Marine Biology
June 2022, Volume 169 Issue 6 Pages 82 (15p.)
https://doi.org/10.1007/s00227-022-04063-6
https://archimer.ifremer.fr/doc/00773/88500/

Long-term exposure to an extreme environment induces species-specific responses in corals' photosynthesis and respiration rates

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Abstract :

Extreme reef environments have become useful natural laboratories to investigate physiological specificities of species chronically exposed to future-like climatic conditions. The lagoon of Bouraké in New Caledonia (21°56′56.16″ S; 125°59′36.82″ E) is one of the only reef environments studied where the three main climatic stressors predicted to most severely impact corals occur. In this lagoon, temperatures, seawater pHT and dissolved oxygen chronically fluctuate between extreme and close-to-normal values (17.5–33.85 °C, 7.23–7.92 pHT units and 1.87–7.24 mg O2 L−1, respectively). In March 2020, the endosymbiont functions (chl a, cell density and photosynthesis) and respiration rates were investigated in seven coral species from this lagoon and compared with those of corals from an adjacent reference site using hour-long incubations mimicking present-day and future conditions. Corals originating from Bouraké displayed significant differences in these variables compared to reference corals, but these differences were species-specific. Photosynthetic rates of Bouraké corals were all significantly lower than those of reference corals but were partially compensated by higher chlorophyll contents. Respiration rates of the Bouraké corals were either lower or comparable to those of reference corals. Conversely, photosynthesis and respiration rates of most studied species were similar regardless of the incubation conditions, which mimicked either present-day or future conditions. This study supports previous work indicating that no unique response can explain corals' tolerance to sub-optimal conditions and that a variety of mechanisms will be at play for corals in a changing world.

Keywords : Coral reefs, Extreme environments, Ocean acidification, Photosynthesis, Respiration, Climate change

Abbreviations

Chl	Chlorophyll
Day R	Day respiration
DO	Dissolved oxygen
P	Photosynthesis
P_{chl}	Photosynthesis per chlorophyll *a*
P_g	Gross photosynthesis
P_S	Photosynthesis per surface area
R/V	Research vessel
T	Temperature

Introduction

Coral-dominated ecosystems are predicted to decline by 99% under a temperature increase of 2 °C (Hoegh-Guldberg et al. 2019), which remains an optimistic scenario for 2100 given our current pathway (IPCC 2019). As a result, it seems likely that most reef ecosystems will disappear or significantly degrade in the coming decades. However, outlying coral populations are being identified in extreme environments, which are characterized by one or more abiotic conditions outside of corals' usual range of tolerance (Kleypas et al. 1999). The identification of these resistant corals (Grottoli et al. 2017; Camp et al. 2018a) provides new insights into how coral populations could persist in a warm, acidified and deoxygenated ocean, which is the trio of climate-induced

stressors predicted to most impact corals in the future (IPCC 2019).

Ocean acidification is driven by the dissolution of atmospheric CO_2 in the ocean, which is increasing due to elevated anthropogenic CO_2 emissions. As a result, sea surface pH_T has been declining by a range of 0.01–0.03 units per decade since the late 1980s (Hoegh-Guldberg et al. 2017), and is predicted to decrease another 0.28–0.29 units by 2100 (RCP8.5 scenario; IPCC 2019). Ocean acidification leads to a decline in the saturation state of calcium carbonate, as well as a concomitant decrease in $[CO_3^{2-}]$ and increase in $[HCO_3^-]$, which is thought to decrease corals' calcification rates (Hoegh-Guldberg et al. 2008). Ocean deoxygenation, i.e. the decrease in partial pressure of oxygen (pO_2), is due to global warming and local eutrophication, which lead to lower O_2 saturation and increased microbial O_2 demands (Breitburg et al. 2018). The impacts of deoxygenation on coral reefs have received little attention, and hypoxia thresholds of main scleractinian groups remain unknown (Hughes et al. 2020). However, the proximity of tropical dead zones to reef ecosystems suggests that it could constitute an important threat (Altieri et al. 2017).

