

Spatial heterogeneity of oxygen concentrations within a coral reef ecosystem

Exploring variations in dissolved oxygen concentrations between different coral morphologies, depths, and locations in a reef.

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Abstract

Rising ocean temperatures, associated with climate change, are expected to cause prolonged and extreme oxygen levels in marine environments. Despite oxygen's crucial role in coral reef ecosystems, very few reefs are monitored for oxygen, limiting our knowledge regarding in situ oxygen availability and thresholds. Here we monitor dissolved oxygen (DO) concentrations using a HOBO U26-001 logger at a coral reef in the Philippines. DO concentrations were found to vary in a reef depending on coral morphologies, depths, and location in the reef. Based on these findings, preliminary conclusions can be drawn regarding which corals and what parts of a reef are most susceptible to extreme oxygen levels. Corals located at shallow depths were more exposed to extreme oxygen levels, including both hyperoxia and hypoxia, compared to deeper corals, which may serve as refuges in the future. Table corals and corals located in the middle of a reef experience higher oxygen concentrations compared to other coral morphologies and the edge of the reef. These findings shed light on the spatial heterogeneity of oxygen concentrations in a coral reef ecosystem and can be used for developing conservation and management strategies in the face of environmental threats.

Keywords

Oxygen concentrations, coral morphology, hypoxia, hyperoxia, coral bleaching, climate change, branching coral, table coral, massive coral, coral reefs.

Popular summary

The warming of our oceans, associated with climate change, is causing oxygen levels in the ocean to decrease. Despite oxygen's crucial role in coral reefs, very few reefs are monitored for oxygen, leaving a gap in our understanding of oxygen availability in these vital habitats. To address this gap, oxygen concentrations have been monitored at a coral reef in the Philippines. The results reveal that oxygen concentrations in a reef vary between different coral morphologies, which is the physical shape and structure of a coral colony, where table corals experience higher oxygen concentrations compared to other coral morphologies. Furthermore, corals located at shallower depths were more exposed to extreme oxygen levels compared to deeper corals. Oxygen concentrations were also compared between the middle and edge of the reef, where corals in the middle experienced higher oxygen concentrations than the edge of the reef. These findings shed light on the oxygen availability in coral reefs and can be used for developing conservation and management strategies in the face of environmental threats.

Ethical and social aspects

The aim of the study was to investigate oxygen concentrations in a coral reef using a HOBO U26-001 logger. The logger was placed in the reef without harming any corals or other marine animals.

List of Abbreviations

Abbreviation	Definition
DO	Dissolved oxygen
SSTs	Sea surface temperatures
DOmax	The highest DO concentration during a day
DOmin	The lowest DO concentration during a night
DOrange	The oxygen range during a day (DOmax-DOmin)
M ± SD	Mean ± Standard Deviation
DBL	Diffusive boundary layer
S/V	Surface-to-volume ratio
PAR	Photosynthetically active radiation
ROS	Reactive oxygen species
UV	Ultraviolet

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Introduction

Tropical coral reefs have been significantly impacted by the adverse effects of climate change, undergoing profound degradation in recent decades (Keller et al., 2009; Stone et al., 1999). This damage has led to a notable decline in coral cover, ranging from 50-75% across most tropical regions (Bates et al., 2019), alongside reduced species diversity, and fish abundance (Bruno et al., 2001). Coral bleaching, recognized as the primary cause of hard coral (order Scleractinia) mortality, occurs due to various stressors such as elevated sea surface temperatures (SSTs) and solar ultraviolet (UV) radiation, triggering the expulsion of endosymbiotic algae and photosynthetic pigments within the individual zooxanthellae (Hoegh-Guldberg, 1999; Lesser, 1997). While elevated SSTs have long been identified as the primary driver of mass bleaching events, the impact of oxygen levels, both excessively high and low, is a potential significant stressor often overlooked (Altieri et al., 2017).

The concentration of dissolved oxygen (DO) has an crucial role in maintaining the function and health of coral reef ecosystems (Hughes et al., 2022). Vital ecological processes such as respiration, reproduction, productivity, and calcification are all dependent on the availability of oxygen (Nelson & Altieri, 2019). Moreover, oxygen levels have direct connections to phenomena like acidification and eutrophication (Nelson & Altieri, 2019). Oxygen production within coral reefs originates from both free-living primary producers and the endosymbiotic zooxanthellae residing within corals. This essential oxygen resource is then utilized by nearly all reef organisms, including the corals themselves (Nelson & Altieri, 2019).

Oxygen levels in the ocean are steadily decreasing, a phenomenon commonly referred to as ocean deoxygenation (Oschlies et al., 2018). Ocean warming drives ocean deoxygenation through both direct effects, such as solubility changes, and indirect impacts, including changes in circulation, mixing and oxygen respiration (Oschlies et al., 2018). Oxygen becomes less soluble in warmer water (Best et al., 2007), while marine organisms such as algae, fish, corals and microbes undergo heightened metabolic rates in response to higher temperatures, consequently leading to an increased demand for oxygen (Schulte, 2015). Additionally, higher SSTs may increase upper ocean stratification, preventing mixing and oxygenating of the bottoms (Altieri & Gedan, 2015). Coastal coral reefs are at an even greater risk of deoxygenation due to possible nutrient pollution by land-based runoff (Altieri & Gedan, 2015). Over the past few decades, large areas of the subsurface tropical oceans have experienced decreasing oxygen levels (Stramma et al., 2010). It is estimated that about 15% of all coral reefs are at an elevated risk of deoxygenation, and this figure is likely greatly underestimated (Altieri et al., 2017; Hughes et al., 2020; Johnson et al., 2021).

Tropical coral reefs experience large natural oxygen fluctuations, with high oxygen levels during the day when more oxygen is produced via photosynthesis than being consumed through respiration, and low levels at night when only respiration (oxygen consumption) is active (Nelson & Altieri, 2019). DO concentrations in a reef can range from 50% to 200% oxygen saturation corresponding to 3.4 to 13.6 mg O₂/L seawater at 27°C (Nelson & Altieri, 2019). Although corals and other reef organisms are adapted to variable oxygen levels,

conditions can become hyperoxic and hypoxic, reaching a threshold where they act as stressors and negatively impact their overall condition (Brahimi-Horn & Pouysségur, 2007; Nelson & Altieri, 2019). For instance, corals' photosynthetic and calcification rates are reduced under hyperoxic, hypoxic, or anoxic conditions (Castrillón-Cifuentes et al., 2023; Mass et al., 2010; Nelson & Altieri, 2019). Hyperoxia refers to a condition characterized by an excess of oxygen at the tissue level or within a body of water, where dissolved oxygen levels exceed 100% air saturation, corresponding to DO levels above 6.38 mg O₂/L at 27°C (Hughes et al., 2020; Nelson & Altieri, 2019). Normoxia describes the “normal oxygen conditions”, the concentration most commonly found in nature, and is typically defined as 80% - 100% oxygen saturation or 5.4 - 6.8 mg O₂/L at 27° in coral reefs (Castrillón-Cifuentes et al., 2023; Welker et al., 2013). Hypoxia is a state where the supply of oxygen at the tissue level is insufficient for normal functioning, or an environmental condition characterized by low oxygen levels in water bodies (Hughes et al., 2020). Anoxic conditions are defined as a complete lack of oxygen (Nelson & Altieri, 2019). Corals have the ability to withstand different levels of hypoxia through a combination of mechanisms, including increasing anaerobic respiration, activating transcriptional hypoxia response systems and adapted behavioral abilities (Pezner et al., 2023; Shashar et al., 1993). These adaptations involve the extension of tentacles and inflation of polyps, not only for feeding but also to reduce oxygen limitation. This extension enhances the S/V ratio and exposed surface area of their tissue, thereby promoting diffusion rates (Dodds et al., 2007; Shashar et al., 1993). However the efficacy of these strategies can vary among coral species and might not be viable under prolonged or repeated hypoxic conditions (Pezner et al., 2023). If oxygen levels reach the hypoxic or hyperoxic thresholds for an organism, it can trigger behavioral changes and reduce growth, fecundity, and survival in marine organisms (Gardella & Edmunds, 1999; Raj et al., 2020; Trowbridge et al., 2017). The specific oxygen concentrations for these thresholds varies between organisms, depending on factors such as exposure time, temperature, taxa, life stage and previous oxygen history (Hughes et al., 2020; Haas et al., 2014; Vaquer-Sunyer & Duarte, 2008, 2011). Thus, oxygen thresholds are almost entirely unknown for reef-building corals (Hughes et al., 2020).

Bleaching events do not necessarily affect all corals in a reef, and the intensity can differ spatially within and between reefs as well as between different coral taxa (Berkelmans et al., 2004; Marshall & Baird, 2000). Coral bleaching has been observed to vary at different depths, where intensity is highest at shallower depths (3-5m) and decreases with depth (Muir et al., 2017; Penin et al., 2007). A positive correlation between bleaching and coral cover has been observed, where areas with higher live coral density exhibited relatively greater bleaching regardless of depth (Muir et al., 2017). Furthermore, coral's susceptibility to bleaching has been shown to vary between different coral genera and morphologies, which is the physical shape and structure of a coral colony (Loya et al., 2001; Marshall & Baird, 2000; Ortiz et al., 2009; Stimson et al., 2002). Several studies have found that branching corals are more susceptible to bleaching and subsequent coral mortality, while massive and encrusting colonies show better resilience in mass bleaching events (Glynn, 1996; Li et al., 2008; Loya et al., 2001; Marshall & Baird, 2000; Muir et al., 2017; Nelson & Altieri, 2019; Stimson et al.,

2002). The differences in bleaching susceptibility between coral morphologies have been attributed to several factors, including growth rate (Marshall & Baird, 2000), tissue thickness (Loya et al., 2001), zooxanthellae density (Li et al., 2008), the genetic constitution of the symbiotic algae (Rowan, 2004; Stimson et al., 2002), mass transfer rate (Patterson, 1992) and surface area to volume (S/V) ratio (van Woesik et al., 2012). However, coral morphology has also been shown to have a significant impact on the magnitude of hyperoxia and hypoxia corals experience, where branching corals seem to be more sensitive compared to encrusting, massive, and table corals (Hughes et al., 2020; Nelson & Altieri, 2019). This raises the question of whether there is potential variation in DO concentrations within the microenvironment surrounding different coral morphologies, which can influence coral's susceptibility to bleaching and survival in mass bleaching events. Microenvironments refer to localized physical and chemical conditions within a specific area or niche where corals are situated and incorporate factors like water flow, light availability, nutrient concentrations, temperature, and oxygen levels. These microenvironments can vary within a reef ecosystem at small scales, creating distinct conditions that influence the physiological rates and ecological processes affecting corals and other marine organisms (Done, 2011). Understanding the connections between bleaching spatial patterns and oxygen conditions can enhance future bleaching predictions and help develop strategies to conserve and manage coral reef ecosystems.

Despite the crucial role of DO in the coral reef ecosystem, our knowledge of how extreme oxygen concentrations might pose potential threats to corals remains very limited. While marine organisms in coral reefs are adapted to large oxygen fluctuations, the influence of climate change and other anthropogenic factors may subject corals to prolonged and extreme oxygen conditions, resulting in stress and potential bleaching (Altieri et al., 2017). Few reefs are monitored for oxygen, so the knowledge regarding in situ oxygen availability and the normal range of oxygen variability at the reef scale is still limited (Nelson & Altieri, 2019). Furthermore, the relationship between oxygen concentrations, coral physiology, and oxygen thresholds has only been studied for a few species (Nelson & Altieri, 2019). Investigating how oxygen concentrations vary in a coral reef is crucial since it can be compared to the patchiness observed in bleaching events and indicate a potential causal relationship (Berkelmans et al., 2004). Understanding which corals are more susceptible to extreme oxygen levels is essential to predict how corals will respond to environmental changes and will help developing strategies to conserve and manage coral reef ecosystems. Therefore, this study aims to investigate how DO concentrations vary within a reef by answering the following research questions:

- i) Does DO concentration in the surrounding seawater of corals vary between different morphologies: branching, table, and massive?
- ii) Does DO concentrations differ between the edge and middle of a reef?
- iii) Does DO concentrations vary with depth?
- iv) What are the in-situ oxygen availability in the reef and the normal range of oxygen variability over the diurnal cycle?

In this study, it is hypothesized that the microenvironment surrounding branching corals will experience more extreme oxygen concentrations, including both hyperoxia and hypoxia, compared to table and massive corals. This is anticipated due to branching corals more complex morphological structure, which can result in reduced water flow, causing the water inside the branches to become stagnant and less oxygenated during the night. The risk of nocturnal hypoxia should be highest in regions where the net primary production (total photosynthesis minus respiration) is at its lowest. This predication suggest that such locations are predominantly situated within the middle of a reef, where respiring biomass is present in all surrounding directions. It is expected that the oxygen concentration will gradually decrease during the night, reaching its lowest point in the early morning. With regards to the variation of DO concentrations with depth, it is expected that oxygen levels will show a decline in DO concentrations with increasing depth, due to the reduction in light availability and primary production.

To the best of this authors knowledge, this is the first study to investigate potential DO concentration variability in the water surrounding different coral morphologies.

Method

Study site and field conditions

The study was conducted at the reef site *Masaplod Sur* during November and December 2022 in Dauin Municipality, Negros Oriental, Philippines (9°10'02.9" N, 123°14'45.4" E) (Fig. 1). Masaplod Sur is a marine protected area with an area of 6 ha, established in 2002 (Bianchessi & Lumbab, 2012). The site consists of a shallow fringing coral reef (0-6 m in depth) and a steep slope ranging from approximately 10m to a maximum depth of 22 m. Outside the shallow coral reef, the bottom is mainly composed of sand with some sparsely scattered coral colonies. The shallow coral reef has a history of habitat disturbance by Crown of Thorns Starfish (COTS) and is still recovering from an outbreak in 2021. Average water temperature in the shallow coral reef was $29 \pm 0.4^{\circ}\text{C}$ (range 28.2-30.1°C). The average temperature at the two deeper sites (9m and 22m) was $28.6 \pm 0.2^{\circ}\text{C}$ (range 27.7-28.9 °C).

