

Morphological variability of *Pocillopora damicornis* in marine environmental adaptation on Sembilan Islands, Sinjai District, Indonesia

RIDHA ALAMSYAH^{1,2,✉}, NEVIATY P. ZAMANI^{2,3,✉}, DIETRIECH G. BENGEN², I WAYAN NURJAYA²

¹Department of Aquatic Resources Management, Faculty of Agriculture, Universitas Muhammadiyah Sinjai. Jl. Teuku Umar No. 8, Sinjai 92611, South Sulawesi, Indonesia

²Department of Marine Science and Technology, Faculty of Fisheries and Marine Sciences, Institut Pertanian Bogor. Jl. Raya Dramaga, Bogor 16680, West Java, Indonesia. Tel./fax.: +62-482-22954, ✉email: ridhaalamsyah@apps.ipb.ac.id, ✉neviaty@apps.ipb.ac.id

³Center for Transdisciplinary and Sustainability Sciences, Institut Pertanian Bogor. Jl. Raya Pajajaran 27, Bogor 16127, West Java, Indonesia

Manuscript received: 19 July 2024. Revision accepted: 18 September 2024.

Abstract. Alamsyah R, Zamani NP, Bengen DG, Nurjaya IW. 2024. Morphological variability of *Pocillopora damicornis* in marine environmental adaptation on Sembilan Islands, Sinjai District, Indonesia. *Biodiversitas* 25: 3116-3124. *Pocillopora damicornis* (Linnaeus, 1758) is a coral species that is very plastic and allows it to adapt to environmental conditions. *Pocillopora* corals are important species of coral reef ecosystems, but it was not easy to interpret morphological variations and species boundaries. Morphological variation is so high that misidentification often occurs. This research aims to understand the morphological differences between apex branches, secondary branches, and primary branches at reef flat, lagoon, and reef slope sites in the waters of Sembilan Islands. The results obtained, except for corallite width, corallite spacing, branch width, branch length, branch angle, and interbranch spacing, were significantly different at the apex branch, secondary branch, and primary branch. Corallite width is larger at the apex branch, while corallite spacing is very small. The largest distance between corallites is found in the secondary branches. The highest branch width is on the primary branch. Branch width on secondary branches is more consistent. The branching angle is greater in the primary branch, especially in the reef flat and reef slope. The apex branch tends to form a smaller angle. The largest interbranch spacing was found at the apex branch for all regions. Both primary and secondary branches show small variations. The morphology of *P. damicornis* on the reef slope is more influenced by salinity and current speed. In reef flat areas, the environmental factors that most influence coral morphology are organic matter, turbidity, TSS, and light intensity, including wave height, temperature, and pH. For the lagoon area group, there is no strong influence of environmental parameters.

Keywords: Environmental, morphology, plasticity, *Pocillopora damicornis*, Sembilan Islands

INTRODUCTION

Coral reef ecosystems have the highest level of diversity on earth. Coral reefs are suitable habitats for 25% of aquatic species in the ocean. This coral diversity is concentrated in the world's coral triangle, including Indonesia, the Philippines, Malaysia, Papua New Guinea, Timor Leste, and the Solomon Islands. The Indonesian region has at least 569 coral species from 83 genera (Hadi et al. 2020). Coral reefs are complex habitats that have very high biodiversity and provide different ecosystem services (Yuanike et al. 2019; El-Naggar 2020; Wagner et al. 2020; Hafezi et al. 2021; Kartikasari et al. 2021; Insafitri et al. 2023).

High diversity requires complex specifications to differentiate one type from another; carefulness is required in identifying coral taxonomy. Coral taxonomy is the science of classifying and naming corals and is the key to understanding this extraordinary marine biodiversity (Kongjandtre et al. 2012; Huang et al. 2014, 2016; Voolstra et al. 2021; Reshma et al. 2023; Sobha et al. 2023). The classification that is commonly carried out is the traditional classification, which is based on macro and micro framework structures (Soto et al. 2018; Zhao et al. 2021; Ho et al. 2023). Coral structures will provide important

information about evolution (Quattrini et al. 2020), kinship relationships (Stolarski et al. 2021), and corals ecology (Thompson 2022). Taxonomy on macro and micro skeletal structures is an important science for understanding marine biodiversity. Traditional classification of corals helps scientists and the general public to identify coral species. The goal of studying taxonomy is to understand their family relationships and evolution and develop strategies to protect them (Bostrom-Einarsson et al. 2020; Thirukanthan et al. 2023).

Differentiating between one species and another in the field is sometimes difficult. Even the morphological forms of the same species sometimes look different due to plasticity mechanisms. Morphological plasticity is an important adaptation that allows organisms to survive in a variety of environmental conditions (Sommer 2020; Pazzaglia et al. 2021; Snell-Rood and Ehlman 2021; Jardeleza et al. 2022). Phenotypic plasticity often referred to as polyphenism, is the ability of an organism to show different phenotypes in response to environmental differences (Sommer 2020; Pfennig 2021; Sultan 2021; Million et al. 2022). Plasticity includes changes in morphology, physiology, or behavior (Tariel et al. 2020; Caspi et al. 2022). The plasticity ability of corals is very complex, but more research needs to be carried out on the

plasticity of coral morphology. Understanding phenotypic plasticity is critical for correct species identification, accurate estimates of diversity, implementation of appropriate conservation and management efforts, and providing information about the mechanisms responsible for morphological variation and its evolutionary potential (Paz-García et al. 2015).

Pocillopora, often called cauliflower coral, is a genus of hard coral that can generally be found in coral reef ecosystems throughout the world (Glynn and Ault 2000; Steinberg et al. 2024). This genus is characterized by its smooth, branching branches and branching colonies (Schmidt-Roach et al. 2014; Oury et al. 2021a). *Pocillopora* corals are a very plastic species. They can adapt to a wide range of environmental conditions. *Pocillopora*'s plasticity ability is a form of adaptation response to various environmental conditions and increases their chances of survival and reproduction. *Pocillopora* coral is an important coral species and makes a major contribution to the coral reef ecosystem. They prepare habitat for other marine organisms and help protect shorelines from erosion.

Pocillopora corals illustrate how difficult it is to interpret morphological variation and species boundaries. Identification of species belonging to this genus is mainly based on the morphology of the colony skeleton, the shape and size of branches and verrucae, and the characteristics of the corallites (Glynn et al. 2017; Soto et al. 2018; Oury et al. 2023). Studies on the morphological plasticity of corals, especially *Pocillopora damicornis* (Linnaeus, 1758), still need to be carried out in order to understand their morphological characteristics. Misidentification and neglect of species complexes, which have been widely

practiced so far, have many had many consequences. Bias towards assessing biodiversity and connectivity. This results in a misunderstanding of ecosystems and impacts on the design and management of effective conservation plans in the future (Oury et al. 2021b).

MATERIALS AND METHODS

Study area

Sampling was carried out in the waters of Sembilan Islands, which is located in Bone Bay. *Pocillopora damicornis* was chosen because it has a wide distribution throughout the Sembilan Islands area. This island is a group of very small islands consisting of nine islands located in a semicircle; sampling was carried out in areas representing each site. The site consists of a reef flat, a lagoon, and a reef slope. The research location is shown in Figure 1.

