collected by carefully removing mats from substrates using a syringe. Samples were collected only where mats were visibly established, immediately preserved in 50 mL Falcon tubes with 96% ethanol, and stored at −20 °C. Samples were transported to the Naturalis Biodiversity Center (Leiden, The Netherlands) for molecular analysis.

The molecular analysis includes DNA extraction, Polymerase Chain Reaction (PCR), and sequencing. DNA was extracted using Bioke NucleoSpin PowerSoil (Machery-Nagel) kits following the manufacturer's protocol, with the adjustment that 50 µL of Proteinase-K (QIAGEN) at a concentration of 28.8 mg/mL was added before lysis (see Supplementary Material Text S1). Tissue weights ranged from 0.08 to 0.15 g. Extraction success was verified by gel electrophoresis on a 1% agarose gel in TBE buffer, stained with SYBR Safe, using 5 µL of extract and 1 µL of loading dye. The 16S rRNA V4-V5 regions were amplified via PCR using the primers 515F—Y (5′-GTGYCAGCMGCCGCGGTAA) and 926R (5′-CCGYCAATTYMTTTRAGTTT) (Parada et al., 2016). These primers target bacterial and archaeal communities and have demonstrated reduced amplification biases in mock marine microbial communities (Parada et al., 2016). Each sample was amplified in triplicate using 1 µL of undiluted DNA extract, 5 µL of KAPA HiFi ReadyMix, 0.3 µL of each primer, and 3.4 µL of Milli-Q water. Cycling conditions were 95 °C for 5 min for the initial denaturation, followed by 25 cycles of denaturation at 98 °C for 30 s, annealing at 50 °C for 30 s, and extension at 72 °C for 1 min. This was then followed by a final extension at 72 °C for 7 min. After this, we first examined the results by selecting a random sample of wells from each amplification replicate, including negative controls, with gel electrophoresis. The triplicate amplifications were pooled and purified using Macherey-Nagel (MN) beads (0.9 µL beads per 10 µL PCR sample). The final pooled library was purified using MN-beads, and its DNA concentration was assessed using a Tape Station (D5000 Agilent reagent kit) (see Supplementary Material Text S2). This final library was sent to BaseClear B.V. (Leiden, the Netherlands) for sequencing on MiSeq.

Raw sequencing data (demultiplexed FASTQ) were processed using the dada2 R package (v. 1.28.0) (Callahan et al., 2016) with the R program, version 4.3.3 (R Core Team, 2025). Paired-end ASVs were merged using *mergePairs* based on overlapping reads, and chimeras were subsequently identified and removed using *removeBimeraDenovo*. Taxonomic assignment of final ASVs was performed using the assignTaxonomy and addSpecies functions against the CyanoSeq_1.1.2_SILVA138.1_dada2 database (Lefler et al., 2023), with species-level assignments restricted to 100% sequence matches. The number of species identified reflects the taxonomic resolution of the metabarcoding data reference. In general, more ASVs can be identified to the genus level than to the species level. While many ASVs could be reliably classified to the genus level, only a subset could be confidently assigned to the species level due to limitations in reference databases; i.e., in the database, not many species have sequence references. Moreover, following the database's standard convention, provisional genera that form distinct monophyletic clades but cannot be assigned to an existing genus are denoted by the family name followed by "_X" (e.g., *Desertifilaceae*_X). These "_X" suffixes are presented in non-italicized font to distinguish them from formal genus names. Further filtering removed ASVs outside the expected 16S V4-V5 amplicon length range (350–390 bp), given an expected length of 371 bp (Parada et al., 2016). Contaminant ASVs were identified and removed using the Contaminant function from the decontam R package (v. 1.20.0) (Davis et al., 2018).

2.5. Statistical analysis

We checked chlorophyll *a*, temperature, turbidity, pH, salinity, and dissolved oxygen and dissolved inorganic nutrient concentrations (NH_4^+, NO_2^-, NO_3^-, PO_4^{3-}) for normality and homogeneity using the Shapiro-Wilk and Levene's tests. Shapiro-Wilk tests revealed significant deviations from normality for all variables ($p < 0.05$) (Table S.2). Therefore, we applied non-parametric tests because the data did not meet the parametric assumptions. We used the Kruskal-Wallis test to examine differences among sites and site types (*Non-Populated, Populated,* and *River Mouth*). Significant Kruskal-Wallis results were followed by Dunn's post-hoc tests with Bonferroni correction. A significance level of $\alpha = 0.05$ was used for all tests. To investigate spatial variation in nutrient signatures, we tested whether nitrogen ($\delta^{15}N$) differed across locations and site types for each of the three macroalgae species (*Halimeda, Padina, Dictyota*) individually. However, not all species could be tested consistently across all locations due to limited sample availability at some sites.

To evaluate variation in BCMs community composition across locations and among site types, we first assessed data quality by trimming forward reads to 280 bp and reverse reads to 210 bp (Fig. S2). Forward and reverse-read error models were then generated (Fig. S3). We then examined sequencing depth across samples and compared it with a minimum depth of 10,000 reads (Fig. S4). Samples below this cutoff were excluded. After that, we applied an additional Amplicon Sequence Variant (ASV) to remove low-quality sequences, and an ASV-level filtering step to reduce noise from rare taxa. We removed ASVs that appeared only once across all samples and required a minimum prevalence of 10% of samples to retain a taxon, as such low-abundance features are often attributed to sequencing noise or contamination (Callahan et al., 2016; Nearing et al., 2022). Prior to quality control and rarefaction, 139,676 ASVs were identified, which were reduced to 696 ASVs after filtering. The bacterial rarefaction curves indicated that the sequencing depth was adequate (Fig. S5). Second, to assess taxonomic resolution and dataset structure after filtering, we quantified the number of unique taxa represented at each rank, from Phylum to Species. We also calculated the number of ASVs per sample. After filtering, the ASV abundances (amplicon sequence data) were normalized using Total Sum Scaling (TSS) (Lin and Peddada, 2020). This normalization enabled direct comparison of community composition across samples and with other studies, without the bias introduced by replacing zeros with pseudo-counts (Tsilimigras and Fodor, 2016; Greenacre, 2026) (Supplementary Material Text S3). Because our primary analyses rely on distance-based ordination and distance-based redundancy analysis (dbRDA), which are robust to sparsity and widely used in microbial ecology, we determined that TSS-based approaches were more appropriate for our dataset. We also note that TSS-normalized relative abundances facilitate interpretability and comparability with existing literature. Normalized data were used to calculate diversity and Bray-Curtis distances for ordination analyses (Tsilimigras and Fodor, 2016). After normalization, ASVs were used to assess the microbial community.

To investigate differences in microbial community structure, we first summarized taxonomic profiles at the phylum level and then aggregated relative abundances across samples. The ten most abundant phyla were retained for visualization, while all remaining phyla collapsed into a "Other" category. Relative contributions of these phyla were then calculated per site and site type and displayed as stacked bar plots. To extend this analysis at finer taxonomic resolution, we generated a heatmap of the 50 most abundant taxonomic groups. Differences in microbial community composition among sites and site types were assessed using PERMANOVA. Pairwise comparisons among sites and site types were performed using the pairwise.adonis2 function with the Holm correction. Furthermore, the differences in alpha diversity (Shannon index, reflecting richness and evenness) (Alberdi and Gilbert, 2019) and richness (Chao1) among sites and site types were compared using Kruskal–Wallis tests followed by Dunn's post hoc analysis with Benjamini-Hochberg correction to control the false discovery rate, a standard approach in microbiome studies (e.g., Armstrong, 2014; Kim et al., 2017; Vesterbacka et al., 2017). Beta diversity (Bray-Curtis) was assessed to evaluate differences in microbial composition between samples and site types.

To evaluate which water quality parameters and inorganic nutrient

variables explained microbial variation, distance-based redundancy analysis (dbRDA) was used. First, environmental variables were standardized using a *scale* function, and then a correlation test for multicollinearity was performed. Then, we cleaned the environmental data by selecting numeric variables, removing missing values, and filtering out highly collinear variables (Pearson's $|r| > 0.7$) (Table S.3). After accounting for these correlations, the dataset was reduced by excluding highly collinear variables ($r < 0.75$) (Fig. S6). Multivariate analyses were performed using Bray-Curtis dissimilarity matrices derived from TSS-normalized abundances, with scaled environmental variables. The significance of the full model and specific predictors was determined via 999 permutations. Ordinations and PERMANOVA were executed using the *vegan* package (Oksanen et al., 2025).