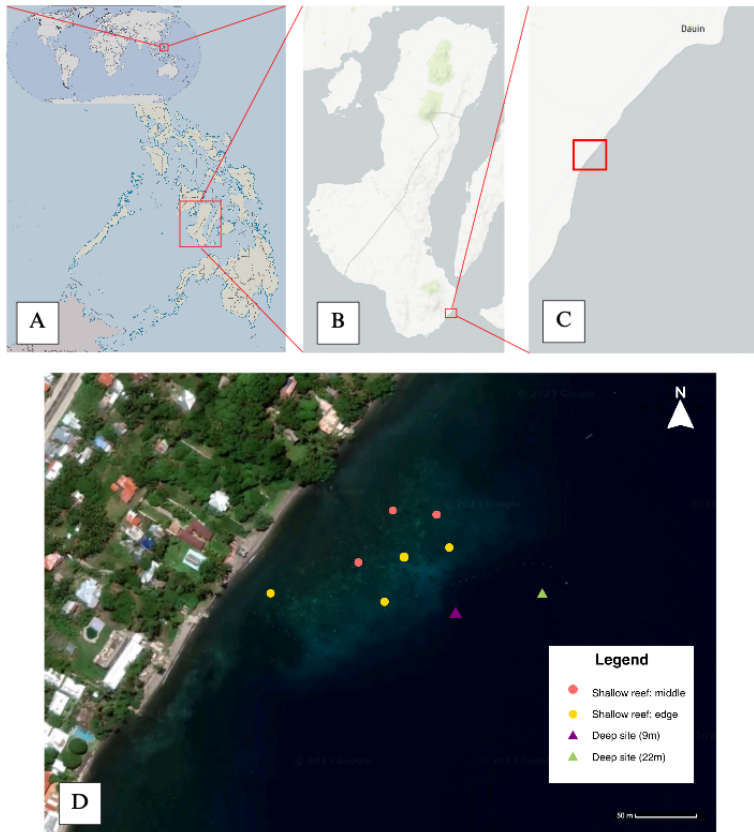


Figure 1. The study site Masaplod Sur located in the Philippines (A), Negros Oriental (B), Dauin Municipality (C). A satellite image of the reef site Masaplod Sur and the oxygen sensor deployment locations (approximately) (D). A combination of Google Images, Google Earth, and Allen Coral Atlas was used to generate the maps (A–D).

Data collection

DO concentration ($\text{mg O}_2/\text{L}$) and temperature ($^{\circ}\text{C}$) were measured *in situ* using a HOBO U26-001 oxygen logger. The logger has an optical sensor (Supplementary Fig 1), offering accuracy within 0.2 mg/L . The logger was calibrated according to manufacturer protocols, first to 100% saturation by placing it in water-saturated air, and then to 0% by placing it in sodium sulfite. An additional dissolved oxygen instrument (sensor) was utilized for comparison, confirming that the logger exhibited DO values within the expected range. DO concentrations and temperature were logged every ten minutes for the duration of the deployment. The logger was placed hidden under the corals of respective morphology and location in the reef for a minimum of three days until moved to the next location. A weight was attached to the logger to secure it from drifting away (Fig. 2).



Figure 2. The HOBO (U26-001) logger with attached weight.

Data was collected at the shallow reef (0.5-5 m in depth) for each of the three coral morphologies investigated: *branching*, *tabular* and *massive* at both reef locations investigated: *middle* and *edge* of the reef. The middle of a reef was defined as a location with high live coral cover, where corals could be found in all surrounding directions. The edge of the reef was defined as a location with relatively lower coral cover, where live corals could not be found in all surrounding directions. The logger was placed at the outer edge of the reef for all coral morphologies, towards the open ocean. Additional placement of the logger was at the inner edge of the reef, towards the shore, for a branching coral colony. The logger was placed at two deeper sites, located at 9 m and 22 m, to investigate how oxygen concentrations varied with depth. Photo documentation of all coral colonies was carried out to evaluate the genus and health status of the corals, ensuring that corals within each group belong to the same genus. Additionally, measurements were taken using transect tape to ensure that the colonies compared within each morphology exhibited similar shape and size.

Coral genus and morphologies

Massive corals were of the genus *Porites*, and branching and table corals were of the genus *Acropora*. The massive corals were boulder-shaped and of similar size, approximately 3.5 meters in diameter and 2 meters in height (Fig. 3a). The massive corals investigated in this study all suffered from Porites Ulcerative White Spot disease (PUWS) like most Porites colonies at this site (Fig. 3b). The table corals were characterized by their broad horizontal surfaces and ranged from 1-1.5 meters in diameter. The branching corals were defined by having secondary branching coming off the first branch, and since they were of the genus *Acropora*, they had an axial polyp at the tip of their branches (Fig. 4). The coral genera were selected based on their presence at the chosen site.

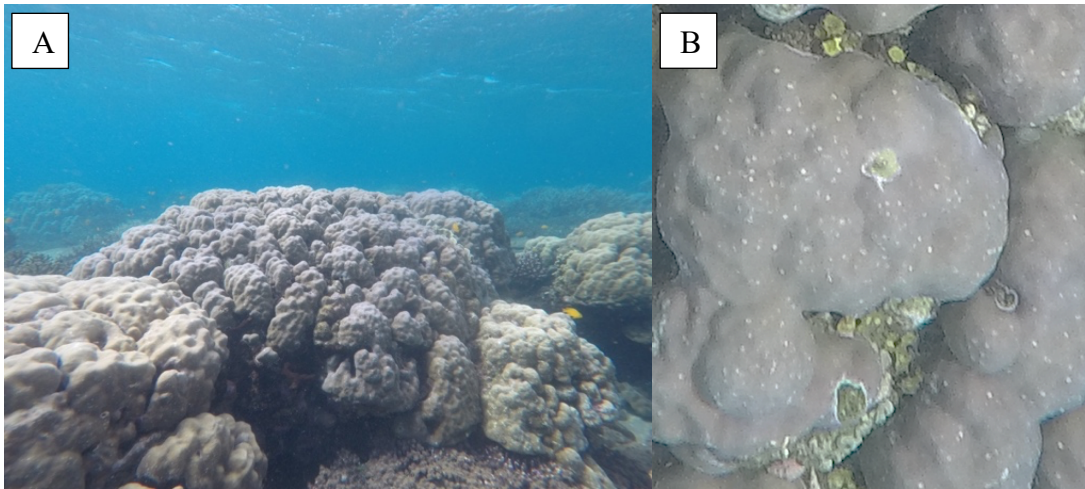


Figure 3. Massive coral of the genus *Porites* suffering from PUWS (A), which can be identified by the white spots on the coral (B).



Figure 4. The HOBO U26-001 oxygen logger deployed adjacent to branching corals of genus *Acropora*.

Oxygen thresholds

The threshold for a hypoxic marine environment is typically defined as ≤ 2 mg O₂/L, but varies based on factors such as exposure time, taxa, life stage and temperature (Johnson et al., 2021; Vaquer-Sunyer & Duarte, 2008). Lethal low oxygen threshold for reef organisms has been found to be as high as 4 mg O₂/L, and sublethal stress thresholds might be even higher for some sensitive species, especially in combination with higher water temperatures (Haas et al., 2014; Jain et al., 2023). This indicates that a hypoxic threshold of ≤ 2 mg O₂/L does not accurately reflect the range of potentially lethal and sublethal effects of low oxygen concentrations on coral reef species. Therefore, in this study four hypoxia thresholds was used to capture different levels of oxygen depletion: ‘weak hypoxia’ (4-5 mg O₂/L or 65-80% saturation), which is a conservative threshold that includes sublethal effect for the most sensitive benthic marine species (Pezner et al., 2023; Vaquer-Sunyer & Duarte, 2008), ‘mild hypoxia’ (3-4 mg O₂/L or 45-65%), ‘moderate hypoxia’ (2-3 mg O₂/L or 30-45%) and ‘severe

hypoxia' (<2 mg O₂/L or <30%). Anoxia is commonly defined as the complete absence of oxygen but is defined as ≤0.5 mg O₂/L (or ≤ 7.5%) in this study due to the uncertainty associated with the oxygen logger measurements (Jane et al., 2023).

While hyperoxia is defined as oxygen saturation levels above 100% (Hughes et al., 2020; Nelson & Altieri, 2019), hyperoxic thresholds for marine organisms generally fall within the range of 150-200% and varies with factors such as temperature, salinity, and pressure (Gardella & Edmunds, 1999; Osinga et al., 2017). There are very few studies of hyperoxia thresholds on corals (Nelson & Altieri, 2019), but the effect of hyperoxia has been shown to vary between different coral morphology and taxa (Shick, 1990), indicating that one single threshold may not capture the range of sublethal and lethal impacts of high oxygen concentrations. Thus, this study will use four thresholds for hyperoxia: 'weak hyperoxia' (105-115% saturation), 'mild hyperoxia' (115-125% saturation), moderate hyperoxia (125-150% saturation), and 'severe hyperoxia' (>150% saturation).

Data analysis

The collected data was transferred to the software HOBOWare Pro (version 3.7.25), where the DO concentration got adjusted for salinity (34 permille) and for barometric pressure (1010 mbar) to get the oxygen concentration in percent saturation. The data was exported with the following information: DO (mg/L), DO (%), temperature (°C), date, and time. Mean daily values of oxygen concentration (mg/L), oxygen saturation (%), and temperature (°C) were calculated and presented as mean ± standard deviation (M ± SD) at each reef site (Supplementary Table 1). The computation of both the highest (DO_{max}) and lowest (DO_{min}) oxygen concentrations involved the selection of the three most extreme values from each day's dataset, a process aimed at excluding potential outliers. To assess the range of oxygen fluctuations over a single day within a reef environment, a daily range (DO_{range}) was established by calculating the difference between DO_{max} and DO_{min} for each 24-hour period. Mean daily exposure time of the different oxygen thresholds for hyperoxia and hypoxia was calculated and presented as mean ± standard deviation (minutes) at each reef site (Supplementary Table 2). The daytime (6 am to 6 pm) and nighttime (6 pm to 6 am) intervals were based on the timing of the sunrise and sunset. The overall day length varied by only five minutes over the entire study length and thus did not need to be changed over time (Sunrise & Sunset Times, 2022). Weather history data were obtained from the "Time and Date" website to observe potential weather and DO concentration trends (timeanddate, 2022).

Since data was collected on different days, the oxygen saturation data (%) was used for the statistical analyses when comparing DO concentrations between different morphologies and reef sites. Oxygen saturation (%) is calculated as the percentage of DO present in the water at a given temperature and pressure relative to the maximum amount of oxygen that can be dissolved in the water at that temperature and pressure. Oxygen saturation is a normalized measure that provides a standardized comparison of DO levels regardless of water temperature.

The statistical analyses were done using DATAtab: Online Statistics Calculator (2023) and R (2021.09.1 Build 371). All variables DOmax (%), DOmin (%), and DOrange (%) were tested for significance against the parameters i) coral morphology: massive, branching and table, ii) reef locations: middle and edge, iii) and depth (shallow (0.5-5 m), deep (9 m), deep (22 m)). The three different coral morphology groups were compared against the variables using one-way analysis (ANOVA). Differences among the morphology groups were assessed with the Tukey post hoc test. The assumptions for ANOVA were tested using a Levene test of variance equality and the Shapiro-Wilk test of normality, which is preferred for small sample sizes (<50) (Mishra et al., 2019). Comparisons between the middle and edge of the reef against the variables were performed using one-sample T-test and Mann-Whitney U-Tests for the non-parametric test. DOmax (%) did not meet the assumptions of equality of variance (p-value: 0.024, Levene-test), and DOmin (%) did not meet the assumptions for normal distribution in the middle of the reef (p-value: 0.026, Shapiro-Wilk). The three depths were compared against the variables using ANOVA and the non-parametric test Kruskal Wallis Test. DOmax (%) did not meet the assumptions of equality of variance (p-value: 0.017, Levene-test), and DOmin (%) did not meet the assumptions for normal distribution at the shallow depth (p-value: 0.023, Shapiro-Wilk). Differences among the depths were assessed with the Bonferroni Post hoc test. The exposure time of the different oxygen thresholds was tested for significance against reef location (middle and edge) and coral morphology. Potential differences in exposure times between the edge and middle of the reef were tested using the non-parametric Wilcoxon Rank Sum Test. Furthermore, comparisons between the morphology groups against exposure time were performed using the non-parametric Kruskal Wallis Test.

Results

Does DO vary between the coral morphologies?

The daily oxygen maximum differed significantly between the coral morphologies (p-value: 0.035, ANOVA), where table corals experienced higher DOmax (Mean: 120.3%, Std. Deviation: 7.8%) compared to massive corals (M: 109.9%, SD: 2.8%) (p-value: 0.027, TukeyHSD) (Fig. 5). The DOmax did not differ between branching and massive corals (p-value: 0.339, TukeyHSD) or between branching and table corals (p-value: 0.26, TukeyHSD). DOmin and DOrange did not differ between the coral morphologies (p-value: 0.13, ANOVA, p-value: 0.78, ANOVA).

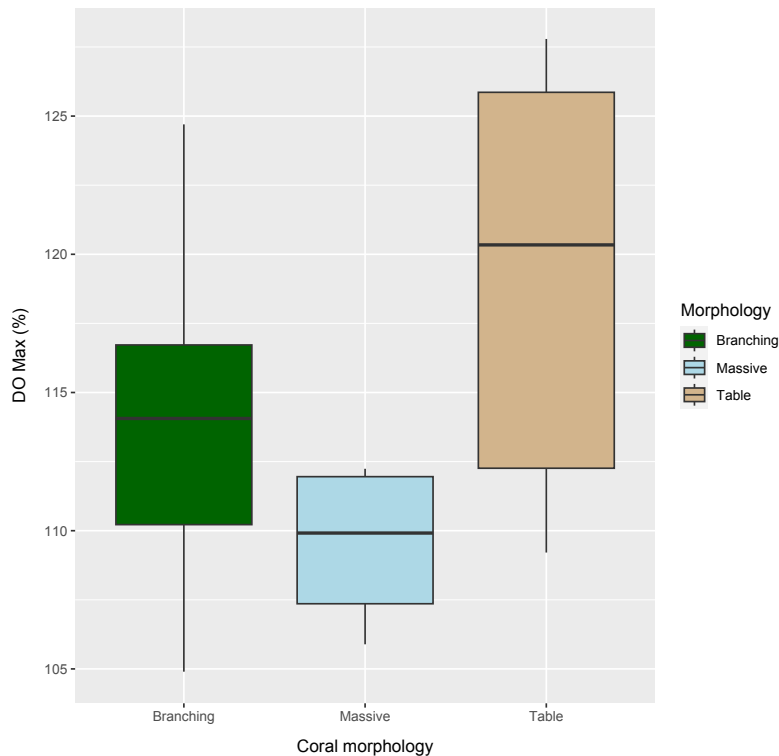


Figure 5. The daily maximum DO concentration (% oxygen saturation) for the different morphologies: branching, massive and table corals. The line inside the box shows the median, and the box itself represent the interquartile range (25th percentile - 75th percentile). The whiskers show the entire range of the data, extending from the minimum to the maximum value.

Does DO vary between the middle and edge of the reef?

The daily maximum oxygen concentration differed significantly between the edge and middle of the reef (p-value: 0.01, t-test), where the middle of the reef experienced higher DOmax (M: 117.4%, SD: 6.9%) than the edge (M: 110.3%, SD: 4.4) (Fig. 6a). DOmin did not differ between the edge and middle of the reef (p-value: 0.53, t-test). Oxygen availability in the middle of the reef ranged from 127.8% at maximum to 60.1% at a minimum oxygen saturation (Fig. 6b). Meanwhile, at the reef's edge, the range was between 116.7% and 70.3% oxygen saturation (Fig. 6b). The diel DOrange differed between the middle and edge of the reef (p-value: 0.04, t-test), where the middle of the reef experienced larger diel oxygen variations (M: 39.2%, SD: 10.1%) compared to the edge of the reef (M: 29.96%, SD: 8.77%) (Fig. 6c).