Some marginal and extreme environments expose corals to climate conditions comparable to or exceeding those predicted for the end of the century. Such environments provide natural laboratories where corals have developed in ecologically realistic and complex systems, which cannot be fully reproduced in tank experiments. Additionally, they allow one to investigate long-term mechanisms involved in corals' tolerance to climatic stressors, which do not have time to occur in most tank experiments that rarely exceed a year. Long-term acclimatory or adaptive mechanisms could play an important role in corals' ability to cope with future climatic conditions as climate change likely occurs at a speed allowing for acclimation and rapid adaptation processes to take place in coral populations (Kenkel et al. 2018; Logan et al. 2014; Palumbi et al. 2014; Torda et al. 2017). To characterize these long-term processes, an increasing number of studies are using marginal and extreme reef sites as natural laboratories to study corals' responses to future conditions (reviewed by Camp et al. 2018b). Currently, most studies have focused on sites displaying high and highly variable temperatures, such as back-reef pools (Oliver and Palumbi 2011; Schoepf et al. 2015) or the Red Sea (Howells et al. 2016; Grottoli et al. 2017), and sites displaying low pCO_2, such as CO_2 vents (Fabricius et al. 2011; Inoue et al. 2013; Rodolfo-Metalpa et al. 2011; Strahl et al. 2015). However, a significant limit to most sites is that they display a single stressor and consequently fail to inform on the combined effects of low pH, low dissolved oxygen (DO), and high temperature (T) that will simultaneously affect corals in the future. While no natural site described can serve as a realistic analogue to all upcoming climatic and environmental conditions, the recently identified site of Bouraké in New Caledonia is unique because it combines these three main stressors (Camp et al. 2017). The site of Bouraké is a semi-enclosed lagoon surrounded by mangroves and characterized by low pH, low DO and high T, all fluctuating according to tidal and diel cycles. To date, it is among the only sites in the world where healthy and diverse coral populations have been identified despite values of pH and DO exceeding those forecasted for the open ocean by 2100 (Bopp et al. 2013; IPCC 2019), and temperatures of 1–3 °C higher than surrounding local values (Camp et al. 2017).

One of the most sensitive aspects of corals' physiology under climate change is their energy budget. Prolonged heat stress can cause corals to bleach, a process in which Symbiodiniaceae are expelled from their host, depriving them of the transfer of photosynthates, their main energy source when healthy (Muscatine 1990; Grottoli et al. 2006). Additionally, ocean acidification is expected to marginally increase the energy costs required to maintain calcification rates and growth (McCulloch et al. 2012). It has been suggested that corals developing in acidified environments could display increased respiration rates to compensate for their additional energy requirements, but this remains inconclusive. So far, studies have shown equivocal results, as the effects of high pCO_2 on corals' photosynthesis and respiration rates have appeared to be species-specific and dependant on experimental designs (e.g., Crawley et al. 2010; Rodolfo-Metalpa et al. 2011; Edmunds 2012; Comeau et al. 2017; McLachlan et al. 2020) and feeding levels (Schoepf et al. 2013). Concerning photosynthesis, a meta-analysis showed that the latter was not affected by short-term exposure to acidified conditions during lab experiments (Kroeker et al. 2010, 2013), but the few studies using low pH environments showed that photosynthesis rates were increased in acclimatized coral populations (Inoue et al. 2013; Strahl et al. 2015; Biscéré et al. 2019). The combined effects of acidification and warming on corals' photosynthesis and respiration rates have only been investigated during short-term experiments, which cannot account for realistic and adaptive processes (Anthony et al. 2008; Schoepf et al. 2013; Hoadley et al. 2015; Brown et al. 2019). Consequently, an important knowledge gap remains in the understanding of how corals' photosynthesis and respiration rates will be affected by climate change, and whether corals could rely on their metabolic plasticity under extreme environmental conditions.

This study investigated the photosynthesis, respiration rates and symbiotic parameters of corals originating from a natural environment combining elevated T, decreased pH and decreased DO. To do so, we carried out incubations of corals originating from Bouraké in present-day or end-of-the-century conditions and compared their photosynthesis and respiration rates with those of corals from an adjacent reference site incubated in similar conditions. This

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experiment was conducted at the end of the austral summer season, i.e., when corals were exposed to the most extreme environmental conditions. We hypothesized that long-term adaptive processes would prevail on the short-term plasticity of the corals' photosynthesis and respiration rates, meaning that (1) endosymbiotic functions, photosynthesis and respiration rates of corals from Bouraké would differ from those of corals from the reference reef; (2) incubating corals from either site in contrasting conditions (present-day or future conditions) would not modify their photosynthesis and respiration rates.