Coral skeleton sampling

The skeletal morphology of *P. damicornis* on Sembilan Islands was characterized by examining differences in reef flat, lagoon, and reef slope sites. Coral fragments are collected by diving to a depth of 5 to 10 m. Colonies resembling the morphology of *P. damicornis* were identified (Dai and Horng 2009). Coral fragments were collected from each location and taken to the laboratory. The framework is then marked, cleaned, bleached, rinsed, and dried for character analysis.

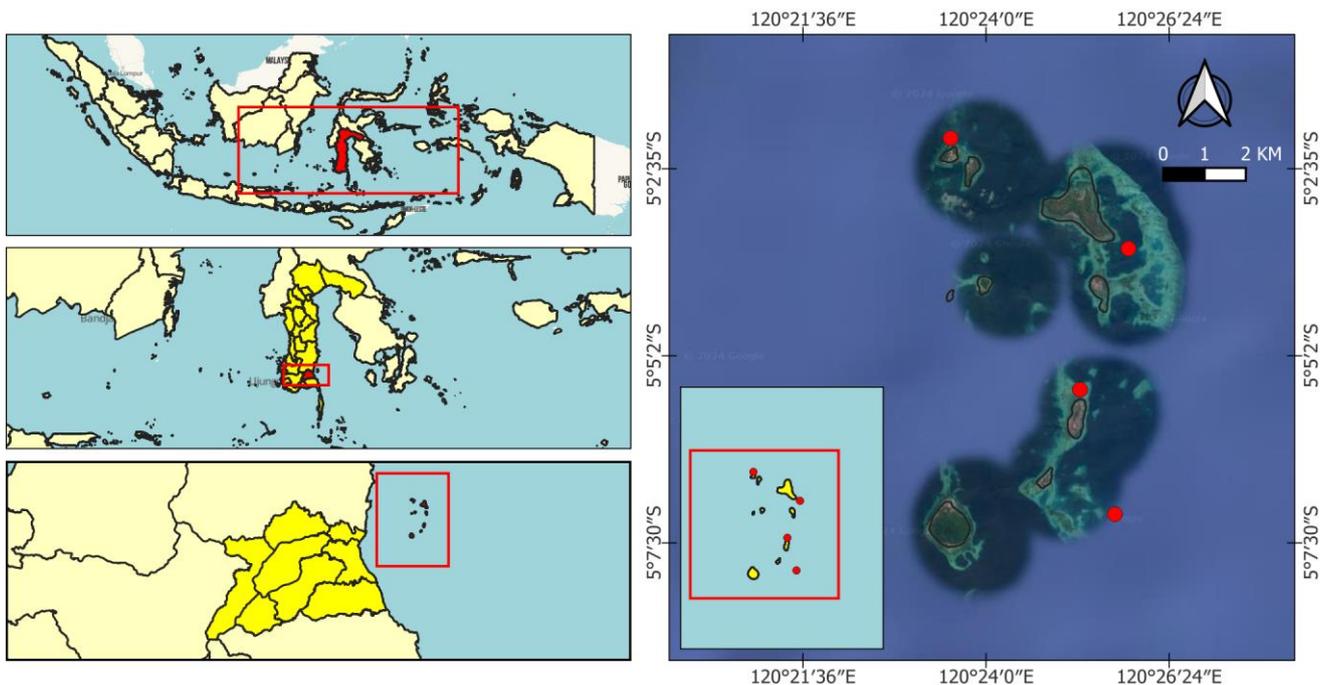


Figure 1. Location of *Pocillopora damicornis* sampling in Sembilan Islands, Sinjai, South Sulawesi, Indonesia

A total of 45 coral fragments were taken to measure their macro and micro morphological characteristics. There are 12 macro characters, while there are 6 micro characters. Each coral skeleton is divided into three parts, namely the apex branch, secondary branch, and primary branch. Macro characters consist of Apex Branch Width (ABW), Apex Branch Length (ABL), Secondary Branch Width (SBW), Secondary Branch Length (SBL), Primary Branch Width (PBW), Primary Branch Length (PBL), Apex Branch Angel (ABA), Secondary Branch Angel (SBA), Primary Branch Angel (PBA), Apex Interbranch Spacing (AIB), Secondary Interbranch Spacing (SIB), and Primary Interbranch Spacing (PIS). Micro characters Apex Branch Corallite Width (ABCW), Apex Branch Corallite Spacing (ABCS), Secondary Branch Corallite Width (SBCW), Secondary Branch Corallite Spacing (SBCS), Primary Branch Corallite Width (PBCW), and Primary Branch Corallite Spacing (PBCS). Macro character measurements use a caliper, while micro character measurements use a digital microscope. The environmental parameters measured are temperature, salinity, pH, turbidity, organic matter, TSS, light intensity, wave height, and current.

Data analysis

Differences in morphological characters of each coral group using the Kruskal-Wallis test. A comparison of the distribution range of character data for each group and site is displayed using a boxplot. Statistical tests were carried out using R version 4.3.3 and R Studio (Qian 2016). The relationship between morphological characteristics, environmental parameters, and location was evaluated using principle component analysis (Greenacre et al. 2022; Amao 2023). To ensure that the observed species is *P. damicornis*, a DNA barcoding test was carried out, which produced the results in Table 1.

RESULTS AND DISCUSSION

The morphological character of *P. damicornis* consists of macro and micro characters. The shape of the character can be seen in Figure 2. The results of the Kruskal-Wallis test show differences in character between the three sites, namely reef flat, lagoon, and reef slope. The results are shown in Table 2. Variables or characters such as corallite spacing, branch width, branch length, branch angle, and interbranch spacing show significant differences between the sections tested, with very small p-values. This indicates that the results have strong statistical significance. Meanwhile, the corallite width character did not show a significant difference (P-value = 0.1331).

Table 1. Basic Local Alignment Search Tool (BLAST) analysis result based on NCBI for species identification

Sample Id	Query cover (%)	Per. ident (%)	Species identified
1	98	100	<i>Pocillopora damicornis</i>
2	97	100	<i>Pocillopora damicornis</i>
3	100	100	<i>Pocillopora damicornis</i>
4	100	100	<i>Pocillopora damicornis</i>
5	100	100	<i>Pocillopora damicornis</i>

Table 2. Results of the Kruskal-Wallis test to test differences in branch character

Character	Chi-squared	df	P-value
Corallite width	4.0341	2	0.1331
Corallite spacing	41.775	2	0.000000008485
Branch width	34.441	2	0.00000003321
Branch length	20.075	2	0.00004373
Branch angle	32.478	2	0.0000000886
Interbranch spacing	40.026	2	0.00000002035