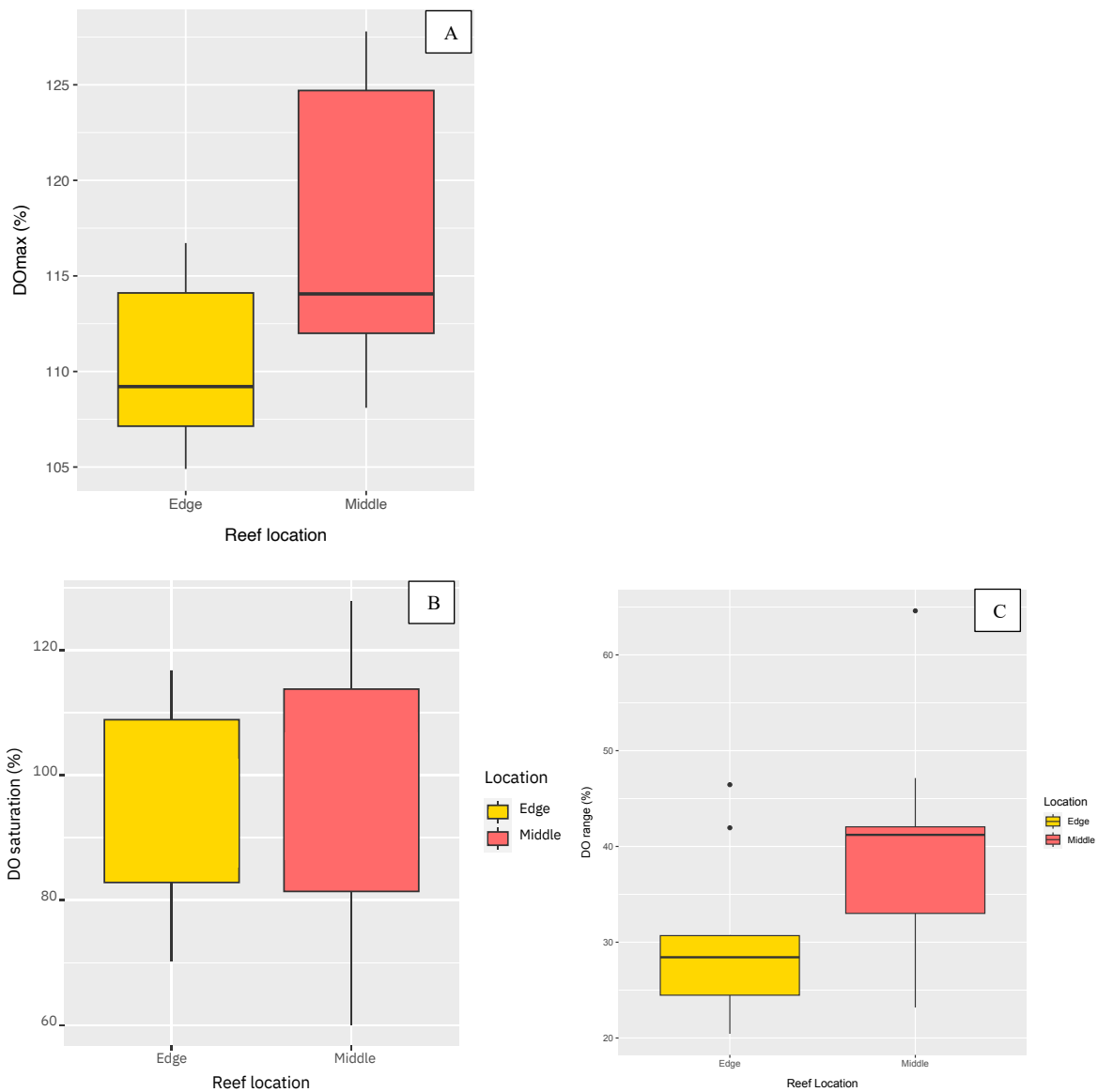


Figure 6. DOmax (% oxygen saturation) (A), oxygen availability (% oxygen saturation) (B), and DOrange (% oxygen saturation) (B) at the two reef locations: edge and middle of the reef. The line inside the box shows the median, and the box represent the interquartile range (25th percentile - 75th percentile). Outliers, points that significantly deviate to the rest of the dataset, are plotted as dots outside the whiskers.

How does oxygen vary with depth?

The daily maximum oxygen concentration varied with depth (p-value: 0.0001, Kruskal-Wallis Test), where corals at shallow depth (0.5-5 m) experienced a higher DOmax (M: 114.5%, SD: 6.9%) compared to corals at deeper depths (Fig. 7a). The DOmax was significantly lower at both 9 m (M: 102.5%, SD: 0.3%) (Adjusted p-value: 0.04, Dunn-Bonferroni-Tests) and at 22m (M: 99.7%, SD: 1%) (Adjusted p-value: 0.007, Dunn-Bonferroni-Tests). However, no significant difference in DOmax was found between the two deeper depths (Adjusted p-value: 0.3, Dunn-Bonferroni-Tests).

The oxygen availability in the shallow depths (0.5-5 m) ranged from a maximum of 127.8% to a minimum of 60.1% oxygen saturation, mirroring the previously stated values observed in the middle of the reef, as the middle reef is considered a part of the shallow reef (Fig. 7b). At the deeper depth (9 m), the oxygen availability ranged from 102.8% at maximum to 81.3% oxygen saturation at minimum (Fig. 7b). At the deepest depth (22 m), the oxygen availability ranged from 100.8% to 86.1% oxygen saturation (Fig. 7b). The diel DOrange varied with depth (p-value: 0.001, Kruskal-Wallis Test), where corals in the shallow reef experienced larger daily oxygen variations (M: 35.4%, SD: 10.46%) compared to corals at the deeper depths (Fig. 7c). The daily oxygen range was significantly lower at both 9 m (M: 19.37%, SD: 2.51%) (Adjusted p-value: 0.005, Dunn-Bonferroni-Tests) and at 22 m (M: 10.36%, SD: 2.14%) (Adjusted p-value: 0.003, Dunn-Bonferroni-Tests). However, no significant difference in DOrange was found between the two deeper depths (Adjusted p-value: 0.3, Dunn-Bonferroni-Tests).

DOmin varied with depth (p-value: 0.029, Kruskal-Wallis Test), where the shallow corals (M: 79.1%, SD: 7.4%) experienced lower oxygen concentrations during the night compared to the deepest site (22 m) (M: 89.3%, SD: 3%) (Adjusted p-value: 0.026, Dunn-Bonferroni-Tests) (Fig. 7d). No difference in DOmin was found between the two deeper depths (Adjusted p-value: 0.45, Dunn-Bonferroni-Tests) or between shallow and the depth 9 m (Adjusted p-value: 1, Dunn-Bonferroni-Tests).

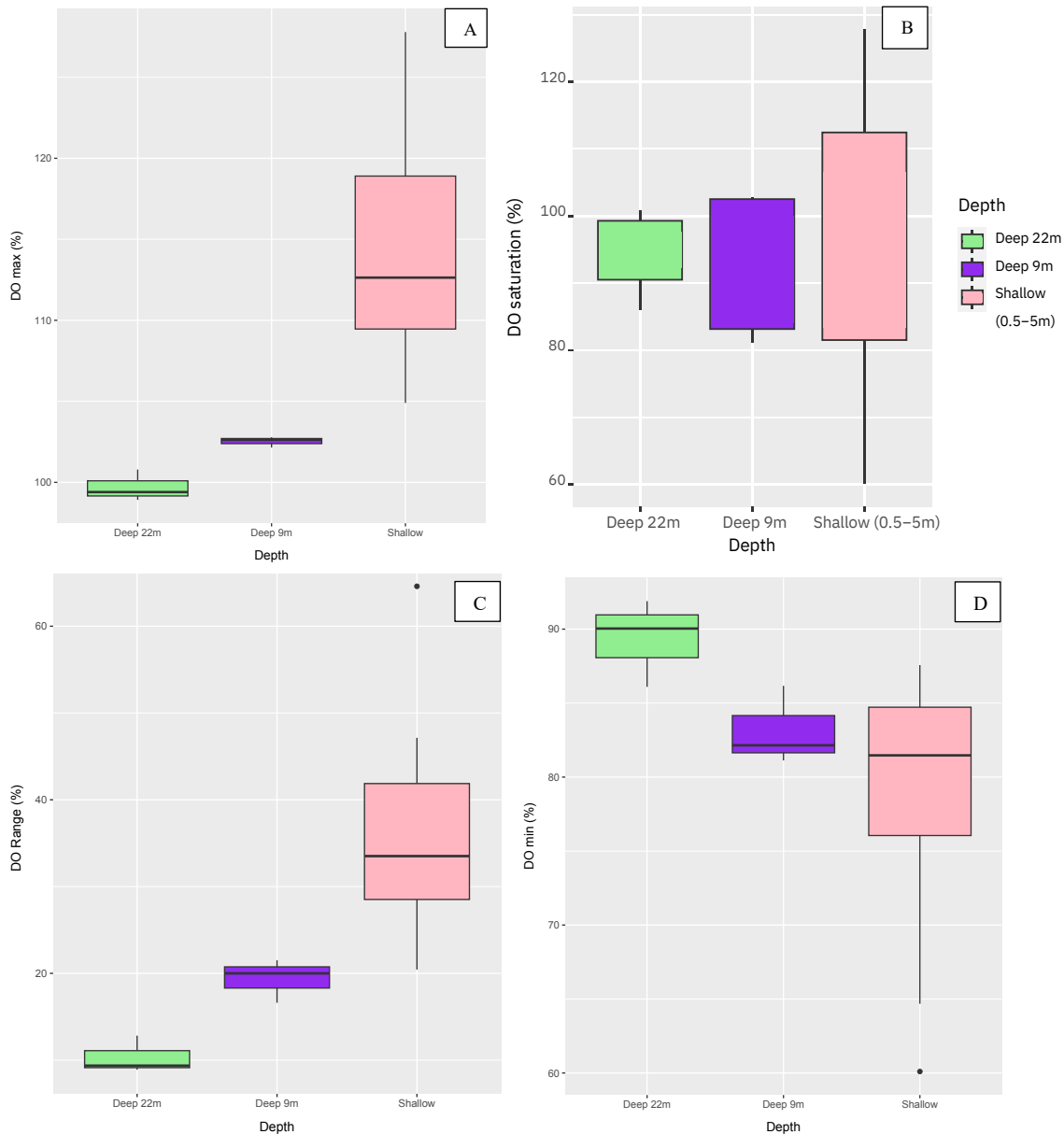


Figure 7. The daily DOmax (%) (A), oxygen availability (B), DOrange (%) (C) and DODmin (%) (D) at the different depths investigated: Shallow (0.5-5m), Deep 9m and Deep 22m.

Oxygen thresholds and exposure times

Hypoxia

According to the hypoxic thresholds set in this study, 55% of the study sites in the shallow reef experienced nocturnal oxygen deficiency. However, no hypoxia was recorded at the two deeper sites (9m and 22m) since the lowest DO concentration recorded was 5.11 mg O₂/L, which is above the highest threshold (>80%). Weak hypoxia (65-80% oxygen saturation) was recorded in both the middle and edge of the reef for branching and table corals, while massive corals only experienced weak hypoxia in the middle of the reef (Supplementary Table 2). The exposure time of weak hypoxia ranged from 0.3h to a maximum of 4.5h a night. The middle of the reef had a longer daily exposure time of weak hypoxia (M: 68, SD: 101 minutes)

compared to the edge of the reef (M: 24.2, SD: 40.3 minutes), but no significant difference was found (p-value: 0.31, Mann-Whitney U-Test). Mild hypoxia was only recorded in the middle of the reef for branching and massive corals and had an exposure time of 0.5h during a night as the longest. Moderate (30-45%) and severe (<30%) hypoxia was not recorded at any point during the study (Supplementary Table 2).

Hyperoxia

Based on the hyperoxic thresholds set, all coral morphologies experienced weak hyperoxia (105-115%) in both the middle and edge of the reef. The exposure time of weak hyperoxia ranged from 10 minutes up to 5.8h a day. Mild hyperoxia (115-125%) was recorded in branching and table coral colonies in both the edge and middle of the reef and had an exposure time of 4.2h at the longest. The exposure time of mild hyperoxia differed between reef locations (p-value: 0.029, Wilcoxon Rank Sum Test), where the middle of the reef had a higher exposure time compared to the edge (Fig. 8). Furthermore, the exposure time of mild hyperoxia also differed between coral morphologies (p-value: 0.025, Kruskal-Wallis Test), where table corals had higher exposure time compared to massive corals (Adjusted p-value: 0.02, Dunn-Bonferroni Post Hoc Test). Moderate hyperoxia (125-150%) only occurred in the middle of the reef for branching and table corals. Severe hyperoxia (>150%) was not recorded at any point during the study. No hyperoxia was recorded at the two deeper sites (9m and 22m) since the highest DO concentration recorded was 6.6 mg O₂/L (<105%).

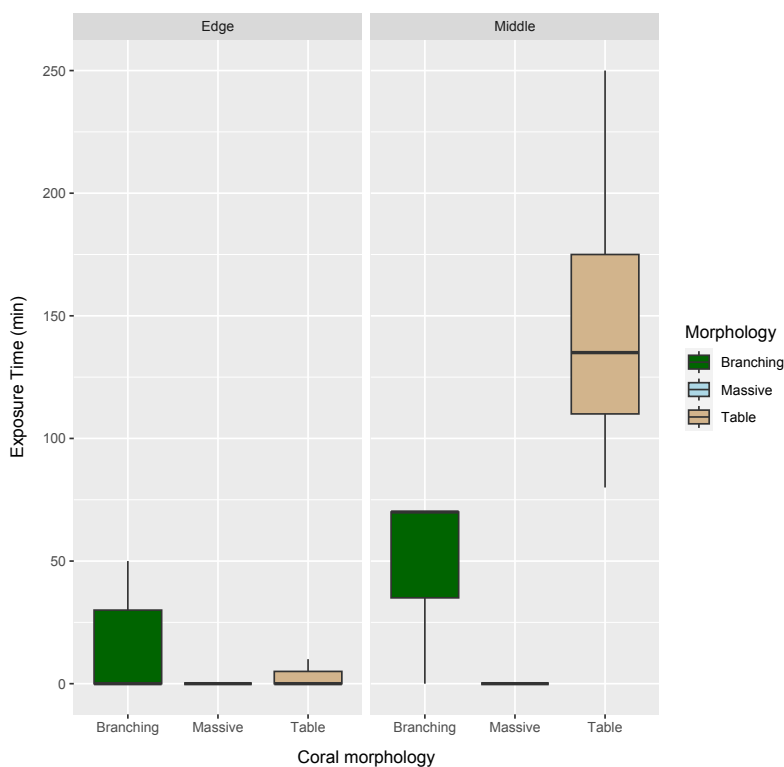


Figure 8. The daily exposure time (min) of mild hyperoxia (115-125% air saturation) at the two reef locations, middle and edge, and at the coral morphologies; branching, massive and table.