Material and methods

Study site

Corals were sampled from shallow reefs (1–2 m depth) in the lagoon of Bouraké (site B2, 21°56′56.16″ S; 125°59′36.82″ E) and in an adjacent fringing reef (site R1, 21°58′13.12″ S; 165°56′45.66″ E), located on the west coast of New Caledonia in the Southwest Pacific Ocean (Fig. 1) on the 12th and 13th of March 2020. The Bouraké lagoon (described in Camp et al. 2017) is connected to the ocean by a channel approximately 4–5 m wide which enters a mangrove forest and forms large back pools 5–7 m deep. It displays a diverse and abundant coral population (66 coral species, up to 96% coral cover; Maggioni et al. 2021) that develops despite acidified (pH_T down to 7.23), warm (up to 33.85 °C) and deoxygenated (down to 2.28 mg O_2 L^{-1}) conditions. Water parameters in the Bouraké lagoon also undergo large fluctuations following tidal and diel cycles, during which they regularly exceed forecasted values for 2100 (Camp et al. 2018b). The lowest values for pH, DO and the highest for T are reached at low tide, while high tides display values close to present-day conditions. In contrast, R1 displays present-day and relatively stable conditions for pH, T and DO, and is outside of the area influenced by the mangrove ecosystem (Table 1). As such, it is used in this study as a reference site.

A fine-scale abiotic and biotic characterization of both sites has been conducted since 2016 (Camp et al. 2017; Maggioni et al. 2021). Here, we used data collected from Maggioni et al. (2021) to characterize the two study sites. Data were collected during a four-year-long monitoring campaign (from 03/2016 to 04/2020) and accounted for both diel and seasonal fluctuations, compiling several thousands of measurements (Table 1). Seawater temperature (°C), dissolved oxygen content (DO, mg L^{-1}), and seawater pH_T

