Unraveling the physiological responses of morphologically distinct corals to low oxygen (#95392)

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Unraveling the physiological responses of morphologically distinct corals to low oxygen

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Background. Low oxygen in marine environments, intensified by climate change and local pollution, poses a substantial threat to global marine ecosystems, especially impacting vulnerable coral reefs and causing metabolic crises and bleaching-induced mortality. Yet, our understanding of the potential impacts in tropical regions is incomplete. Furthermore, uncertainty surrounds the physiological responses of corals to hypoxia and anoxia conditions. **Methods.** We initially monitored *in situ* dissolved oxygen (DO) levels at Kham Island in the lower Gulf of Thailand. Subsequently, we conducted a 72-hour experimental exposure of corals with different morphologies—*Pocillopora acuta*, *Porites lutea*, and *Turbinaria mesenterina*—to low oxygen conditions, while following a 12/12-hour dark/light cycle. Three distinct dissolved oxygen (DO) conditions were employed: control (DO 6.0±0.5 mg/L), hypoxia (DO 2.0±0.5 mg/L), and anoxia (DO < 0.5 mg/L). We measured and compared photosynthetic efficiency, Symbiodiniaceae density, chlorophyll concentration, respiratory rates, primary production, and calcification across the various treatments. **Results.** Persistent hypoxia was observed at the study site. Subsequent experiments revealed that low oxygen levels led to a notable decrease in the maximum quantum yield over time in all the species tested, accompanied by declining rates of respiration and calcification. Our findings reveal the sensitivity of corals to both hypoxia and anoxia, particularly affecting processes crucial to energy balance and structural integrity. Notably, *P. lutea* and *T. mesenterina* exhibited no mortality over the 72-hour period, while *P. acuta*, exposed to anoxia, experienced mortality with tissue loss within 24 hours. This study underscores species-specific variations in susceptibility associated with different morphologies under low oxygen conditions. The results demonstrate the substantial impact of deoxygenation on coral growth and health, with the compounded challenges of climate change and coastal pollution exacerbating oxygen availability,

leading to increasingly significant implications for coral ecosystems.

Unraveling the Physiological Responses of Morphologically Distinct Corals to Low Oxygen

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Abstract

Background. Low oxygen in marine environments, intensified by climate change and local pollution, poses a substantial threat to global marine ecosystems, especially impacting vulnerable coral reefs and causing metabolic crises and bleaching-induced mortality. Yet, our understanding of the potential impacts in tropical regions is incomplete. Furthermore, uncertainty surrounds the physiological responses of corals to hypoxia and anoxia conditions.
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Introduction

Oceans worldwide are experiencing a decline in oxygen levels as the climate warms and coastal pollution accelerates, which could have adverse effects on the diversity and richness of marine organisms (Bopp et al., 2013; Breitburg et al., 2018; Camp et al., 2018; Sampaio et al., 2021). 'Hypoxia' is defined by oxygen levels of 2 to 3.5 mg O_2/L or less, and this is a condition that some studies have suggested may impose more severe impacts on marine life than ocean warming, ocean acidification, or their combined effects (Vaquer-Sunyer & Duarte, 2008; Bijma et al., 2013; Haas et al., 2014).

According to the Intergovernmental Panel on Climate Change (IPCC) and their representative concentration pathways (RCP 2.6-8.5), the dissolved oxygen content is projected to decrease by between 1.7% and 4% by 2100 due to climate change drivers (IPCC, 2022). Over the past 50 years, certain tropical areas, including the Central Pacific and the Indian Ocean, have experienced a significant decline, with up to a 40% reduction in their dissolved oxygen levels (Schmidtko, Stramma & Visbeck, 2017). This decrease is primarily attributed to the absorption of rising atmospheric CO_2 from human activities and the impact of consequent excessive heat (Levin & Bris, 2015; Henson, Beaulieu & Lampitt, 2016). As the oceans warm, the solubility of oxygen in seawater decreases, and simultaneously, the physiological oxygen requirements for many organism's increase. This scenario can lead to altered behavior, migrations, decreased growth rates, reduced fecundity, and higher mortality rates (Levin & Bris, 2015; Breitburg et al., 2018). In addition, coastal areas are experiencing hypoxic or anoxic conditions due to factors such as, eutrophication and restricted circulation (Nakamura, Yamasaki & Van Woesik, 2003; Ulstrup, Hill & Ralph, 2005; Keeling, Körtzinger & Gruber, 2009).

Hermatypic scleractinian corals are pivotal as the primary reef-building species, thriving in shallow, warm water environments with adequate light. They play a vital role in supporting a diverse array of marine species by providing food, shelter, and substrate (Liao, Xiao & Li, 2019; Raphael et al., 2020). Their metabolic needs, constituting up to 90% of metabolism, are fulfilled through a mutualistic interaction with endosymbiotic dinoflagellate algae known as Symbiodiniaceae (Muscatine, 1990). However, unfavorable environmental factors can lead to the disruption of this essential symbiosis (Zhu et al., 2004; Suggett & Smith, 2020), with hypoxia acknowledged as one of the primary drivers.

The extent and consequences of low oxygen are increasingly recognized (Hughes et al., 2020). Previous findings underscore a growing concern as they highlight the widespread deaths of

corals and coral reef associated animals attributed to hypoxia and dead zones (Altieri & Gedan, 2015; Altieri et al., 2017). Notably, the consequences of coral mass mortality extend beyond direct impacts, as many faunas associated with coral reef habitats are also affected (Alderdice et al., 2020). It has been established that inadequate oxygen hampers cellular processes, deteriorating coral health and rendering it susceptible to severe bleaching under hypoxia (Alderdice et al., 2020; Figuerola et al., 2021; Jain et al., 2023). Our recent study along the Andaman coast of Thailand reveals that hypoxia significantly impacts various coral health parameters, resulting in reduced photosynthetic efficiency, Symbiodiniaceae density, chlorophyll concentration, and overall coral growth in certain species. The study further emphasizes distinct susceptibility levels to hypoxia among the different tested coral species, underscoring the importance of identifying species-specific responses for effective management strategies (Jain et al., 2023).

The present study by Kham Island in the southern Gulf of Thailand was initiated by measuring *in situ* dissolved oxygen. Building upon these data, an experimental approach was employed to assess the susceptibility to low oxygen conditions among three morphologically distinct dominant coral species at Kham Island: *P. acuta*, *P. lutea*, and *T. mesenterina*. The investigation explored changes in the physiological performances and metabolism of these corals across a range of dissolved oxygen levels categorized as hypoxia and anoxia. As the first findings from the lower Gulf of Thailand and complementing our previous study, this research aims to offer guidance for prioritizing management initiatives to alleviate the adverse effects of low oxygen in tropical shallow-water coral reefs. Within the broader context of global climate change, the study provides essential baseline information to enhance ecological risk assessment.

Materials & Methods

Assessment of *in situ* environmental parameters:

The study site is located at the northern part of Kham Island (6°58’24.3” N 100°51’24.8” E), situated in the lower Gulf of Thailand within Songkhla Province (Fig. 1). The depth in the study area ranges within 3-5 meters. According to the Department of Marine and Coastal Resources, Thailand (DMCR) survey conducted in 2019, the primary reef areas in both the northern and southern regions of the island were reported to be in very good condition.

To establish baseline conditions for experimental simulations, we recorded environmental parameters at the study site. One HOBO® U26-001 data logger (Onset, USA) was strategically positioned at a depth of 5 meters in the northern part of the reef area of Kham Island. This logger was programmed to record DO values at hourly intervals from 22 June 2021 to 30 June 2022 (except for 20 Jan 2022- 4 Mar 2022), contributing to a detailed temporal profile of the DO dynamics within the specified aquatic environment. Additionally, we employed the AAQ-RINKO 176 multiprobe (JFE Advantech Co. Ltd., Hyogo, Japan) to collect data on various

parameters, including temperature, salinity, chlorophyll *a* concentration, pH and irradiance. Detailed information is provided in Supplementary Table 1.

Figure 1. Sampling site location, southern Gulf of Thailand

Coral sampling and acclimation

In June 2022, healthy colonies (n = 8) of each of the coral species *P. acuta, P. lutea* and *T. mesenterina* were collected using stainless hammer and chisel. These are the dominant coral species at Kham Island. The research permission in the Non-Hunting Area was approved by the Department of National Parks, Wildlife and Plant Conservation (permission number: 21685). Coral collection was permitted by the Department of Fisheries, Ministry of Agriculture and Cooperatives (permission number: 409) under Wild Animal Conservation and Protection Act, B.E. 2562 (A.D. 2019). The live samples were transferred to the aquarium facility of Coastal Oceanography and Climate Change Research Center (COCC) at Prince of Songkla University (PSU) within 2 hours. Here, they were acclimated in a 600 L holding tank that simulated the environmental conditions (light 120 µmol photons m^{-2} s^{-1}, temperature 29°C, salinity 33 psu, and pH 8.20) of the sampling area. Following a week of acclimation in the holding tank, each colony was cut into 3–5 cm nubbins (totaling 72 nubbins, with 24 nubbins per species) and subjected to an additional week of acclimation.

Experiment design

The experiment of this study was conducted according to the Animals for Scientific Purposes Act, B.E. 2558 (A.D. 2015) and approved by Institutional Animal Care and Use Committee**,** Prince of Songkla University (ref.46/2021). A total of 72 coral nubbins were placed into individual chambers, subjected to three different treatments, each with 8 nubbins per species. The treatments were as follows: 1) Ambient with dissolved oxygen (DO) levels ranging from 6.0 to 6.5 mg/L, 2) Hypoxia with DO levels ranging from 1.5 to 2.5 mg/L, and 3) Anoxia with DO levels ranging from 0 to 0.5 mg/L (refer to Fig. 2 for graphical representation). Dissolved oxygen (DO) levels were adjusted in 50 L stock seawater tanks using a nitrogen high-pressure regulator (IM-TCH, China) with an air compressor pressure regulator (Xcpc, China). Prepared seawater was added to each chamber, and coral nubbins were gently placed inside. All chambers were then sealed with parafilm (Bemis, USA).

The experiment ran for 72 hours in a 12:12 dark/light cycle, commencing in a dark condition. Throughout the experiment, light, temperature, and salinity were controlled and maintained at the same conditions as during the acclimation period. The seawater in each chamber underwent renewal every 12 hours, synchronized with the light cycle, utilizing freshly prepared seawater specific to the treatment. Dissolved oxygen (DO) and pH measurements were recorded before and after each 12-hour incubation period, alongside simultaneous collection of water samples for total alkalinity measurement. The maximum quantum yield of all nubbins was assessed at the

onset of dark/light conditions. Coral nubbins were collected at the initiation and conclusion of the experiment, subsequently stored in a -80°C liquid nitrogen tank for later analysis of Symbiodiniaceae density and chlorophyll content. The experimental design is summarized in Fig. 2.

Figure 2. Experimental design and sampling parameters

Measurement protocols

Chlorophyll fluorescence

The photosynthetic efficiency represented by the maximum quantum yield (MQY) was evaluated at 9:30 and 22:30 following dark adaptation. Quantification of MQY for *P. acuta*, *P. lutea*, and *T. mesenterina* in each treatment was conducted every 12 hours using a Diving-PAM fluorometer (Walz GmbH, Germany) connected to a 6 mm diameter fiberoptic probe. The PAM settings were held constant with a measuring light intensity (MEAS-INT) of 5, electronic signal gain (GAIN) set to 2, saturation pulse intensity (SAT-INT) at 8, and the width of the saturating light pulse (SATWIDTH) at 0.6 s.