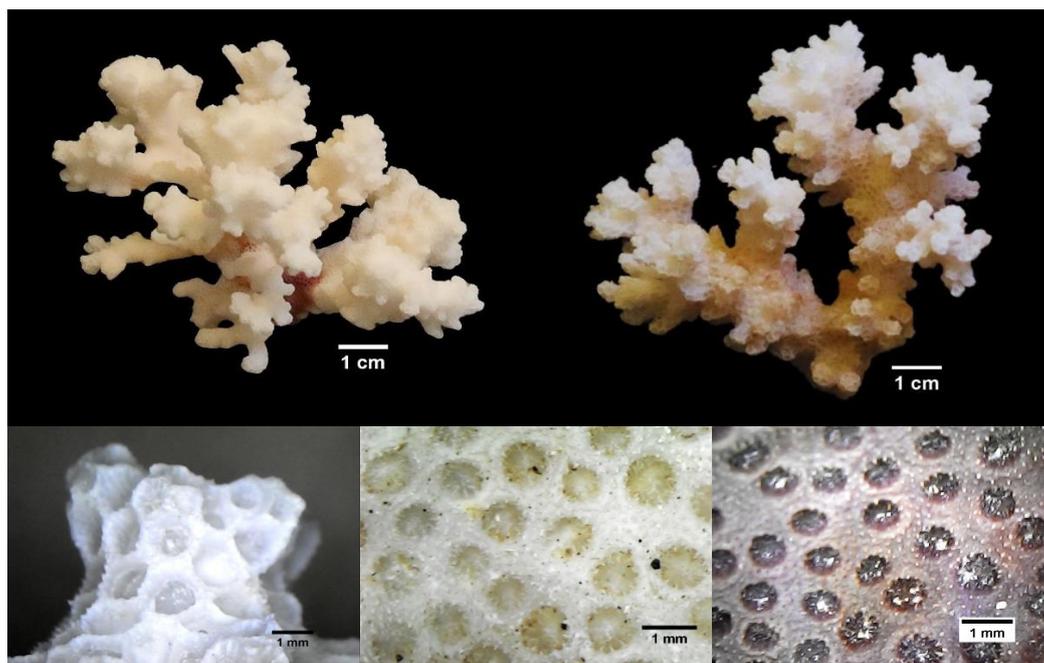


Figure 2. Macro (top) and Micro (bottom) morphological characters of *Pocillopora damicornis*

The boxplot visualization results of the distribution of *P. damicornis* characters show variability in corallite width sizes at three different sites. At the reef flat site, the corallite width (Figure 3.A) tends to be normally distributed at the apex, while the variation is high at the primary branch and secondary branch. For the lagoon site, the variability in corallite width at the apex branch and primary branch tends to be the same with a width range that is not much different. Meanwhile, for the reef slope site, the size variability at the apex branch and secondary branch tends to be the same. There are several outliers at the reef flat site, namely in the primary branch and secondary branch, which indicates that the variation in corallite width size is quite high. Likewise, at the lagoon and reefslope sites, there are outliers in the secondary branches and primary branches.

Variations in the size of corallite spacing (Figure 3.B) at three different sites show the same pattern. The smallest distance is at the apex branch, and the largest distance is at the secondary branch. At the apex branch, the corallite spacing is very low, below 0.4 mm, which indicates a large number of corallites. The corallite spacing size is highest in the secondary branch, with the highest variability at the reef flat site. The highest variability is in the secondary branch, especially at the reef flat site. Outliers were obtained at the lagoon site for the apex and primary sections and the reef slope site for the secondary branch section.

Macro characters in branch width variations (Figure 4.A) at the apex branch have higher variability; the range of branch widths at the highest reef slope location and the lowest lagoon location. Overall, the primary branch has the largest branch width. Meanwhile, branch width on secondary branches tends to be more consistent. The highest branch length (Figure 4.B) was obtained on the primary branch in the reef flat. Branch length at the reef

slope site tends to be the same for the apex, secondary, and primary branches, but the variability in the size of the branch length at the apex branch is quite high. Branch angles have the same pattern for all three sites, where the apex branch has the smallest angle range (Figure 4.C). Large angles are obtained on primary branches, especially on reef flat and reef slope sites. The largest variation in interbranch spacing was found at the apex branch for all sites (Figure 4.D). Primary branches and secondary branches show small and narrow variations in the three branch sections observed.

The results of the PCA test can be seen in Figure 5, showing that the first principal component has the largest dispersion with a high variance of 29.6%. The second principal component explained 14.3% of the variability. Although less information is described, it is important because it captures aspects of variability in the data that are not captured by the first principal component. The grouping at each site is completely separate and states the differences in character between the three; specific relationships between environmental factors and coral morphology. The Vector Variables Salinity (Sal) and Current Speed (CS) lead to the reef slope group, which explains that salinity and current variables influence coral morphology on the reef slope. This also indicates that corals on the reef slope have adapted to conditions of higher salinity and stronger currents. Variables whose vectors point towards the reef flat consist of Organic Matter (OM), Turbidity (Tur), TSS, and Light Intensity (LI). It has a positive correlation and has a greater role in influencing coral morphology at this location. Wave Height (WH), Temperature (Tem) and pH are also related to the reef flat area, but the level of correlation is low. For the lagoon site group, there is no strong influence of environmental parameters.