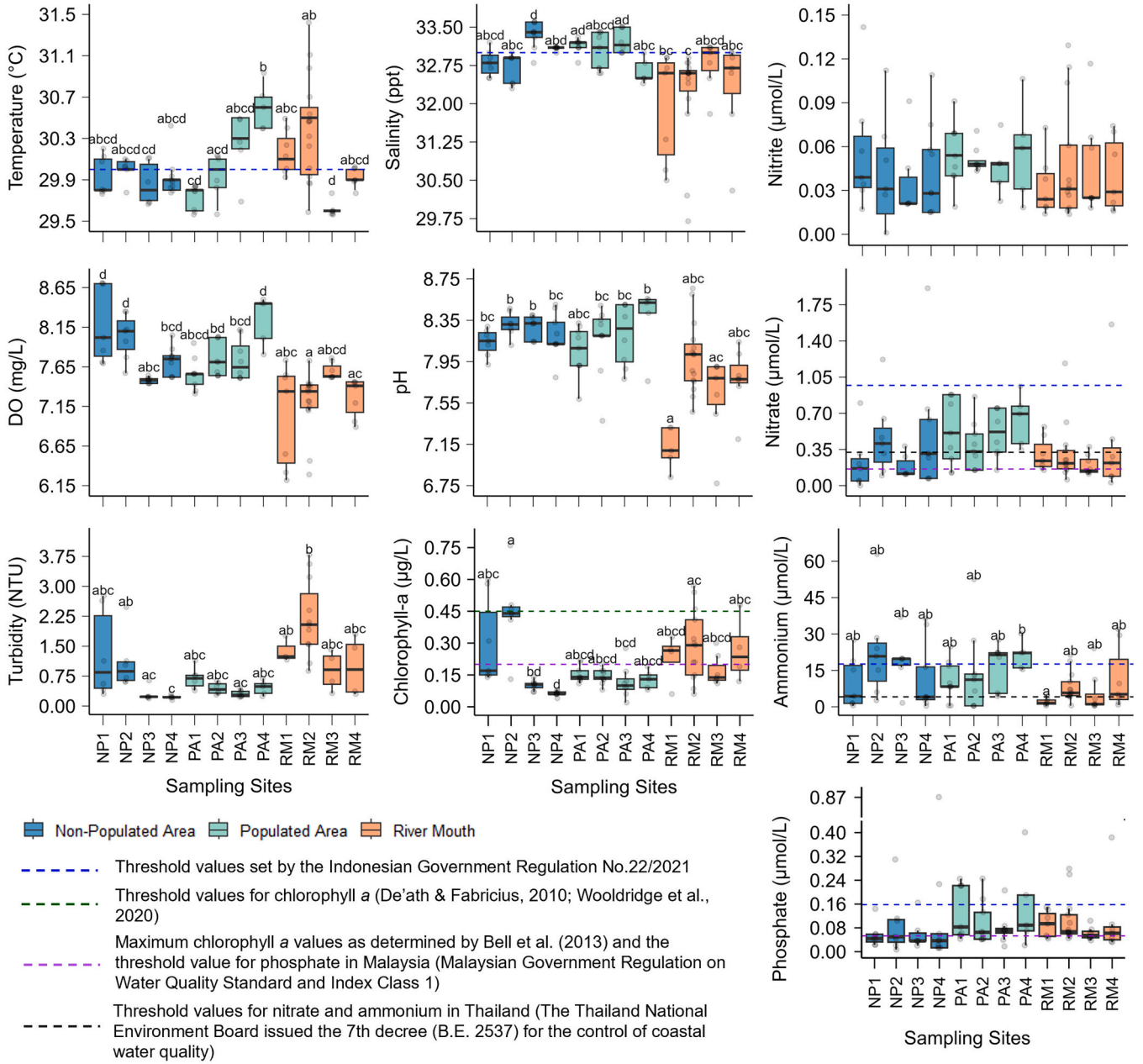


Fig. 2. Variation in water quality parameters across sampling sites in Lease, Indonesia. Boxplots show the distribution of temperature, dissolved oxygen (DO), turbidity, salinity, pH, chlorophyll *a*, nitrite, nitrate, ammonium and phosphate measured at individual sampling sites (for a complete list of locations, see Table S.1). Each boxplot represents samples collected at 50 cm depth; samples taken at different distances from the coast to the diving sites were considered replicates in this analysis. Boxes represent the interquartile range, with median lines and individual observations overlaid. Black letters (a, b, c, d) above boxes indicate statistically significant differences among sites for each parameter ($p < 0.05$, Dunn's test with Bonferroni correction). Sites that have no or the same letter do not differ significantly, and vice versa. The blue-dashed line represents the threshold set by Indonesian Government Regulation No. 22/2021. Dark green line represents threshold values for chlorophyll *a* on the Great Barrier Reefs, Australia (De'ath and Fabricius, 2010; Wooldridge, 2020). The purple dashed line indicates the optimal maximum chlorophyll *a* values determined by Bell et al. (2014), and the phosphate threshold value in Malaysia under the Malaysian Marine Water Quality Standards (MMWQS). Black dashed lines show threshold values for nitrate and ammonium in Thailand, based on the Thailand National Environmental Board's 7th Decree (BE.2537) for the control of coastal water quality. NP: *Non-Populated*, PA: *Populated*, RM: *River Mouth*.

3. Results

3.1. Spatial variation in water quality

At the individual site level, water quality measures displayed high spatial heterogeneity with some variation among sites (Fig. 2). Pairwise comparisons revealed sporadic, site-specific differences (e.g., in temperature between PA1 and PA4, $p = 0.003$), no consistent patterns were found across individual sampling sites (Fig. 2; Table S. 4). In contrast, when aggregating sites into anthropogenic categories (*Non-Populated, Populated,* and *River Mouth*), clear significant patterns were revealed (Fig. S7; Table S.5) except for temperature. Pairwise comparisons showed that the *River Mouth* was the most distinct site, characterized by significantly lower mean salinity, lower mean dissolved oxygen, lower pH, higher chlorophyll *a*, lower ammonium, and higher turbidity compared to both the *Populated* and *Non-Populated* sites. *Populated* and *Non-Populated* sites did not differ significantly for those parameters (Fig. S7). Significant differences were found between *Non-Populated* and *Populated* sites in phosphate, nitrate, and nitrite levels, with higher levels in the *Populated* sites. Phosphate levels in *River Mouth* sites were comparable to *Populated* sites, while nitrate and nitrite in *River Mouth* were similar to *Non-Populated* sites (Fig. S7).

Our results also showed that many of the measured dissolved inorganic nutrient levels exceeded the limits set by the official national water quality standards. When assessed against the regulatory thresholds set by the Government of Indonesia (Regulation No. 22/2021), 37% of the total sampling points exceeded the limits for nitrate, nitrite, and ammonium. Phosphate thresholds were exceeded at 21% of the total sampling points, while chlorophyll *a* thresholds were exceeded at 36% of the total sampling points across 12 sites (Fig. 2).

Analysis of the land-sea gradient (1–75 m) showed some differences in physical gradients and nutrient distributions (Fig. 3). Physical parameters displayed sharp coast-to-ocean gradients; both turbidity and salinity changed significantly across the transect ($p = 0.0021$ and $p =$

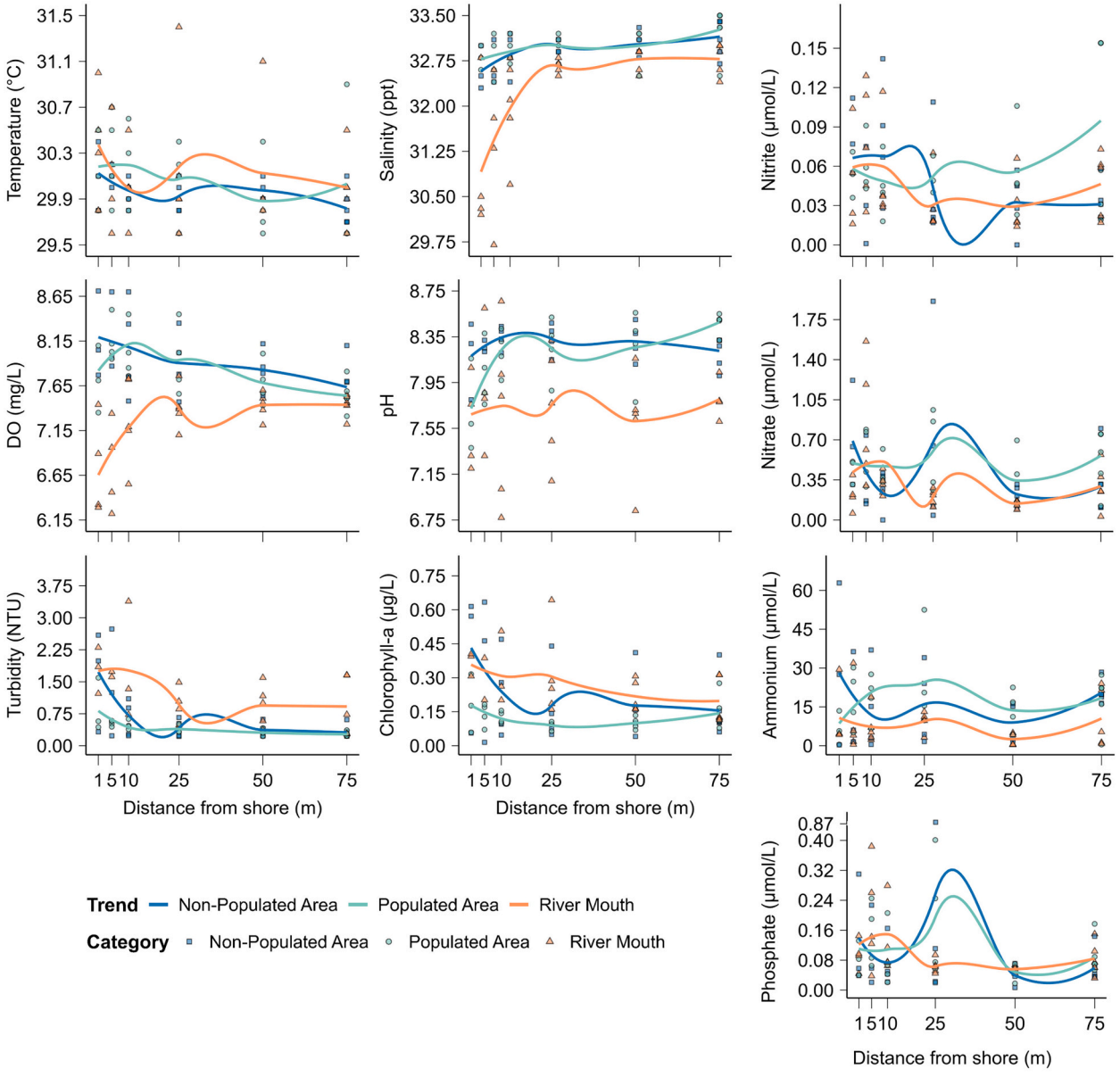


Fig. 3. Physical gradients at the land-sea interface. The figure illustrates the variation of water quality parameters with distance from shore (0–75 m). Individual panels show measurements of temperature, dissolved oxygen (DO), turbidity, salinity, pH, chlorophyll *a*, nitrite, nitrate, ammonium, and phosphate. Data are grouped by anthropogenic site type: *Non-Populated* Area (squares - blue), *Populated Area* (circles - green), and *River Mouth* (triangles - oranges). All measurements were taken ~50 cm below the water surface.

0.0022, respectively). Post-hoc tests confirmed that turbidity was significantly higher at 1 m than at 75 m ($p = 0.001$), while salinity was significantly lower at 1 m and 5 m compared to 75 m ($p < 0.02$). In contrast, Kruskal-Wallis tests showed no significant relationship with distance from the coast for phosphate ($p = 0.225$), ammonium ($p = 0.243$), or nitrite ($p = 0.184$). Nitrate was the only nutrient to show a significant, albeit weak, relationship with distance ($p = 0.044$). The nearshore zone (1–25 m from the coast) was characterized by high variability, with coefficients of variation for turbidity, dissolved oxygen, and temperature frequently exceeding 1.0 (Table S. 6). Dissolved inorganic nutrient concentrations showed lower variability and greater consistency at distances of 50–75 m from the coast, particularly for phosphate (Fig. 3, Table S. 7).