Symbiodiniaceae density and chlorophyll content

The symbiotic relationship with Symbiodiniaceae was investigated by employing the density of Symbiodiniaceae and chlorophyll content as proxies. Each frozen coral nubbin underwent air-blasting to separate the coral tissue from the skeleton, followed by dissolution in 50 mL artificial seawater (3.2% NaCl solution). The resulting tissue slurries were then centrifuged at 1,000 rpm for 10 min, and 1 mL of each sample was extracted for Symbiodiniaceae cell counting using a hemocytometer under a light microscope.

The remaining slurry was resuspended in 3 mL of 90% acetone and stored in darkness for 24 h at 4°C. Subsequently, it was centrifuged at 5,000 rpm for 5 min, and the photosynthetic pigments (chlorophyll *a* and chlorophyll c_2) were measured using a spectrophotometer (SP8001, Metertech, Taiwan) by taking absorbance readings at 630, 664, and 750 nm. The standard spectrophotometric method described by Ritchie (2006) was employed for chlorophyll analysis. Symbiodiniaceae density and chlorophyll concentration were determined per the surface area of the coral nubbin. The paraffin wax method was utilized to determine the coral's surface area (Stimson & Kinzie, 1991).

Respiration and primary production

Dissolved oxygen (DO) levels in all chambers were monitored in both dark and light conditions using a multiparameter benchtop meter (inoLab® Multi 9630 IDS, Xylem Analytics, Oberbayern, Germany).

Respiration rate (R) and net primary production (NPP) were subsequently calculated based on the oxygen consumption in dark conditions and the oxygen release in light conditions, respectively. The calculations followed the methodology by Cohen, Dubinsky, and Erez (2016). The equation for R (or NPP) is as follows.

$$NPP \ \ or \ \ R \ (\text{mg } O_2 \text{ cm}^{-2} \text{ h}^{-1}) = \frac{(O2 \ end - O2 \ start) * V}{Time * Surface \ area}$$

Here, V represents the volume of the chamber, time is the duration of the measurement (12 h), and the surface area is the surface area of the coral nubbin. This approach allows for estimating the gross primary production as follows.

$$Gross \ primary \ production \ (\text{mg } O_2 \text{ cm}^{-2} \text{ h}^{-1}) = Net \ primary \ production - Respiration \ rate$$

Calcification rate

The HI84502 mini titrator (HANNA Instruments, Woonsocket, RI, USA) was employed to perform titrations on seawater for the determination of total alkalinity (TA). As coral calcification is a light-enhanced process (Mallon et al., 2022), the change in total alkalinity during light conditions was utilized to calculate the calcification rate, employing the equation outlined by Cohen, Dubinsky, and Erez (2016). The equation is as follows:

$$Calcification \ rate \ (\mu\text{mol } O_2 \text{ cm}^{-2}\text{h}^{-1}) = \frac{\frac{\Delta TA}{2} * V * 1000 * 1.028}{Time * Surface \ area}$$

Here, ΔTA represents the difference between the initial (TA start) and the final (TA end) total alkalinities, V is the chamber volume, 1.028 is the seawater density (1.028 L × Kg^{-1}), the division by 1000 converts mmol to µmol, time is the duration of the measurement (12 hours), and Surface area is the surface area of each coral nubbin. This formula allows for the quantitative assessment of calcification rate per unit surface area over the specified time period and chamber conditions.

Statistical analysis

All parameters underwent a Shapiro-Wilk Test to assess normality, and in cases of non-normal distribution, square root or log10 transformation was applied. Two-way ANOVA was employed to identify significant differences in MQY, net primary production, gross primary production, respiration rate, and calcification rate among treatments and days. For the specific species *P. acuta*, which died within one day of anoxia, one-way ANOVA was utilized to detect significant differences between treatments in parameters such as net primary production, gross primary production, respiration rate, and calcification rate. To assess significant differences in Symbiodiniaceae density and chlorophyll concentration among treatments, one-way ANOVA

was applied. All statistical tests were conducted at a 95% confidence level threshold. *Post hoc* comparisons were performed using the Tukey Honestly Significant Difference (HSD) test.

Results

In-situ dissolved oxygen

Between June 2021 and June 2022, DO loggers consistently monitored the dissolved oxygen levels at 12:00 and 24:00 daily in the reef region to the north of Kham Island. The annual average dissolved oxygen concentration, excluding February 2022, was found to be 4.84 mg/L. Our data suggests the presence of recurring hypoxic events in the reef area of the northern part of Kham Island, particularly between September and November 2021. Over this three-month period, the dissolved oxygen in the reef area consistently fell below 4 mg/L, with numerous instances of levels dropping even lower, reaching below 2 mg/L (refer to Fig. 3). Analyzing the monthly trends, we observed a notable decline in DO levels almost every month from July 2021 through the middle of October 2021. This downward trend continued, with DO levels plummeting to 1 mg/L in October 2021. Hypoxia was identified during 7 out of the 11 recorded months.

Figure 3. DO record in coral reef at Kham Island throughout the period from June 2021 to June 2022.

Chlorophyll fluorescence

Significantly lower values of MQY were observed in the anoxia treatment compared to the control treatment during nighttime, across all the studied species (Fig. 4). A significant interaction between treatment and time was detected for all three species ($p<0.001$, see Supplementary Table 1a). In the case of *P. acuta* subjected to anoxia scenario, there was a notable decline in MQY after the initial 12 hours in dark condition, leading to a complete loss of coral tissue within 24 h. Similarly, corals exposed to hypoxic conditions exhibited significantly reduced photosynthetic efficiency compared to the control group after a 24 h treatment period (Fig. 4a), with the effects being less pronounced than those observed under anoxia. Significant variations between treatments were evident in *P. lutea* ($p<0.001$). In anoxic conditions, corals exhibited significantly decreased photosynthetic efficiency when treated in the dark compared to the control; however, the efficiency was notably recovered when the light was on (Fig. 4b).

The performance of *T. mesenterina*, particularly concerning the MQY, stood out among the three species. Time exerted a substantial influence on MQY ($p<0.001$), as observed in both nighttime and daytime measurements. Notably, during the dark treatment period, MQY was significantly lower than during the light treatment condition (Fig. 4c).

In the comparison of treatments, corals subjected to anoxia exhibited a significant reduction in photosynthetic efficiency during the initial 12 hours of treatment. In contrast, corals under hypoxic conditions displayed a slower response compared to the anoxia treatment. Notably, both groups of corals ultimately recovered by the end of the experiment (72 h). These findings underscore the unique temporal and treatment-specific dynamics influencing the photosynthetic performance of *T. mesenterina*.

Figure 4: Maximum quantum yield (MQY) of *P. acuta* (a), *P. lutea* (b), and *T. mesenterina* (c) under hypoxia and anoxia during a 72-h experiment. The shaded area represents nighttime. Capital letters indicate differences between times. Lowercase letters denote differences between treatments.

Symbiodiniaceae density and chlorophyll content

The photosynthetic symbiont and pigments exhibited a lesser impact under low oxygen conditions (hypoxia and anoxia). In *P. acuta* corals, both hypoxia and anoxia treatments led to a significantly lower density of Symbiodiniaceae compared to the initial group collected at the beginning of the experiment ($p = 0.049$), so there was tissue loss. However, no significant difference in Symbiodiniaceae density was observed in *P. lutea* and *T. mesenterina*. Additionally, anoxia treatment resulted in significantly lower concentrations of chlorophyll *a* and chlorophyll c_2, reflecting the impact of tissue loss. In *T. mesenterina*, hypoxia treatment led to a significant decrease in chlorophyll *a* concentration ($p = 0.014$). Notably, *P. lutea* showed no discernible effect from hypoxia and anoxia in these three parameters.

Figure 5: Comparison of Symbiodiniaceae density (a), chlorophyll *a* concentration (b), and chlorophyll c_2 concentration (c) in *P. acuta*, *P. lutea*, and *T. mesenterina* under hypoxia and anoxia before (initial) and after a 72 h experiment. Lowercase letters indicate differences between treatments.

Respiration and primary production

Respiration

Hypoxia and anoxia conditions exerted significant impacts on respiration of all the species (Fig. 6, Supplementary Table). The effects of treatments were statistically significant ($p < 0.001$). However, there were no significant differences observed between the days of sampling for *P. lutea* and *T. mesenterina* ($p = 0.796$ and $p = 0.860$, respectively). Additionally, no interaction effects were identified for *P. lutea* ($p = 0.896$) and *T. mesenterina* ($p = 0.595$).

Figure 6: Respiration rates of *P. acuta* (a), *P. lutea* (b), and *T. mesenterina* (c) from day 1 to day 3 under control, hypoxic, and anoxic conditions. Lowercase letters denote differences between treatments, while uppercase letters indicate differences between days.

Primary production

While *P. acuta* exhibited no significant effect on net primary production rates under hypoxia and anoxia (p=0.053), *P. lutea* displayed variability in net primary production. Specifically, under hypoxic conditions, *P. lutea* showed no difference in net primary production. However, under anoxic conditions, it exhibited a significantly higher net primary production rate compared to other treatments across all three days (p<0.001). Importantly, there was no discernible impact from the days of incubation, and no interaction effects were observed (p=0.849 and p=0.876, respectively). On the other hand, an interaction effect between treatment and day was observed in *T. mesenterina* (p=0.034). The net primary production rates of *T. mesenterina* were significantly affected by hypoxia and anoxia (p<0.001). Furthermore, under anoxic conditions, *T. mesenterina* exhibited significantly higher net primary production rates from the first day.

Figure 7: Net primary production from day 1 to day 3 of *P. acuta* (a), *P. lutea* (b), and *T. mesenterina* (c) under control, hypoxia, and anoxia conditions. Lowercase letters denote differences between treatments, while uppercase letters indicate differences between days.

In terms of gross primary production, *P. acuta* exhibited a significant reduction in the gross primary production rates under both hypoxia and anoxia conditions (p=0.001). In contrast, *P. lutea* only displayed a lower gross primary production rate on the first day of the experiment (p=0.002). Unlike *P. acuta* and *P. lutea*, *T. mesenterina* showed significantly lower gross primary production rates specifically under anoxia (p=0.042) on the third day of the experiment (p=0.016).

Figure 8: Gross primary production from day 1 to day 3 for *P. acuta* (a), *P. lutea* (b), and *T. mesenterina* (c) under control, hypoxia, and anoxia conditions. Lowercase letters denote differences between treatments, while uppercase letters indicate differences between days.

Calcification

The calcification rate of *P. acuta* was significantly affected by anoxia (p=0.020). In the case of *P. lutea*, calcification rates were influenced by both hypoxia and anoxia (p<0.001). A significantly lower calcification rate under hypoxia was observed on the second day, while under anoxia, the calcification rate of *P. lutea* exhibited an effect across all three days. Calcification rates of *T. mesenterina* were significantly influenced by treatment (p < 0.001), day (p < 0.01), and with an interaction between these factors (p < 0.001). Initially, on the first day of stress, the calcification rate of *T. mesenterina* remained unaffected by hypoxia or anoxia. However, a notable reduction was observed on the second and third days under these conditions.