In situ oxygen availability and diel oxygen fluctuations

A wide range of oxygen conditions was observed among the different study sites, with means and extremes differing between reef locations, coral morphologies, and depths (Supplementary Table 1). Diel oxygen variability was observed at all study locations, with higher oxygen concentrations during the day and lower at night (Fig. 9 and Supplementary Figs. 2 and 3). The mean DO concentration across all sites was $97.1 \pm 8.9\%$ (6.1 ± 0.6 mg O₂/L), and the mean daily DO range was $31 \pm 12.8\%$ (1.9 ± 0.8 mg O₂/L). The smallest daily range in oxygen (8.9% or 0.56 mg O₂/L) was observed at the deepest site (22m depth), while the largest daily range (66.6% or 4.1 mg O₂/L) occurred in a branching coral colony in the middle of the shallow reef (1.8m depth) (Fig. 9 and Supplementary Fig. 3). The highest (130.3% or 8.2 mg O₂/L) and lowest (59.1% or 3.8 mg O₂/L) DO concentrations were recorded in the middle of the shallow reef. The mean oxygen maximum across all sites was $111.6 \pm 8.3\%$ (7.1 ± 0.5 mg O₂/L), and the mean oxygen minimum was $80.6 \pm 7.4\%$ (5.1 ± 0.5 mg O₂/L), with variations between the different reef sites (Figs. 6 and 7a and Supplementary Table 1). The oxygen concentrations were typically highest mid-afternoon (12:00-15:00) and lowest in the early morning (03:00-06:00) (Supplementary Figs. 4 and 5). However, oxygen concentrations did not continuously decrease but fluctuated throughout the night. The oxygen variations revealed a pattern of an initial decline in oxygen levels after sunset (around 6:00 PM), followed by a subsequent increase in oxygen saturation, often occurring around midnight, before returning to lower levels in the early morning. These oxygen variations were observed at all reef sites, but the most substantial nocturnal fluctuation occurred within the middle reef's branching coral colony, with oxygen saturation levels ascending markedly from 59% to 98% during the first night (Fig. 9). Similarly, at the reef's edge, the largest fluctuation was observed in a branching colony where the oxygen saturation increased from 69% to 96% (Supplementary Fig 2). The deeper sites also exhibited nocturnal oxygen fluctuations, although to a lesser extent, where saturation levels rose from 80% to 98% at 9 m and 88% to 99% at 22 m (Supplementary Figs. 3 & 4).

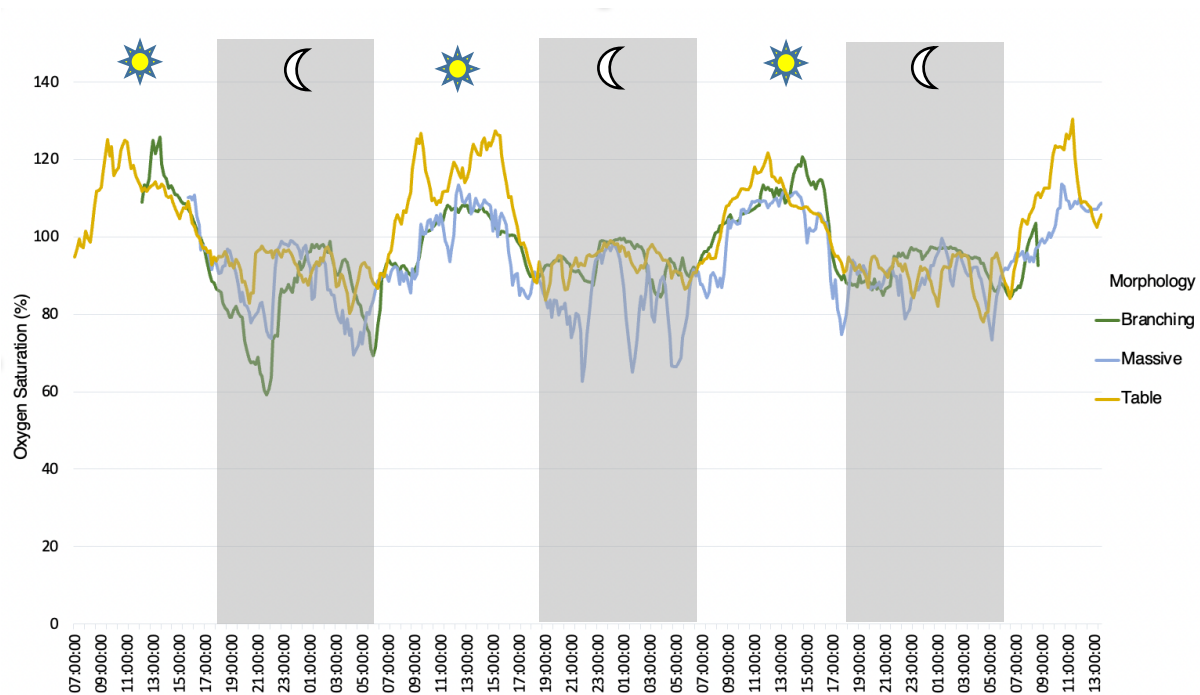


Figure 9. Diel oxygen fluctuations in the middle of the reef. Oxygen saturation (%) was measured over time (3 days) in the middle of the reef for the three different morphologies: branching, massive and table corals. The data for the different coral morphologies were all measured on different days. The sun represents the daytime intervals (6 am to 6 pm) and the shadowed areas with the moon represent the nighttime intervals (6 pm to 6 am).

Discussion

DO concentrations variations between different coral morphologies

The findings of this study indicate variations in DO concentration across the different coral morphologies. DO_{max} and the exposure time to mild hyperoxia (115-125% oxygen saturation) were significantly higher for table corals compared to massive corals. Both branching and table corals experienced weak, mild, and moderate hyperoxia, while massive corals only experienced weak hyperoxia (105-115% oxygen saturation) (Supplementary Table 2). Several factors can explain why the DO concentration in the surrounding seawater of massive corals seems to be less hyperoxic compared to other coral morphologies:

Thickness of the diffusive boundary layer

- i) Massive corals have, on average, a thicker diffusive boundary layer (DBL), which is a thin layer of stagnant water surrounding the coral colony, compared to other morphologies, such as branching corals (Shashar et al., 1993). The transfer of oxygen in and out of the coral occurs through passive diffusion, which is the process of molecules transferring from a region of higher concentration to a location of lower

concentration (Ott, 2013; Patterson et al., 1991). The DBL regulates these mass transfers between coral tissue and the surrounding seawater, and the diffusion rate is inversely proportional to the thickness of the DBL (Shashar et al., 1996). Thus, a thicker DBL results in a reduced rate of oxygen molecule diffusion from the coral to the seawater. This phenomenon could explain the relatively lower levels of measured oxygen concentrations (DO_{max}) in the surrounding seawater during daylight hours for the massive corals.

Waterflow

- ii) Branching and table corals of the genus *Acropora*, have relatively more complex morphological structures than massive *Porites* corals, which can limit the water flow, causing the water inside the spaces between branches to become stagnant (Nelson & Altieri, 2019). This can contribute to the accumulation of DO and oxygen radicals, creating potentially harmful hyperoxic conditions during the daytime (Nelson & Altieri, 2019). In contrast, massive corals with simpler and flatter morphologies experience faster waterflow, thus being less susceptible to the accumulation of DO (Nelson & Altieri, 2019; Patterson, 1992). These differences in water flow due to coral morphology have been observed to significantly affect coral health and survival in bleaching events (Loya et al., 2001; Nelson & Altieri, 2019) and could explain why branching and table corals experienced higher DO levels (DO_{max}) than massive corals during the daytime.

Surface-to-volume ratio

- iii) Table and branching corals have a higher surface-to-volume ratio (S/V) compared to massive corals, which enhances diffusion and gas exchange rates (Ong et al., 2012; Shashar et al., 1993). This includes the diffusion of carbon dioxide into the coral tissue and photosynthetically produced oxygen from the coral to the surrounding water (Osinga et al., 2017).

Thickness of coral tissue

- iv) Massive coral species have, on average, a thicker and deeper coral tissue compared to branching and table coral species, which allows for better expansion and contraction of the tissue (Loya et al., 2001). This provides tissue flexibility and the ability to self-shade against radiant energy reaching the zooxanthellae, making them less susceptible to high oxygen production and potential hyperoxia (Loya et al., 2001).

No significant differences in DO_{max}, DO_{min}, and DO_{orange} were observed between branching and table corals. The two morphology groups shared the same genus, *Acropora*, which suggests that they share similar physiological traits, which in turn can influence their oxygen demand. *Acropora* corals, known for their fast growth rate and higher metabolism, require more oxygen compared to slower-growing massive corals like *Porites*, which exhibit a lower metabolism and oxygen demand (Haas et al., 2014; Raj et al., 2020). Similar oxygen production and respiration rates due to their shared coral genus may have contributed to the similarity in DO concentrations in the surrounding seawater. Another potential factor is the

proximity of corals within the reef environment. Table and branching corals were commonly located adjacent to each other (Fig.10). This suggest that the DO measurements encompassed a blend of their combined oxygen production and respiration, making it challenging to detect any potential differences in DO concentrations. In contrast, massive corals typically grow solitary, minimizing the influence of neighbouring corals' oxygen production and respiration on the water's oxygen concentration.

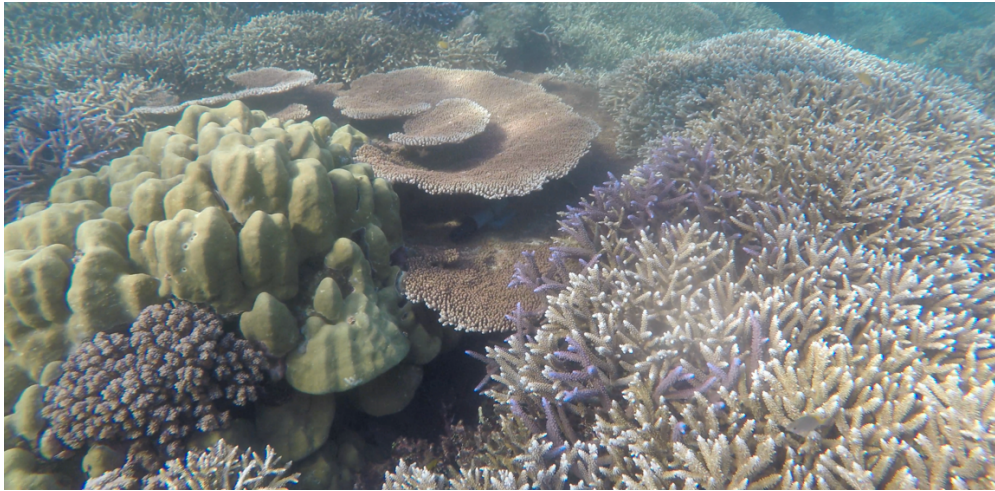


Figure 10. An image showing table and branching corals located adjacent to each other in the middle of the reef. In this image the oxygen logger is placed on the bottom shelf of the table coral and below the middle shelf, to measure the oxygen concentration for a table coral in the middle of the reef.

Moreover, the study did not find any significant disparity in DO concentrations (DO_{max}, DO_{min} and DO_{range}) between massive and branching corals, contradicting the initial hypothesis of this study. This result does not align with the factors that account for the observed variance in DO_{max} between table and massive corals (DBL thickness, water flow, mass transfer, coral tissue thickness, and S/V ratio) since these factors are also relevant to branching corals. However, several factors could potentially explain this discrepancy:

i) The study had a small sample size (<50) with high variability in some morphology groups, which may have influenced the observed result. The variability of DO_{max} was high for both branching and table corals (Fig.6), which could have affected the statistical power and reduced the possibility to detect significant differences. Branching corals (both at the edge and in the middle of the reef) had a substantially higher variance of DO_{max} within the groups compared to the two other coral morphologies (Supplementary Table 4). The variability of DO_{max} was lower for massive corals, increasing the likelihood of detecting significant differences. Furthermore, since the study's sample size was small, environmental factors such as weather are more likely to influence the result.

ii) All data was collected on different days, where environmental variability in factors such as light availability, temperature, nutrient levels, and water flow could have influenced the DO concentrations (Nelson & Altieri, 2019). Weather conditions, such as cloud coverage, could have affected the DO concentration in the reef by influencing the availability of light and radiant energy reaching the zooxanthellae (Kühl et al., 1995). During the study period, variations in cloud coverage were observed, which could have influenced the recorded

DO_{max} values. For instance, branching corals exhibited notably lower DO_{max} concentrations during days characterized by persistent cloud coverage, compared to days with clear weather (Supplementary Table 3). The timing of DO_{max} also seemed to vary in response to weather conditions. DO_{max} typically occurred mid-afternoon (12:00 -15:00), regardless of reef site, but a notable deviation was observed when DO_{max} occurred at 09:30 (Supplementary Table 3). This was the earliest recorded DO_{max} during the entire study period and occurred during a day when it was sunny in the morning and cloudy during the mid-afternoon. These results indicate that varying light availability due to cloud coverage may have influenced DO_{max} measurements. However, there are some disparate results, where despite cloud coverage on certain days, no substantial difference in DO_{max} concentration was observed compared to sunny days. This was the case for table corals, indicating that other environmental factors or physiological and morphological characteristics of different colonies influence the DO concentration. Table corals are generally found at deeper depths than other coral morphologies (Ow & Todd, 2010). Their flat, plate-like growth forms allow them to capture and utilize light more efficiently, making them well-adapted to low-light conditions (Erftemeijer et al., 2012). Table corals can sustain growth with as little as 4% of the surface light energy, while massive colonies require at least 20% and branching 60% of the surface light (Hallock, 2005). Branching coral's lower ability to capture light compared to table corals during low-light conditions (cloudy weather) could explain their higher DO_{max} variance within the groups, which could have affected the statistical power to detect significant differences. In addition to cloud coverage, other environmental factors, such as turbidity, could have impacted the light availability. Turbidity decreases the transparency of water due to the presence of suspended and dissolved substances, which reduce the photosynthetically active radiation (PAR), resulting in decreased zooxanthellae productivity (Erftemeijer et al., 2012).

To accurately assess potential differences in DO concentrations among various coral morphology structures, future studies should consider deploying multiple oxygen loggers. This approach would mitigate the impact of diverse environmental factors, thereby ensuring the reliability of the results obtained.