3.2. Macroalgae δ15N

The distribution of macroalgae was patchy, with target genera encountered at only 8 of the 12 study sites. *Halimeda* was the most frequent ($n = 6$ sites), followed by *Dictyota* ($n = 5$) and *Padina* ($n = 3$). Our intended sampling of three individuals per species per site was not achievable; the number of specimens collected varied by sites and species, depending on local availability. This uneven and limited occurrence precluded a balanced cross-site comparison for each individual genus. The $\delta^{15}N$ signatures within the most frequent species, *Halimeda*, did not differ significantly across sampling sites in which the species was encountered (Fig. 4A). We did observe significant differences ($p < 0.05$) among species when data were pooled across all locations (Fig. 4B). Significant differences in $\delta^{15}N$ were identified between *Padina* and *Halimeda* as well as between *Padina* and *Dictyota* ($p < 0.05$). In contrast, isotopic signatures in *Dictyota* and *Halimeda* were statistically not different.

3.3. BCM community composition

A total of 42 BCMs samples were collected in 10 sites at the Lease Islands (Table S.8). BCMs were absent at two sites, RM2 (*River Mouth*) and NP1 (*Non-Populated*). Taxonomic classification of amplicon sequence variants (ASVs) of the mats assigned to 17 phyla, 30 classes, 67 orders, 96 families, 169 genera. However, only 32 ASVs could be confidently resolved to the species level due to limitations in reference databases. The most abundant phyla across all samples were Proteobacteria (343 ASVs), Bacteroidota (145 ASVs), and Planctomycota (76 ASVs), followed by Verrucomicrobiota (28 ASVs), Cyanobacteriota (27 ASVs), and Firmicutes (22 ASVs).

Overall, the phylum Proteobacteria was the most abundant (Fig. S8), and potentially pathogenic bacteria, such as *Vibrio*, were consistently abundant across all sites (Fig. 5). *Non-Populated* sites showed relatively higher abundances of Firmicutes and Verrucomicrobia. *Populated* sites showed a higher abundance of Cyanobacteria (e.g., genus *Parasynechococcus*) and Fusobacteriota (e.g., genus *Propionigenium*). *River Mouth* sites were dominated by Proteobacteria (e.g., genus *Vibrio*, *Photobacterium*, and *Pseudoalteromonas*). The genus of *Catenococcus, Cognatishimia,* Desertifilaceae_X, *Planktothicoides, Moorena, and* Prochlorotrichaceae_X, were absent in *River Mouth* sites but present in both *Non-Populated* and *Populated* sites (Fig. 5).

Assessment Chao1 richness, calculated at the ASV level, did not differ among individual sites, but it varied significantly by site types (Kruskal-Wallis, $p = 0.025$) (Fig. S9). Chao1 taxonomic microbial richness differed significantly ($p = 0.02$) between *River Mouth* and *Populated* sites. Shannon diversity showed no variation across sites and site types. Beyond individual richness, BCM communities were compositionally distinct across site type at the ASV level, with *River Mouth* sites hosting the most divergent microbial communities. Permutational multivariate analysis of variance confirmed that both individual sites ($R^2 = 0.282$, $p = 0.001$) (Table S.8) and site types ($R^2 = 0.094$, $p = 0.001$) (Table S.9) were significant predictors of overall microbial community structure. *River Mouth* microbial communities were significantly distinct from those in both *Non-Populated* ($R^2 = 0.11$, $p = 0.001$) and *Populated* sites ($R^2 = 0.09$, $p = 0.001$). In contrast, microbial communities in *Non-Populated* and *Populated* sites were not significantly different from each other. This pattern is visually apparent in the ordination, where river mouth samples form a separate cluster from the other sites (Fig. 6). Tests for homogeneity of dispersion (PERMDISP) confirmed that these compositional differences were not an artifact of unequal group variances.

Distance-based redundancy analysis (dbRDA) identified that turbidity, temperature, nitrite, phosphate, and ammonium explained the variation in the BCM community composition. The first constrained axis explained 28.19% and the second axis explained 19.49% of the total constrained variation. Together, 47.68% of the variation was explained by the environmental variables (Fig. 6). The ordination showed a clear spatial structuring among site types, a trend supported by pairwise PERMANOVA results (Table S.9). *River Mouth* sites clustered in the upper left quadrant and were showing significant differentiation from both *Non-Populated* and *Populated* sites ($p < 0.005$, Table S.10), and were associated with high turbidity levels. In contrast, BCM assemblages at *Non-Populated* and *Populated* sites overlap in ordination space, consistent with the lack of significant statistical separation between these two categories (Table S.10). Within these sites, variation in the BCMs community composition was associated with phosphate, with sites distributed mostly across the top-right and lower-left quadrants.

4. Discussion

Our integrated assessment of physicochemical water quality, macroalgal stable isotopes, and BCM microbial communities across the Lease

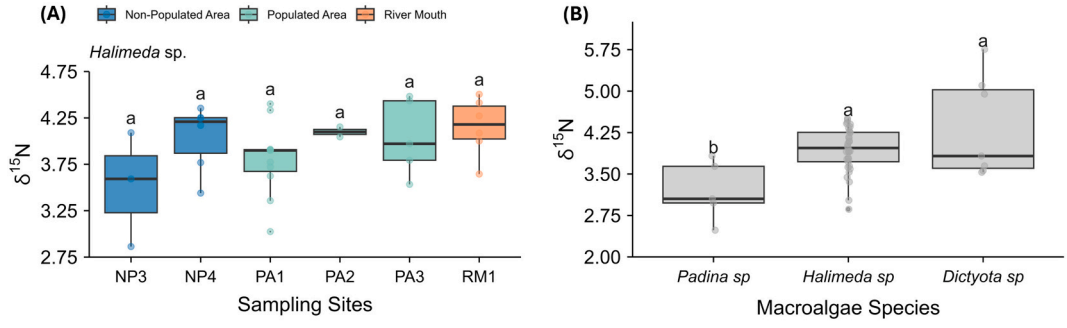


Fig. 4. Macroalgal $\delta^{15}N$ signatures (in ‰) differ by species but not by sites. (A) Boxplots of $\delta^{15}N$ values in *Halimeda* sp. collected from sites categorized as *Non-Populated* Area (NP), *Populated Area* (PA), and *River Mouth* (RM). No significant spatial pattern is evident across sites and site types ($p = 0.279$). (B) Pooled $\delta^{15}N$ values for all three macroalgal genera across the sampling sites. Each point represents an individual sample. Boxes show the interquartile range; the center line is the median. Species that do not share the same superscript letter (a, b) are significantly different (Dunn's test with Bonferroni correction, $p < 0.05$).