Figure 9: Calcification rate from day 1 to day 3 of *P. acuta* (a), *P. lutea* (b), and *T. mesenterina* (c) under control, hypoxia, and anoxia conditions. Lowercase letters denote differences between treatments, while uppercase letters indicate differences between days.

Discussion

A comprehensive inquiry into the effects of oxygen limitation on coral ecosystems within the lower Gulf of Thailand is motivated by the urgent need to address the growing threat of deoxygenation events to coral health globally (Altieri et al., 2017; Hughes et al., 2020; Nelson & Altieri, 2019). Given the limited availability of dissolved oxygen data in Thailand, we initiated regular monitoring, revealing persistent hypoxic conditions in the study site (Fig. 3). Recorded data reveals a consistent decrease in seawater oxygen levels, reaching hypoxia (oxygen less than 2 mg/L), particularly during two periods: from the end of September to mid-October and in mid-May, aligning with elevated temperatures (Fig. S1). The solubility of oxygen and metabolic requirements in aquatic ectotherms is intricately linked to water temperature (Roman et al., 2019). Moreover, the proximity to mainland of Kham Island, situated just 2 km from the estuarine and close to the coastal area (Fig. 1), makes it susceptible to anthropogenic activities and freshwater runoff, contributing to the phenomenon of ocean deoxygenation (Laffoley & John, 2019; Mancini et al., 2023).

Based on these data, our objective was to investigate the impact of hypoxia and anoxia conditions on the physiological performance of the predominant coral species, *P. acuta*, *P. lutea*, and *T. mesenterina*. Our findings reveal that diminished oxygen levels significantly influence various physiological processes, reducing the integrity of photosystem II, and decreasing respiration, primary production, and calcification rates. Importantly, the observed effects are contingent upon the specific oxygen levels (hypoxia or anoxia) and associated with the morphological variations among different coral species.

Our investigation highlights a significant impact of low oxygen conditions on the photosynthetic performance of the three coral species. The decline in photosynthetic efficiency is attributed to a structural alteration in photochemical reaction centers and/or the donor and acceptor sides and a reduction in photosystem II density, affecting electron transport, as corroborated by previous studies (Gorbunov et al., 2001; Hill et al., 2004; Smith, Suggett & Baker, 2005; Duarte et al., 2017; Franzitta et al., 2020; Deleja et al., 2022; Smythers et al., 2023). However, the recent findings of Deleja et al. (2022) propose that although photochemical reaction centers remain unchanged during nighttime hypoxia, there is an observed modification in the connectivity between the PSII antennae. This alteration results in a reduced absorption of the photon flux by the pigment antenna, ultimately leading to an insufficient amount of transported energy to the reaction centers (Duarte et al., 2015; Strasser & Stirbet, 2001). Furthermore, this photoinhibition may arise from oxidative stress (Deleja et al., 2022), impeding repair of the photosystem and exacerbating damage. Our findings indicate that the effects on photosynthesis related parameters were primarily observed in the maximum quantum yield and, to a certain extent, in the gross photosynthesis rates. However, there was no significant impact on Symbiodiniaceae density or

chlorophyll content. From these observations, we propose that the influence of low oxygen conditions is predominantly on the functionality of the photosynthetic machinery rather than causing a disruption in the symbiotic relationship between coral and Symbiodiniaceae or triggering the onset of bleaching. This finding aligns with our earlier research (Jain et al., 2023) and is consistent with findings from other studies (Alva García et al., 2022; Deleja et al., 2022). It suggests that chlorophyll fluorescence parameters may serve as effective biomarkers for detecting hypoxic and anoxic stresses in *P. acuta*, *P. lutea*, and *T. mesenterina*. Moreover, it is noteworthy that the impacts of hypoxia exhibited significant variations between periods with and without light, corresponding to daytime and nighttime conditions. This pattern may be attributed to the ongoing photosynthetic activity during the day, contributing to oxygen production and alleviating tissue oxygen levels. In contrast, during nighttime, when photosynthetic activity ceases and respiration consumes oxygen, the impact of oxygen deprivation intensifies.

Cellular respiration, a vital process for generating energy for cellular functions, was significantly impacted by low oxygen in our study. Under these conditions, *P. acuta*, *P. lutea*, and *T. mesenterina* exhibited reduced respiration rates. The observed influence of oxygen limitation on coral respiration aligns with findings from previous studies (Dodds et al., 2007; Nelson & Altieri, 2019; Alva García et al., 2022; Gravinese et al., 2022). Certain cnidarians have demonstrated the ability to tolerate acute hypoxic and anoxic conditions by transitioning from aerobic respiration to the less efficient anaerobic respiration pathway, enabling them to survive extended exposure periods (Martinez, Smith & Richmond, 2012; Murphy & Richmond, 2016; Gravinese et al., 2022). Consequently, the decrease in respiratory oxygen consumption during hypoxic and anoxic stress observed in our study may be linked to a gradual shift towards anaerobic respiration (Nelson & Altieri, 2019; Gravinese et al., 2022). However, this metabolic shift comes at the cost of energy production and may lead to an energy deficit stage (Murphy & Richmond, 2016). While our measurements were conducted using the holobionts, it is crucial to acknowledge the tight coupling of coral respiration with the photosynthesis of symbiotic algae. Previous studies have demonstrated that the carbon dioxide necessary for photosynthesis by Symbiodiniaceae is derived from coral cellular respiration (Muscatine, Porter & Kaplan, 1989). Consequently, low oxygen not only limits coral and Symbiodiniaceae respiration but also indirectly inhibits symbiotic algal photosynthesis by restricting the supply of carbon dioxide from coral respiration (Harland & Davies, 1995; Gardella & Edmunds, 1999). Furthermore, we propose that the decrease in respiratory rates serves as the primary contributor to a slight increase in net primary production observed in some species in our study. It's important to note that, considering the lower MQY and gross photosynthetic rates, any increase in net primary production should not be interpreted as a positive impact for corals.

Calcification, an essential process for coral growth, exhibited high sensitivity to low oxygen levels in our study. Under these conditions, *P. acuta*, *P. lutea*, and *T. mesenterina* displayed reduced calcification rates. Coral calcification, a "photosynthesis-driven" process, relies on the

energy derived from the photosynthesis of Symbiodiniaceae (Colombo-Pallotta, Rodríguez-Román & Iglesias-Prieto, 2010). Additionally, the products of photosynthesis play a crucial role in fueling corals' aerobic respiration and the deposition of calcium carbonate, which demands a significant portion (13–30%) of the total metabolic energy budget from corals through aerobic respiration (Cohen & Holcomb, 2009; Colombo-Pallotta, Rodríguez-Román & Iglesias-Prieto, 2010; Allemand et al., 2011). Hence, the availability of oxygen plays a vital role not only in respiration and photosynthesis but also in restricting calcification by influencing both respiration and photosynthesis (Colombo-Pallotta, Rodríguez-Román & Iglesias-Prieto, 2010; Wijgerde et al., 2012). Previous studies consistently highlight the significant impact of oxygen on corals' calcification in both dark and light conditions (Al-Horani, Tambutté & Allemand, 2007; Colombo-Pallotta, Rodríguez-Román & Iglesias-Prieto, 2010; Wijgerde et al., 2012, 2014; Nakamura, Nadaoka & Watanabe, 2013; Zhang et al., 2023). These findings underscore the sensitivity of coral calcification to oxygen levels, emphasizing potential implications for overall coral health and growth. Notably, observations of *Pocillopora* species' growth rates showed a substantial 43.3% reduction at relatively lower oxygen levels, as reported by Castrillón-Cifuentes et al. (2023).

Considerable differences in responses among morphologically distinct corals have been documented, with branching and solitary coral colonies being more susceptible to severe hypoxic conditions compared to massive, sub-massive, and encrusting corals (Guzmán et al., 1990; Simpson, Cary & Masini, 1993; Adjeroud, Andréfouët & Payri, 2001).

In our study, *P. acuta* exhibited the highest sensitivity to anoxic conditions, resulting in tissue loss and mortality within 24 hours. This response mirrored the findings in the branching coral *Acropora cervicornis*, which also experienced tissue loss and mortality within a day of exposure to dissolved oxygen levels of 1.0 mg/L (Johnson et al., 2021). These observations underscore the vulnerability of branching corals to stress. Given the susceptibility of *P. acuta* and similar branching species, it is crucial that management efforts prioritize these corals when developing conservation plans and strategies. In contrast, *P. lutea* and *T. mesenterina* did not show any mortality over a 72-hour period, indicating a higher tolerance to hypoxia, consistent with previous records for massive corals such as *P. lutea* and *Orbicella faveolata* (Johnson et al., 2021; Alderdice et al., 2022). This difference in tolerance by morphology also aligns with our recent findings from the Andaman Coast (Jain et al., 2023). However, the variability in hypoxia thresholds is not only evident among genera but also among coral species. For example, within the same genus and morphology, *Acropora selago* and *Acropora yongei* exhibited bleaching under hypoxic conditions within 12 hours, while *Acropora tenuis* showed no bleaching under the same stress (Alderdice et al., 2020; Haas et al., 2014). Effective conservation efforts in the face of climate change should place importance on understanding the biology of corals, considering both the variation within and among species. Tailoring conservation strategies to specific coral

species, especially those with distinct sensitivities to environmental stressors like hypoxia, is critical for the long-term health and resilience of coral reef ecosystems.

Conclusions

In summary, our experiments highlight the sensitivity of corals to hypoxia and anoxia conditions, impacting essential processes related to energy balance and structural integrity. Variability in resilience was evident among species, with *P. acuta* identified as the most susceptible. This study emphasizes species specific variations in vulnerability, linked to different morphologies, under low oxygen conditions, corroborating the earlier suggestion that branching corals are more sensitive to stress.

Our research gains particular relevance considering the persistent hypoxia in the natural environment of our study site. As challenges related to oxygen availability intensify due to climate change and coastal pollution, the implications for coral ecosystems become increasingly significant. A comprehensive understanding of these physiological processes is not only crucial for predicting the consequences of deoxygenation, as well as of climate change in general, but also for developing effective strategies to assess and mitigate the impacts of deoxygenated events on tropical corals.

Consent Statement

The research permission in the Non-Hunting Area was approved by the Department of National Parks, Wildlife and Plant Conservation (permission number: 21685). Coral collection was permitted by the Department of Fisheries, Ministry of Agriculture and Cooperatives (permission number: 409) under Wild Animal Conservation and Protection Act, B.E. 2562 (A.D. 2019). The experiment of this study was conducted according to the Animals for Scientific Purposes Act, B.E. 2558 (A.D. 2015) and approved by Institutional Animal Care and Use Committee**,** Prince of Songkla University (ref.46/2021).

Funding

This research was supported by Prince of Songkla University (Grant number: ENV6402039S) and student grant was provided by PSU-TUYF Charitable Trust Fund under a project “Coral reef biodiversity conservation and connectivity in southern Gulf of Thailand to support reef resilience and sustainable use”.