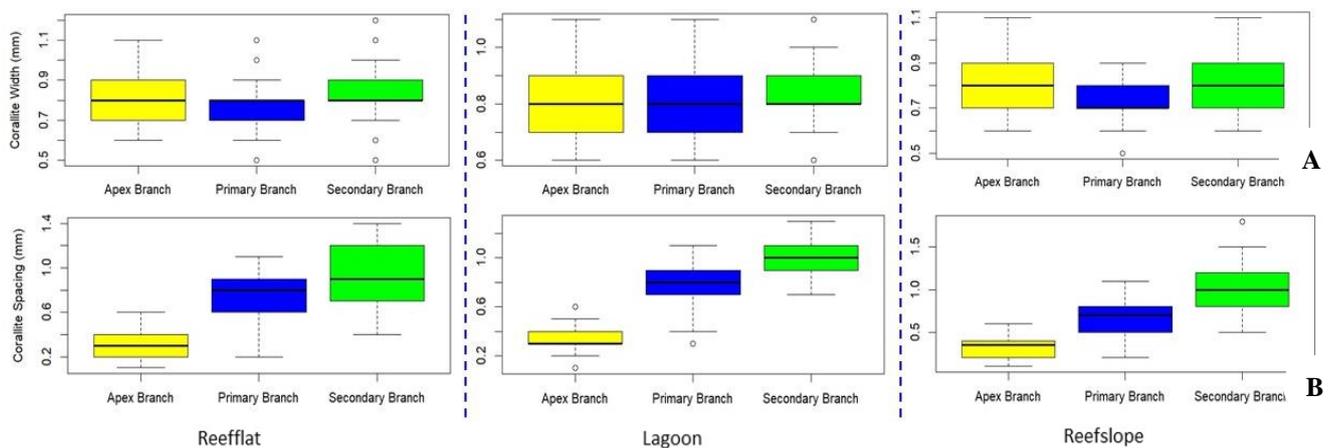


Figure 3. Microcharacter boxplot of *Pocillopora damicornis*

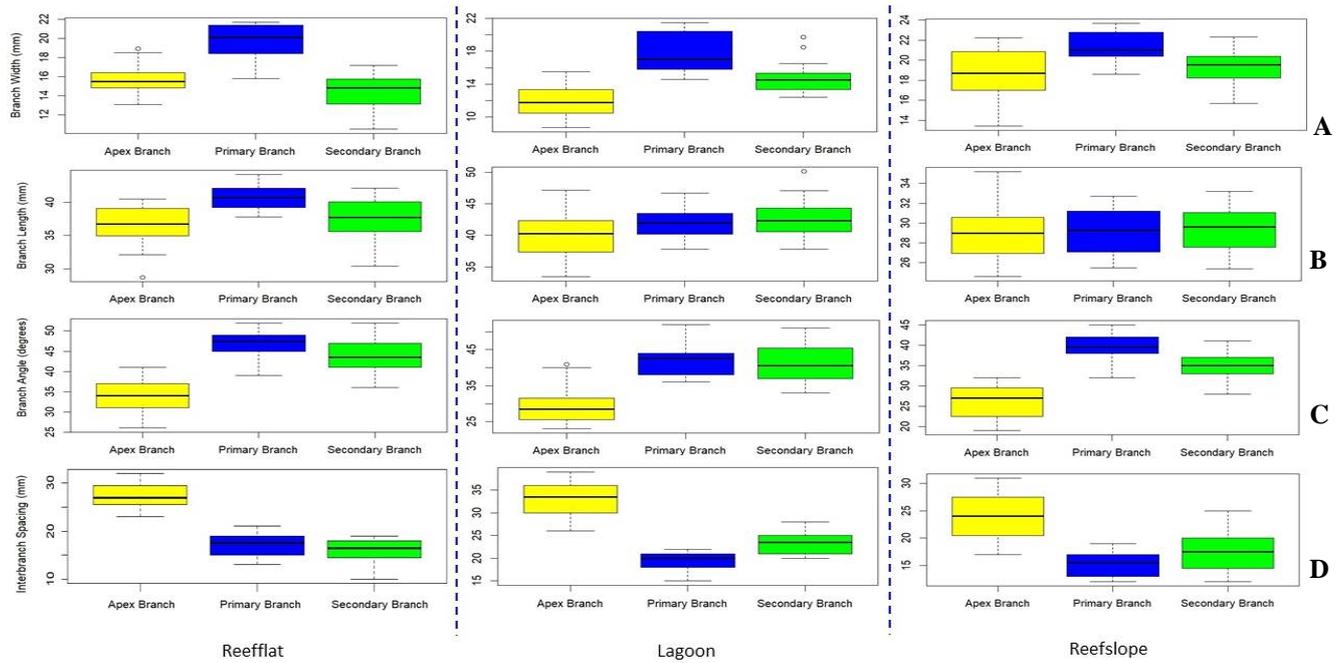


Figure 4. Macrocharacter boxplot of *Pocillopora damicornis*

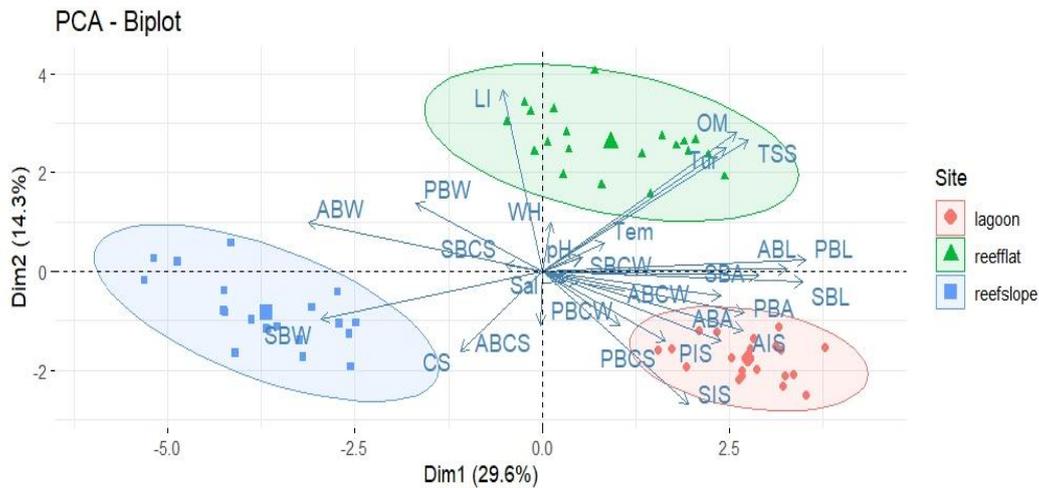


Figure 5. Main component analysis of *Pocillopora damicornis* morphological characters and environmental aspects

Discussion

Analysis of micromorphological characters in *P. damicornis* based on variable corallite width and corallite spacing provides a detailed picture of how this species adapts to different environmental factors such as reef flat, lagoon, and reef slope. The corallite width at the apex branch in reef flat areas, which tends to be greater, is an indication of adaptation to environmental conditions with high turbidity and fluctuating light intensity (Jones et al. 2021; Sheppard 2021). A large corallite width indicates that the coral polyps are also larger. This will maximize particle capture and light absorption, which is hampered in turbid water conditions (Cacciapaglia and van Woesik 2016). The very small corallite spacing on reef flats

indicates an adaptation to maximize the number of corallites. Large amounts of corallite will increase the efficiency of building coral structures in conditions that frequently experience physical disturbances such as waves and currents (Wang et al. 2019).

The high median corallite width value in the lagoon area indicates adaptation to more stable water flow and nutrient availability (Hoegh-Guldberg et al. 2017). Larger corallite spacing in secondary branches is a response to the need for more efficient water exchange or to reduce competition between coral polyps. In the reef slope area, the median corallite width is wider in the secondary branch compared to the apex and primary branches. This condition shows adaptation to an environment with stronger currents

and more consistent light availability (Kahng et al. 2019). Greater corallite spacing on a secondary branch on the reef slope also reflects an adaptation strategy to current and nutrient fluctuations (Howells et al. 2016).

The variability seen in each location illustrates the complexity of the morphological adaptation of *P. damicornis* to different local conditions. This diverse corallite morphology provides important knowledge about coral survival strategies that are closely related to environmental conditions (Hoegh-Guldberg 2014). There is natural selection that continues to encourage the diversification of corallite morphological forms in response to environmental variations in coral habitats (Dishon et al. 2020; Roff 2021).

Branch width in macro morphological characters is higher at the branch apex. Branch structure compaction occurs, where the growth in coral branch width is the result of various interrelated factors in a complex marine ecosystem. The growth of different coral branch widths is related to the interaction of several ecological and biological factors (Drury et al. 2017). However, it is the ideal environmental conditions that play a pivotal role in supporting growth, including branch width. Optimal water temperature, sufficient sunlight, and suitable currents are crucial factors (Xu et al. 2020; Sanna et al. 2023). Genetic variations between coral species also result in some types of coral tending to grow wider than others (Drury et al. 2017; Prada and Hellberg 2021; Million et al. 2022). The highest primary branch width throughout the coral indicates the need to support larger and heavier coral structures. This is done as a form of adaptation to greater physical disturbances.

The existence of a more consistent branch width in secondary branches reflects a balance between structural strength and hydrodynamic adaptation to currents. Large branches function to withstand physical stress without experiencing significant damage. The highest branch length on primary branches in reef flats is related to the need to reach upwards to get maximum light or to spread polyps to capture nutrients in high turbidity conditions efficiently.

Branching angles tend to be larger on primary branches, especially on reef flats and reef slopes. The main factors contributing to this phenomenon include defense mechanisms against physical disturbances such as waves and currents (Reidenbach et al. 2021; Sheppard 2021; Ghiasian 2022). Polyps require more surface space for photosynthetic activity particle capture in environments with limited light or higher competition. Larger branching angles provide the structural stability necessary to support coral vertical and horizontal growth (Mistr and Bercovici 2003). This adaptability illustrates the evolutionary tendency of *Pocillopora* in response to environmental pressure and competition in marine habitats. Wider branches can also increase coral resistance to stronger currents or other mechanical disturbances. Branching at the apex branch tends to form smaller angles with a more compact and aerodynamic coral structure, reducing resistance to currents and hydrodynamic pressure. This facilitates vertical growth in an effort to maximize light capture.