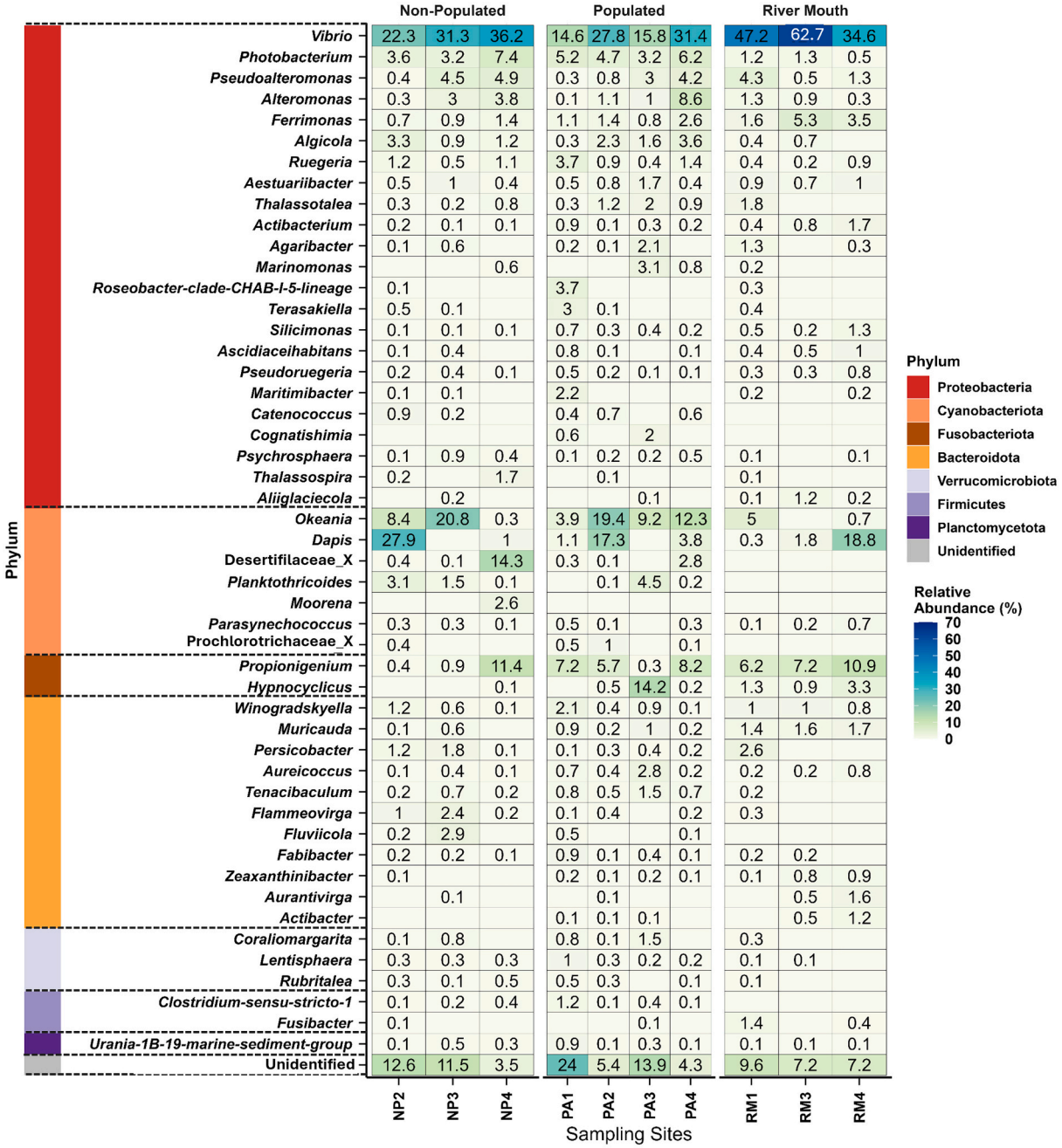


Fig. 5. Relative abundance of the 50 bacterial taxonomic groups across multiple sites per site type *(Non-Populated, Populated, River Mouth)* in the Lease Islands, Indonesia. Each row of the heatmap represents a taxonomic group, and each column corresponds to a site. Tile colors represent relative abundance with darker blue indicating higher abundance; the lightest tiles indicate zero abundance, and numeric values represent the exact percentage of each taxonomic group per site. Values represent relative abundance (0%). Labels are shown only for values ≥0.1%. Left sidebar: Phylum-level classification for each taxonomic group, displayed as a categorical colour bar with distinct colors for each phylum. NP: *Non-Populated Area*, PA: *Populated Area*, and RM: *River Mouth* (complete list of locations Table S.1). Note that unclassified Desertifilaceae and Prochlorotrichaceae in the reference database are labeled as Desertifilaceae_X and Prochlorotrichaceae_X, following the CyanoSeq convention for provisional genera (Lefler et al., 2023). *Urania-1B-19-marine-sediment-group* is an environmental/candidate group designation from the same reference database (Lefler et al., 2023). The "_X" suffix and unidentified genera are presented in non-italicized font.

Islands, Indonesia, tested three hypotheses: whether nutrients decline along a coast-to-ocean gradient, whether *Populated* and *River Mouth* sites differ from *Non-Populated* sites, and whether nutrients can explained BCM compositions. In summary, salinity and turbidity showed clear coast-to-ocean patterns (1–75 m), but phosphate, ammonium, and nitrite did not; nitrate showed a weak gradient. The nearshore zone (1–25 m) had high nutrient variability, while the 50–75 m zone showed greater consistency, particularly for phosphate. Regarding site-type differences: *Populated* and *River Mouth* sites had higher nutrient levels than *Non-Populated* sites, and BCM compositions differed significantly among site types. However, macroalgal $\delta^{15}N$ did not differ significantly among sites, and its application was limited by patchy species distribution (present at only 8 of 12 sites). Lastly, BCM community compositions differed significantly among sites, with environmental factors (temperature, turbidity, nitrite, ammonium, phosphate) explained 47.68% of the variation in BCM composition. Copiotroph and potentially pathogenic taxa (e.g., *Photobacterium, Vibrio*) were prevalent across all sites. Together, these findings demonstrate that an integrated assessment

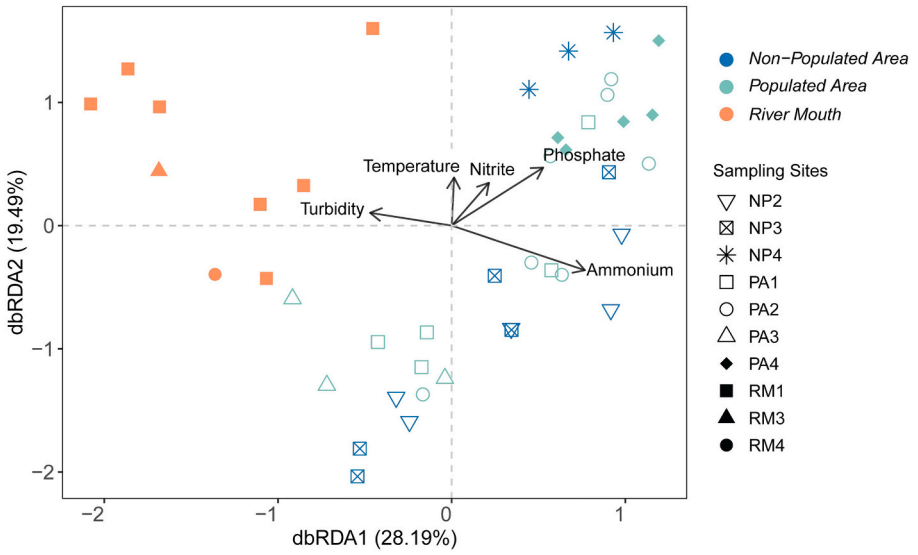


Fig. 6. Distance-based redundancy analysis (dbRDA) of the microbial community composition of benthic cyanobacterial mats in the Lease Islands, Maluku, Indonesia. Samples are colored by site type, with shapes denoting individual sampling sites. Points representing Amplicon Sequence Variants (ASVs) are scaled by abundance, with Lingoes' correction applied to account for non-Euclidean distances. Sites located near each other have similar community compositions. Sites positioned in the direction of an environmental variable arrow have higher values for that specific environmental variable. Only significant environmental variables with a statistical significance of $p < 0.05$ are shown as arrows. The first two constrained axes account for 28.19% and 19.49% of the constrained variance, respectively.

across complementary methods may capture land-based nutrient pollution, with BCM communities showing potential promise as indicators of nutrient pollution, and warranting further investigation.

4.1. Complex spatial dynamics of water quality

Our results demonstrate that water quality in the Lease Islands does not manifest as a simple or predictable coast-to-reef gradient, but instead shows pronounced small-scale spatial heterogeneity. While salinity and turbidity showed clear coast-to-ocean gradients, dissolved inorganic nutrients were less clear. However, nutrient concentrations differed significantly by site type, with higher levels at *Populated* and *River Mouth* sites than at *Non-populated sites*. The higher nutrient concentrations observed in *Populated* relative to *Non-Populated* sites suggest that coastal settlements may impose a persistent source of nutrient inputs, likely through untreated sewage and diffuse coastal runoff, rather than relying only on river inputs. These findings align with regional evidence that small-scale island communities lacking centralized wastewater treatment disproportionately contribute to reef eutrophication (Adyasari et al., 2021). Furthermore, river and groundwater inputs also inflict significant physicochemical stressors such as hyposaline conditions and increased turbidity, which can further exacerbate nutrient enrichment and favor algae over corals (Duprey et al., 2016; Houk et al., 2022).

Our findings suggest that physicochemical water quality monitoring conducted at kilometer scales is likely failing to capture the nearshore interface. We observed high spatial variability within the first 50 m. Phosphate, ammonium, and nitrite showed high variability in the nearshore zone (1–25 m), whereas the 50–75 m zone showed greater consistency, particularly for phosphate. While a phosphate signal is likely present, the high variance in this zone needs a much higher sampling density. This pattern suggests rapid biological assimilation or dilution of terrestrial inputs occurs immediately upon entry. Rapid physical mixing, tidal exchange, and strong regional circulation, for example, can also greatly reduce nutrient residence time, causing nutrient inputs from land to be rapidly diluted, exported, or assimilated before accumulation is detectable (Koop et al., 2001; Eyre et al., 2008; Dzwonkowski et al., 2023; Olorunsaye and Heiss, 2024). As a result, the absence of a clear gradient at fine spatial scales should not be interpreted as an absence of anthropogenic pressure, but rather as a combination of nutrient inputs and snapshot measurements. Similar findings have been reported in Jakarta Bay and other Indonesian reef systems, where chronic nutrient loading is well documented despite weak gradients in measured inorganic nutrients (van der Wulp et al., 2016; Damar et al., 2019). Immediate dilution of terrestrial inputs upon entry masks nutrient-enrichment signals, which align with recent high-resolution observations in Curaçao and the Caribbean, where nutrient and pH/DO variability in inland bays and nearshore zones (5–20 m) were only detectable through small-scale measurements (de Jong et al., 2025). In current practice, monitoring typically involves low-frequency sampling at distances where terrestrial inputs have already been diluted or assimilated, potentially underestimating nutrient stress.

It is important to note that this study is based on a single sampling campaign conducted in April–May 2022, at the onset of the wet season in the Maluku region. To contextualize the sampling period of this study, meteorological data from BMKG indicate that April to May 2022 corresponded to a transitional wet-season phase across the Maluku region, with monthly rainfall ranging from approximately 100 to over 400 mm (BMKG, 2022). These rainfall conditions suggest that coastal systems were still influenced by precipitation-driven freshwater inputs at the time of sampling. This period was intentionally chosen to maximize the detection of land-based runoff signals, while also accounting for logistical constraints during peak rainy seasons when sea conditions are unsafe for fieldwork. In order to improve our understanding of long-term water quality and land–sea connectivity, future research could incorporate multi-seasonal sampling across both wet and dry periods, as well as targeted sampling before and after rainfall events. Such high-frequency monitoring, combined with biological indicators of nutrient exposure, would provide a more comprehensive assessment of eutrophication risk in small island reef systems. However, in practice, most monitoring in Indonesian MPAs is typically conducted only once a year (Trialfhianty et al., 2025).

4.2. Opportunities and limitations of macroalgae $\delta^{15}N$ for identifying nitrogen sources

δ15N analysis of macroalgae provided limited evidence of anthropogenic nitrogen influence, as its interpretive power was confounded by species availability, biological variability, and localized biogeochemical cycling. Based on previous studies (Costanzo et al., 2001; Gartner et al., 2002; Dailer et al., 2010), we hypothesized that sites characterized by sewage-derived nitrogen would be easily identifiable by high $\delta^{15}N$ values. While certain samples in this study exhibited $\delta^{15}N$ values >4‰, falling within ranges commonly associated with sewage-derived nitrogen in tropical coastal systems (Risk et al., 2009; Lapointe et al., 2019). The signal was likely masked by physiological factors and kinetic fractionation, a process in which macroalgae alter the isotope signal during nitrogen uptake (Swart et al., 2014). In oligotrophic environments such as coral reefs, where primary production is high, algae may manifest higher $\delta^{15}N$ values simply because the local nitrate pool becomes enriched. High turbidity may have suppressed light intensity and phototrophic activity, further complicating the relationship between nutrient concentrations and isotopic signatures. Species-specific differences were also evident, consistent with previous studies that have demonstrated macroalgal physiology, nutrient storage capacity, and tissue turnover rates strongly influence isotopic signatures (Umezawa et al., 2002; Viana and Bode, 2013).