Acknowledgements

We would like to thank the staff of, and the instrument and material support by the Coastal Oceanography and Climate Change Research Center (COCC) and the Marine and Coastal Resources Institute (MACORIN), Faculty of Environmental Management, Prince of Songkla University; as well as Muhammad Arif Samshuri, Verdiana Vellani, Thanyapat Chamnina, Wilawan Hwan-air, Natchanon Kiatkajornphan, Rattanaporn Sengkhim, Natthaya Sotthiphan,

Jittapon Patcharat, Watchara Samsuvan for their helpful assistance in the field and the laboratory.

References

Adjeroud M, Andréfouët S, Payri C. 2001. Mass mortality of macrobenthic communities in the lagoon of Hikueru atoll (French Polynesia). *Coral Reefs* 19:287–291. DOI: 10.1007/PL00006962.

Alderdice R, Hume BCC, Kühl M, Pernice M, Suggett DJ, Voolstra CR. 2022. Disparate inventories of hypoxia gene sets across corals align with inferred environmental resilience. *Frontiers in Marine Science* 9:834332. DOI:10.3389/fmars.2022.834332.

Alderdice R, Suggett DJ, Cárdenas A, Hughes DJ, Kühl M, Pernice M, Voolstra CR. 2020. Divergent expression of hypoxia response systems under deoxygenation in reef-forming corals aligns with bleaching susceptibility. *Global Change Biology* 27:312–326. DOI: 10.1111/GCB.15436.

Al-Horani FA, Al-Moghrabi SM, De Beer D. 2003. The mechanism of calcification and its relation to photosynthesis and respiration in the scleractinian coral *Galaxea fascicularis*. *Marine Biology* 142:419–426. DOI: 10.1007/s00227-002-0981-8

Al-Horani FA, Tambutté É, Allemand D. 2007. Dark calcification and the daily rhythm of calcification in the scleractinian coral, *Galaxea fascicularis*. *Coral Reefs* 26:531–538. DOI: 10.1007/s00338-007-0250-x

Allemand D, Tambutté E, Zoccola D, Tambutté S. 2011. Coral calcification, cells to reefs. In: Dubinsky Z, Stambler N, eds. *Coral reefs: an ecosystem in transition*. New York: Springer Press. 119-150.

Altieri AH, Gedan KB. 2015. Climate change and dead zones. *Global Change Biology* 21:1395–1406. DOI: 10.1111/GCB.12754.

Altieri AH, Harrison SB, Seemann J, Collin R, Diaz RJ, Knowlton N. 2017. Tropical dead zones and mass mortalities on coral reefs. *Proceedings of the National Academy of Sciences of the United States of America* 114:3660–3665. DOI: 10.1073/PNAS.1621517114.

Alva García J V., Klein SG, Alamoudi T, Arossa S, Parry AJ, Steckbauer A, Duarte CM. 2022. Thresholds of hypoxia of two Red Sea coral species (*Porites* sp. and *Galaxea fascicularis*). *Frontiers in Marine Science* 9:945293. DOI: 10.3389/FMARS.2022.945293.

Beer S, Björk M, Beardall J. 2014. *Photosynthesis in the Marine Environment*. Hoboken: John Wiley and Sons.

Bijma J, Pörtner HO, Yesson C, Rogers AD. 2013. Climate change and the oceans – What does the future hold? *Marine Pollution Bulletin* 74:495–505. DOI: 10.1016/J.MARPOLBUL.2013.07.022.

Bopp L, Resplandy L, Orr JC, Doney SC, Dunne JP, Gehlen M, Halloran P, Heinze C, Ilyina T, Séférian R, Tjiputra J, Vichi M. 2013. Multiple stressors of ocean ecosystems in the 21st century: Projections with CMIP5 models. *Biogeosciences* 10:6225–6245. DOI: 10.5194/BG-10-6225-2013.

Breitburg D, Levin LA, Oschlies A, Grégoire M, Chavez FP, Conley DJ, Garçon V, Gilbert D, Gutiérrez D, Isensee K, Jacinto GS, Limburg KE, Montes I, Naqvi SWA, Pitcher GC, Rabalais NN, Roman MR, Rose KA, Seibel BA, Telszewski M, Yasuhara M, Zhang J. 2018. Declining oxygen in the global ocean and coastal waters. *Science* 359. DOI: 10.1126/SCIENCE.AAM7240.

Camp EF, Schoepf V, Mumby PJ, Hardtke LA, Rodolfo-Metalpa R, Smith DJ, Suggett DJ. 2018. The future of coral reefs subject to rapid climate change: Lessons from natural extreme environments. *Frontiers in Marine Science* 5:307197. DOI: 10.3389/FMARS.2018.00004/BIBTEX.

Castrillón-Cifuentes AL, Zapata FA, Wild C. 2023. Physiological responses of *Pocillopora* corals to upwelling events in the Eastern Tropical Pacific. *Frontiers in Marine Science* 10. DOI: 10.3389/FMARS.2023.1212717.

Cohen AL, Holcomb M. 2009. Why corals care about ocean acidification uncovering the mechanism. *Oceanography* 22:118–127. DOI: 10.5670/oceanog.2009.102

Cohen I, Dubinsky Z, Erez J. 2016. Light enhanced calcification in hermatypic corals: New insights from light spectral responses. *Frontiers in Marine Science* 2:122. DOI: 10.3389/fmars.2015.00122.

Colombo-Pallotta MF, Rodríguez-Román A, Iglesias-Prieto R. 2010. Calcification in bleached and unbleached *Montastraea faveolata*: Evaluating the role of oxygen and glycerol. *Coral Reefs* 29:899–907. DOI: 10.1007/s00338-010-0638-x

Deleja M, Paula JR, Repolho T, Franzitta M, Baptista M, Lopes V, Simão S, Fonseca VF, Duarte B, Rosa R. 2022. Effects of hypoxia on coral photobiology and oxidative stress. *Biology* 11. DOI: 10.3390/BIOLOGY11071068.

Department of Marine and Coastal Resources (2019). *Report on survey and assessment of the status of marine and coastal resources: Corals and seagrass, fiscal year 2018*. Technical Report. 306 pp. (in Thai).

Dodds LA, Roberts JM, Taylor AC, 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* 349:205–214. DOI: 10.1016/J.JEMBE.2007.05.013.

Duarte B, Cabrita MT, Gameiro C, Matos AR, Godinho R, Marques JC, Caçador I. 2017. Disentangling the photochemical salinity tolerance in *Aster tripolium* L.: connecting biophysical traits with changes in fatty acid composition. *Plant Biology* 19:239–248. DOI: 10.1111/PLB.12517.

Duarte B, Goessling JW, Marques JC, Caçador I. 2015. Ecophysiological constraints of *Aster tripolium* under extreme thermal events impacts: Merging biophysical, biochemical and genetic insights. *Plant Physiology and Biochemistry* 97:217–228. DOI: 10.1016/J.PLAPHY.2015.10.015.

Figuerola B, Grossman EL, Lucey N, Leonard ND, O'Dea A. 2021. Millennial-scale change on a Caribbean reef system that experiences hypoxia. *Ecography* 44:1270–1282. DOI: 10.1111/ECOG.05606.

Franzitta M, Feijão E, Cabrita MT, Gameiro C, Matos AR, Marques JC, Goessling JW, Reis-Santos P, Fonseca VF, Pretti C, Caçador I, Duarte B. 2020. Toxicity going nano: Ionic *versus* engineered Cu nanoparticles impacts on the physiological fitness of the model diatom *Phaeodactylum tricornutum*. *Frontiers in Marine Science* 7:539827. DOI: 10.3389/fmars.2020.539827.

Gardella DJ, Edmunds PJ. 1999. The oxygen microenvironment adjacent to the tissue of the scleractinian *Dichocoenia stokesii* and its effects on symbiont metabolism. *Marine Biology* 135:289–295. DOI: 10.1007/s002270050626.

Gorbunov MY, Kolber ZS, Lesser MP, Falkowski PG. 2001. Photosynthesis and photoprotection in symbiotic corals. *Limnology and Oceanography* 46:75–85. DOI: 10.4319/LO.2001.46.1.0075.

Gravinese PM, Douwes A, Eaton KR, Muller EM. 2022. Ephemeral hypoxia reduces oxygen consumption in the Caribbean coral *Orbicella faveolata*. *Coral Reefs* 41:13–18. DOI: 10.1007/s00338-021-02197-5.

Guzmán H, Cortés J, Glynn P, Richmond R. 1990. Coral mortality associated with dino-flagellate blooms in the eastern Pacific (Costa Rica and Panama). *Marine Ecology Progress Series* 60:299–303. DOI: 10.3354/MEPS060299.

Haas AF, Smith JE, Thompson M, Deheyn DD. 2014. Effects of reduced dissolved oxygen concentrations on physiology and fluorescence of hermatypic corals and benthic algae. *PeerJ* 2014: e235. DOI: 10.7717/peerj.235.

Harland AD, Davies PS. 1995. Symbiont photosynthesis increases both respiration and photosynthesis in the symbiotic sea anemone *Anemonia viridis*. *Marine Biology* 123:715–722. DOI: 10.1007/BF00349114.

Henson SA, Beaulieu C, Lampitt R. 2016. Observing climate change trends in ocean biogeochemistry: when and where. *Global Change Biology* 22:1561–1571. DOI: 10.1111/GCB.13152.

Hill R, Larkum AWD, Frankart C, Kühl M, Ralph PJ. 2004. Loss of functional photosystem II reaction centres in Symbiodiniaceae of corals exposed to bleaching conditions: Using fluorescence rise kinetics. *Photosynthesis Research* 82:59–72. DOI: 10.1023/B:PRES.0000040444.41179.09.

Hughes DJ, Alderdice R, Cooney C, Kühl M, Pernice M, Voolstra CR, Suggett DJ. 2020. Coral reef survival under accelerating ocean deoxygenation. *Nature Climate Change 2020 10:4* 10:296–307. DOI: 10.1038/s41558-020-0737-9.

IPCC. 2022: Summary for Policymakers [H.-O. Pörtner, D.C. Roberts, E.S. Poloczanska, K. Mintenbeck, M. Tignor, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem (eds.)]. In: *Climate Change 2022: Impacts, Adaptation, and Vulnerability*. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 3-33, doi:10.1017/9781009325844.001.

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* 11:403. DOI: 10.3390/JMSE11020403/S1.

Johnson MD, Swaminathan SD, Nixon EN, Paul VJ, Altieri AH. 2021. Differential susceptibility of reef-building corals to deoxygenation reveals remarkable hypoxia tolerance. *Scientific Reports* 11:1–12. DOI: 10.1038/s41598-021-01078-9.

Keeling RF, Körtzinger A, Gruber N. 2009. Ocean deoxygenation in a warming world. *Annual Review of Marine Science* 2:199–229. DOI: 10.1146/ANNUREV.MARINE.010908.163855.

Laffoley D, John M. Baxter. 2019. *Ocean deoxygenation: everyone's problem. Causes, impacts, consequences and solutions*. IUCN, International Union for Conservation of Nature. DOI: 10.2305/IUCN.CH.2019.13.en.

Levin LA, Bris NL. 2015. The deep ocean under climate change. *Science* 350:766–768. DOI: 10.1126/SCIENCE.AAD0126.