The greatest interbranch spacing variability was found at the apex branch at all locations. This is indicative of high phenotypic plasticity in response to local variability of environmental conditions. Primary and secondary branches show smaller and narrower variations, indicating that environmental conditions at the depths where they are located are more stable or less fluctuating. These overall patterns represent complex morphological adaptations, which refer to the physical changes in an organism's structure or form in response to its environment, and are related to environmental factors such as light, currents, and turbidity (Putnam et al. 2016; Kahng et al. 2019; Morgan et al. 2020). Considering these environmental factors is critical to understanding coral ecology and morphological evolution. More focused studies on the relationship between morphology and environmental conditions could provide further insight into coral adaptation processes in different ecosystems.

The distribution of groups of PCA test results at each reef flat, lagoon, and reef slope site shows grouping based on the characteristics of each site. The reef flat group (green) tends to be clustered and separated from the lagoon group (red) and reef slope group (blue). These separate groupings indicate significant differences in biological conditions or composition between the three sites. This could indicate that there are location-specific factors that have a strong influence on the measured parameters.

Organic Matter (OM), Total Suspended Solid (TSS), Turbidity (Tur), and Light Intensity (LI) have long and unidirectional vectors. This condition shows that the four environmental variables increase simultaneously and have an influence on the morphology of *P. damicornis* in reef-flat areas. High turbidity in reef flat areas is caused by the influence of waves and water activity, which stir up sand and sediment from the seabed (Macdonald 2015; Omori 2019; Jones et al. 2021). TSS tends to be high because sand and other particles are lifted from the bottom by the continuous movement of water. Organic matter also becomes highly enriched by organic matter from land that is carried to the reef flat via currents or waves (Bainbridge et al. 2018; Nelson et al. 2023). The shallow depth allows sunlight to penetrate more easily, so the light intensity is high. Even though high turbidity affects the intensity of light in the water, shallow water conditions still allow light to penetrate to the bottom of the water.

The variables temperature, pH, and wave height have a relatively small influence on the PCA biplot. The direction of the vector reflects the significant relationship between these variables and the specific characteristics of the reef flat. Low water depth and high exposure to sunlight tend to have greater temperature variations compared to other areas. These higher temperatures can affect many biological processes, including the metabolism of coral organisms and the solubility of oxygen in water (Hughes et al. 2020; Szabó et al. 2020; Rädercker et al. 2021). pH is an indicator of chemical balance, which is influenced by factors such as photosynthesis, respiration, and the decomposition of organic matter (Cornwall et al. 2022; Sakin et al. 2024). Photosynthesis by zooxanthellae algae can increase pH during the day and CO₂ absorption (Raven et al. 2020;

Titlyanov and Titlyanova 2020). Conversely, high decomposition of organic matter can reduce pH due to increased carbonic acid production (Middelburg et al. 2020; Renforth and Campbell 2021; Shajedul 2023). Although the contribution of sea waves is low, it is able to increase aeration, which affects oxygenation levels and CO₂ balance, thus affecting pH (Halevy and Bachan 2017).

The interaction between temperature, pH, and wave height at reef flat sites provides important information about the physical and chemical conditions that influence coral reef ecosystems. Variations in these parameters have direct and indirect effects on species composition, coral reef health, and overall ecological dynamics. Further research into these relationships could provide a better understanding of how these physical and chemical processes interact and influence marine biota.

Salinity and current speed indicate a more significant correlation with conditions found on the reef slope compared to other areas, such as lagoons or reef flats. Reef slopes are areas where there is a steeper depth gradient. This naturally allows an increase in salinity caused by the influence of more open water. The current speed in the reef slope area is also influenced by seabed topography (Johansen 2014; Wolanski et al. 2024), where steeper areas tend to experience more dynamic water movement due to the influence of waves and changes in depth (Yu et al. 2016; Zheng et al. 2024). Strong current speeds can also help maintain salinity stability by bringing in new water from the deep sea, which has a higher salt concentration.

The interaction between environmental factors is not so visible in the lagoon area. It is likely caused by ecological and geophysical factors unique to lagoons. Lagoons are generally better protected from the direct influence of waves and open ocean currents (Soria et al. 2022). Its position is located behind the main reef or due to natural barriers such as atolls or coral islands (Claudino-Sales 2019). Lagoons produce more stable environmental conditions with less intensity of change. The temperature in the lagoon is more homogeneous and does not experience extreme fluctuations (Rajput and Ramakrishnan 2021; Lacoste et al. 2023). The lagoon's pH can also be more stable due to the lack of vigorous stirring and lower wave activity, which results in a more constant chemical balance. Low waves cause less sediment stirring and a decrease in turbidity and TSS. Thus, the coral's visible morphology does not vary much compared to the reef flat and reef slope areas.

Morphological forms influenced by environmental factors in the short term are temporary responses to changes in environmental conditions. Further research is needed to understand the most influential environmental variables and genetic analysis to see if the variation is hereditary. Thus, understanding the environmental context and conducting more in-depth investigations can help determine whether morphological variation is temporary or the result of a longer evolutionary process. Collecting data from multiple locations and statistical analysis of the relationships between these factors and coral morphology allows for a better understanding of how environmental

conditions affect colony shape and health. It provides a basis for management and conservation recommendations.

Overall, it is evident that the morphological adaptation of *P. damicornis* is strongly influenced by the specific environmental conditions at each location. Variations in corallite and branch morphology reflect complex adaptive responses to factors such as turbidity, light intensity, current velocity, and nutrient availability. This deeper understanding of the relationship between coral morphology and these environmental conditions provides important insights into coral survival strategies in the face of diverse environmental stressors. Further research is needed to deepen the understanding of the interactions between these environmental factors and how they influence the evolution of coral morphology in different ecosystems.

ACKNOWLEDGEMENTS

Gratitude to the Indonesian Minister of Education, Culture, Research and Technology. Directorate of Higher Education Research and Technology for funding studies and research through the Domestic Postgraduate Education Scholarship so that this research can run and the results can be published in this Journal. Thank you to the Dean of the Faculty of Agriculture, Universitas Muhammadiyah Sinjai, Indonesia for supporting the use of equipment, and the Head of the Chemical Oceanography Laboratory of Universitas Hasanuddin, Indonesia who has provided a lot of support and assistance that this research can be completed.