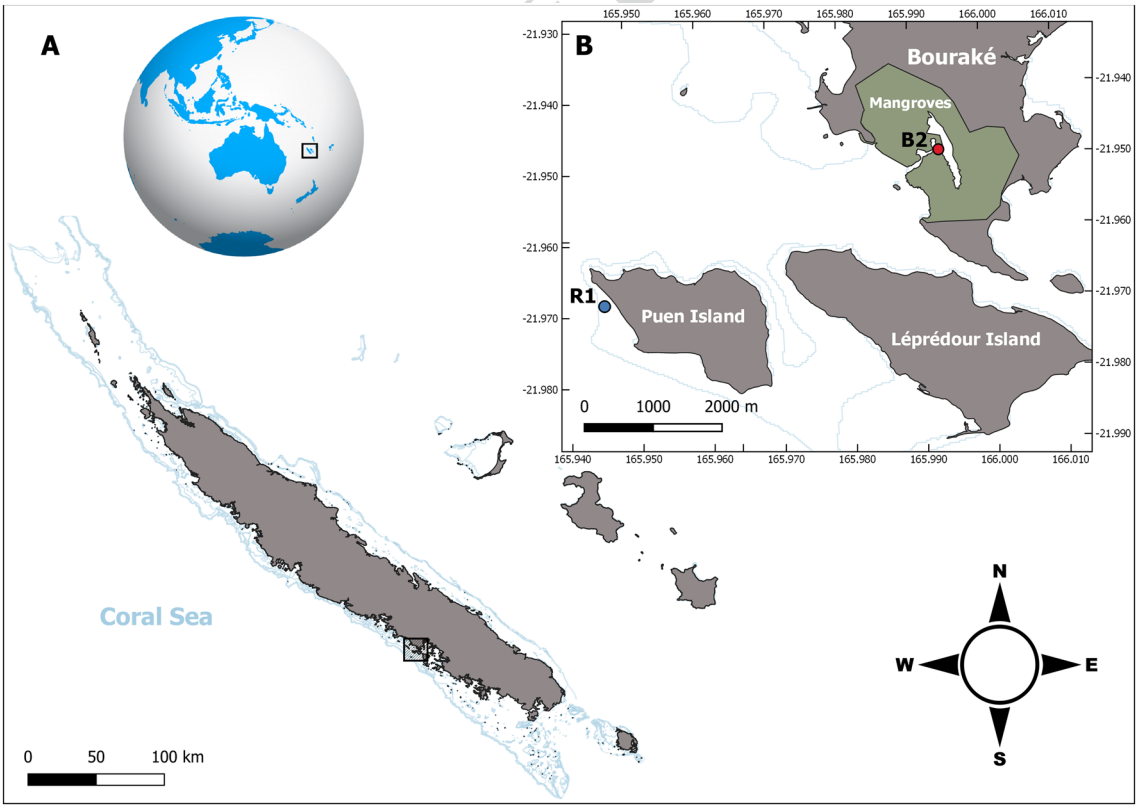

Fig. 1 **A** Location of New Caledonia within the Pacific South-West and **B** location of the two study sites: the Bouraké lagoon (B2) and the reference site (R1). Map tiles were collected from www.georep.nc (© Georep contributors)

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Table 1 Main environmental parameters measured at the reference (R1) and at the Bouraké site (B2)

		R1	B2
Temperature (°C)	Mean ± SD	25.25 ± 1.89	26.13 ± 2.67
	Min	19.98	17.49
	Max	30.54	33.85
pH_T (total scale)	Mean ± SD	8.01 ± 0.04	7.67 ± 0.23
	Min	7.91	7.23
	Max	8.18	8.06
pCO_2 (µatm)	Mean ± SD	353.4 ± 7.24	1318.9 ± 819.8
	Min	343.3	464.7
	Max	361.5	2860.7
DO (mg L^{-1})	Mean ± SD	6.45 ± 0.95	5.23 ± 0.89
	Min	3.06	2.28
	Max	10.65	7.10
Salinity	Mean ± SD	35.44 ± 0.049	36.97 ± 1.18
	Min	35.24	35.59
	Max	36.65	39.37

Mean (± SD), minimum (min) and maximum (max) values of temperature, pH_T (in total scale), dissolved oxygen (DO), salinity, and calculated pCO_2. Values for temperature, pH, pCO_2 and DO were obtained through a four-year long monitoring (from 03/2016 to 04/2020) considering both diel and seasonal fluctuations, and compiling several thousands of measurements (Maggioni et al. 2021). Salinity was averaged between two sets of continuous measurements: during the winter of 2019 (from 15/07/2019 to 18/07/2019), and the summer of 2020 (from 29/11/2020 to 04/12/2020)

(total scale), were periodically recorded using 600 OMS-M (YSI, USA), SeaFET pH loggers (Sea-Bird, USA), and Hobo water temperature Pro V2 (Onset, USA), all settled at a 10-min logging interval. Salinity was measured only during the winter of 2019 (from the 15th to the 18th of July), and the summer of 2020 (from the 29th of November to the 4th of December, see Maggioni et al. (2021) for further details on the probe deployments).

Coral sampling

Six coral fragments (3–5 cm long) of *Acropora tenuis* (Dana, 1846), *Pocillopora damicornis* (Linnaeus, 1758) and *Montipora digitata* (Dana, 1846) were collected at B2 and R1 on the 8th of March 2020. Coral fragments were collected from distinct mother colonies ($n = 6$ at both sites) at least 10 m apart from each other, using a plier. In B2, corals were collected along a reef of ca 150 × 20 m, while in R1 they were collected in a larger area of about 250 × 20 m. Additionally, $n = 5$–7 coral fragments of *Acropora samoensis* (Brook, 1891), *Acropora tenuis* (Dana, 1846), *Echinopora* spp. (Lamark, 1816), *Montipora stellata* (Bernard, 1897), and *Porites cylindrica* (Dana, 1846) were collected using the same sampling methodology on the 12th and 13th of March 2020. Only one fragment was sampled from each mother colony. Fragments collected on the 8th of March were immediately frozen at − 20 °C and fragments collected on the 12th and 13th were frozen after being incubated for photosynthesis and respiration measurements on that same day.

Symbiont density, chlorophyll concentration and surface measurements

All fragments collected were unfrozen and measured for symbiont density and chlorophyll concentrations throughout March and April 2020. This resulted in the analysis of $n = 12$ fragments of *A. tenuis*, $n = 5$–7 fragments of the 4 other species used in the incubations, and $n = 6$ fragments of *M. digitata* and *P. damicornis*.