In the Lease Islands, patchy macroalgal distributions and their absence at several sites constrained our sampling replication and underscored a limitation of this approach in reef systems. In many regions of Indonesia, macroalgae are sparse, and species distributions are patchy (Cleary et al., 2016; Draisma et al., 2018; Win et al., 2022; Aji et al., 2025). In other words, it is hard to find the same species consistently and in high enough numbers at each site to allow adequate comparison. Furthermore, highly disturbed reefs in Indonesia do not necessarily transition to macro-algal dominance (Reverter et al., 2021), as is more commonly the case in the Caribbean and Australia (Lapointe et al., 2004; Bruno et al., 2009; Mumby, 2009). This implies that, while isotopic analysis remains a valuable complementary tool for identifying pollution, its application in Indonesian reef systems should be carefully evaluated. When applied strategically by targeting abundant species and interpreting results with other indicators, $\delta^{15}N$ can help identify dominant nitrogen sources (Salo and Salovius-Laurén, 2022). However, our results also suggest the need to explore other, more widespread taxa, such as phototrophic soft corals, as potential indicators for stable isotope analysis.

4.3. BCM microbial communities' composition as an integrative indicator of nutrient pollution and reef degradation

The microbial composition of BCMs shows strong, consistent spatial differentiation and a potential association with anthropogenic influence. This finding supports a growing body of nutrient enrichment, organic loading, and imbalance microbial in reef systems (Brocke et al., 2015b; Reverter et al., 2020). The dominance of Proteobacteria across all sites, and particularly the enrichment of pathogenic genera such as *Vibrio* at *River Mouth* sites is concerning, as it has been linked to the black-band disease of corals (Glasl et al., 2017). The high relative abundance of *Vibrio* across site types, therefore, may signal compromised microbial conditions, with possible implications for coral disease risk and reduced recovery potential. Furthermore, our results show a higher relative abundance of copiotrophic microbial communities, such as *Photobacterium* and *Pseudoalteromonas*, across all sites, with the highest abundance in *the Populated Area* sites. Copiotroph bacteria are fast-growing microbes adapted to nutrient-rich conditions. In coral reefs near densely populated islands without sewage treatment, copiotroph taxa are enriched (Kegler et al., 2018). Our results may signal that even *Non-Populated* sites in the Lease Islands experience nutrient enrichment. Previous work on microbial communities across the Central Pacific, Caribbean, and Indian Ocean consistently links the increased abundance of copiotroph taxa to degraded reefs, where elevated organic matter and nutrient inputs promote opportunistic pathogens (Haas et al., 2016).

Populated sites showed a higher relative abundance of *Cyanobacteriota* and *Fusobacteriota* compared to *Non-Populated* sites, suggesting a change toward microbial communities adapted to elevated phosphorus availability. Experimental and field studies demonstrate that phosphorus enrichment, particularly when nitrogen becomes relatively limiting, favors the proliferation of cyanobacteria and nitrogen fixation (D'Angelo and Wiedenmann, 2014; Brocke et al., 2015b; Burberg et al., 2020; Yin et al., 2025). Furthermore, elevated phosphate levels decrease beneficial microbial diversity on corals and can promote the dominance of harmful bacteria such as *Aquarickettsia* (Williams et al., 2022).

We noted that the nutrient data used in this study represent surface-water concentrations and should be interpreted as indicators of broader water-column nutrient regimes influenced by surface-water conditions rather than direct measurements of benthic microenvironmental conditions at the BCM-sediment interface. Within this context, the dbRDA results indicate that phosphate, ammonium, and nitrite were among the environmental variables associated with variation in BCM community composition. Such patterns are consistent with evidence that BCMs communities integrate nutrient exposure at the sediment–water interface, where nutrient concentrations can be higher than those measured in the overlying water column (Tout et al., 2014).

BCM community composition may represent a symptom of nutrient enrichment and reef degradation. BCMs respond to nutrient conditions at microbial scales (nanometers to millimeters), potentially detecting reef deterioration earlier than visible changes in benthic cover (Barott et al., 2012; Vega-Thurber et al., 2014; Glasl et al., 2017). Their microbial consortia may concentrate nutrients, create localized hypoxia, and harbor high densities of copiotroph and pathogenic bacteria (Thomson-Laing et al., 2020). These conditions can suppress coral recruitment and survival, locking the system into a degraded state (Zaneveld et al., 2016). Our findings suggest that BCM community composition may provide a useful tool for monitoring nutrient exposure and indicating lower water quality, as different taxa within the mats respond differently to specific biogeochemical stressors. For instance, while *Proteobacteria* are often linked to nitrogen enrichment, increased relative abundances of *Cyanobacteria* are closely associated with phosphate enrichment (Ford et al., 2018). Overall, BCM community composition shows potential promise as an indicator of land-based nutrient pollution, complementing water sampling and isotope analysis. Further studies should evaluate: (1) the temporal integration period, e.g., via repeated sampling or transplant experiment to assess whether different seasons show different BCM community responses, (2) the causal relationship via experimental nutrient manipulation to confirm that enrichment drives BCM community shifts, (3) spatial generality across other Indonesian reef systems, and (4) possibly integrating BCM assessments into routine reef monitoring.

5. Conclusion

This study tested three hypotheses regarding nutrient pollution in the Lease Islands using an integrated assessment of water quality, macroalgal $\delta^{15}N$, and BCM microbial communities, highlighting both the potential and the limitations of current monitoring approaches. Our study suggests that nutrient pollution in the Lease Islands does not always follow a linear coast-to-reef trajectory, but rather manifests as a complex, small-scale mosaic that may be overlooked by single-time-point measurement of physicochemical parameters. While physical parameters such as salinity and turbidity followed predictable gradients, the high nearshore heterogeneity of dissolved inorganic nutrients illustrates the difficulty of capturing terrestrial loading through snapshot water samples. *Populated Area* sites showed higher nutrient concentrations than *Non-Populated* sites. Macroalgal $\delta^{15}N$ isotopes did provide some evidence of sewage-derived nitrogen, but the evidence was

constrained by patchy species distribution. In contrast, the molecular microbial composition of BCMs offered a promising integrative perspective, potentially reflecting ecological signatures of nutrient and organic enrichment that were less apparent in the physicochemical data. The observed correlations among BCM microbial composition, environmental factors, and the presence of copiotroph taxa suggest a subtle yet persistent change in microbial community structure. Recognizing that reef health monitoring is typically conducted once or twice per year, we suggest that BCM molecular profiles show promise as potential indicators of land-based nutrient pollution and warrant further exploration, including seasonal replication and experimental nutrient manipulations. By exploring these multi-trophic indicators, this research highlights how biological responses may help bridge the gaps left by direct water-column measurements. These findings encourage reconsideration of current monitoring practices, suggesting that incorporating BCM assessments alongside routine water-quality sampling may provide a more comprehensive understanding of nutrient pollutions influencing coral reef resilience.

Acknowledgments

This work was financially supported by the Indonesia Endowment Fund for Education (LPDP) - the Ministry of Finance of the Republic of Indonesia [contact number: S-3570/LPDP.4/2020] and the Dutch Research Council (NWO) project VI.Vidi.193.137. We extend our gratitude to the World Wildlife Fund's (WWF) Russell E. Train Education for Nature (EFN) Program for the first author. We would like to thank the following people who provided help with fruitful discussion, logistics and/or fieldwork: Prof. Marten Scheffer, Mahu Lodge Lease, Prandito Simanjuntak, Harlly Aldo Matruty, Benrilo Mubarok Asdin, Meysella Anugrah, Lalu M. Iqbal Sani, Ronald van Bommel, Gulsah Dogruer, Andreas Haas, Coral Triangle Center, and DKP Maluku. We are grateful to the National Research and Innovation Agency (BRIN) for providing a research permit (B-9/IV/KS.01.04/1/2022) and to KLHK and BKSDA for the sampling permits SK.309/KKHSG/PSG1/KSA.2/5/2022 and S.16/K.19/SATS.DN/05/2022, 14733.IV/SATS-LN/2022. Additionally, we are grateful for the reviewers' valuable suggestions and constructive feedback.

CRediT authorship contribution statement

Agustin Capriati: Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Stephanie J. Martinez:** Writing – review & editing, Methodology, Formal analysis. **Thomas Kemenes van Uden:** Writing – review & editing, Validation, Methodology. **Marcel T.J. van der Meer:** Writing – review & editing, Resources. **Purwanto:** Writing – review & editing, Resources. **Ingrid A. van de Leemput:** Writing – review & editing, Supervision, Resources, Conceptualization. **Leontine E. Becking:** Writing – review & editing, Supervision, Resources, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Agustin Capriati reports financial support was provided by Indonesia Endowment Fund for Education. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2026.115096.

Data availability

Data will be made available on request.

References

Adyasari, D., Pratama, M.A., Teguh, N.A., Sabdaningsih, A., Kusumaningtyas, M.A., Dimova, N., 2021. Anthropogenic impact on Indonesian coastal water and ecosystems: Current status and future opportunities. Marine Pollution Bulletin 171. https://doi.org/10.1016/j.marpolbul.2021.112689.

Aji, L.P., de Leeuw, C.A., Riekenberg, P., Capriati, A., Maas, D.L., Christianen, M.J.A., Murk, A.J., van der Meer, M.T.J., Becking, L.E., 2025. Marine ecosystems with elevated temperature and terrestrial input support simplified food webs. Mar. Ecol. Prog. Ser. 771, 15–32. https://doi.org/10.3354/meps14958.

Aji, L.P., Maas, D.L., Capriati, A., Ahmad, A., De Leeuw, C., Becking, L.E., 2024. Shifts in dominance of benthic communities along a gradient of water temperature and turbidity in tropical coastal ecosystems. PeerJ 12 (4), 1–33. https://doi.org/10.7717/peerj.17132.

Alberdi, A., Gilbert, M.T.P., 2019. A guide to the application of hill numbers to DNA-based diversity analyses. Mol. Ecol. Resour. 19 (4), 804–817.

Andrello, M., Darling, E.S., Wenger, A., Suárez-Castro, A.F., Gelfand, S., Ahmadia, G.N., 2022. A global map of human pressures on tropical coral reefs. Conserv. Lett. 15 (1), 1–12. https://doi.org/10.1111/conl.12858.