REFERENCES

- Amao SR. 2023. Application of principal component analysis on the body morphometric of Nigerian indigenous chickens reared intensively under southern guinea savanna condition of Nigeria. *J Environmental Issues Agric Dev Ctries* 10 (1): 1-12.
- Bainbridge Z, Lewis S, Bartley R, Fabricius K, Collier C, Waterhouse J, Garzon-Garcia A, Robson B, Burton J, Wenger A, Brodie J. 2018. Fine sediment and particulate organic matter: A review and case study on ridge-to-reef transport, transformations, fates, and impacts on marine ecosystems. *Mar Pollut Bull* 135: 1205-1220. DOI: 10.1016/j.marpolbul.2018.08.002.
- Boström-Einarsson L, Babcock RC, Bayraktarov E, Ceccarelli D, Cook N, Ferse SC, Hancock B, Harrison P, Hein M, Shaver E, Smith A, Suggett D, Stewart-Sinclair PJ, Vardi T, McLeod IM. 2020. Coral restoration - A systematic review of current methods, successes, failures and future directions. *PLoS One* 15 (1) : e0226631. DOI: 10.1371/journal.pone.0226631.
- Cacciapaglia C, van Woesik R. 2016. Climate-change refugia: Shading reef corals by turbidity. *Glob Chang Biol* 22 (3): 1145-1154. DOI: 10.1111/gcb.13166.
- Caspi T, Johnson JR, Lambert MR, Schell CJ, Sih A. 2022. Behavioral plasticity can facilitate evolution in urban environments. *Trends Ecol Evol* 37 (12): 1092-1103. DOI: 10.1016/j.tree.2022.08.002.
- Claudino-Sales V. 2019. Lagoons of New Caledonia, France BT - Coastal World Heritage Sites. Springer Netherlands, Dordrecht.
- Cornwall CE, Harvey BP, Comeau S, Cornwall DL, Hall-Spencer JM, Peña V, Wada S, Porzio L. 2022. Understanding coralline algal responses to ocean acidification: Meta-analysis and synthesis. *Glob Chang Biol* 28 (2): 362-374. DOI: 10.1111/gcb.15899.
- Dai C-f, Horng S. 2009. Scleractinia fauna of Taiwan. II. The Robust Group. National Taiwan University, Taipei.
- Dishon G, Grossowicz M, Krom M, Guy G, Gruber DF, Tchernov D. 2020. Evolutionary traits that enable scleractinian corals to survive

- mass extinction events. *Sci Rep* 10: 3903. DOI: 10.1038/s41598-020-60605-2.
- Drury C, Manzello D, Lirman D. 2017. Genotype and local environment dynamically influence growth, disturbance response and survivorship in the threatened coral, *Acropora cervicornis*. *PLoS One* 12 (3): e0174000. DOI: 10.1371/journal.pone.0174000.
- El-Naggar HA. 2020. Human Impacts on Coral Reef Ecosystem. In: Edward R (eds.). *Natural Resources Management and Biological Sciences*. IntechOpen, London. DOI: 10.5772/intechopen.88841.
- Glynn PW, Manzello DP, Enochs IC. 2017. Coral Reefs of the Eastern Tropical Pacific: Persistence and Loss in a Dynamic Environment. Springer Nature, Miami. DOI: 10.1007/978-94-017-7499-4.
- Ghiasian SMR. 2022. Structural Morphogenesis of Green/Gray Coastal Infrastructure: Paradigms for Shoreline Protection. [Dissertation]. University of Miami, Coral Gables.
- Glynn PW, Ault JS. 2000. A biogeographic analysis and review of the far eastern Pacific coral reef region. *Coral Reefs* 19: 1-23. DOI: 10.1007/s003380050220.
- Greenacre M, Groenen PJF, Hastie T, D'Enza AI, Markos A, Tuzhilina E. 2022. Principal component analysis. *Nat Rev Methods Primers* 2: 100. DOI: 10.1038/s43586-022-00184-w.
- Hadi Ta, Muhammad A, Giyanto, Prayudha B, Johan O, Budiyo A, Rezza A, Alifatri LO, Sulha S, Shar Ss. 2020. The Status of Indonesian Coral Reefs 2019. Research Center for Oceanography-Indonesian Institute of Sciences, Jakarta.
- Hafezi M, Stewart RA, Sahin O, Giffin AL, Mackey B. 2021. Evaluating coral reef ecosystem services outcomes from climate change adaptation strategies using integrative system dynamics. *J Environ Manag* 285: 112082. DOI: 10.1016/j.jenvman.2021.112082.
- Halevy I, Bachan A. 2017. The geologic history of seawater pH. *Science* 355 (6329): 1069-1071. DOI: 10.1126/science.aal4151.
- Ho M, Idujuni S, Payne JL, Koeshidayatullah A. 2023. Hierarchical multi-label taxonomic classification of carbonate skeletal grains with deep learning. *Sediment Geol* 443: 106298. DOI: 10.1016/j.sedgeo.2022.106298.
- Hoegh-Guldberg O. 2014. Coral reef sustainability through adaptation: Glimmer of hope or persistent mirage? *Curr Opin Environ Sustain* 7: 127-133. DOI: 10.1016/j.cosust.2014.01.005.
- Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S. 2017. Coral reef ecosystems under climate change and ocean acidification. *Front Mar Sci* 4: 158. DOI: 10.3389/fmars.2017.00158.
- Howells EJ, Abrego D, Meyer E, Kirk NL, Burt JA. 2016. Host adaptation and unexpected symbiont partners enable reef-building corals to tolerate extreme temperatures. *Glob Chang Biol* 22 (8): 2702-2714. DOI: 10.1111/gcb.13250.
- Huang D, Benzoni F, Fukami H, Knowlton N, Smith ND, Budd AF. 2014. Taxonomic classification of the reef coral families Merulinidae, Montastraeidae, and Diploastraeidae (Cnidaria: Anthozoa: Scleractinia). *Zool J Linn Soc* 171 (2): 277-355. DOI: 10.1111/zooj.12140.
- Hughes DJ, Alderdice R, Cooney C, Kühl M, Pernice M, Voolstra CR, Suggett DJ. 2020. Coral reef survival under accelerating ocean deoxygenation. *Nat Clim Change* 10: 296-307. DOI: 10.1038/s41558-020-0737-9.
- Insafitri I, Nursalim N, Kholilah N, Kurniasih EM, Cahyani NK, Nugraha WA, Ambariyanto A. 2023. DNA barcode of seven species coral from Sepulu, Madura Island, Indonesia. *Biodiversitas* 24 (1): 317-323. DOI: 10.13057/biodiv/d240138.