Coral tissue was extracted in 20 mL of filtered seawater (GF/F 47 mm filters) using an air pick, and the slurry obtained was homogenised with a potter tissue grinder. For symbiont density measurement, 2 mL of the slurry was sampled to count the number of Symbiodiniaceae using a Neubauer's cell under a stereomicroscope. Four to six replicates were measured for each sample. For chl content measurement, 10 mL of the slurry was centrifuged at 5,000 g for 10 min, after which the supernatant was discarded. The remaining algal pellet was re-suspended in 10 mL of pure acetone, and pigments were extracted over 24 h at 4 °C in darkness. The extract was then centrifuged at 10,000 g for 15 min, and the supernatant was sampled to measure its absorbance at 630, 663 and 750 nm using a spectrophotometer (Evolution 201, Thermo Scientific). Chlorophyll *a* and c_2 concentrations were calculated using the spectrophotometric equations by Jeffrey and Humphrey (1975). Surface area of coral fragments was measured using the single wax method (Veal et al. 2010).

Experimental design of the incubations

The incubations were performed on board the research vessel (R/V) Alis, which was moored in front of the study sites. The incubations were designed to test the effects of short- and long-term exposure to present-day and future-like conditions on corals' photosynthesis, day respiration and symbiont content. Effects of long-term exposure were tested by comparing these variables between corals originating from two contrasting environmental conditions: i) the site of Bouraké (B2), where corals have been chronically exposed to fluctuating and extreme conditions; ii) the reference site (R1), where conditions are those of a typical fringing reef. Effects of short-term exposure were tested by comparing the photosynthesis and respiration rates of corals during hour-long incubations carried out under both present-day and future-like conditions. The incubation reproducing future-like conditions displayed temperatures higher by 2 ±

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0.2 °C, pH lower by 0.3 ± 0.03 units and DO lower by 1.3 ± 0.02 mg L^{-1} than the incubation in present-day conditions (Table 2). Incubations under present-day conditions were achieved by collecting seawater in the lagoon of Bouraké during high tide, while incubations under future-like conditions were achieved by collecting seawater in the lagoon of Bouraké during falling tide when values of T, pH and DO reach their extremes. Consequently, both coral groups were incubated in seawater collected from the lagoon of Bouraké, which was an opportunity to carry out our experiment using ecologically realistic conditions rather than artificially reproduced ones. The experimental design thus encompassed four types of incubations, to account for the two groups of corals both incubated under two seawater conditions. Corals from the Bouraké and the reference site were collected and incubated following the same methodology on two different days (respectively the 12th and 13th of March 2020) because of logistic constraints. Characteristics of seawater collected at Bouraké were found to be in very close ranges on both incubation days (Table 2), ensuring comparable incubation conditions for both coral groups.

Experimental set up of incubations

The coral fragments ($n = 5–7$) of *Acropora samoensis* (Brook, 1891), *Acropora tenuis* (Dana, 1846), *Echinopora* spp. (Lamark, 1816), *Montipora stellata* (Bernard, 1897), and *Porites cylindrica* (Dana, 1846) collected from the Bouraké site on the 12th of March 2020, and from the reference site on the 13th of March 2020 were used for the photosynthesis and respiration measurements. Fragments were collected during the morning, one hour before the high tide (11:19 am and 11:53 am local time on the 12th and 13th of March, respectively) to avoid any bias due to diurnal variations (Edmunds and Davies, 1988). Fragments were transported onboard the R/V in individual hermetic plastic bags containing seawater and immersed in a cooler. Fragments were then transferred in a 100 L tank in the indoor laboratory of the vessel where the temperature was maintained close to the one that was measured with a dive computer in situ during collection. The tank was equipped with a submersible pump and an air stone for water circulation, and filled with seawater freshly collected in Bouraké. A low light level (ca. 70 µmol m^{-2} s^{-1}) was provided by the same source of light used for the incubations (see below) to allow corals to recover for an hour.