Anthony, K.R.N., Marshall, P.A., Abdulla, A., Gooch, M., Graham, N.A.J., Green, A., Heron, S.F., 2015. Operationalizing resilience for adaptive coral reef management under global environmental change, pp. 48–61. https://doi.org/10.1111/gcb.12700.

Armstrong, R.A., 2014. When to use the B onferroni correction. Ophthalmic Physiol. Opt. 34 (5), 502–508.

Bailes, I.R., Gröcke, D.R., 2020. Isotopically labelled macroalgae: A new method for determining sources of excess nitrogen pollution. Rapid Commun. Mass Spectrom. 34 (24), e8951.

de Bakker, D.M., van Duyl, F.C., Bak, R.P.M., Nugues, M.M., Nieuwland, G., Meesters, E. H., 2017. 40 years of benthic community change on the Caribbean reefs of Curaçao and Bonaire: the rise of slimy cyanobacterial mats. Coral Reefs 36 (2), 355–367. https://doi.org/10.1007/s00338-016-1534-9.

Barott, K.L., Rodriguez-Mueller, B., Youle, M., Marhaver, K.L., Vermeij, M.J.A., Smith, J. E., Rohwer, F.L., 2012. Microbial to reef scale interactions between the reef-building coral Montastraea annularis and benthic algae. Proc. R. Soc. B Biol. Sci. 279 (1733), 1655–1664. https://doi.org/10.1098/rspb.2011.2155.

Barr, N.G., Dudley, B.D., Rogers, K.M., Cornelisen, C.D., 2013. Broad-scale patterns of tissue-δ15N and tissue-N indices in frondose Ulva spp.; developing a national baseline indicator of nitrogen-loading for coastal New Zealand. Mar. Pollut. Bull. 67 (1–2), 203–216.

Bell, P.R., Elmetri, I., Lapointe, B.E., 2014. Evidence of large-scale chronic eutrophication in the great barrier reef: quantification of chlorophyll a thresholds for sustaining coral reef communities. Ambio 43 (3), 361–376.

Bell, P.R.F., 1991. Status of Eutrophication in the Great Barrier Reef Lagoon, 23.

Bell, P.R.F., 1992. Eutrophication and coral reefs-some examples in the Great Barrier Reef lagoon. War. Res. 26 (5).

Biessy, L., Wood, S.A., Chinain, M., Roué, M., Smith, K.F., 2021. Exploring benthic cyanobacterial diversity and co-occurring potentially harmful dinoflagellates in six islands of the South Pacific. Hydrobiologia 848 (11), 2815–2829. https://doi.org/10.1007/s10750-021-04599-6.

BMKG, 2022. Curah Hujan di Provinsi Maluku. 2022.

Bourne, D., Iida, Y., Uthicke, S., Smith-Keune, C., 2008. Changes in coral-associated microbial communities during a bleaching event. ISME J. 2 (4), 350–363. https://doi.org/10.1038/ismej.2007.112.

Brocke, H. J., Piltz, B., Herz, N., Abed, R. M. M., Palinska, K. A., John, U., Haan, J. den, de Beer, D., & Nugues, M. M. (2018). Nitrogen fixation and diversity of benthic cyanobacterial mats on coral reefs in Curaçao. Coral Reefs, 37(3), 861–874. Doi: https://doi.org/10.1007/s00338-018-1713-y.

Brocke, H.J., Polerecky, L., De Beer, Dirk., Weber, M., Claudet, J., Nugues, M.M., 2015b. Organic matter degradation drives benthic cyanobacterial mat abundance on Caribbean coral reefs. PLoS One 10 (5). https://doi.org/10.1371/journal.pone.0125445.

Brocke, H.J., Wenzhoefer, F., De Beer, D., Mueller, B., Van Duyl, F.C., Nugues, M.M., 2015a. High dissolved organic carbon release by benthic cyanobacterial mats in a Caribbean reef ecosystem. Sci. Rep. 5. https://doi.org/10.1038/srep08852.

Bruno, J.F., Sweatman, H., Precht, W.F., Selig, E.R., Schutte, V.G.W., 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 90 (6), 1478–1484. https://doi.org/10.1890/08-1781.1.

Burberg, C., Petzoldt, T., von Elert, E., 2020. Phosphate limitation increases content of protease inhibitors in the cyanobacterium Microcystis aeruginosa. Toxins 12 (1). https://doi.org/10.3390/toxins12010033.

Burke, L., Reytar, K., Spalding, M., Perry, A., 2011. Reefs at Risk Revisited. www.wri.org.

Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A., Holmes, S.P., 2016. DADA2: high-resolution sample inference from Illumina amplicon data. Nat. Methods 13 (7), 581–583. https://doi.org/10.1038/nmeth.3869.

Chagas, F.O., Hargreaves, P.I., Trindade, V.G.S., Silva, T.B.M., Ferreira, G. de A., Pestana, Y., Alves, M.A., Salomon, P.S., Bielinski, V.A., Borges, R.M., 2024. Chemical diversity of marine filamentous benthic Cyanobacteria. Phycology 4 (4), 589–604. https://doi.org/10.3390/phycology4040032.

Christianen, M.J.A., Middelburg, J.J., Holthuijsen, S.J., Jouta, J., Compton, T.J., van der Heide, T., Piersma, T., Sinninghe Damsté, J.S., van der Veer, H.W., Schouten, S.,