DO concentrations differ between the middle and edge of the reef

The middle of the reef experienced significantly higher DO_{max} and DO_{orange} than the reef's edge, which could be explained by a difference in the surrounding coral cover between the two locations. During the day, coral's zooxanthellae and other primary producers produce oxygen through photosynthesis, thus a higher coral cover should result in a higher oxygen concentration, aligning with our result. During the night, when light is absent, photosynthesis ceases while respiration continues (Nelson & Altieri, 2019). Corals need to extract oxygen from their environment as the internal oxygen supply from zooxanthellae diminishes (Al-Horani et al., 2007), and consequently, corals shift from being net oxygen producers during the day to becoming net oxygen consumers at night (Al-Horani et al., 2007). A location with higher coral cover should therefore experience larger differences in DO concentrations between day and night, which explains why the middle of the reef experience higher DO_{max} and DO_{orange} than the reef's edge.

This study hypothesized that the middle of the reef, characterized by a greater coral cover and expectedly higher respiring biomass, would exhibit lower nighttime oxygen concentrations compared to the reef's edge. Nonetheless, our study did not find any significant difference in DO_{min} between the two reef locations. This suggests the potential influence of environmental factors such as water flow patterns and tidal fluctuations on nighttime oxygen concentrations, maintaining a comparable DO_{min} between the middle and edge of the reef. Another alternative explanation could be that there exists a difference in DO_{min} between the two locations; however, due to the limited dataset, this study was unable to detect any significant differences. Notably, the lowest DO concentrations were observed in the middle of the reef, suggesting a trend of reduced DO levels in this region during the night (Supplementary Table 1).

DO vary with depth

The result from this study revealed variations in DO concentrations at different depths. The deeper sites at 9 m and 22 m experienced lower DO_{max} concentrations compared to the shallow reef. Several factors may explain this result. First, light intensity and PAR decrease with depth (Jokiel et al., 1997). This reduction in light availability can lead to lower photosynthetic rates and, consequently, reduced net oxygen production by corals located at deeper depths. Second, the density of zooxanthellae in corals has been observed to decrease with water depth (Li et al., 2008). This decrease is likely due to varying sunlight intensity and water clarity. Shallower depths benefit from greater exposure to sunlight and clearer water conditions, promoting higher zooxanthellae density and, consequently, higher net oxygen production to the surrounding seawater. Lastly, the exchange of gases, including oxygen, occurs in the air-water interface (Garbe et al., 2014). Oxygen from the air dissolves into the surface water, increasing the DO at shallower depths. Water movement and turbulence tend to be higher in shallow waters due to wave actions, tides, and currents, which create mixing and promote higher DO concentrations. In contrast, deeper waters may experience slower water mixing, limiting the exchange of gases and resulting in lower DO concentrations.

The shallow reef site (0.5-5 m) experienced lower oxygen concentrations (DO_{min}) during the night, compared to the deepest reef site (22 m). This result, in combination with higher oxygen concentrations (DO_{max}) during the day, explains why the shallow reef exhibited larger daily variations (DO_{range}) in oxygen concentrations compared to the deepest reef site. This finding aligns with previous studies indicating that deeper reef environments have smaller diel variations in oxygen (Nelson & Altieri, 2019), most likely as a result of lower biomass both producing oxygen through primary production and consuming oxygen through respiration.

Intriguingly, the study revealed that the deeper sites at 9 m and 22 m did not exhibit hypoxia or hyperoxia, unlike the shallow reef site where both conditions were recorded. These results align with the deep reef refugia hypothesis, which posits that corals located at greater depths may experience more stable and favorable environmental conditions, making them less susceptible to stressors that can cause coral bleaching (Bongaerts et al., 2010). This indicates

that corals located at deeper depths are less exposed to extreme oxygen concentrations and suggest that deeper reef areas may serve as critical habitats sustaining coral populations in the face of rising sea temperatures and stressors such as too low or too high oxygen concentrations.

However, it is important to note that the shallow and deep reef environments in this study differed regarding coral cover. The reef environment at the deeper sites was characterized by corals sparsely scattered on a mainly sandy bottom, in contrast to the shallow reef environment with substantially higher coral cover. A lower coral cover results in reduced oxygen production and coral respiration, leading to lower DO_{max} values, higher DO_{min} values, and, consequently, a smaller daily range of oxygen. To gain a comprehensive understanding of DO concentrations in deep reef environments, future studies should prioritize deep (>10 m) reef environments with high coral cover. By examining these sites, further conclusions about the relationship between coral cover, oxygen dynamics, and water depth can be made.

Did oxygen act as a stressor on the corals in the reef?

Hypoxia

It has been demonstrated that exposure to low oxygen conditions at night, followed by reoxygenation during the daytime, can have both sublethal and lethal effects on tropical corals across a range of oxygen concentrations (Haas et al., 2014; Pezner et al., 2023). Weak and mild nocturnal hypoxia was recorded in the study, but based on the exposure time, the oxygen deficiency was not likely severe enough to act as a stressor. Weak hypoxia (65-80%) has not yet been recorded to alone cause stress to scleractinia corals and based on the exposure time (4.5h a night at longest), it is not likely severe enough to cause any lethal or sublethal effects to the corals. Mild nocturnal hypoxia (45-65% or 3-4 mg O₂/L) has been shown to cause both lethal and sublethal effects to branching *Acropora* corals (exposure time: 12h each night), including bleaching, reductions in calcification rates and photosynthetic capacity, tissue loss and DNA damage (Haas et al., 2014). However, since the longest recorded exposure time of mild hypoxia in this study was 30 minutes, it is likely not long enough to cause stress to the corals.

It is important to note that these DO concentrations were measured in the surrounding water, which can differ from the DO levels found in the coral tissue (Shashar et al., 1993). The restricted release of DO from the coral tissue into the seawater due to the diffusive boundary layer can cause an accumulation of oxygen within the coral tissues, which can exceed 250% oxygen saturation during the day (Gardella & Edmunds, 1999; Shashar et al., 1993). In contrast, at night, the limited influx of oxygen combined with the continued respiratory consumption can result in extreme hypoxic conditions (<2% saturation) within the coral tissues (Gardella & Edmunds, 1999; Shashar et al., 1993). Therefore, the measured oxygen concentration in the surrounding water cannot fully indicate the level of hyperoxic or hypoxic stress the coral experience. The recorded concentration of DO in the seawater is likely lower

compared to the concentration of oxygen found in the coral tissues during the day and vice versa at night (Fig.11).

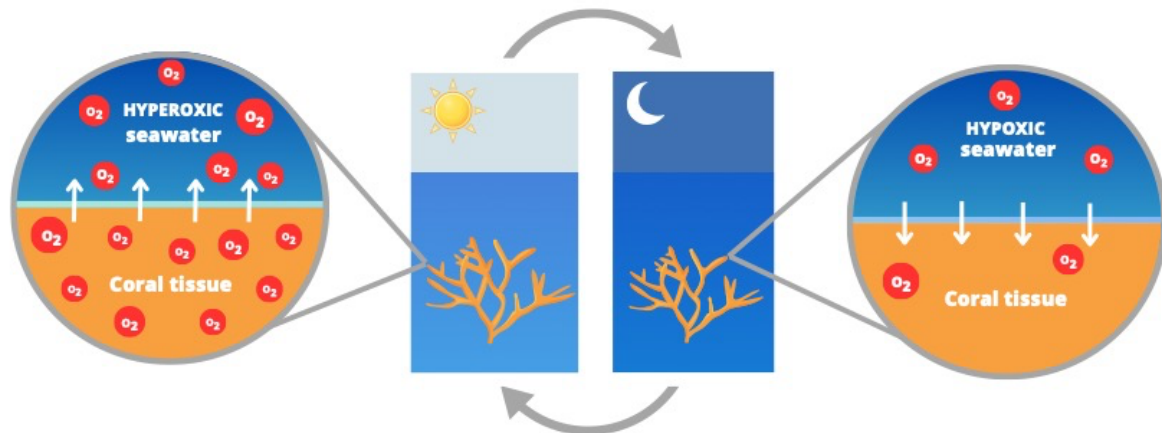


Figure 11. The diel oxygen cycle in coral reefs shifts from hyperoxic during the day to hypoxic at night. During the day, corals are net oxygen producers since oxygen production by zooxanthellae exceeds the oxygen consumption, leading to an excess of oxygen released into the surrounding seawater. At night, with no photosynthesis and continued coral respiration, corals become net oxygen consumers and rely on the environment for oxygen. (Figure inspired by Fig. 3 in Nelson & Altieri (2019)).

Hyperoxia

In the present study, weak (105-115%), mild (115-125%), and moderate (125-150%) hyperoxia was recorded at the coral reef, with varying exposure times (Supplementary Table 2). While severe ($>150\%$) hyperoxia was not recorded, it is of high interest to discuss whether the recorded hyperoxic levels were severe enough to cause any sub-lethal stress to the corals. Oxygen, which accumulate during photosynthesis, can impose stress on corals through a various of processes (Shick, 1990). High levels of oxygen can indirectly inhibit photosynthesis by promoting the process of photorespiration or by generating excessive levels of radical oxygen species (ROS) (Mass et al., 2010). ROS are highly reactive molecules and natural byproducts of various cellular processes, including photosynthesis and play important roles in signaling and stress responses (Abdal Dayem et al., 2017). However, excessive levels of ROS can cause antioxidants to not be able to neutralize them effectively, resulting in significant cellular damage (disrupting proteins, membranes, and nucleic acids) to components responsible for calcification and photosynthesis in corals (Lesser, 2006; Mass et al., 2010; Wijgerde et al., 2012).

Nevertheless, hyperoxic conditions can provide benefits to corals beyond serving as stressors. Diel hyperoxia has been shown to elevate thermal thresholds of marine organisms, including corals, and improve their capacity to withstand and recover from hypoxic events, such as those that occurring during the night (Giomi et al., 2019; Parry, 2021). Additionally, an initial increase of oxygen has been shown to boost photosynthesis, before reaching a certain threshold, where an accumulation of oxygen decreases photosynthetic rates because of photorespiration or ROS (Gardella & Edmunds, 1999). Hyperoxic treatments of 150% oxygen saturation have been found to enhance photosynthesis (exposure time: 24 hours) (Gardella &

Edmunds, 1999), while hyperoxic treatments of >200% have been shown to inhibit and decrease photosynthesis rates. Based on these literature thresholds (Gardella & Edmunds, 1999; Mass et al., 2010), the recorded hyperoxia (weak, mild, and moderate) was not severe enough to alone act as a stressor to the corals. The recorded hyperoxic conditions in this study more likely boosted the photosynthesis rates of the corals, than caused stress. However, further investigation is needed to determine the shape and threshold concentrations of the curve between oxygen and photosynthetic rates in corals to better understand hyperoxia's impact on corals.

No comprehensive health assessments were conducted on the corals in this study, except for visual assessments of potential bleaching and coral diseases. While no instances of bleaching were observed in any of the study corals, the coral disease PUWS was identified on all the massive corals. Coral diseases can induce stress in corals and can also emerge as a result of stress, as researcher has found that bleaching and thermal stress can reduce corals' resilience against coral diseases (Miller et al., 2009). Considering that massive corals exhibited the lowest hyperoxic levels among all the coral morphologies, it is not likely that the high prevalence of PUWS is due to increased stress in massive corals compared to other coral morphologies due to hyperoxia. Instead, elevated nutrient and organic carbon levels are more likely contributing factors (Kaczmarek & Richardson, 2011).

Assessing Spatial Variability: Bleaching Patterns and Oxygen Conditions

Coral morphology

Based on bleaching observation across the Indian and Pacific Oceans, coral genera can be ranked in order of decreasing vulnerability to bleaching as follows: *Acropora* > *Stylophora* > *Pocillopora* > *Montipora* > *Heliopora* > *Favia* > *Porites* (Stimson et al., 2002). Notably, the top three most sensitive genera in this list are all dominated by branching coral species, while the remaining genera mostly consists of massive corals. However, there are some disparate results since Williams et al., (2010) found no relation between coral morphologies and bleaching severity, and Ortiz et al., 2009 found that massive corals experience more bleaching severity compared to branching corals. This was explained by the massive coral colonies being located in sandy patches, where the carbonate sand is highly reflective and amplifies the light intensity, which can increase the production of harmful ROS (Ortiz et al., 2009). The susceptibility of table corals to bleaching remains poorly understood, with existing literature primarily focusing on the vulnerabilities of branching and massive corals. To address this gap, it is recommended that future studies investigate the bleaching dynamics of table corals in comparison to other morphologies, thus providing a more comprehensive understanding of coral bleaching variability.

This study revealed that oxygen conditions varied between table and massive corals, with table corals experiencing heightened oxygen concentrations during the day relative to massive corals. The impact of high oxygen levels as a stressor, as previously discussed, can be linked to the generation of ROS and photoinhibition (Mass et al., 2010). If massive corals demonstrate less vulnerability to hyperoxic conditions, this phenomenon could contribute to

their observed reduced probability of bleaching when compared to other coral morphology groups. Nonetheless, it is crucial to acknowledge that certain traits, like the relatively thicker coral tissue, which can reduce massive corals susceptibility to hyperoxia, may also decrease their vulnerability to other stressors such as UV radiation. Therefore, hyperoxia is likely to function as an additional stressor in combination with other stressors, leading to cumulative stress effects.

Branching coral species have been observed to exhibit a higher degree of bleaching compared to other coral morphologies (Stimson et al., 2002). However, the findings from this study suggest that varying oxygen conditions do not account for these differences among the morphology groups. The result does not support the hypothesis that either hyperoxia or hypoxia serves as stressors influencing the susceptibility of branching corals to bleaching. Nevertheless, it is recommended to conduct a more comprehensive study with a larger dataset, since certain results still suggest the potential for variations in dissolved oxygen concentration between branching corals and other morphologies. Unfortunately, this study was unable to detect such differences due to the limited amount of available data.

Middle and edge of the reef

Previous research has shown a positive correlation between coral cover and bleaching, suggesting that areas with denser coral populations tend to exhibit more pronounced bleaching, regardless of the depth (Muir et al., 2017). In this study, higher daytime oxygen concentrations were observed in the middle of the reef compared to the reef edge, accompanied by greater diel fluctuations in dissolved oxygen. Given the higher coral cover in the middle of the reef, these findings suggest a potential link between coral cover and dissolved oxygen concentration, which may in turn elucidate the correlation between coral bleaching and coral cover.

Depth

Coral bleaching displays depth-dependent variations, with more pronounced occurrences at shallower depths (3-5 m) and a notable decline in intensity with increasing depth (Muir et al., 2017; Penin et al., 2007). This study's findings demonstrate distinct variations in oxygen concentrations (DO_{max}, DO_{min} and DO_{orange}) along the depth gradient. The deeper sites at 9 m and 22 m exhibited no instances of hypoxia or hyperoxia, in contrast to the shallow reef site, where both conditions were recorded. It is plausible that the presence of hypoxic and hyperoxic stress may contribute to the heightened susceptibility of shallow reefs to coral bleaching. However, it is crucial to consider the potential influence of other depth-dependent stressors, such as temperature differentials and UV radiation, in this context.