Fragments were first incubated twice for 50 ± 10 min in the morning under high tide conditions. The first incubation was carried out in the dark to measure day respiration (day R) rates and the second in the light to measure net photosynthesis (P_n) rates. P_n rates were measured using saturating light intensity (250 ± 10 µmol m^{-2} s^{-1}) provided by one bank of four T5 bulbs (10,000°K, Giesemann, Germany). Seawater in beakers was renewed between the dark and the light incubations using the same sample of seawater collected in Bouraké during sampling. After the first two incubations (i.e., dark and light), corals were let to recover for two hours under a low light level in fresh seawater collected in Bouraké at intermediate conditions between high and low tide. During the afternoon falling tide, when the seawater in the lagoon reached values close to projected future conditions, fresh seawater was collected again and the corals were gently transferred and let to recover in the collected seawater for about one hour. Two incubations were then carried out in the afternoon to measure the P_n and R rates of corals under low tide conditions, using the same methodology as the incubations carried out in the morning. Because pO_2 levels are low at the falling tide, P_n was conducted first in the afternoon so that R would not be constrained by low pO_2. This resulted in a total of four sets of incubations of the same 30 coral fragments collected in the morning (see also Supplementary Figure S1 for a summarized representation of the incubation chronology). This exact sampling procedure and incubation protocol were carried out on the 12th of March with corals from Bouraké, and on the 13th of March with corals from the reference site.

Photosynthesis and day respiration rates

The experimental set-up used (i.e., incubation duration and volume of beakers) was as in Biscéré et al. (2019), which allows to measure clear DO variations without variations exceeding 15–20% during the incubation. For each incubation, coral fragments ($n = 5–7$) of the five species were placed in individual 100 mL Pyrex glass beakers ($n = 30$) filled with seawater and hermetically sealed underwater with transparent cellophane and a rubber band after all air bubbles were removed, to avoid any bias from O_2 exchanges

Table 2 Values of pH_T (in total scale), temperature (T) and dissolved oxygen (DO) used during the four incubations of corals from the reference (R1) and Bouraké (B2) sites under present-day, and future conditions

Seawater	Incubation R1 corals			Incubation B2 corals		
Conditions	pH_T	T (°C)	DO (mg L^{-1})	pH_T	T (°C)	DO (mg L^{-1})
Present-day	8.03	29.8	6.0	7.98	29.4	5.9
Future	7.73	32.0	4.6	7.65	31.3	4.8

with air (Biscéré et al. 2019). Three control beakers, in which no coral fragment was placed, were used to measure the metabolic microbial activity of the water. Control beakers were emptied and filled again with fresh seawater for each new incubation. Beakers were placed on two submersible multi-stirring plates with $n = 18$ individual stirring positions each (Fig. S1), which continuously stirred the seawater in each beaker, and were semi-submersed in a thermostatic water bath settled at ± 0.5 °C from the temperature of the collected seawater (Table 2). After five minutes of incubation, and at the end of each incubation, concentrations of DO were measured in each beaker, where O_2 sensor spots were fixed, using an optical fiber (PreSens Fibox 4 trace). Rates of P_n and day R were calculated using the change of DO concentrations in each beaker, corrected by the mean of the microbial activity measured in three empty beakers, and normalized by the incubation duration, the volume of seawater in each beaker, and either the coral's surface or its content in chl *a* (Edmunds and Gates 2002).

Rates of gross photosynthesis P_g were calculated as the sum of $|P_n|$ and |R|. Photosynthesis to respiration ratio (P_g: day R) was calculated as:

$$P_g : \text{day } R = \frac{P_g \times \text{hours of daylight}}{\text{day } R \times 24}$$

with P_g and day R in µmol O_2 cm^{-2} h^{-1}. The value of hours of daylight equalled 12.2 on March 13th in New Caledonia. At the end of each incubation pair (dark and light), coral fragments were frozen at −20 °C for subsequent measurements of chlorophyll (chl) concentration and symbiont density and surface area. Values of P_g are presented hereafter as normalized by the chl content (P_{chl}) or by the surface area (P_S) of each coral fragment.