Olff, H., 2017. Benthic primary producers are key to sustain the Wadden Sea food web: stable carbon isotope analysis at landscape scale. Ecology 98 (6), 1498–1512. https://doi.org/10.1002/ecy.1837.
Cissell, E.C., Eckrich, C.E., McCoy, S.J., 2022. Cyanobacterial mats as benthic reservoirs and vectors for coral black band disease pathogens. Ecol. Appl. 32 (6). https://doi.org/10.1002/eap.2692.
Cissell, E.C., McCoy, S.J., 2021. Shotgun metagenomic sequencing reveals the full taxonomic, trophic, and functional diversity of a coral reef benthic cyanobacterial mat from Bonaire, Caribbean Netherlands. Sci. Total Environ. 755. https://doi.org/10.1016/j.scitotenv.2020.142719.
Cleary, D.F.R., Polónia, A.R.M., Renema, W., Hoeksema, B.W., Rachello-Dolmen, P.G., Moolenbeek, R.G., Budiyanto, A., Yahmantoro, Tuti, Y., Giyanto, Draisma, S.G.A., Prud'homme van Reine, W.F., Hariyanto, R., Gittenberger, A., Rikoh, M.S., de Voogd, N.J., 2016. Variation in the composition of corals, fishes, sponges, echinoderms, ascidians, molluscs, foraminifera and macroalgae across a pronounced in-to-offshore environmental gradient in the Jakarta Bay–Thousand Islands coral reef complex. Mar. Pollut. Bull. 110 (2), 701–717. https://doi.org/10.1016/j.marpolbul.2016.04.042.
Cohen, R.A., Fong, P., 2005. Experimental evidence supports the use of δ15N content of the opportunistic green macroalga Enteromorpha intestinalis (Chlorophyta) to determine nitrogen sources to estuaries. J. Phycol. 41 (2), 287–293. https://doi.org/10.1111/j.1529-8817.2005.04022.x.
Costanzo, S.D., Oödonohue, M.J., Dennison, W.C., Loneragaǹà, N.R., Thomas, M., 2001. A New Approach for detecting and mapping sewage impacts.
Dailer, M.L., Knox, R.S., Smith, J.E., Napier, M., Smith, C.M., 2010. Using δ15N values in algal tissue to map locations and potential sources of anthropogenic nutrient inputs on the island of Maui, Hawai'i, USA. Mar. Pollut. Bull. 60 (5), 655–671. https://doi.org/10.1016/j.marpolbul.2009.12.021.
Damar, A., Hesse, K.J., Colijn, F., Vitner, Y., 2019. The eutrophication states of the Indonesian sea large marine ecosystem: Jakarta Bay, 2001–2013. Deep-Sea Research Part II: Topical Studies in Oceanography 163, 72–86. https://doi.org/10.1016/j.dsr2.2019.05.012.
D'Angelo, C., Wiedenmann, J., 2014. Impacts of nutrient enrichment on coral reefs: new perspectives and implications for coastal management and reef survival. Curr. Opin. Environ. Sustain. 7, 82–93. https://doi.org/10.1016/j.cosust.2013.11.029.
Davis, N.M., Proctor, Di.M., Holmes, S.P., Relman, D.A., Callahan, B.J., 2018. Simple statistical identification and removal of contaminant sequences in marker-gene and metagenomics data. Microbiome 6 (1). https://doi.org/10.1186/s40168-018-0605-2.
De'ath, G., Fabricius, K., 2010. Water quality as a regional driver of coral biodiversity and macroalgae on the great barrier reef. Ecol. Appl. 20 (3), 840–850.
Draisma, S.G.A., Prud'homme van Reine, W.F., Herandarudewi, S.M.C., Hoeksema, B.W., 2018. Macroalgal diversity along an inshore-offshore environmental gradient in the Jakarta Bay – Thousand Islands reef complex, Indonesia. Estuar. Coast. Shelf Sci. 200, 258–269. https://doi.org/10.1016/j.ecss.2017.11.010.
Duprey, N.N., Yasuhara, M., Baker, D.M., 2016. Reefs of tomorrow: eutrophication reduces coral biodiversity in an urbanized seascape. Glob. Chang. Biol. 22 (11), 3550–3565. https://doi.org/10.1111/gcb.13432.
Dzwonkowski, B., Kang, X., Sahoo, B., Veeramony, J., Mitchell, S., & Xia, M. (2023). Mixing and transport in estuaries and coastal waters a special issue in estuarine coastal and shelf science. In Estuar. Coast. Shelf Sci. (Vol. vol. 288). Academic Press. Doi: https://doi.org/10.1016/j.ecss.2023.108370.
Edward, E., Kusnadi, A., 2023. Review on monitoring of water quality of the Jakarta Bay, Indonesia. E3S Web of Conferences 454. https://doi.org/10.1051/e3sconf/202345402003.
Eyre, B.D., Glud, R.N., Patten, N., 2008. Mass coral spawning: A natural large-scale nutrient addition experiment. Limnol. Oceanogr. 53 (3), 997–1013. https://doi.org/10.4319/lo.2008.53.3.0997.
Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar. Pollut. Bull. 50 (2), 125–146. https://doi.org/10.1016/j.marpolbul.2004.11.028.
Fabricius, K.E., 2011. Factors determining the resilience of coral reefs to eutrophication: A review and conceptual model. In: Coral Reefs: An Ecosystem in Transition. Springer Netherlands, pp. 493–505. https://doi.org/10.1007/978-94-007-0114-4_28.
Fabricius, K.E., De'ath, G., Humphrey, C., Zagorskis, I., Schaffelke, B., 2013. Intra-annual variation in turbidity in response to terrestrial runoff on near-shore coral reefs of the Great Barrier Reef. Estuar. Coast. Shelf Sci. 116, 57–65. https://doi.org/10.1016/j.ecss.2012.03.010.
Fernandes, M., Benger, S., Sharma, S.K., Gaylard, S., Kildea, T., Hoare, S., Braley, M., Irving, A.D., 2012. The use of δ 15 N signatures of translocated macroalgae to map coastal nutrient plumes: improving species selection and spatial analysis of metropolitan datasets. J. Environ. Monit. 14 (9), 2399–2410.
Fong, C.R., Gaynus, C.J., Carpenter, R.C., 2020. Extreme rainfall events pulse substantial nutrients and sediments from terrestrial to nearshore coastal communities: a case study from French Polynesia. Sci. Rep. 10 (1). https://doi.org/10.1038/s41598-020-59807-5.
Ford, A.K., Bejarano, S., Nugues, M.M., Visser, P.M., Albert, S., Ferse, S.C.A., 2018. Reefs under siege-the rise, putative drivers, and consequences of benthic cyanobacterial mats. Front. Mar. Sci. 5. https://doi.org/10.3389/fmars.2018.00018.
Ford, A.K., Van Hoytema, N., Moore, B.R., Pandihau, L., Wild, C., Ferse, S.C.A., 2017. High sedimentary oxygen consumption indicates that sewage input from small islands drives benthic community shifts on overfished reefs. Environ. Conserv. 44 (4), 405–411. https://doi.org/10.1017/S0376892917000054.
Ford, A.K., Visser, P.M., van Herk, M.J., Jongepier, E., Bonito, V., 2021. First insights into the impacts of benthic cyanobacterial mats on fish herbivory functions on a nearshore coral reef. Sci. Rep. 11 (1). https://doi.org/10.1038/s41598-021-84016-z.
Gartner, A., Lavery, P., Smit, A.J., 2002. Use of δ15N signatures of different functional forms of macroalgae and filter-feeders to reveal temporal and spatial patterns in sewage dispersal. Mar. Ecol. Prog. Ser. 235, 63–73.
Glasl, B., Webster, N.S., Bourne, D.G., 2017. Microbial indicators as a diagnostic tool for assessing water quality and climate stress in coral reef ecosystems. Mar. Biol. 164 (4). https://doi.org/10.1007/s00227-017-3097-x.
Gorman, D., Turra, A., Connolly, R.M., Olds, A.D., Schlacher, T.A., 2017. Monitoring nitrogen pollution in seasonally-pulsed coastal waters requires judicious choice of indicator species. Mar. Pollut. Bull. 122 (1–2), 149–155.
Greenacre, M., 2026. Annual review of statistics and its application compositional data analysis, 21, 59. https://doi.org/10.1146/annurev-statistics-042720.
Haas, A.F., Fairoz, M.F.M., Kelly, L.W., Nelson, C.E., Dinsdale, E.A., Edwards, R.A., Giles, S., Hatay, M., Hisakawa, N., Knowles, B., Lim, Y.W., Maughan, H., Pantos, O., Roach, T.N.F., Sanchez, S.E., Silveira, C.B., Sandin, S., Smith, J.E., Rohwer, F., 2016. Global microbialization of coral reefs. Nat. Microbiol. 1 (6). https://doi.org/10.1038/nmicrobiol.2016.42.
Houk, P., Castro, F., McInnis, A., Rucinski, M., Starsinic, C., Concepcion, T., Manglona, S., Salas, E., 2022. Nutrient thresholds to protect water quality, coral reefs, and nearshore fisheries. Mar. Pollut. Bull. 184 (June), 114144. https://doi.org/10.1016/j.marpolbul.2022.114144.
Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., Baird, A.H., Baum, J.K., Berumen, M.L., Bridge, T.C., Claar, D.C., Eakin, C.M., Gilmour, J.P., Graham, N.A.J., Harrison, H., Hobbs, J.-P.A., Hoey, A.S., Hoogenboom, M., Lowe, R.J., Wilson, S.K., 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359 (6371), 80–83.
Hydes, D.J., Aoyama, M., Aminot, A., Bakker, K., Becker, S., Coverly, S., Daniel, A., Dickson, A.G., Grosso, O., Kerouel, R., Van Ooijen, J., Sato, K., Tanhua, T., Woodward, E.M.S., Zhang, J.Z., 2010. Determination of Dissolved Nutrients (N, P, Si) in Seawater with High Precision and Inter-Comparability Using Gas-Segmented Continuous Flow Analysers.
de Jong, C., van Os, I., Sepúlveda-Rodríguez, G., de Baat, M.L., Schoepf, V., 2025. High-resolution temporal assessment of physicochemical variability and water quality in tropical semi-enclosed bays and coral reefs. Sci. Total Environ. 968. https://doi.org/10.1016/j.scitotenv.2025.178810.
Kegler, H.F., Hassenrück, C., Kegler, P., Jennerjahn, T.C., Lukman, M., Jompa, J., Gärdes, A., 2018. Small tropical islands with dense human population: differences in water quality of near-shore waters are associated with distinct bacterial communities. PeerJ 6, e4555.
Kim, B.R., Shin, J., Guevarra, R.B., Lee, J.H., Kim, D.W., Seol, K.H., Lee, J.H., Kim, H.B., Isaacson, R.E., 2017. Deciphering diversity indices for a better understanding of microbial communities. J. Microbiol. Biotechnol. 27 (12), 2089–2093. https://doi.org/10.4014/jmb.1709.09027.
Koop, K., Boothà, D., Broadbent, A., Brodie, J., Bucheràà, D., Capone, D., Coll, J., Dennison, W., Erdmannàààà, M., Harrisonàà, P., Hoegh-Guldberg, O., Hutchings, P., Jones, G.B., Larkum, A.W.D., O'neil, J., Steven, A., Tentori, E., Wardàà, S., Williamson, J., Yellowleesàààà, D., 2001. ENCORE: The Eect of Nutrient Enrichment on Coral Reefs. Synthesis of Results and Conclusions. Mar. Pollut. Bull. 42 (2).
Kubicek, A., Breckling, B., Hoegh-Guldberg, O., Reuter, H., 2019. Climate change drives trait-shifts in coral reef communities. Sci. Rep. 9 (1). https://doi.org/10.1038/s41598-019-38962-4.
Lapointe, B.E., Barile, P.J., Matzie, W.R., 2004. Anthropogenic nutrient enrichment of seagrass and coral reef communities in the lower Florida keys: discrimination of local versus regional nitrogen sources. J. Exp. Mar. Biol. Ecol. 308 (1), 23–58. https://doi.org/10.1016/j.jembe.2004.01.019.
Lapointe, B.E., Brewton, R.A., Herren, L.W., Porter, J.W., Hu, C., 2019. Nitrogen enrichment, altered stoichiometry, and coral reef decline at Looe key, Florida keys, USA: a 3-decade study. Mar. Biol. 166 (8). https://doi.org/10.1007/s00227-019-3538-9.
Le, Q.D., Haron, N.A., Tanaka, K., Ishida, A., Sano, Y., Dung, L.V., Shirai, K., 2017. Quantitative contribution of primary food sources for a mangrove food web in Setiu lagoon from east coast of peninsular Malaysia, stable isotopic (δ13C and δ15N) approach. Reg. Stud. Mar. Sci. 9, 174–179. https://doi.org/10.1016/j.rsma.2016.12.013.
Lefler, F.W., Berthold, D.E., Laughinghouse, H.D., 2023. Cyanoseq: A database of cyanobacterial 16S rRNA gene sequences with curated taxonomy. J. Phycol. 59 (3), 470–480. https://doi.org/10.1111/jpy.13335.
Lin, H., Peddada, S. Das, 2020. Analysis of microbial compositions: a review of normalization and differential abundance analysis. NPJ Biofilms Microbiomes 6 (1). https://doi.org/10.1038/s41522-020-00160-w. Nature Research.
Maslukah, L., Zainuri, M., Wirasatriya, A., Salma, U., 2019. Spatial distribution of chlorophyll-*a* and its relationship with dissolved inorganic phosphate influenced by rivers in the north coast of Java. Journal of Ecological Engineering 20 (7), 18–25. https://doi.org/10.12911/22998993/108700.
Mumby, P.J., 2009. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. Coral Reefs 28 (3), 761–773. https://doi.org/10.1007/s00338-009-0506-8.
Nearing, J.T., Douglas, G.M., Hayes, M.G., MacDonald, J., Desai, D.K., Allward, N., Jones, C.M.A., Wright, R.J., Dhanani, A.S., Comeau, A.M., Langille, M.G.I., 2022. Microbiome differential abundance methods produce different results across 38 datasets. Nat. Commun. 13 (1). https://doi.org/10.1038/s41467-022-28034-z.
Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Weedon, J., 2025. Vegan: community ecology package. CRAN. package. vegan, 10.32614.

Olorunsaye, O., Heiss, J.W., 2024. Stability of saltwater-freshwater mixing zones in beach aquifers with geologic heterogeneity. Water Resour. Res. 60 (8). https://doi.org/10.1029/2023WR036056.

Parada, A.E., Needham, D.M., Fuhrman, J.A., 2016. Every base matters: assessing small subunit rRNA primers for marine microbiomes with mock communities, time series and global field samples. Environ. Microbiol. 18 (5), 1403–1414. https://doi.org/10.1111/1462-2920.13023.

Puyana, M., Prato, J.A., Nieto, C.F., Ramos, F.A., Castellanos, L., Pinzón, P., Zárate, J.C., 2019. Experimental approaches for the evaluation of allelopathic interactions between hermatypic corals and marine benthic cyanobacteria in the colombian caribbean. Acta Biologica Colombiana 24 (2), 243–254. https://doi.org/10.15446/abc.v24n2.72706.