Liao B, Xiao B, Li Z. 2019. Coral Reef Ecosystem. *Symbiotic Microbiomes of Coral Reefs Sponges and Corals*:1–15. DOI: 10.1007/978-94-024-1612-1_1.

Mallon J, Cyronak T, Hall ER, Banaszak AT, Exton DA, Bass AM. 2022. Light-driven dynamics between calcification and production in functionally diverse coral reef calcifiers. *Limnology and Oceanography* 67:434–449. DOI: 10.1002/LNO.12002.

Mancini AM, Bocci G, Morigi C, Gennari R, Lozar F, Negri A. 2023. Past analogues of deoxygenation events in the Mediterranean Sea: A tool to constrain future impacts. *Journal of Marine Science and Engineering* 11:562. DOI: 10.3390/JMSE11030562.

Martinez JA, Smith CM, Richmond RH. 2012. Invasive algal mats degrade coral reef physical habitat quality. *Estuarine, Coastal and Shelf Science* 99:42–49. DOI: 10.1016/J.ECSS.2011.12.022.

Murphy JWA, Richmond RH. 2016. Changes to coral health and metabolic activity under oxygen deprivation. *PeerJ* 4:e. DOI: 10.7717/PEERJ.1956.

Muscatine L. 1990. The role of symbiotic algae in carbon and energy flux in reef corals. *Coral Reefs* 25, 75–87.

Muscatine L, Porter JW, Kaplan IR. 1989. Resource partitioning by reef corals as determined from stable isotope composition. *Marine Biology* 100:185–193. DOI: 10.1007/BF00391957.

Nakamura T, Nadaoka K, Watanabe A. 2013. A coral polyp model of photosynthesis, respiration and calcification incorporating a transcellular ion transport mechanism. *Coral Reefs* 32:779–794. DOI: 10.1007/s00338-013-1032-2.

Nakamura T, Yamasaki H, Van Woesik R. 2003. Water flow facilitates recovery from bleaching in the coral *Stylophora pistillata*. *Marine Ecology Progress Series* 256:287–291. DOI: 10.3354/MEPS256287.

Nelson HR, Altieri AH. 2019. Oxygen: the universal currency on coral reefs. *Coral Reefs 2019 38:2* 38:177–198. DOI: 10.1007/S00338-019-01765-0.

Raphael A, Dubinsky Z, Iluz D, Netanyahu NS. 2020. Neural network recognition of marine benthos and corals. *Diversity* 12:29. DOI: 10.3390/D12010029.

675 Richier S, Furla P, Plantivaux A, Merle PL, Allemand D. 2005. Symbiosis-induced adaptation to
676 oxidative stress. *Journal of Experimental Biology* 208:277–285. DOI: 10.1242/JEB.01368.
677 Richier S, Merle PL, Furla P, Pigozzi D, Sola F, Allemand D. 2003. Characterization of
678 superoxide dismutases in anoxia- and hyperoxia-tolerant symbiotic cnidarians. *Biochimica et*
679 *Biophysica Acta (BBA) - General Subjects* 1621:84–91. DOI: 10.1016/S0304-4165(03)00049-7.
680 Ritchie RJ. 2006. Consistent sets of spectrophotometric chlorophyll equations for acetone,
681 methanol and ethanol solvents. *Photosynthesis Research* 89:27–41. DOI: 10.1007/S11120-006-
682 9065-9/METRICS.
683 Roman MR, Brandt SB, Houde ED, Pierson JJ. 2019. Interactive effects of hypoxia and
684 temperature on coastal pelagic zooplankton and fish. *Frontiers in Marine Science* 6:404311.
685 DOI: 10.3389/FMARS.2019.00139.
686 Sampaio E, Santos C, Rosa IC, Ferreira V, Pörtner HO, Duarte CM, Levin LA, Rosa R. 2021.
687 Impacts of hypoxic events surpass those of future ocean warming and acidification. *Nature*
688 *Ecology & Evolution* 5:311–321. DOI: 10.1038/s41559-020-01370-3.
689 Schmidtko S, Stramma L, Visbeck M. 2017. Decline in global oceanic oxygen content during the
690 past five decades. *Nature* 542:335–339. DOI: 10.1038/nature21399.
691 Simpson CJ, Cary JL, Masini RJ. 1993. Destruction of corals and other reef animals by coral
692 spawn slicks on Ningaloo Reef, Western Australia. *Coral Reefs* 12:185–191. DOI:
693 10.1007/BF00334478.
694 Smith DJ, Suggett DJ, Baker NR. 2005. Is photoinhibition of Symbiodiniaceae photosynthesis
695 the primary cause of thermal bleaching in corals? *Global Change Biology* 11:1–11. DOI:
696 10.1111/j.1529-8817.2003.00895.x.
697 Smythers AL, Crislip JR, Slone DR, Flinn BB, Chaffins JE, Camp KA, McFeeley EW, Kolling
698 DRJ. 2023. Excess manganese increases photosynthetic activity via enhanced reducing center
699 and antenna plasticity in *Chlorella vulgaris*. *Scientific Reports 2023 13:1* 13:1–14. DOI:
700 10.1038/s41598-023-35895-x.
701 Stimson J, Kinzie RA. 1991. The temporal pattern and rate of release of Symbiodiniaceae from
702 the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-enrichment and control
703 conditions. *Journal of Experimental Marine Biology and Ecology* 153:63–74. DOI:
704 10.1016/S0022-0981(05)80006-1.
705 Strasser RJ, Stirbet AD. 2001. Estimation of the energetic connectivity of PS II centres in plants
706 using the fluorescence rise O–J–I–P: Fitting of experimental data to three different PS II models.
707 *Mathematics and Computers in Simulation* 56:451–462. DOI: 10.1016/S0378-4754(01)00314-7.
708 Suggett DJ, Smith DJ. 2020. Coral bleaching patterns are the outcome of complex biological and
709 environmental networking. *Global Change Biology* 26:68–79. DOI: 10.1111/GCB.14871.
710 Ulstrup KE, Hill R, Ralph PJ. 2005. Photosynthetic impact of hypoxia on in hospite
711 Symbiodiniaceae in the scleractinian coral *Pocillopora damicornis*. *Marine Ecology Progress*
712 *Series* 286:125–132. DOI: 10.3354/MEPS286125.

713 Vaquer-Sunyer R, Duarte CM. 2008. Thresholds of hypoxia for marine biodiversity.
714 *Proceedings of the National Academy of Sciences of the United States of America* 105:15452–
715 15457. DOI: 10.1073/pnas.0803833105
716 Wijgerde T, Jurriaans S, Hoofd M, Verreth JAJ, Osinga R. 2012. Oxygen and heterotrophy
717 Affect calcification of the scleractinian coral *Galaxea fascicularis*. *PLoS ONE* 7:e52702. DOI:
718 10.1371/JOURNAL.PONE.0052702.
719 Wijgerde T, Silva CIF, Scherders V, Van Bleijswijk J, Osinga R. 2014. Coral calcification under
720 daily oxygen saturation and pH dynamics reveals the important role of oxygen. *Biology Open*
721 3:489–493. DOI: 10.1242/BIO.20147922.
722 Zhang K, Wu Z, Liu Z, Tang J, Cai W, An M, Zhou Z. 2023. Acute hypoxia induces reduction of
723 algal symbiont density and suppression of energy metabolism in the scleractinian coral
724 *Pocillopora damicornis*. *Marine Pollution Bulletin* 191:114897. DOI:
725 10.1016/J.MARPOLBUL.2023.114897.
726 Zhu B, Wang G, Huang B, Tseng CK. 2004. Effects of temperature, hypoxia, ammonia and
727 nitrate on the bleaching among three coral species. *Chinese Science Bulletin* 49:1923–1928.
728 DOI: 10.1007/BF03184283.
729

Figure 1

Sampling site location, southern Gulf of Thailand

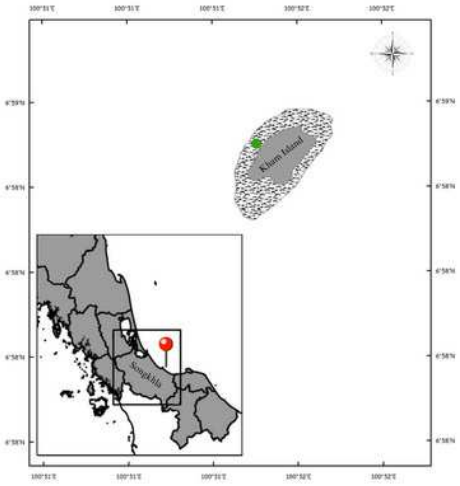


Figure 2

Experimental design and sampling parameters

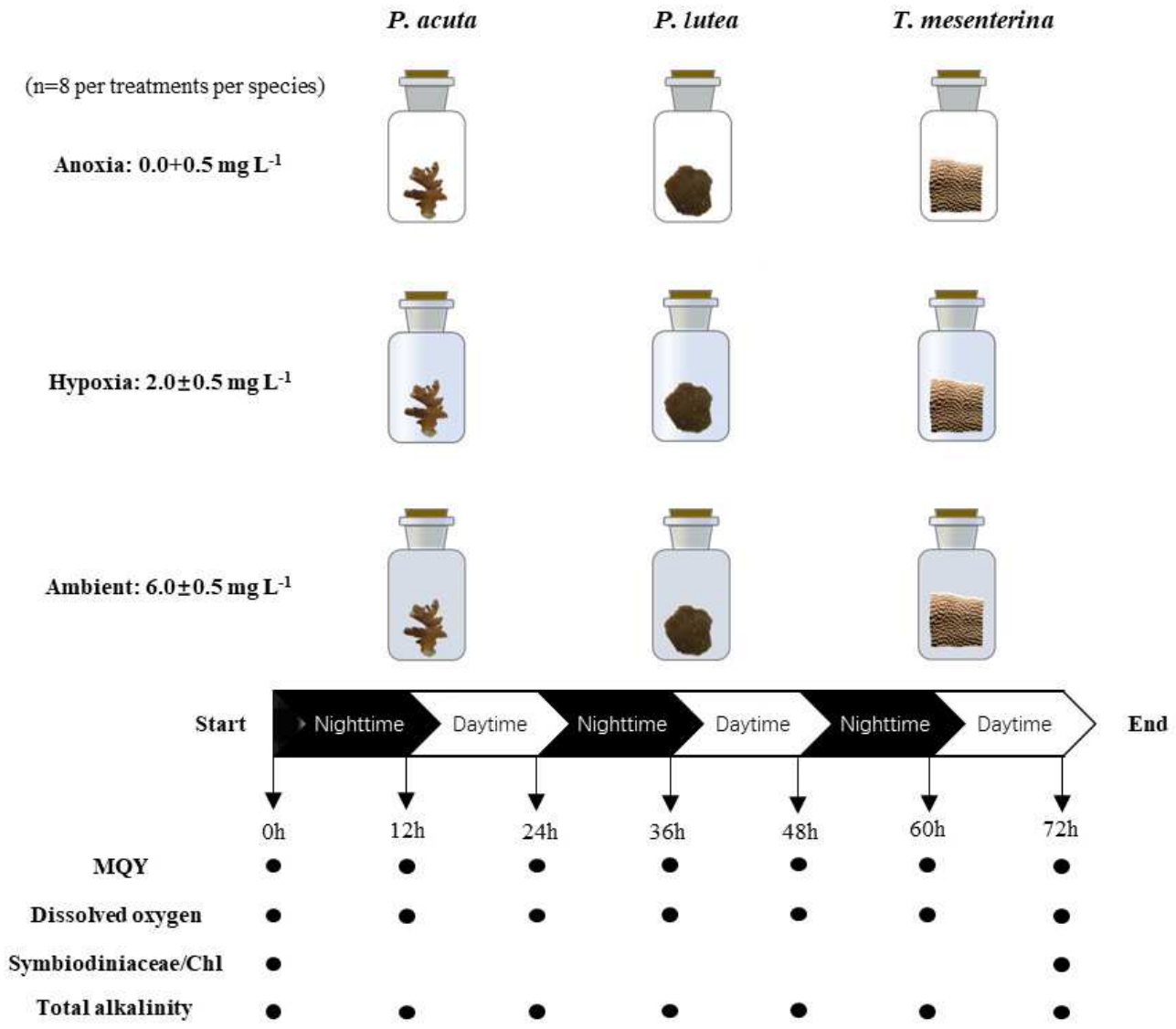


Figure 3

DO record in coral reef at Kham Island throughout the period from June 2021 to June 2022.