Statistical analyses and data presentation

Statistical analyses were carried out and figures were produced using RStudio v.4.1.0 (2021), including the packages {ggplot2}, {stats}, {ARTool} and {car}. Data were first visually inspected and abnormal values were deleted. Homogeneity of variance was tested using the Bartlett test and the distribution of variances within groups was checked graphically on a normal P-P plot (i.e., expected vs observed). Chlorophyll and Symbiodiniaceae contents did not meet the assumptions of normality so values from both sites were compared using the non-parametrical Kruskal–Wallis test. Day R, P_{chl}, P_s and P_g: day R rates verified normality and homoscedasticity conditions, so a 2 × 2-way ANOVA was run to test for the effect of long-term exposure (i.e. site of origin: reference and Bouraké) and the effect of short-term exposure (i.e. incubation conditions: present-day and future), and their interaction on corals' P and R rates. As no interaction term was significant, post hoc Tukey HSD tests were not performed. P-levels were not adjusted. Data were presented using boxplots displaying median values (line) ± 25th and 75th percentiles (box), minimum and maximum values (whiskers), and mean values (dots).

Results

Environmental parameters at the study sites

Environmental data collected from 2016 to 2020 (see Maggioni et al. (2021) for full data set) clearly demonstrated the large differences between the reference site R1 and the Bouraké site (Table 1). While the environmental parameters for seawater measured at the reference site *R*1 were all within the normal range known for New Caledonia, seawater temperature was on average 1 °C higher in Bouraké, and up to 3 °C higher during the hot season. Measured pH was ca. 0.2 pH_T units lower, reaching the extreme value of 7.23 pH_T and pCO_2 was three times higher in Bouraké than at *R*1. Measured DO was on average 1 mg L^{-1} lower than at R1 and salinity was on average 1 point higher, reaching extreme values during the summer (+ 3 points). Dissolved oxygen, temperature, pH and salinity fluctuated in relation to the tide, respectively up to 4.91 mg O_2 L^{-1}, 6.50 °C, 0.69 pH_T units, and 3.42 points within a day.

Chlorophyll and Symbiodiniaceae content

Chlorophyll and symbiont contents in coral fragments significantly differed between the Bouraké and the reference site (Fig. 2; Table 3). Bouraké fragments displayed significantly higher content of chl *a* for 4 out of 7 species; higher content of chl c_2 for *A. tenuis* and *M. stellata,* higher symbiont density for *A. samoensis, A. tenuis* and *P. cylindrica* and higher chl *a* per symbiont for *A. tenuis* and *M. stellata*.

Photosynthesis and day respiration rates

ANOVA showed no significant effect of incubation conditions (present day vs. future) on the photosynthesis and respiration rates of corals (Fig. 3 for the corals from the Bouraké site, Fig. S2 for corals from the reference site and Table 4 for statistical values).

In contrast, significant differences between corals from different sites were observed for the P_{chl} of all coral species, the P_s of three coral species, the P_g: day R of two species and the day R rates of *Echinopora* spp. (Table 4). Figure 4 presents the values of the four measured variables for fragments from both sites, after having pooled together both incubation conditions. Mean photosynthesis rates per chl *a* (P_{chl}) were lower for all corals originating from Bouraké compared

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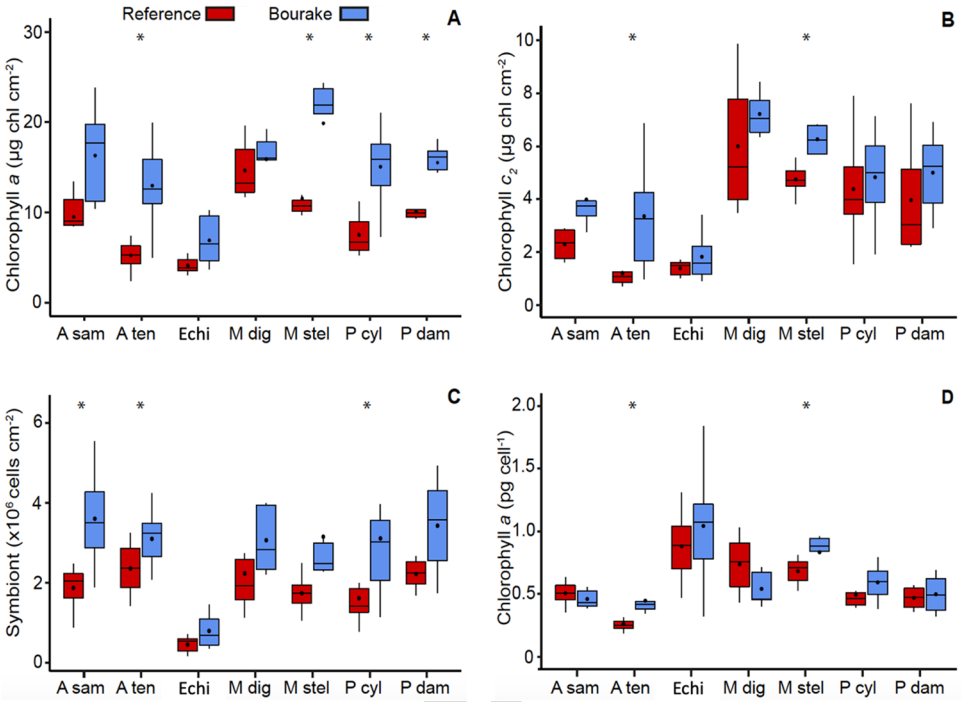