Diel fluctuations and oxygen availability in the reef

Oxygen concentrations in the reef displayed a clear diurnal pattern, characterized by higher DO levels during the daylight hours when photosynthesis is active, and reduced levels at night due to cessation of photosynthesis while respiration persist (Nelson & Altieri, 2019). The average diurnal variation in oxygen concentration across the shallow reef was $31 \pm 12.81\%$

and peaked at 67% (range: 59.1% to 125.7% oxygen saturation over a diurnal cycle) in the middle of the shallow reef. This range of natural daily fluctuation underscores coral's adaptive capacity and could provide insight to coral's level of resistance to future shifts in oxygen availability that could arise due to climate change and other stressors.

Contrary to the initial hypothesis of a gradual oxygen decline during the night, the observed fluctuating nocturnal oxygen concentrations sometimes increased from 60% up to 100% saturation. This significant range suggests the presence of additional factors influencing nighttime oxygen dynamics. One plausible explanation for these nocturnal oxygen fluctuations is the contribution of reef fish behaviour. Nocturnally active fish seek refuge within coral crevices and branches, a behaviour that offers protection from predators and enhances water circulation in the reef (Gauff et al., 2018). Furthermore, some coral fish species have developed behavioural adaptive strategies to cope with low oxygen conditions, such as sleep swimming (Nilsson & Renshaw, 2004). Fanning their fins at night increases water flow between coral structures, which can elevate oxygen saturation levels from 20% up to 80% (Goldshmid et al., 2004). Notably, evidence suggests that corals harbouring fish overnight are less susceptible to bleaching due to reduced risks of hypoxic stress (Chase et al., 2018; Holbrook et al., 2008). Another contributing factor to the observed oxygen fluctuations at night could be the influence of water currents and tides. The movement of water caused by currents and tides can enhance the exchange of oxygen and other gases between the air-sea interface and the water column and reef ecosystem (Kraines et al., 1996). Although nocturnal fluctuations were observed at all reef sites, the fluctuations were largest in the middle of the reef. The middle of the reef could host a greater abundance of prey organisms such as zooplankton and smaller fish, which attracts nocturnal predators. These interactions could create localized turbulence and increased water movement, impacting the oxygen dynamics in the reef.

The oxygen availability within the studied reef, ranged from the highest recorded value of 130.3% to the lowest of 59.1%. These observed values comfortably fall within the established range of DO concentration found in reef ecosystems (50-200%), as deduced from a comprehensive assessment conducted by Nelson & Altieri (2019). While the observed range can provide insights into the oxygen conditions that support a reef's overall health, it might not serve as a direct oxygen threshold for coral health. Corals and other reef organisms have specific oxygen requirements that vary based on species and environmental conditions (Vaquer-Sunyer & Duarte, 2008). Nevertheless, the recorded range can be used as a reference for future studies to monitor changes in oxygen availability related to climate change. By regularly measuring oxygen levels over time, deviations from established ranges can be detected, which might indicate shifts in the reef ecosystem's dynamics. Sudden or prolonged shifts outside the established range might indicate disturbances such as pollution events, algal blooms or other factors affecting oxygen availability. However, long-term monitoring of oxygen concentration over a full year is advisable, to comprehend seasonal variations. Different seasons can influence factors such as temperature, water movement and biological activity, which impact DO concentrations (Camacho-Cruz et al., 2022).

Oxygen's role in bleaching events

Mass coral bleaching events are widely attributed to elevated SSTs, and while it might be the primary trigger, the interplay between temperature and oxygen levels needs further investigation. Hypoxic zones are expected to increase globally (Altieri et al., 2017) and might not only occur at a local scale in reefs with restricted water movement but globally as a contributing stressor in mass bleaching events. The timing of coral bleaching could provide insights in oxygen's potential role in these events. It has been found that regions near the equator, characterized by relatively consistent night lengths over a year, experience bleaching peaks during the warmest phase of the summer (Andersson, 2020). Contrarily, in locations where night lengths varied by 38 minutes or more within a month, bleaching events occurred not during the highest temperature periods but later in the summer. This pattern coincided with months characterized by longer nights and relative lower water temperatures (Andersson, 2020). This suggests that the role of nocturnal hypoxia could be significant in coral bleaching events during the late summer. To further understand oxygen's potential role in bleaching, studies should investigate i) the precise timing of bleaching onset during the day, ii) compare the expulsion rates of zooxanthellae during both the daytime and nighttime. If the bleaching starts at night, it strongly suggests a connection to oxygen depletion.

Conclusions

In this investigation of in-situ oxygen availability in a coral reef, a diverse range of oxygen conditions was revealed, influenced by factors such as reef location, coral morphology, and depth. Based on the findings of this study, we can draw preliminary insights regarding which corals and what parts of a reef are most susceptible to extreme oxygen levels:

- 1. Corals located at shallower depths (<5m) (both hypoxia and hyperoxia)**
- 2. Corals located in the middle of a reef (hyperoxia)**
- 3. Table corals (hyperoxia)**

These corals and reef locations appear to be most exposed to extreme oxygen levels, potentially making them primary areas of interest for the assessment of future changes in oxygen dynamics. However, it is plausible that these corals have developed a better adaptation to extreme oxygen, enabling them to withstand potential alterations more effectively. To understand whether these locations are more vulnerable or resistance to extreme oxygen conditions, further research is required, focusing on spatial variability in bleaching events, ideally in conjunction with continuous monitoring of oxygen conditions.

Hypoxic events in tropical coral reefs are poorly understood and not well documented, possibly because research on oxygen deficiency has mainly focused on temperate areas rather than tropical ones (Altieri et al., 2017). Furthermore, die-offs following a potential hypoxic event is often discovered when water chemistry has returned to normal conditions, which makes it difficult to determine if mortality was driven by oxygen deficiency (Kealoha et al.,

2020). As ocean temperatures continue to rise due to climate change, the occurrence of extreme oxygen concentration is expected to increase in the future, which poses a significant threat to coral reefs. These findings suggest that oxygen concentration measurements should be included in standard protocol when monitoring coral reefs to fully assess a reef's health and identify oxygen-driven bleaching. Moreover, this study sheds light on the spatial heterogeneity of oxygen concentrations in a coral reef ecosystem and can be used for developing conservation and management strategies in the face of environmental threats.

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References

- Abdal Dayem, A., Hossain, M., Lee, S., Kim, K., Saha, S., Yang, G.-M., Choi, H., & Cho, S.-G. (2017). The Role of Reactive Oxygen Species (ROS) in the Biological Activities of Metallic Nanoparticles. *International Journal of Molecular Sciences*, *18*(1), 120. <https://doi.org/10.3390/ijms18010120>
- Al-Horani, F. A., Tambutté, É., & Allemand, D. (2007). Dark calcification and the daily rhythm of calcification in the scleractinian coral, *Galaxea fascicularis*. *Coral Reefs*, *26*(3), 531–538. <https://doi.org/10.1007/s00338-007-0250-x>
- Altieri, A. H., & Gedan, K. B. (2015). Climate change and dead zones. *Global Change Biology*, *21*(4), 1395–1406. <https://doi.org/10.1111/gcb.12754>
- Altieri, A. H., Harrison, S. B., Seemann, J., Collin, R., Diaz, R. J., & Knowlton, N. (2017). Tropical dead zones and mass mortalities on coral reefs. *Proceedings of the National Academy of Sciences*, *114*(14), 3660–3665. <https://doi.org/10.1073/pnas.1621517114>
- Andersson, E. (2020). Nocturnal hypoxia in coral reefs: an unknown factor contributing to coral bleaching? (Unpublished bachelor's thesis). Stockholm University, Stockholm.

Bates, A. E., Cooke, R. S. C., Duncan, M. I., Edgar, G. J., Bruno, J. F., Benedetti-Cecchi, L., Côté, I. M., Lefcheck, J. S., Costello, M. J., Barrett, N., Bird, T. J., Fenberg, P. B., & Stuart-Smith, R. D. (2019). Climate resilience in marine protected areas and the ‘Protection Paradox.’ *Biological Conservation*, 236, 305–314. <https://doi.org/10.1016/j.biocon.2019.05.005>

Berkelmans, R., De’ath, G., Kininmonth, S., & Skirving, W. J. (2004). A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: Spatial correlation, patterns, and predictions. *Coral Reefs*, 23(1), 74–83. <https://doi.org/10.1007/s00338-003-0353-y>

Best, M. A., Wither, A. W., & Coates, S. (2007). Dissolved oxygen as a physico-chemical supporting element in the Water Framework Directive. *Marine Pollution Bulletin*, 55(1–6), 53–64. <https://doi.org/10.1016/j.marpolbul.2006.08.037>

Bianchessi, Annalisa & Lumbab, Vincent. (2012). A Case Study of the Municipality of Dauin, Negros Oriental, Philippines: A Global Bright Spot for Marine Conservation. Inhouse publication by Rare.

Bongaerts, P., Ridgway, T., Sampayo, E. M., & Hoegh-Guldberg, O. (2010). Assessing the ‘deep reef refugia’ hypothesis: Focus on Caribbean reefs. *Coral Reefs*, 29(2), 309–327. <https://doi.org/10.1007/s00338-009-0581-x>

Brahimi-Horn, M. C., & Pouysségur, J. (2007). Oxygen, a source of life and stress. *FEBS Letters*, 581(19), 3582–3591. <https://doi.org/10.1016/j.febslet.2007.06.018>

Bruno, J., Siddon, C., Witman, J., Colin, P., & Toscano, M. (2001). El Niño related coral bleaching in Palau, Western Caroline Islands. *Coral Reefs*, 20(2), 127–136. <https://doi.org/10.1007/s003380100151>

Castrillón-Cifuentes, A. L., Zapata, F. A., Giraldo, A., & Wild, C. (2023). Spatiotemporal variability of oxygen concentration in coral reefs of Gorgona Island (Eastern Tropical Pacific) and its effect on the coral *Pocillopora capitata*. *PeerJ*, 11, e14586. <https://doi.org/10.7717/peerj.14586>

DATAtab Team (2023). DATAtab: Online Statistics Calculator. DATAtab e.U. Graz, <https://datatab.net>

Dodds, L. A., Roberts, J. M., Taylor, A. C., & Marubini, F. (2007). Metabolic tolerance of the cold-water coral *Lophelia pertusa* (Scleractinia) to temperature and dissolved oxygen change. *Journal of Experimental Marine Biology and Ecology*, 349(2), 205–214. <https://doi.org/10.1016/j.jembe.2007.05.013>

Done, T. (2011). Corals: Environmental Controls on Growth. In D. Hopley (Ed.), *Encyclopedia of Modern Coral Reefs* (pp. 281–293). Springer Netherlands. https://doi.org/10.1007/978-90-481-2639-2_10

Erfteemeijer, P. L. A., Riegl, B., Hoeksema, B. W., & Todd, P. A. (2012). Environmental impacts of dredging and other sediment disturbances on corals: A review. *Marine Pollution Bulletin*, 64(9), 1737–1765. <https://doi.org/10.1016/j.marpolbul.2012.05.008>

Fondriest Environmental, Inc. "Measuring Dissolved Oxygen." Fundamentals of Environmental Measurements. 7 Jan. 2014. Web. <https://www.fondriest.com/environmental-measurements/measurements/measuring-water-quality/dissolved-oxygen-sensors-and-methods/>>.

Garbe, C. S., Rutgersson, A., Boutin, J., De Leeuw, G., Delille, B., Fairall, C. W., Gruber, N., Hare, J., Ho, D. T., Johnson, M. T., Nightingale, P. D., Pettersson, H., Piskozub, J., Sahlée, E., Tsai, W., Ward, B., Woolf, D. K., & Zappa, C. J. (2014). Transfer Across the Air-Sea Interface. In P. S. Liss & M. T. Johnson (Eds.), *Ocean-Atmosphere Interactions of Gases and Particles* (pp. 55–112). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-25643-1_2

Gardella, D. J., & Edmunds, P. J. (1999). The oxygen microenvironment adjacent to the tissue of the scleractinian *Dichocoenia stokesii* and its effects on symbiont metabolism. *Marine Biology*, 135(2), 289–295. <https://doi.org/10.1007/s002270050626>

Giomi, F., Barausse, A., Duarte, C. M., Booth, J., Agusti, S., Saderne, V., Anton, A., Daffonchio, D., & Fusi, M. (2019). Oxygen supersaturation protects coastal marine fauna from ocean warming. *Science Advances*, 5(9), eaax1814. <https://doi.org/10.1126/sciadv.aax1814>

Glynn, P. W. (1996). Coral reef bleaching: Facts, hypotheses and implications. *Global Change Biology*, 2(6), 495–509. <https://doi.org/10.1111/j.1365-2486.1996.tb00063.x>

Haas, A. F., Smith, J. E., Thompson, M., & Deheyn, D. D. (2014). Effects of reduced dissolved oxygen concentrations on physiology and fluorescence of hermatypic corals and benthic algae. *PeerJ*, 2, e235. <https://doi.org/10.7717/peerj.235>

Hallock, P. (2005). Global change and modern coral reefs: New opportunities to understand shallow-water carbonate depositional processes. *Sedimentary Geology*, 175(1–4), 19–33. <https://doi.org/10.1016/j.sedgeo.2004.12.027>

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*. <https://doi.org/10.1071/MF99078>

Hughes, D. J., Alderdice, R., Cooney, C., Kühl, M., Mathieu Pernice, Voolstra, C. R., & Suggett, D. J. (2020). Coral reef survival under accelerating ocean deoxygenation. *Nature Climate Change*, 10(4), 296–307. <https://doi.org/10.1038/s41558-020-0737-9>

Hughes, D. J., Alexander, J., Cobbs, G., Kühl, M., Cooney, C., Pernice, M., Varkey, D., Voolstra, C. R., & Suggett, D. J. (2022). Widespread oxyregulation in tropical corals under hypoxia. *Marine Pollution Bulletin*, 179, 113722. <https://doi.org/10.1016/j.marpolbul.2022.113722>

Jain, T., Buapet, P., Ying, L., & Yucharoen, M. (2023). Differing Responses of Three Scleractinian Corals from Phuket Coast in the Andaman Sea to Experimental Warming and Hypoxia. *Journal of Marine Science and Engineering*, 11(2), 403. <https://doi.org/10.3390/jmse11020403>

Jane, S. F., Mincer, J. L., Lau, M. P., Lewis, A. S. L., Stetler, J. T., & Rose, K. C. (2023).