Reverter, M., Jackson, M., Daraghmeh, N., von Mach, C., Milton, N., 2020. 11-yr of coral community dynamics in reefs around Dahab (Gulf of Aqaba, Red Sea): the collapse of urchins and rise of macroalgae and cyanobacterial mats. Coral Reefs 39 (6), 1605–1618. https://doi.org/10.1007/s00338-020-01988-6.

Reverter, M., Jackson, M., Rohde, S., Moeller, M., Bara, R., Lasut, M.T., Segre Reinach, M., Schupp, P.J., 2021. High taxonomic resolution surveys and trait-based analyses reveal multiple benthic regimes in North Sulawesi (Indonesia). Sci. Rep. 11 (1). https://doi.org/10.1038/s41598-021-95905-8.

de V. F., Ribeiro, Caires, T.A., de A. M.A., Simões, Hargreaves, P.I., Villela, L.B., de O. G., Fistarol, Caselgrandi, A.B., Pereira-Filho, G.H., de R.L., Moura, Pereira, R.C., Salomon, P.S., 2022. Benthic Cyanobacterial Diversity and Antagonistic Interactions in Abrolhos Bank: Allelopathy, Susceptibility to Herbivory, and Toxicity. Frontiers in Marine Science 8. https://doi.org/10.3389/fmars.2021.790277.

Risk, M.J., Lapointe, B.E., Sherwood, O.A., Bedford, B.J., 2009. The use of δ15N in assessing sewage stress on coral reefs. Mar. Pollut. Bull. 58 (6), 793–802. https://doi.org/10.1016/j.marpolbul.2009.02.008.

Salo, T., Salovius-Laurén, S., 2022. Green algae as bioindicators for long-term nutrient pollution along a coastal eutrophication gradient. Ecol. Indic. 140. https://doi.org/10.1016/j.ecolind.2022.109034.

Schmid, B., Navalho, S., Schulze, P.S.C., Van De Walle, S., Van Royen, G., Schüler, L.M., Maia, I.B., Bastos, C.R.V., Baune, M.C., Januschewski, E., Coelho, A., Pereira, H., Varela, J., Navalho, J., Rodrigues, A.M.C., 2022. Drying microalgae using an industrial solar dryer: a biomass quality assessment. Foods 11 (13). https://doi.org/10.3390/foods11131873.

Silberberger, M.J., Koziorowska-Makuch, K., Kuliński, K., Kędra, M., 2021. Stable isotope mixing models are biased by the choice of sample preservation and pre-treatment: implications for studies of aquatic food webs. Front. Mar. Sci. 7. https://doi.org/10.3389/fmars.2020.621978.

Silbiger, N.J., Nelson, C.E., Remple, K., Sevilla, J.K., Quinlan, Z.A., Putnam, H.M., Fox, M.D., Donahue, M.J., 2018. Nutrient pollution disrupts key ecosystem functions on coral reefs. Proc. R. Soc. B Biol. Sci. 285 (1880). https://doi.org/10.1098/rspb.2017.2718.

Silva, A.F.R., Abreu, H., Silva, A.M.S., Cardoso, S.M., 2019. Effect of oven-drying on the recovery of valuable compounds from Ulva rigida, Gracilaria sp. and fucus vesiculosus. Mar. Drugs 17 (2). https://doi.org/10.3390/md17020090.

Skinner, C., Cobain, M.R.D., Zhu, Y., Wyatt, A.S.J., Polunin, N.V.C., 2022. Progress and direction in the use of stable isotopes to understand complex coral reef ecosystems: A review. In: Oceanography and marine biology: an annual review, volume 60. CRC press, pp. 373–432. https://doi.org/10.1201/9781003288602-8.

Stuij, T.M., Cleary, D.F.R., Gomes, N.C.M., Mehrotra, R., Visser, P.M., Speksnijder, A.G.C. L., Hoeksema, B.W., 2023. High diversity of benthic cyanobacterial mats on coral reefs of Koh Tao, Gulf of Thailand. Coral Reefs 42 (1), 77–91. https://doi.org/10.1007/s00338-022-02304-0.

Swart, P.K., Evans, S., Capo, T., Altabet, M.A., 2014. The fractionation of nitrogen and oxygen isotopes in macroalgae during the assimilation of nitrate. Biogeosciences 11 (21), 6147–6157. https://doi.org/10.5194/bg-11-6147-2014.

Teichberg, M., Wild, C., Bednarz, V.N., Kegler, H.F., Lukman, M., Gärdes, A.A., Heiden, J. P., Weiand, L., Abu, N., Nasir, A., Miñarro, S., Ferse, S.C.A., Reuter, H., Plass-Johnson, J.G., 2018. Spatio-temporal patterns in coral reef communities of the Spermonde archipelago, 2012-2014, I: comprehensive reef monitoring of water and benthic indicators reflect changes in reef health. Front. Mar. Sci. 5 (FEB). https://doi.org/10.3389/fmars.2018.00033.

Thomson-Laing, G., Puddick, J., Laroche, O., Fulton, S., Steiner, K., Heath, M.W., Wood, S.A., 2020. Broad and fine scale variability in bacterial diversity and cyanotoxin quotas in benthic cyanobacterial Mats. Front. Microbiol. 11. https://doi.org/10.3389/fmicb.2020.00129.

Tout, J., Jeffries, T.C., Webster, N.S., Stocker, R., Ralph, P.J., Seymour, J.R., 2014. Variability in microbial community composition and function between different niches within a coral reef. Microb. Ecol. 67 (3), 540–552. https://doi.org/10.1007/s00248-013-0362-5.

Trialfhianty, T.I., Quinn, C.H., Beger, M., 2025. Engaging customary law to improve the effectiveness of marine protected areas in Indonesia. Ocean Coast. Manag. 261. https://doi.org/10.1016/j.ocecoaman.2025.107543.

Tsilimigras, M.C.B., Fodor, A.A., 2016. Compositional data analysis of the microbiome: fundamentals, tools, and challenges. Ann. Epidemiol. 26 (5), 330–335. Elsevier Inc. https://doi.org/10.1016/j.annepidem.2016.03.002.

Tue, N.T., Hamaoka, H., Sogabe, A., Quy, T.D., Nhuan, M.T., Omori, K., 2012. Food sources of macro-invertebrates in an important mangrove ecosystem of Vietnam determined by dual stable isotope signatures. J. Sea Res. 72, 14–21. https://doi.org/10.1016/j.seares.2012.05.006.

Umezawa, Y., Miyajima, T., Kayanne, H., Koike, I., 2002. Significance of groundwater nitrogen discharge into coral reefs at Ishigaki island, southwest of Japan. Coral Reefs 21 (4), 346–356. https://doi.org/10.1007/s00338-002-0254-5.

Vega-Thurber, R.L., Burkepile, D.E., Fuchs, C., Shantz, A.A., Mcminds, R., Zaneveld, J.R., 2014. Chronic nutrient enrichment increases prevalence and severity of coral disease and bleaching. Glob. Chang. Biol. 20 (2), 544–554. https://doi.org/10.1111/gcb.12450.

Vesterbacka, J., Rivera, J., Noyan, K., Parera, M., Neogi, U., Calle, M., Paredes, R., Sönnerborg, A., Noguera-Julian, M., Nowak, P., 2017. Richer gut microbiota with distinct metabolic profile in HIV infected elite controllers. Sci. Rep. 7 (1), 6269.

Viana, I.G., Bode, A., 2013. Stable nitrogen isotopes in coastal macroalgae: geographic and anthropogenic variability. Sci. Total Environ. 443, 887–895. https://doi.org/10.1016/j.scitotenv.2012.11.065.

Villeneuve, A., Laurent, D., Chinain, M., Gugger, M., Humbert, J.F., 2012. Molecular characterization of the diversity and potential toxicity of cyanobacterial mats in two tropical lagoons in the south pacific ocean. J. Phycol. 48 (2), 275–284. https://doi.org/10.1111/j.1529-8817.2012.01118.x.

Williams, S.D., Klinges, J.G., Zinman, S., Clark, A.S., Bartels, E., Maurino, M.V.D., Muller, E.M., 2022. Geographically driven differences in microbiomes of *Acropora cervicornis* originating from different regions of Florida's coral reef. PeerJ 10. https://doi.org/10.7717/peerj.13574.

Win, N.N., Wai, M.K., Geraldino, P.J.L., Liao, L.M., Aye, C.T.P.P., Mar, N.N., Hanyuda, T., Kawai, H., Tokeshi, M., 2022. Taxonomy and species diversity of Padina (Dictyotales, Phaeophyceae) from the indo-Pacific with the description of two new species. Eur. J. Phycol. 57 (1), 1–17. https://doi.org/10.1080/09670262.2021.1883742.

Wooldridge, S.A., 2020. Excess seawater nutrients, enlarged algal symbiont densities and bleaching sensitive reef locations: 1. Identifying thresholds of concern for the great barrier reef, Australia. Mar. Pollut. Bull. 152, 107667.

USAID SEA Project, 2018. USAID SEA Project Site Profile: Lease Islands-Central Maluku Usaid Sustainable Ecosystems Advanced (Usaid SEA) Project: Lease Islands-Central Maluku.

van der Wulp, S.A., Damar, A., Ladwig, N., Hesse, K.J., 2016. Numerical simulations of river discharges, nutrient flux and nutrient dispersal in Jakarta Bay, Indonesia. Mar. Pollut. Bull. 110 (2), 675–685. https://doi.org/10.1016/j.marpolbul.2016.05.015.

Yin, H., Bao, Y., Huang, T., Zhang, Y., Sun, T., Tao, P., Sun, Q., Chen, K., 2025. Effects of cyanobacterial growth and decline on dissolved organic matter and endogenous nutrients release at the sediment–water interface. Carbon Res. 4 (1). https://doi.org/10.1007/s44246-025-00203-x.

Zaneveld, J.R., Burkepile, D.E., Shantz, A.A., Pritchard, C.E., McMinds, R., Payet, J.P., Welsh, R., Correa, A.M.S., Lemoine, N.P., Rosales, S., Fuchs, C., Maynard, J.A., Thurber, R.V., 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nat. Commun. 7. https://doi.org/10.1038/ncomms11833.