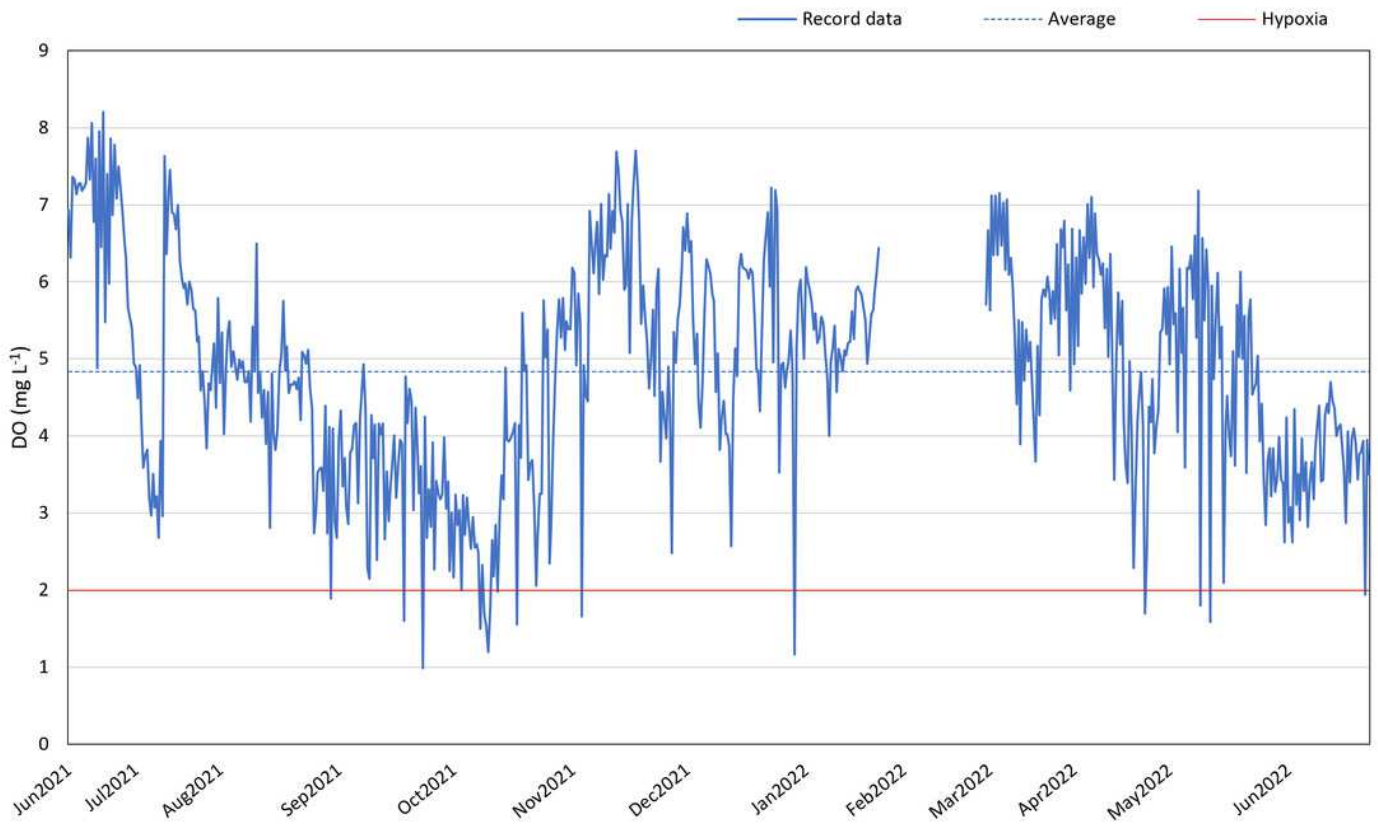


Figure 4

Maximum quantum yield (MQY) of *P. acuta* (a), *P. lutea* (b), and *T. mesenterina* (c) under hypoxia and anoxia during a 72-h experiment.

The shaded area represents nighttime. Capital letters indicate differences between times.

Lowercase letters denote differences between treatments.

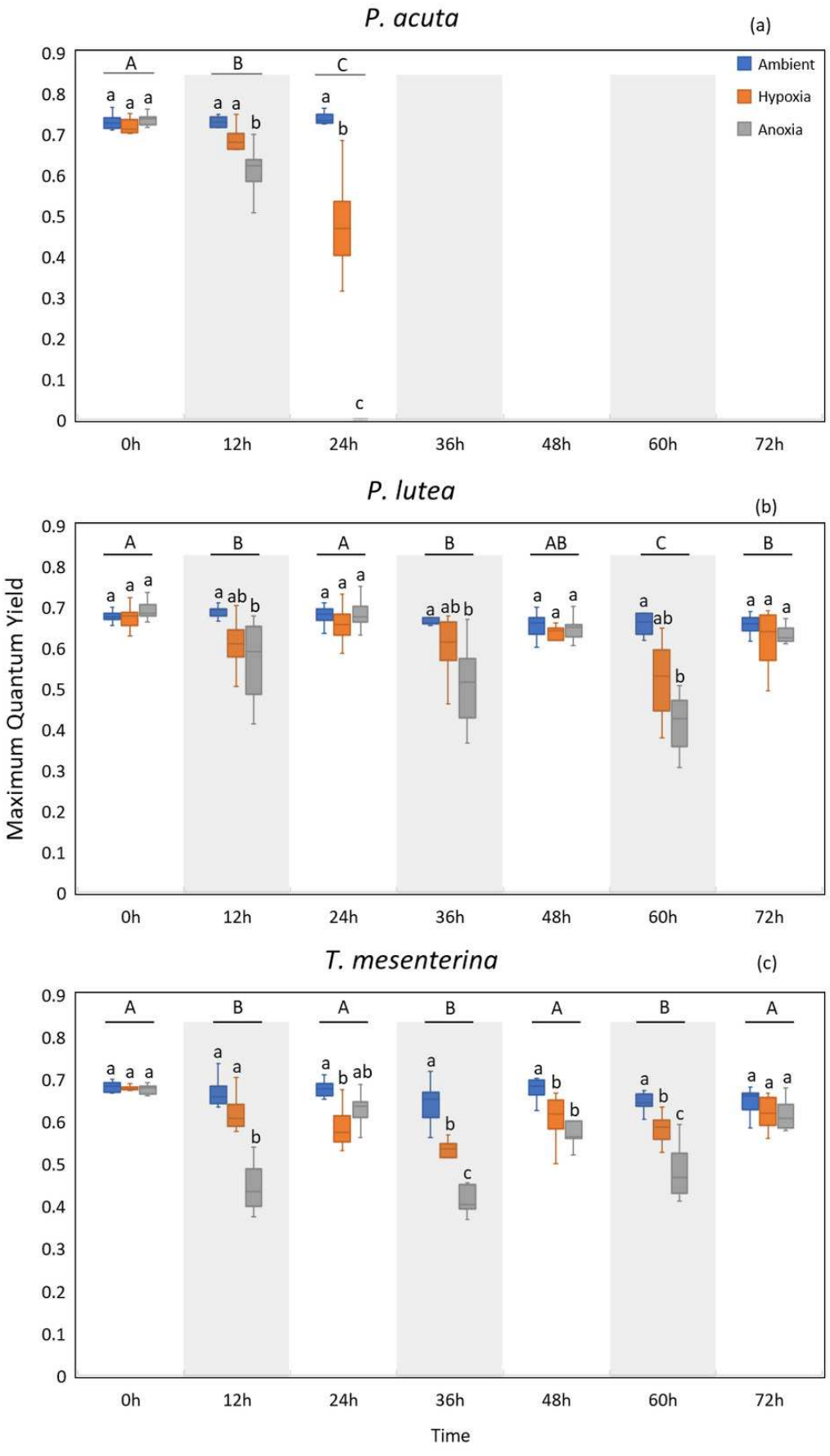
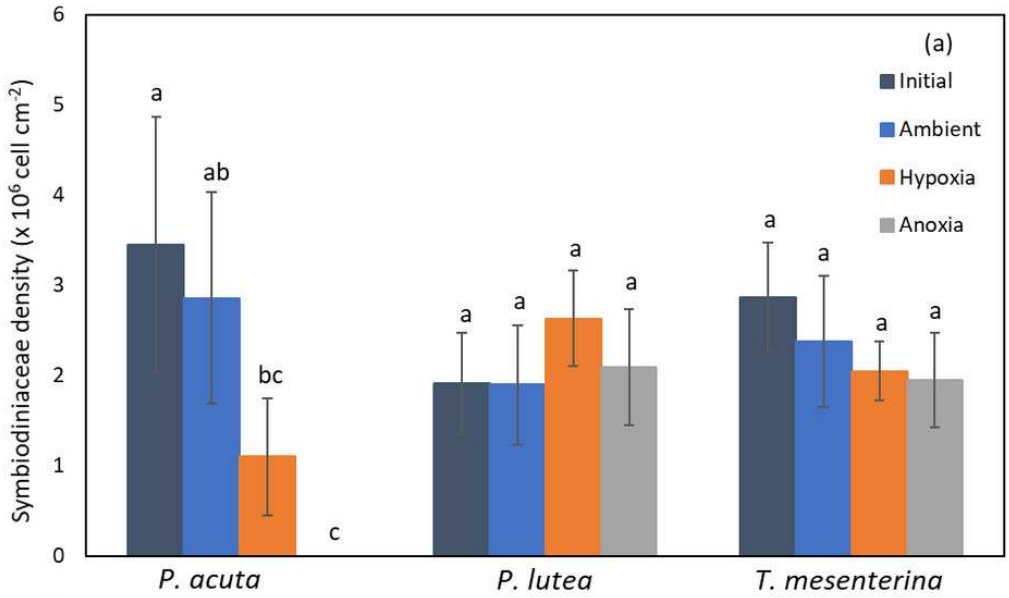
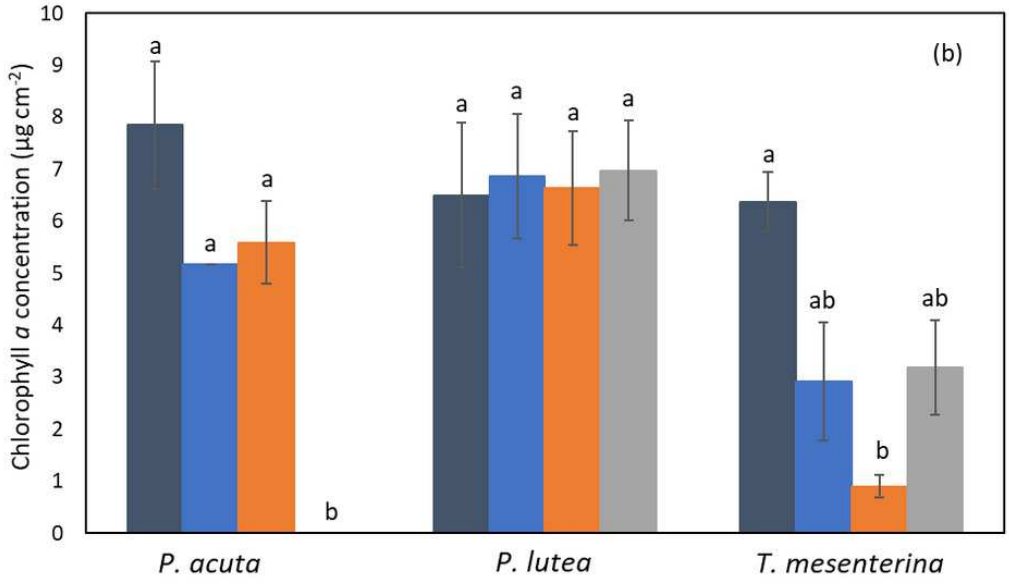