Longer duration of seasonal stratification contributes to widespread increases in lake hypoxia and anoxia. *Global Change Biology*, 29(4), 1009–1023. <https://doi.org/10.1111/gcb.16525>

Johnson, M. D., Swaminathan, S. D., Nixon, E. N., Paul, V. J., & Altieri, A. H. (2021). Differential susceptibility of reef-building corals to deoxygenation reveals remarkable hypoxia tolerance. *Scientific Reports*, 11(1), 23168. <https://doi.org/10.1038/s41598-021-01078-9>

Jokiel, P. L., Lesser, M. P., & Ondrusek, M. E. (1997). UV-absorbing compounds in the coral *Pocillopora damicornis*: Interactive effects of UV radiation, photosynthetically active radiation, and water flow. *Limnology and Oceanography*, 42(6), 1468–1473. <https://doi.org/10.4319/lo.1997.42.6.1468>

Kaczmarek, L., & Richardson, L. L. (2011). Do elevated nutrients and organic carbon on Philippine reefs increase the prevalence of coral disease? *Coral Reefs*, 30(1), 253–257. <https://doi.org/10.1007/s00338-010-0686-2>

Keller, B. D., Gleason, D. F., McLeod, E., Woodley, C. M., Airamé, S., Causey, B. D., Friedlander, A. M., Grober-Dunsmore, R., Johnson, J. E., Miller, S. L., & Steneck, R. S. (2009). Climate Change, Coral Reef Ecosystems, and Management Options for Marine Protected Areas. *Environmental Management*, 44(6), 1069–1088. <https://doi.org/10.1007/s00267-009-9346-0>

Kühl, M., Cohen, Y., Dalsgaard, T., Jørgensen, B., & Revsbech, N. (1995). Microenvironment and photosynthesis of zooxanthellae in scleractinian corals studied with microsensors for O₂, pH and light. *Marine Ecology Progress Series*, 117, 159–172. <https://doi.org/10.3354/meps117159>

Lesser, M. P. (1997). Oxidative stress causes coral bleaching during exposure to elevated temperatures. *Coral Reefs*, 16(3), 187–192. <https://doi.org/10.1007/s003380050073>

Lesser, M. P. (2006). OXIDATIVE STRESS IN MARINE ENVIRONMENTS: Biochemistry and Physiological Ecology. *Annual Review of Physiology*, 68(1), 253–278. <https://doi.org/10.1146/annurev.physiol.68.040104.110001>

Li, S., Yu, K., Shi, Q., Chen, T., Zhao, M., & Zhao, J. (2008). Interspecies and spatial diversity in the symbiotic zooxanthellae density in corals from northern South China Sea and its relationship to coral reef bleaching. *Chinese Science Bulletin*, 53(2), 295–303. <https://doi.org/10.1007/s11434-007-0514-4>

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., & van Woesik, R. (2001). Coral bleaching: The winners and the losers. *Ecology Letters*, 4(2), 122–131. <https://doi.org/10.1046/j.1461-0248.2001.00203.x>

Marshall, P. A., & Baird, A. H. (2000). Bleaching of corals on the Great Barrier Reef: Differential susceptibilities among taxa. *Coral Reefs*, 19(2), 155–163. <https://doi.org/10.1007/s003380000086>

Mass, T., Genin, A., Shavit, U., Grinstein, M., & Tchernov, D. (2010). Flow enhances photosynthesis in marine benthic autotrophs by increasing the efflux of oxygen from the organism to the water. *Proceedings of the National Academy of Sciences*, 107(6), 2527–2531. <https://doi.org/10.1073/pnas.0912348107>

- Miller, J., Muller, E., Rogers, C., Waara, R., Atkinson, A., Whelan, K. R. T., Patterson, M., & Witcher, B. (2009). Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. *Coral Reefs*, 28(4), 925–937. <https://doi.org/10.1007/s00338-009-0531-7>
- Mishra, P., Pandey, C., Singh, U., Gupta, A., Sahu, C., & Keshri, A. (2019). Descriptive statistics and normality tests for statistical data. *Annals of Cardiac Anaesthesia*, 22(1), 67. https://doi.org/10.4103/aca.ACA_157_18
- Muir, P. R., Marshall, P. A., Abdulla, A., & Aguirre, J. D. (2017). Species identity and depth predict bleaching severity in reef-building corals: Shall the deep inherit the reef? *Proceedings of the Royal Society B: Biological Sciences*, 284(1864), 20171551. <https://doi.org/10.1098/rspb.2017.1551>
- Nelson, H. R., & Altieri, A. H. (2019). Oxygen: The universal currency on coral reefs. *Coral Reefs*, 38(2), 177–198. <https://doi.org/10.1007/s00338-019-01765-0>
- Ong, R. H., King, A. J. C., Mullins, B. J., Cooper, T. F., & Caley, M. J. (2012). Development and Validation of Computational Fluid Dynamics Models for Prediction of Heat Transfer and Thermal Microenvironments of Corals. *PLoS ONE*, 7(6), e37842. <https://doi.org/10.1371/journal.pone.0037842>
- Ortiz, J. C., Gomez-Cabrera, M. del C., & Hoegh-Guldberg, O. (2009). Effect of colony size and surrounding substrate on corals experiencing a mild bleaching event on Heron Island reef flat (southern Great Barrier Reef, Australia). *Coral Reefs*, 28(4), 999–1003. <https://doi.org/10.1007/s00338-009-0546-0>
- Oschlies, A., Brandt, P., Stramma, L., & Schmidtko, S. (2018). Drivers and mechanisms of ocean deoxygenation. *Nature Geoscience*, 11(7), 467–473. <https://doi.org/10.1038/s41561-018-0152-2>
- Osinga, R., Derksen-Hooijberg, M., Wijgerde, T., & Verreth, J. A. J. (2017). Interactive effects of oxygen, carbon dioxide and flow on photosynthesis and respiration in the scleractinian coral *Galaxea fascicularis*. *Journal of Experimental Biology*, jeb.140509. <https://doi.org/10.1242/jeb.140509>
- Ott, I. (2013). Biodistribution of Metals and Metalloids. In *Comprehensive Inorganic Chemistry II* (pp. 933–949). Elsevier. <https://doi.org/10.1016/B978-0-08-097774-4.00337-5>
- Ow, Y. X., & Todd, P. A. (2010). Light-induced morphological plasticity in the scleractinian coral *Goniastrea pectinata* and its functional significance. *Coral Reefs*, 29(3), 797–808. <https://doi.org/10.1007/s00338-010-0631-4>
- Parry, A. (2021). *Oxygen Modulation of thermal tolerance in the branching coral Stylophora pistillata* [KAUST Research Repository]. <https://doi.org/10.25781/KAUST-6X45E>
- Patterson, M. R. (1992). A Mass Transfer Explanation of Metabolic Scaling Relations in Some Aquatic Invertebrates and Algae. *Science*, 255(5050), 1421–1423. <https://doi.org/10.1126/science.255.5050.1421>

- Patterson, M. R., Sebens, K. P., & Olson, R. R. (1991). In situ measurements of flow effects on primary production and dark respiration in reef corals. *Limnology and Oceanography*, 36(5), 936–948. <https://doi.org/10.4319/lo.1991.36.5.0936>
- Penin, L., Adjeroud, M., Schrimm, M., & Lenihan, H. S. (2007). High spatial variability in coral bleaching around Moorea (French Polynesia): Patterns across locations and water depths. *Comptes Rendus Biologies*, 330(2), 171–181. <https://doi.org/10.1016/j.crv.2006.12.003>
- Pezner, A. K., Courtney, T. A., Barkley, H. C., Chou, W.-C., Chu, H.-C., Clements, S. M., Cyronak, T., DeGrandpre, M. D., Kekuewa, S. A. H., Kline, D. I., Liang, Y.-B., Martz, T. R., Mitarai, S., Page, H. N., Rintoul, M. S., Smith, J. E., Soong, K., Takeshita, Y., Tresguerres, M., ... Andersson, A. J. (2023). Increasing hypoxia on global coral reefs under ocean warming. *Nature Climate Change*. <https://doi.org/10.1038/s41558-023-01619-2>
- Raj, K. D., Mathews, G., Obura, D. O., Laju, R. L., Bharath, M. S., Kumar, P. D., Arasamuthu, A., Kumar, T. K. A., & Edward, J. K. P. (2020). Low oxygen levels caused by *Noctiluca scintillans* bloom kills corals in Gulf of Mannar, India. *Scientific Reports*, 10(1), 22133. <https://doi.org/10.1038/s41598-020-79152-x>
- Rowan, R. (2004). Thermal adaptation in reef coral symbionts. *Nature*, 430(7001), 742–742. <https://doi.org/10.1038/430742a>
- Schulte, P. M. (2015). The effects of temperature on aerobic metabolism: Towards a mechanistic understanding of the responses of ectotherms to a changing environment. *Journal of Experimental Biology*, 218(12), 1856–1866. <https://doi.org/10.1242/jeb.118851>
- Shashar, N., Cohen, Y., & Loya, Y. (1993). Extreme Diel Fluctuations of Oxygen in Diffusive Boundary Layers Surrounding Stony Corals. *The Biological Bulletin*, 185(3), 455–461. <https://doi.org/10.2307/1542485>
- Shick, J. M. (1990). Diffusion Limitation and Hyperoxic Enhancement of Oxygen Consumption in Zooxanthellate Sea Anemones, Zoanths, and Corals. *The Biological Bulletin*, 179(1), 148–158. <https://doi.org/10.2307/1541749>
- Stimson, J., Sakai, K., & Sembali, H. (2002). Interspecific comparison of the symbiotic relationship in corals with high and low rates of bleaching-induced mortality. *Coral Reefs*, 21(4), 409–421. <https://doi.org/10.1007/s00338-002-0264-3>
- Stone, L., Huppert, A., Rajagopalan, B., Bhasin, H., & Loya, Y. (1999). Mass Coral Reef Bleaching: A Recent Outcome of Increased El Niño Activity? *Ecology Letters*, 2(5), 325–330. <https://doi.org/10.1046/j.1461-0248.1999.00092.x>
- Stramma, L., Schmidtko, S., Levin, L. A., & Johnson, G. C. (2010). Ocean oxygen minima expansions and their biological impacts. *Deep Sea Research Part I: Oceanographic Research Papers*, 57(4), 587–595. <https://doi.org/10.1016/j.dsr.2010.01.005>
- Timeanddate.com. (2022, December). Historic Weather in Dauin, Philippines. Retrieved April 25, 2023 from <https://www.timeanddate.com/weather/@1715369/historic?month=12&year=2022>

Trowbridge, C. D., Davenport, J., Cottrell, D. M., Harman, L., Plowman, C. Q., Little, C., & McAllen, R. (2017). Extreme oxygen dynamics in shallow water of a fully marine Irish sea lough. *Regional Studies in Marine Science*, 11, 9–16. <https://doi.org/10.1016/j.rsma.2017.01.008>

van Woerik, R., Irikawa, A., Anzai, R., & Nakamura, T. (2012). Effects of coral colony morphologies on mass transfer and susceptibility to thermal stress. *Coral Reefs*, 31(3), 633–639. <https://doi.org/10.1007/s00338-012-0911-2>

Vaquer-Sunyer, R., & Duarte, C. M. (2008). Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences*, 105(40), 15452–15457. <https://doi.org/10.1073/pnas.0803833105>

Welker, A. F., Moreira, D. C., Campos, É. G., & Hermes-Lima, M. (2013). Role of redox metabolism for adaptation of aquatic animals to drastic changes in oxygen availability. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 165(4), 384–404. <https://doi.org/10.1016/j.cbpa.2013.04.003>

Wijgerde, T., Jurriaans, S., Hoofd, M., Verreth, J. A. J., & Osinga, R. (2012). Oxygen and Heterotrophy Affect Calcification of the Scleractinian Coral *Galaxea fascicularis*. *PLoS ONE*, 7(12), e52702. <https://doi.org/10.1371/journal.pone.0052702>

Williams, G. J., Knapp, I. S., Maragos, J. E., & Davy, S. K. (2010). Modeling patterns of coral bleaching at a remote Central Pacific atoll. *Marine Pollution Bulletin*, 60(9), 1467–1476. <https://doi.org/10.1016/j.marpolbul.2010.05.009>

Supplementary data

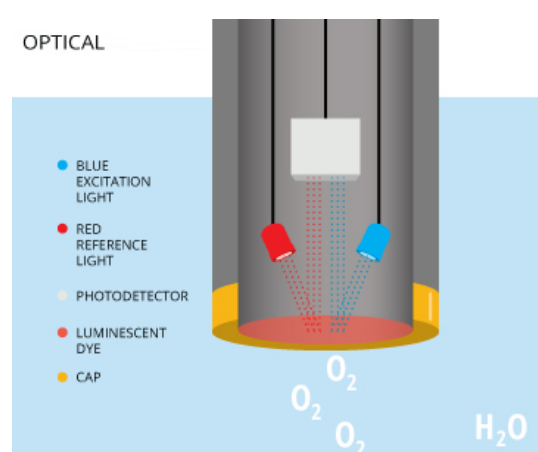


Figure S1. Optical dissolved oxygen sensor uses luminescent dyes reacting to blue LED light. These sensors consist of a membrane, LED, luminescent dye, and photodetector. Oxygen molecules affects the dye's luminescence, measured by the photodetector, inversely correlating with dissolved oxygen concentration via the Stern-Volmer equation. Image taken from Fondriest Environmental, Inc (2014).

Table S1. Mean daily values of oxygen concentration (mg/L), oxygen saturation (%), and temperature (°C) at the different reef sites. Statistics were calculated using a total of N observations over n days (i.e., full 24 hours) and presented as mean ± standard deviation at each reef site.

Reef Site			Dissolved Oxygen (mg/L)			Dissolved Oxygen Saturation (%)			Temperature (°C)				
Depth	Reef location	Morphology	N	n	Mean Daily Range	Mean Daily Min	Mean Daily Max	Mean Daily Range	Mean Daily Min	Mean Daily Max	Mean Daily Range	Mean Daily Min	Mean Daily Max
Shallow	Middle	Branching	414	3	2,6 ± 1,3	4,9 ± 1	7,4 ± 0,5	40,6 ± 21,5	76,9 ± 14,5	117,5 ± 8,5	0,6 ± 0,4	28,6 ± 0,1	29,2 ± 0,4
		Massive	419	3	2,6 ± 0,3	4,4 ± 0,4	7 ± 0	41,5 ± 5,5	70,5 ± 5,7	112 ± 0,2	0,6 ± 0,1	29,5 ± 0	30 ± 0,1
		Table	592	4	2,6 ± 0,1	5,3 ± 0,2	7,9 ± 0,2	42,1 ± 1	82,9 ± 3,2	125 ± 3,3	0,7 ± 0,1	29 ± 0,1	29,6 ± 0,1
	Edge	Branching (inner)	420	3	2,5 ± 0,6	4,7 ± 0,2	7,2 ± 0,4	39,1 ± 9,2	73,5 ± 3	112,5 ± 6,6	0,6 ± 0,2	28,5 ± 0,2	29 ± 0,2
		Branching (outer)	469	3	2 ± 0,1	5,1 ± 0,3	7,2 ± 0,1	31,5 ± 2,3	80,1 ± 3,5	112 ± 2	0,5 ± 0,1	28,3 ± 0,1	28,9 ± 0,2
		Massive	382	3	1,5 ± 0,2	5,2 ± 0,3	6,7 ± 0,1	24,5 ± 4	82,6 ± 5,1	107 ± 1,1	0,5 ± 0,2	29,1 ± 0,3	29,7 ± 0,1
	Table	432	3	1,7 ± 0,3	5,4 ± 0,1	7,1 ± 0,2	26,4 ± 4,3	84,9 ± 2	111,2 ± 2,5	0,4 ± 0,1	28,7 ± 0	29,1 ± 0	
Deep (9m)	N/A	N/A	392	3	1,2 ± 0,2	5,3 ± 0,2	6,5 ± 0	19,4 ± 2,5	83,2 ± 2,7	102,5 ± 0,3	0,5 ± 0,2	28,3 ± 0,2	28,8 ± 0
Deep (22m)	N/A	N/A	423	3	0,6 ± 0,1	5,7 ± 0,2	6,4 ± 0	10,4 ± 2,1	89,3 ± 2,96	99,7 ± 1	0,8 ± 0,3	28 ± 0,3	28,8 ± 0,1

Table S2. Mean daily exposure (minutes) of the different oxygen thresholds (hypoxia and hyperoxia) at the different reef sites. Statistics were calculated using a total of N observations over n days (i.e., full 24 hours) and presented as mean ± standard deviation at each reef site.