- Jardeleza MK, Koch JB, Pearse IS, Ghalambor CK, Hufbauer RA. 2022. The roles of phenotypic plasticity and adaptation in morphology and performance of an invasive species in a novel environment. *Ecol Entomol* 47 (1): 25-37. DOI: 10.1111/een.13087.
- Johansen JL. 2014. Quantifying water flow within aquatic ecosystems using load cell sensors: A profile of currents experienced by coral reef organisms around Lizard Island, Great Barrier Reef, Australia. *PLoS One* 9 (1): e83240. DOI: 10.1371/journal.pone.0083240.
- Jones R, Pineda MC, Luter HM, Fisher R, Francis D, Klonowski W, Slivkoff M. 2021. Underwater light characteristics of turbid coral reefs of the inner central great barrier reef. *Front Mar Sci* 8: 727206. DOI: 10.3389/fmars.2021.727206.
- Kahng SE, Akkaynak D, Shlesinger T, Hochberg EJ, Wiedenmann J, Tamir R, Tchernov D. 2019. Light, Temperature, Photosynthesis, Heterotrophy, and the Lower Depth Limits of Mesophotic Coral Ecosystems. *Mesophotic Coral Ecosystems*. Springer, Cham. DOI: 10.1007/978-3-319-92735-0_42.
- Kartikasari A, Pristianto T, Hanintyo R, Ampou EE, Wibawa TA, Borneo BB. 2021. Representative benthic habitat mapping on Lovina coral reefs in Northern Bali, Indonesia. *Biodiversitas* 22 (11): 4766-4774. DOI: 10.13057/biodiv/d221108.
- Kongjandtre N, Ridgway T, Cook LG, Huelsken T, Budd AF, Hoegh-Guldberg O. 2012. Taxonomy and species boundaries in the coral genus *Favia* Milne Edwards and Haime, 1857 (Cnidaria: Scleractinia) from Thailand revealed by morphological and genetic data. *Coral Reefs* 31: 581-601. DOI: 10.1007/s00338-011-0869-5.
- Lacoste É, Jones A, Callier M, Klein J, Lagarde F, Derolez V. 2023. A review of knowledge on the impacts of multiple anthropogenic pressures on the soft-bottom benthic ecosystem in Mediterranean coastal lagoons. *Estuaries Coasts* 46: 2190-2207. DOI: 10.1007/s12237-023-01188-9.
- Macdonald RK. 2015. Turbidity and Light Attenuation in Coastal Waters of the Great Barrier Reef. [Dissertation]. James Cook University, Cairns.
- Middelburg JJ, Soetaert K, Hagens M. 2020. Ocean alkalinity, buffering and biogeochemical processes. *Rev Geophys* 58 (3): e2019RG000681. DOI: 10.1029/2019RG000681.
- Million WC, Ruggeri M, O'Donnell S, Bartels E, Conn T, Krediet CJ, Kenkel CD. 2022. Evidence for adaptive morphological plasticity in the Caribbean coral, *Acropora cervicornis*. *Proc Natl Acad Sci U S A* 119 (49): e2203925119. DOI: 10.1073/pnas.2203925119.
- Mistr S, Bercovici D. 2003. A theoretical model of pattern formation in coral reefs. *Ecosystems* 6: 61-74. DOI: 10.1007/s10021-002-0199-0.
- Morgan KM, Moynihan MA, Sanwlani N, Switzer AD. 2020. Light limitation and depth-variable sedimentation drives vertical reef compression on turbid coral reefs. *Front Mar Sci* 7: 571256. DOI: 10.3389/fmars.2020.571256.
- Nelson CE, Wegley Kelly L, Haas AF. 2023. Microbial interactions with dissolved organic matter are central to coral reef ecosystem function and resilience. *Ann Rev Mar Sci* 15: 431-460. DOI: 10.1146/annurev-marine-042121-080917.
- Omori M. 2019. Coral restoration research and technical developments: What we have learned so far. *Mar Biol Res* 15 (7): 377-409. DOI: 10.1080/17451000.2019.1662050.
- Oury N, Gélin P, Magalon H. 2021a. High connectivity within restricted distribution range in *Pocillopora* corals. *J Biogeogr* 48 (7): 1679-1692. DOI: 10.1111/jbi.14104.
- Oury N, Gélin P, Rajaonarivelo M, Magalon H. 2021b. Exploring the *Pocillopora* cryptic diversity: A new genetic lineage in the Western Indian Ocean or remnants from an ancient one? *Mar Biodivers* 52 (1): 5. DOI: 10.1007/s12526-021-01246-0.
- Oury N, Noël C, Mona S, Aurelle D, Magalon H. 2023. From genomics to integrative species delimitation? The case study of the Indo-Pacific *Pocillopora* corals. *Mol Phylogenet Evol* 184: 107803. DOI: 10.1016/j.ympev.2023.107803.
- Paz-García DA, Aldana-Moreno A, Cabral-Tena RA, García-De-León FJ, Hellberg ME, Balart EF. 2015. Morphological variation and different branch modularity across contrasting flow conditions in dominant *Pocillopora* reef-building corals. *Oecologia* 178 (1): 207-218. DOI: 10.1007/s00442-014-3199-9.
- Pazzaglia J, Reusch TBH, Terlizzi A, Marín-Guirao L, Procaccini G. 2021. Phenotypic plasticity under rapid global changes: The intrinsic force for future seagrasses survival. *Evol Appl* 14 (5): 1181-1201. DOI: 10.1111/eva.13212.
- Pfennig DW. 2021. Key Questions About Phenotypic Plasticity. CRS Press, London.
- Prada C, Hellberg ME. 2021. Speciation-by-depth on coral reefs: Sympatric divergence with gene flow or cryptic transient isolation? *J Evol Biol* 34 (1): 128-137. DOI: 10.1111/jeb.13731.
- Putnam HM, Davidson JM, Gates RD. 2016. Ocean acidification influences host DNA methylation and phenotypic plasticity in environmentally susceptible corals. *Evol Appl* 9 (9): 1165-1178. DOI: 10.1111/eva.12408.
- Qian SS. 2016. Environmental and ecological statistics with R. Chapman and Hall/CRC, New York.
- Quattrini AM, Rodríguez E, Faircloth BC, Cowman PF, Brugler MR, Farfan GA, Hellberg ME, Kitahara MV, Morrison CL, Paz-García DA, Reimer JD, McFadden CS. 2020. Palaeoclimate ocean conditions shaped the evolution of corals and their skeletons through deep time. *Nat Ecol Evol* 4 (11): 1531-1538. DOI: 10.1038/s41559-020-01291-1.
- Rådecker N, Pogoreutz C, Gegner HM, Cárdenas A, Roth F, Bougoure J, Guagliardo P, Wild C, Pernice M, Raina JB, Meibom A, Voolstra CR. 2021. Heat stress destabilizes symbiotic nutrient cycling in corals.