P. acuta
(a)
Ambient
Hypoxia
Anoxia
P. lutea
(b)
T. mesenterina
(c)
Maximum Quantum Yield
Time
0h
12h
24h
36h
48h
60h
72h

Figure 5

Comparison of Symbiodiniaceae density (a), chlorophyll *a* concentration (b), and chlorophyll c_2 concentration (c) in *P. acuta*, *P. lutea*, and *T. mesenterina.*

Lowercase letters indicate differences between treatments.


(a)
Initial
Ambient
Hypoxia
Anoxia
Symbiodiniaceae density (x 10^6 cell cm^-2)
a
ab
bc
c
a
a
a
a
a
a
a
a
P. acuta
P. lutea
T. mesenterina


(b)
Chlorophyll a concentration (µg cm^-2)
a
a
a
b
a
a
a
a
a
ab
b
ab
P. acuta
P. lutea
T. mesenterina

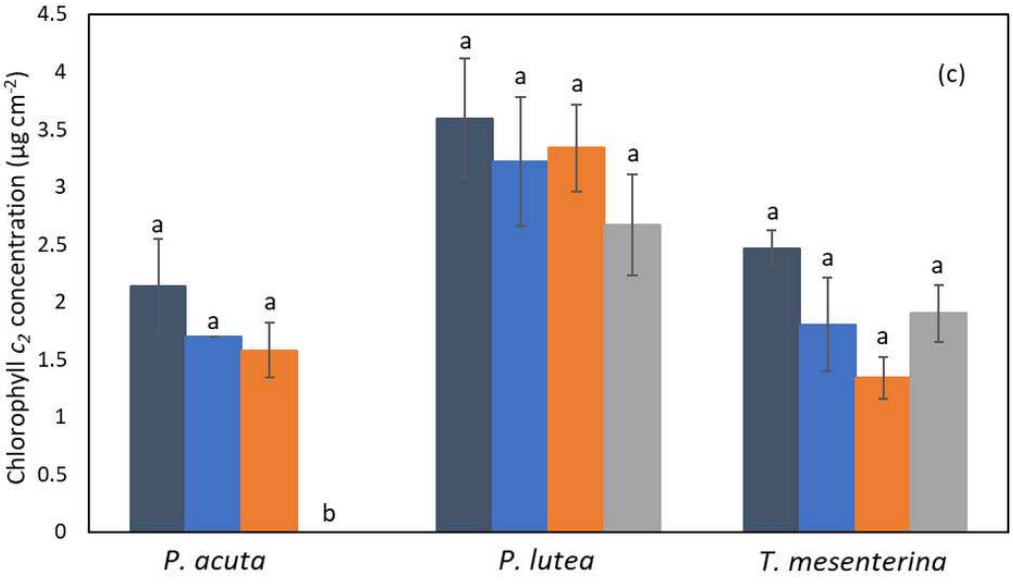

(c)
Chlorophyll c2 concentration (µg cm^-2)
a
a
a
b
a
a
a
a
a
a
a
a
P. acuta
P. lutea
T. mesenterina

Figure 6

Respiration rates of *P. acuta* (a), *P. lutea* (b), and *T. mesenterina* (c) from day 1 to day 3 under control, hypoxic, and anoxic conditions.

Lowercase letters denote differences between treatments, while uppercase letters indicate differences between days.

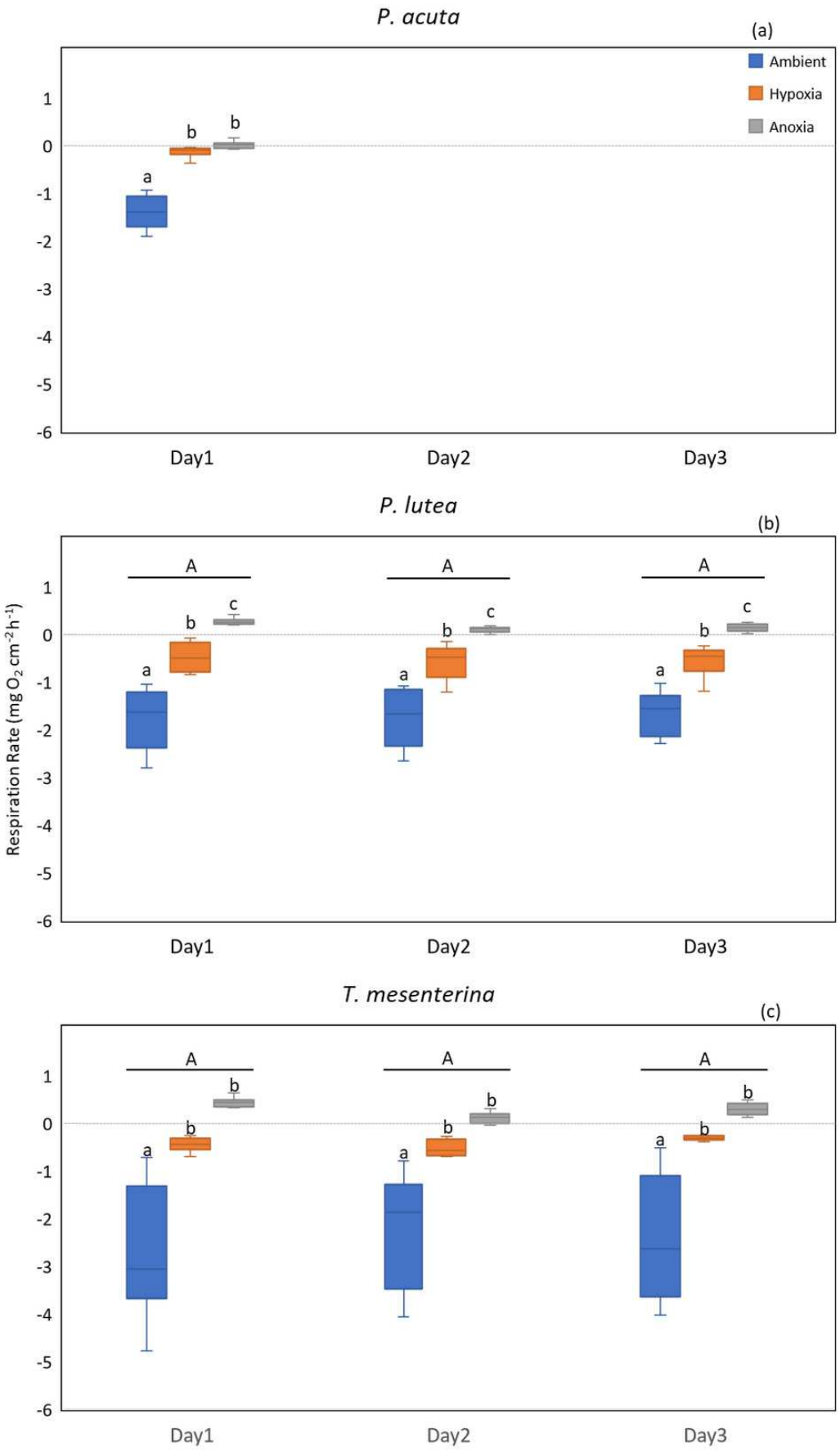

P. acuta
(a)
Ambient
Hypoxia
Anoxia
Day1
Day2
Day3
P. lutea
(b)
Respiration Rate (mg O2 cm-2 h-1)
T. mesenterina
(c)

Figure 7

Net primary production from day 1 to day 3 of *P. acuta* (a), *P. lutea* (b), and *T. mesenterina* (c) under control, hypoxia, and anoxia conditions.

Lowercase letters denote differences between treatments, while uppercase letters indicate differences between days.