Reef Site			Mean daily exposure of the oxygen thresholds (minutes)									
Depth	Reef Location	Morphology	N	n	Weak Hypoxia	Mild Hypoxia	Moderate Hypoxia	Severe Hypoxia	Weak Hyperoxia	Mild Hyperoxia	Moderate Hyperoxia	Severe Hyperoxia
Shallow	Middle	Branching	414	3	63,3 ± 92,9	10 ± 17,3	0	0	240 ± 98,5	46,7 ± 40,4	6,7 ± 5,8	0
		Massive	419	3	160 ± 125,3	3,3 ± 5,8	0	0	253 ± 66,6	0	0	0
		Table	592	4	2,5 ± 5	0	0	0	262,5 ± 53,8	150 ± 72,6	30 ± 31,6	0
	Edge	Branching (inner)	420	3	83,3 ± 35,1	0	0	0	133,3 ± 180,1	30 ± 26,5	0	0
		Branching (outer)	469	3	0	0	0	0	283,3 ± 61,1	0	0	0
		Massive	382	3	13,3 ± 23,1	0	0	0	20 ± 20,5	0	0	0
	Table	432	3	0	0	0	0	263,3 ± 75,1	3,3 ± 5,8	0	0	
Deep (9m)	N/A	N/A	392	3	0	0	0	0	0	0	0	
Deep (22m)	N/A	N/A	423	3	0	0	0	0	0	0	0	

Table S3. Weather data for the morning (8am and 11am) and mid-afternoon (14pm) for each day and site during the study. D_{max} (%) and time of D_{max} included to see potential trends in weather and D_{max}. Weather was classified as ‘Scattered clouds’, ‘Partly sunny’ or ‘Overcast’ (timeanddate, 2022).

Date	Weather morning (08-11am)	Weather mid-afternoon (14.00)	Site	D _{max} (%)	Time of D _{max}
11/21/22	Scattered clouds	Scattered clouds	Massive, Middle	112	12:20
11/22/22	Scattered clouds	Scattered clouds	Massive, Middle	111,8	13:20
11/23/22	Scattered clouds	Scattered clouds	Massive, Middle	112,2	10:30
11/24/22	Overcast/Partly Sunny	Scattered clouds	Massive, Edge	105,9	15:00:00
11/25/22	Partly Sunny	Partly Sunny	Massive, Edge	108	13:20:00
11/26/22	Scattered clouds	Scattered clouds	Massive, Edge	107,1	13:10
11/27/22	Scattered clouds	Overcast	Table, Middle	124,9	09:30:00
11/28/22	Overcast	Overcast	Table, Middle	126,9	15:10:00
11/29/22	Scattered clouds	Scattered clouds	Table, Middle	120,3	12:00:00
11/30/22	Partly Sunny	Overcast	Table, Middle	127,8	11:20:00
12/1/22	Partly Sunny	Partly Sunny	Table, Edge	109,2	11:10:00
12/2/22	Overcast	Overcast	Table, Edge	110,4	14:50:00
12/3/22	Partly Sunny	Partly Sunny	Table, Edge	114,1	14:50:00
12/4/22	Scattered clouds	Scattered clouds	Branching, Middle	124,7	13:30:00
12/5/22	Overcast	Overcast	Branching, Middle	108,1	11:30:00
12/6/22	Partly Sunny	Partly Sunny	Branching, Middle	119,6	14:40:00
12/7/22	Scattered clouds	Partly Sunny	Branching, Edge (inner)	115,9	13:20:00
12/8/22	Overcast	Overcast	Branching, Edge (inner)	116,7	12:10:00
12/9/22	Overcast	Overcast	Branching, Edge (inner)	104,9	12:20:00
12/10/22	Overcast	Scattered clouds	Branching, Edge (outer)	113	12:50:00
12/11/22	Overcast	Overcast	Branching, Edge (outer)	110,2	14:30:00
12/12/22	Partly Sunny	Partly Sunny	Branching, Edge (outer)	114	12:30:00
12/13/22	Partly Sunny	Partly Sunny	Deep, 9m	102,8	16:20:00
12/14/22	Partly Sunny	Partly Sunny	Deep, 9m	102,2	11:00:00
12/15/22	Partly Sunny	Partly Sunny	Deep, 9m	102,6	12:20:00
12/16/22	Partly Sunny	Overcast	Deep, 22m	98,9	17:50:00
12/17/22	NA	Scattered clouds	Deep, 22m	99,4	11:20:00
12/18/22	Overcast	Overcast	Deep, 22m	100,8	12:40:00

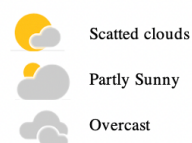


Table S4. Mean, standard deviation, variance, maximum and minimum values of D_{max} (%) at the different reef sites.

		Reef Sites									
		Table, Middle	Table, Edge	Massive, Middle	Massive, Edge	Branching, Middle	Branching, Edge (outer)	Branching, Edge (inner)	Deep, 9m	Deep, 22m	
Frequency		4	3	3	3	3	4	3	3	3	
Domax (%)	Mean	124,98	111,23	112	107	117,47	113,2	113,39	102,53	99,7	
	Std. Deviation	3,34	2,55	0,2	1,05	8,5	7,09	2,06	0,31	0,98	
	Variance	10,98	6,52	0,04	1,11	72,3	50,28	4,2	0,09	0,97	
	Minimum	120,3	109,2	111,8	105,9	108,1	105,2	110,57	102,2	98,9	
	Maximum	127,8	114,1	112,2	108	124,7	118,35	115,44	102,8	100,8	

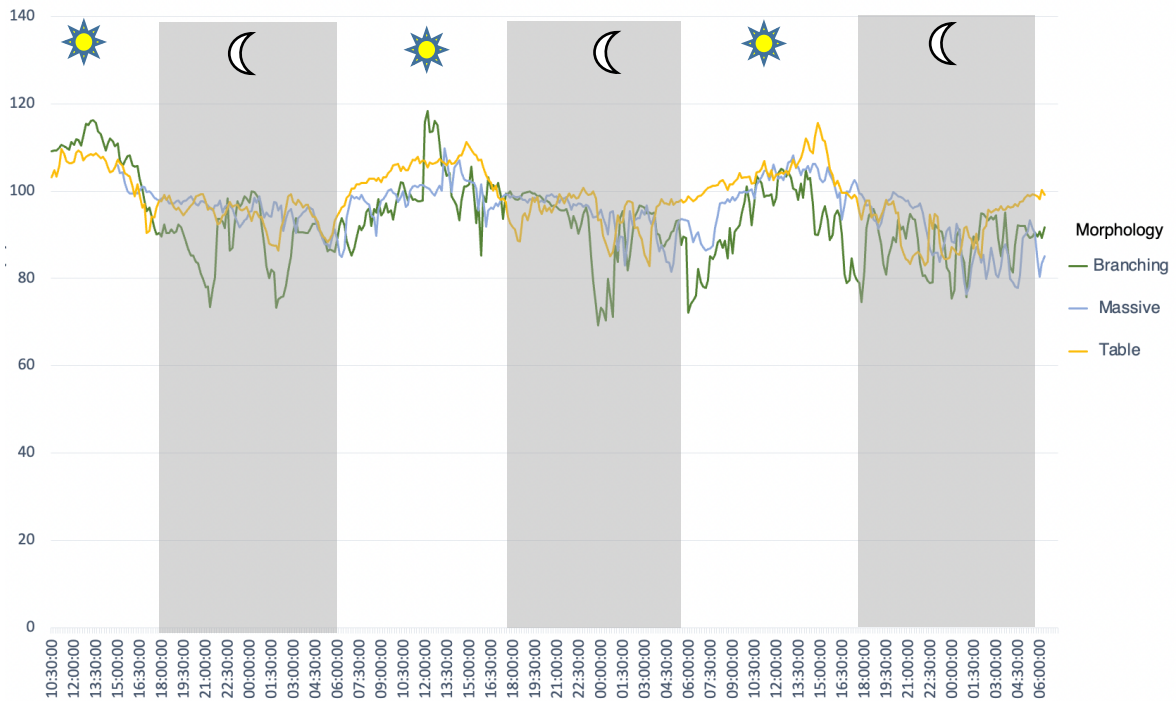


Figure S2. Oxygen saturation (%) measured over time at the edge of the reef for the three different morphologies: branching, massive and table corals. The data for the different coral morphologies were all measured on different days.

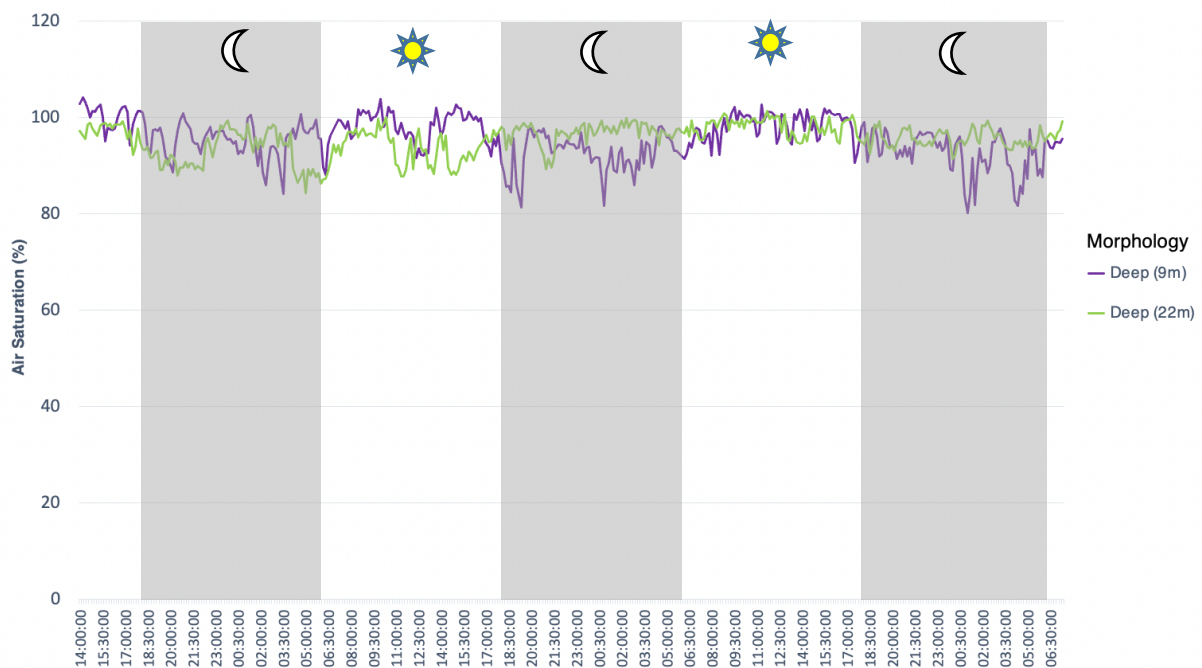


Figure S3. Oxygen saturation (%) measured over time at the deeper depths (9m and 22m). The data for the different depths were measured on different days. The sun represents the daytime intervals (6 am to 6 pm) and the shadowed areas with the moon represent the nighttime intervals (6 pm to 6 am).

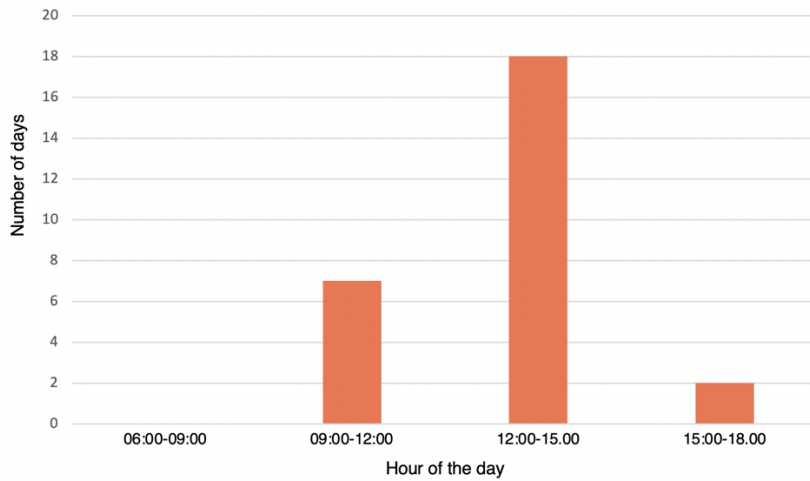


Figure S4. Timing of DOmax occurrence during the day (06:00-18:00). Showing for how many days the DOmax occurred at a certain time interval, 06:00-09:00, 09:00-12:00, 12:00-5:00 and 15:00-18:00.

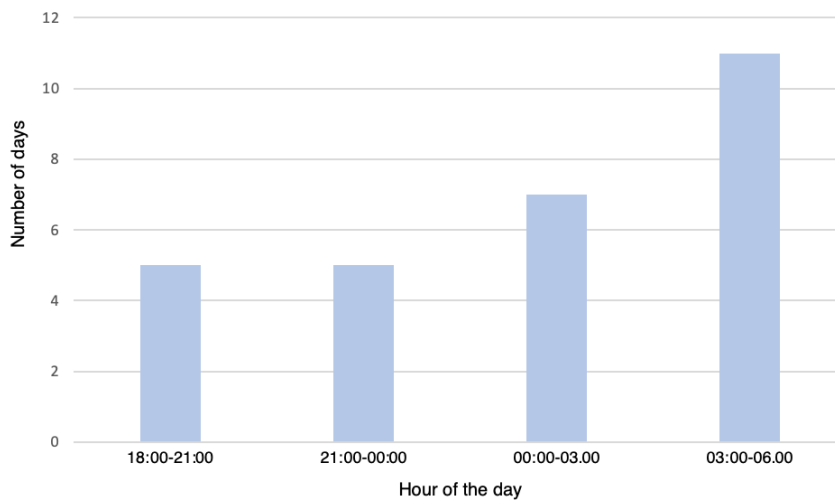


Figure S5. Timing of DOfin occurrence during the night (18:00-06:00-). Showing for how many nights the DOfin occurred at a certain time interval, 18:00-21:00, 21:00-00:00, 00:00-03:00 and 03:00-06:00.