- Proc Natl Acad Sci U S A 118 (5): e2022653118. DOI: 10.1073/pnas.2022653118.
- Rajput P, Ramakrishnan R. 2021. Investigating the Temporal Variability of Sea Surface Temperature over the Enclosed Water Bodies of Coral Reef Lagoon at Lakshadweep Islands, India. In: 2021 IEEE International India Geoscience and Remote Sensing Symposium (InGARSS). DOI: 10.1109/InGARSS51564.2021.9791943.
- Raven JA, Gobler CJ, Hansen PJ. 2020. Dynamic CO₂ and pH levels in coastal, estuarine, and inland waters: Theoretical and observed effects on harmful algal blooms. *Harmful Algae* 91: 101594. DOI: 10.1016/j.hal.2019.03.012.
- Reidenbach MA, Stocking JB, Szczyrba L, Wendelken C. 2021. Hydrodynamic interactions with coral topography and its impact on larval settlement. *Coral Reefs* 40: 505-519. DOI: 10.1007/s00338-021-02069-y.
- Renforth P, Campbell JS. 2021. The role of soils in the regulation of ocean acidification. *Philos Trans R Soc Lond B Biol Sci* 376 (1834): 20200174. DOI: 10.1098/rstb.2020.0174.
- Reshma B, Rahul B, Sreenath KR, Joshi KK, Grinson G. 2023. Taxonomic resolution of coral image classification with convolutional neural network. *Aquat Ecol* 57: 845-861. DOI: 10.1007/s10452-022-09988-0.
- Roff G. 2021. Evolutionary history drives biogeographic patterns of coral reef resilience. *BioScience* 71 (1): 26-39. DOI: 10.1093/biosci/biaa145.
- Sakin E, Yanardağ HI, Firat Z, Çelik A, Beyyavaş V, Suat CU. 2024. Some indicators for the assessment of soil health: A mini review. *MAS J Appl Sci* 9 (2): 297-310. DOI: 10.5281/zenodo.11665000.
- Sanna G, Büscher JV, Freiwald A. 2023. Cold-water coral framework architecture is selectively shaped by bottom current flow. *Coral Reefs* 42: 483-495. DOI: 10.1007/s00338-023-02361-z.
- Schmidt-Roach S, Miller KJ, Lundgren P, Andreakis N. 2014. With eyes wide open: A revision of species within and closely related to the Pocillopora damicornis species complex (Scleractinia; Pocilloporidae) using morphology and genetics. *Zool J Linn Soc* 170 (1): 1-33. DOI: 10.1111/zoj.12092.
- Shajedul MI. 2023. Impact of global change on oceanic dissolved carbon chemistry and acidification: A Review. *J Appl Sci Environ Manag* 27 (3): 473-481. DOI: 10.4314/jasem.v27i3.10.
- Sheppard C. 2021. *Coral Reefs: A Very Short Introduction*. Oxford University Press, Jericho. DOI: 10.1093/acrade/9780199682775.001.0001.
- Snell-Rood EC, Ehlman SM. 2021. *Ecology and Evolution of Plasticity. Phenotypic Plasticity & Evolution*. CRC Press, Boca Raton. DOI: 10.1201/9780429343001-6.
- Sobha TR, Vibija CP, Fahima P. 2023. *Coral Reef: A Hot Spot of Marine Biodiversity. Conservation and sustainable utilization of bioresources*. Springer Nature, Singapore. DOI: 10.1007/978-981-19-5841-0_8.
- Sommer RJ. 2020. Phenotypic plasticity: From theory and genetics to current and future challenges. *Genetics* 215 (1): 1-13. DOI: 10.1534/genetics.120.303163.
- Soria J, Pérez R, Sòria-Pepinyà X. 2022. Mediterranean coastal lagoons review: Sites to visit before disappearance. *J Mar Sci Eng* 10 (3): 347. DOI: 10.3390/jmse10030347.
- Soto D, De Palmas S, Ho MJ, Denis V, Chen CA. 2018. Spatial variation in the morphological traits of *Pocillopora verrucosa* along a depth gradient in Taiwan. *PLoS One* 13 (8): e0202586. DOI: 10.1371/journal.pone.0202586.
- Steinberg RK, Turnbull J, Ainsworth TD, Dafforn KA, Poore AG, Johnston EL. 2024. Impacts of necrotising disease on the endangered cauliflower soft coral *Dendronephthya australis*. *Mar Freshw Res* 75 (3): 1-13. DOI: 10.1071/MF23144.
- Stolarski J, Coronado I, Murphy JG, Kitahara MV, Janiszewska K, Mazur M, Gothmann AM, Bouvier AS, Marin-Carbonne J, Taylor ML, Quattrini AM. 2021. A modern scleractinian coral with a two-component calcite-aragonite skeleton. *Proc Natl Acad Sci* 118: e2013316117. DOI: 10.1073/pnas.2013316117.
- Sultan SE. 2021. Phenotypic Plasticity As an Intrinsic Property of Organisms. In: *Phenotypic Plasticity & Evolution*. CRC Press, Boca Raton. DOI: 10.1201/97804293433001-1.
- Szabó M, Larkum AWD, Vass I. 2020. A Review: The Role of Reactive Oxygen Species in Mass Coral Bleaching. In: Larkum A, Grossman A, Raven J (eds.). *Photosynthesis in Algae: Biochemical and Physiological Mechanisms. Advances in Photosynthesis and Respiration*. Springer, Cham. DOI: 10.1007/978-3-030-33397-3_17.
- Tariel J, Plénet S, Luquet É. 2020. Transgenerational plasticity in the context of predator-prey interactions. *Front Ecol Evol* 8: 548660. DOI: 10.3389/fevo.2020.548660.
- Thirukanthan CS, Azra MN, Lananan F, Sara' G, Grinfelde I, Rudovica V, Vincevica-Gaile Z, Burlakovs J. 2023. The evolution of coral reef under changing climate: A scientometric review. *Animals (Basel)* 13 (5): 949. DOI: 10.3390/ani13050949.
- Thompson DM. 2022. Environmental records from coral skeletons: A decade of novel insights and innovation. *WIREs Climate Change* 13 (1): e745. DOI: 10.1002/wcc.745.
- Titlyanov EA, Titlyanova TV. 2020. Symbiotic relationships between microalgal zooxanthellae and reef-building coral polyps in the process of autotrophic and heterotrophic nutrition. *Russ J Mar Biol* 46: 307-318. DOI: 10.1134/S1063074020050107.
- Voolstra CR, Quigley KM, Davies SW, Parkinson JE, Peixoto RS, Aranda M, Baker AC, Barno AR, Barshis DJ, Benzoni F, Bonito V. 2021. Consensus guidelines for advancing coral holobiont genome and specimen voucher deposition. *Front Mar Sci* 8: 701784. DOI: 10.3389/fmars.2021.701784.
- Wagner D, Friedlander AM, Pyle RL, Brooks CM, Gjerde KM, Wilhelm TA. 2020. Coral reefs of the high seas: Hidden biodiversity hotspots in need of protection. *Front Mar Sci* 7: 567428. DOI: 10.3389/fmars.2020.567428.
- Wang A, Zhang Z, Liu K, Xu H, Shi L, Sun D. 2019. Coral aggregate concrete: Numerical description of physical, chemical and morphological properties of coral aggregate. *Cement Concrete Composites* 100: 25-34. DOI: 10.1016/j.cemconcomp.2019.03.016.
- Wolanski E, Kingsford M, Lambrechts J, Marmorino G. 2024. *The Physical Oceanography of the Great Barrier Reef: A Review. In: Oceanographic Processes of Coral Reefs*. CRC Press, London.
- Xu H, Feng B, Xie M, Ren Y, Xia J, Zhang Y, Wang A, Li X. 2020. Physiological characteristics and environment adaptability of reef-building corals at the Wuzhizhou Island of South China Sea. *Front Physiol* 11: 390. DOI: 10.3389/fphys.2020.00390.
- Yu X, Yang J, Graf T, Koneshloo M, O'Neal MA, Michael HA. 2016. Impact of topography on groundwater salinization due to ocean surge inundation. *Water Resour Res* 52 (8): 5794-5812. DOI: 10.1002/2016WR018814.
- Yuanike Y, Yulianda F, Bengen DG, Dahuri R, Souhoka J. 2019. A biodiversity assessment of hard corals in dive spots within Dampier Straits Marine Protected Area in Raja Ampat, West Papua, Indonesia. *Biodiversitas* 20 (4): 1198-1207. DOI: 10.13057/biodiv/d200436.
- Zhao M, Zhang H, Zhong Y, Xu X, Yan H, Li G, Yan W. 2021. Microstructural characteristics of the stony coral genus *Acropora* useful to coral reef paleoecology and modern conservation. *Ecol Evol* 11 (7): 3093-3109. DOI: 10.1002/ece3.7247.
- Zheng Y, Yang M, Liu H. 2024. Coastal groundwater dynamics with a focus on wave effects. *Earth-Sci Rev* 256: 104869. DOI: 10.1016/j.earscirev.2024.104869.