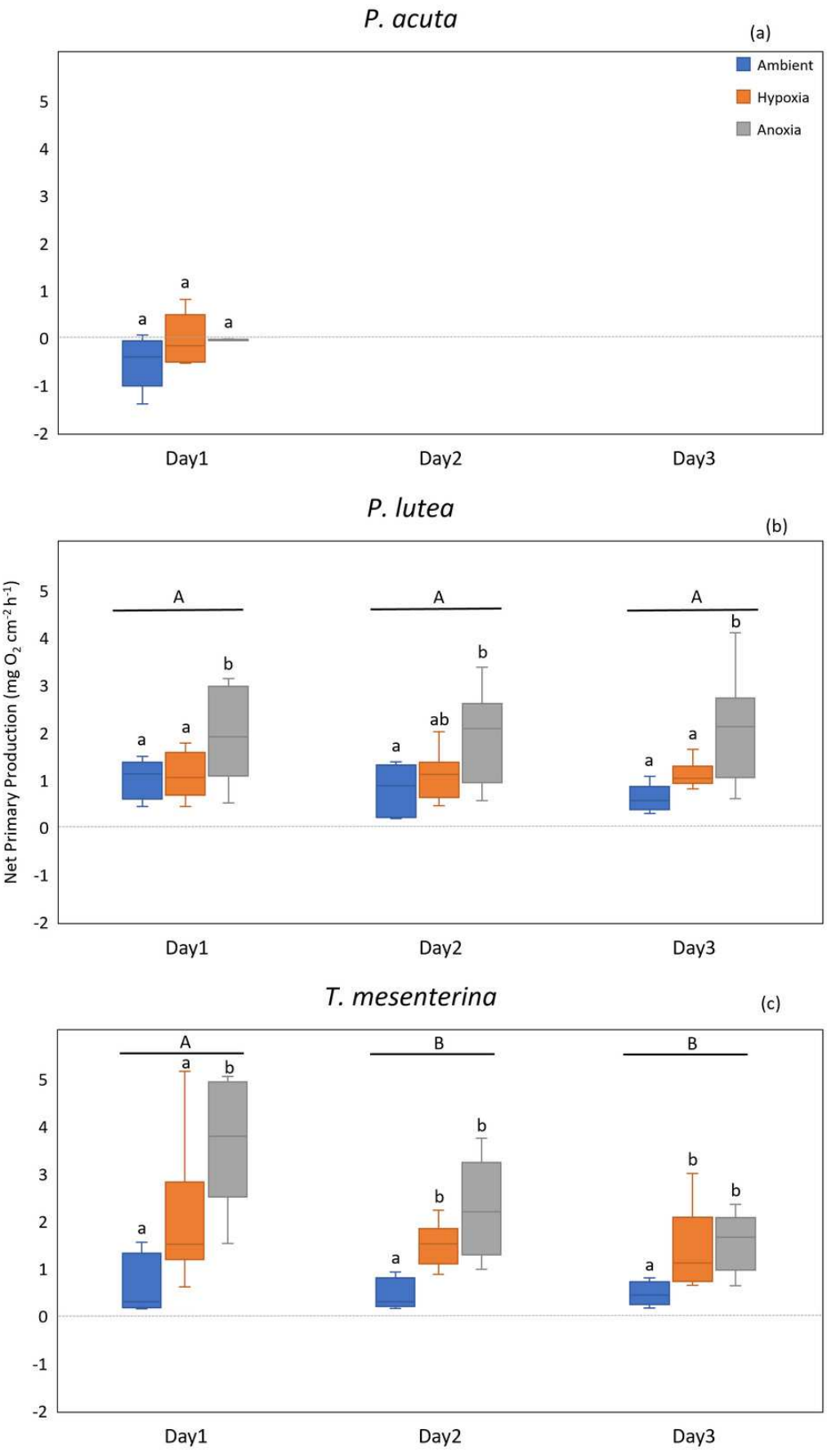

P. acuta
(a)
Ambient
Hypoxia
Anoxia
Day1
Day2
Day3
P. lutea
(b)
Net Primary Production (mg O_2 cm^{-2} h^{-1})
T. mesenterina
(c)

Figure 8

Gross primary production from day 1 to day 3 for *P. acuta* (a), *P. lutea* (b), and *T. mesenterina* (c) under control, hypoxia, and anoxia conditions.

Lowercase letters denote differences between treatments, while uppercase letters indicate differences between days.

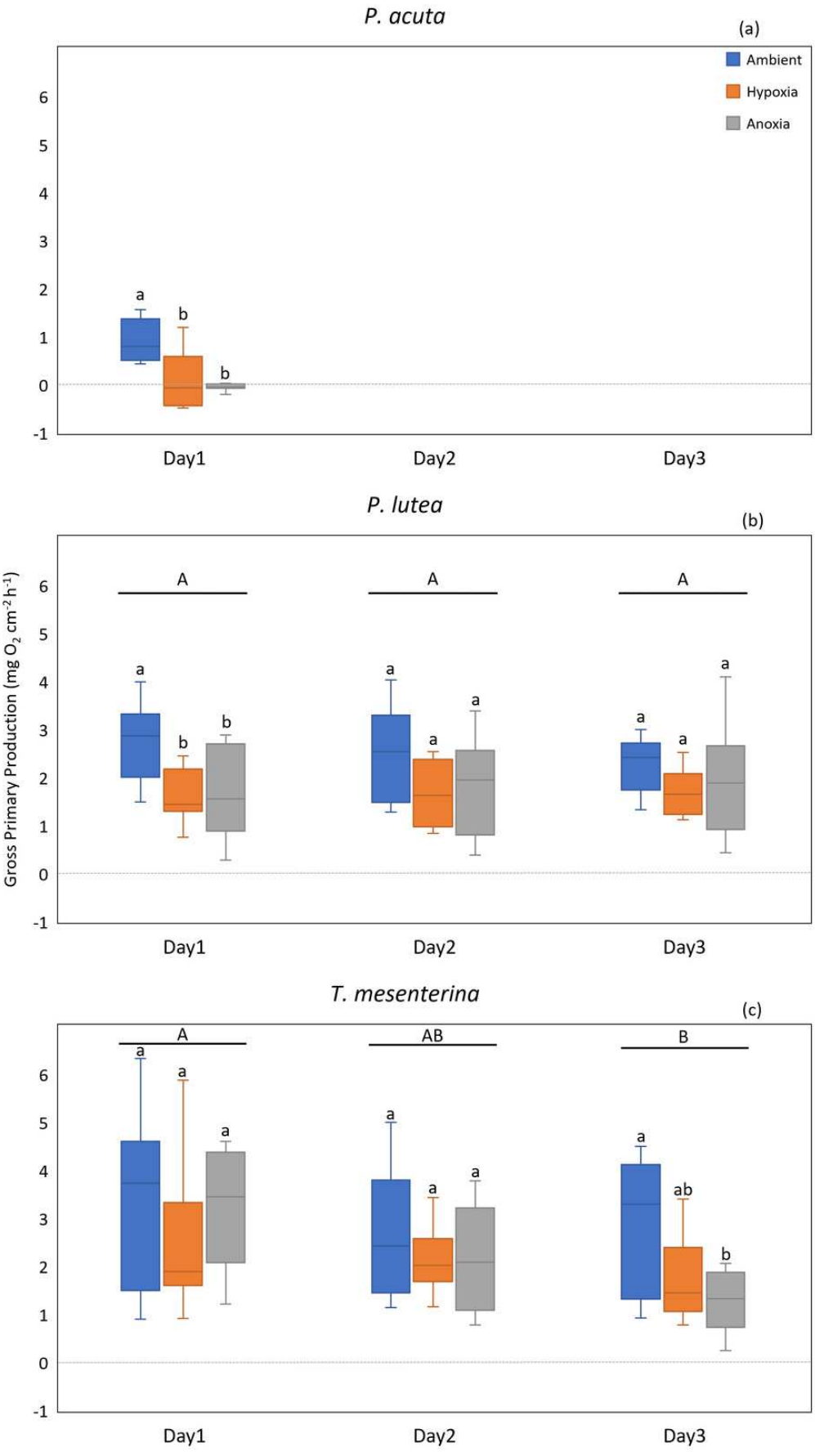
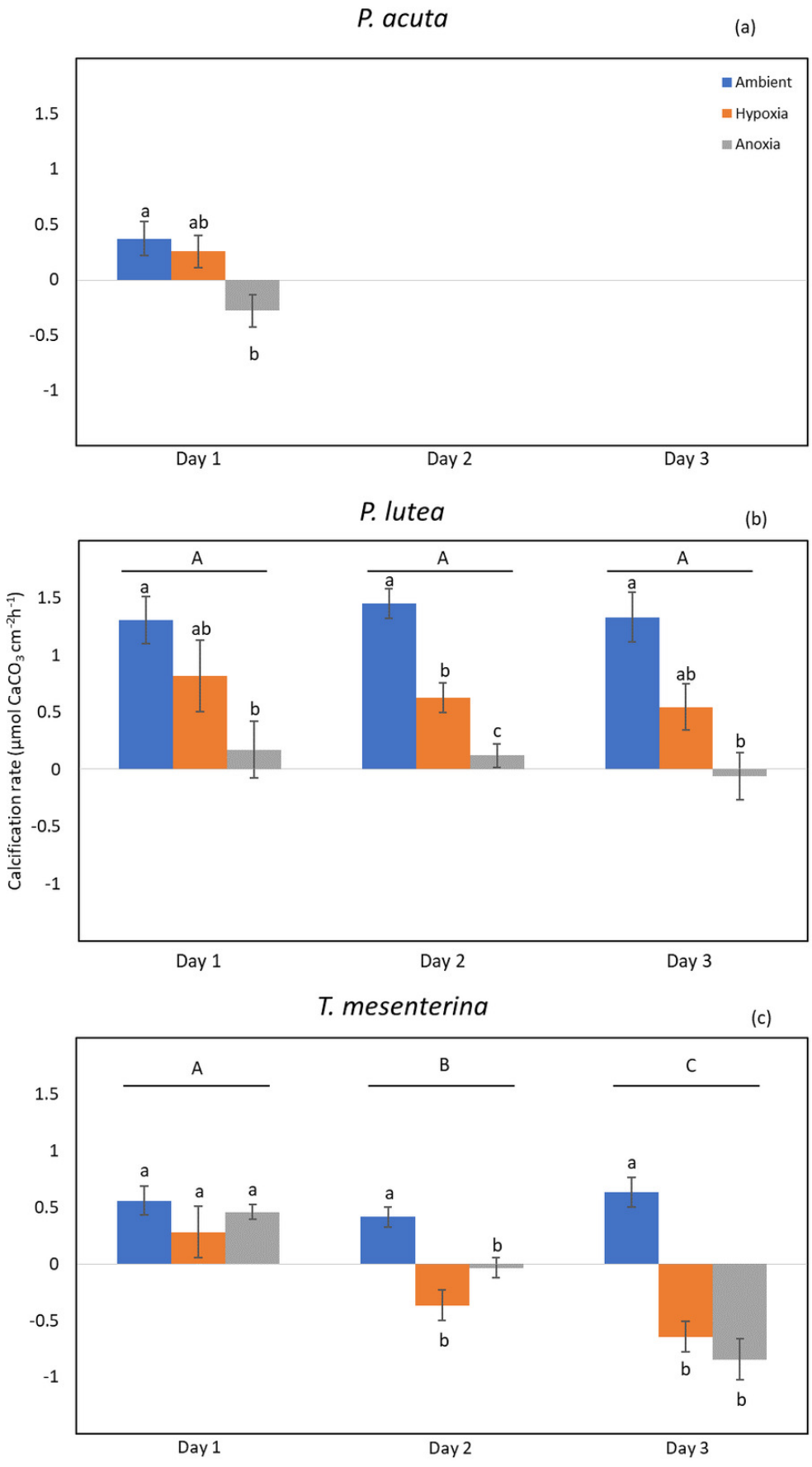

P. acuta
(a)
Ambient
Hypoxia
Anoxia
6
5
4
3
2
1
0
-1
a
b
b
Day1
Day2
Day3
P. lutea
(b)
Gross Primary Production (mg O2 cm-2 h-1)
A
A
A
a
b
b
a
a
a
a
a
a
Day1
Day2
Day3
T. mesenterina
(c)
A
AB
B
a
a
a
a
a
a
a
ab
b
Day1
Day2
Day3

Figure 9

Calcification rate from day 1 to day 3 of *P. acuta* (a), *P. lutea* (b), and *T. mesenterina* (c) under control, hypoxia, and anoxia conditions.

Lowercase letters denote differences between treatments, while uppercase letters indicate differences between days.


P. acuta
(a)
Ambient
Hypoxia
Anoxia
1.5
1
0.5
0
-0.5
-1
a
ab
b
Day 1
Day 2
Day 3
P. lutea
(b)
Calcification rate (μmol CaCO3 cm-2h-1)
A
A
A
a
ab
b
a
b
c
a
ab
b
Day 1
Day 2
Day 3
T. mesenterina
(c)
A
B
C
a
a
a
a
b
a
b
b
b
Day 1
Day 2
Day 3