Fig. 2 **A** Chl *a* and **B** chl c_2 content per unit surface area of the skeleton (µg cm^{-2}); **C** symbiont density per unit surface area ($\times 10^6$ cells cm^{-2}), and **D** chl *a* content per symbiont (pg $cell^{-1}$) measured on corals collected at the reference site and Bouraké site ($n = 12$ for *A. tenuis* and $n = 5$–7 for other species). Data are represented as median value (line) ± 25th and 75th percentiles (box), minimum and maximum values (whiskers) and mean value (dot). Asterisks indicate statistical differences between sites of origin (see Table 3)

to the reference fragments (Fig. 4A). When normalizing P rates per surface area (P_S), contrasting trends were observed depending on the species. While colonies of *P. cylindrica* from Bouraké increased P_S, *A. tenuis* and *Echinopora* spp. displayed decreased P_S, and the two other species had similar P_S compared to colonies from the reference site (Fig. 4B). Mean respiration (day R) rates were lower for *Echinopora* spp. from Bouraké compared to the reference site, and comparable for the other species between both sites (Fig. 4C). The mean P_g: day R ratios of Bouraké fragments were higher for *M. stellata, Echinopora* spp. and *P. cylindrica* but similar for *A. samoensis* and *A. tenuis* compared to fragments from the reference site (Fig. 4D).

Discussion

Zooxanthellae and chlorophyll contents of corals from the Bouraké lagoon were in similar ranges or higher than those of usual tropical corals in New Caledonia and in the GBR: $1–6 \times 10^6$ cells cm^{-2} of symbionts, 5–25 µg cm^{-2} of chl *a* and chl c_2, $2–15 \times 10^{-6}$ pg $cell^{-1}$ of chl *a* (e.g., Connolly et al. 2012; Schoepf et al. 2015; Camp et al. 2020). These results demonstrate that despite developing in a site with extreme conditions, corals from the Bouraké lagoon display healthy levels of symbionts and chlorophyll, even during the hottest period of the year (February to March), when fragments were collected for this study. This is coherent with the field observations made during sampling for this study, during which no sign of bleaching of corals in either site was observed. For a majority of species (five out of seven), chl *a* concentrations per surface area were even found to be higher at the Bouraké site than at the reference site. This resulted from increased symbiont densities and/or increased chl per symbiont in Bouraké corals compared to the reference site. The ability of Bouraké corals to maintain "normal" symbiont and chlorophyll contents under combined stressors could result from genetic adaptations, but several additional mechanisms could explain this ability. A first explanation could be related to the high levels of turbidity in the lagoon, especially at the end of the falling tide when the system empties and receives water rich in organic matter from the surrounding mangrove forest. Although light irradiance in the lagoon has yet to be extensively measured, the attenuation of solar radiations by turbidity has been shown to mitigate the stress exerted on corals from elevated temperatures and UV radiations by reducing photoinhibition and thus bleaching (Lesser and Farrell 2004; Sully and Woesik 2020). Many studies have reported lower bleaching rates at sites displaying higher turbidity levels in comparison to adjacent clear-water reefs (e.g., van Woesik et al. 2012; Morgan et al. 2017), and a similar mechanism could be at play in the Bouraké lagoon. A second mechanism involved could originate from the high nutrient concentrations (Rees and Smith 1991) which are likely to occur in the lagoon in relation to the surrounding mangrove ecosystem (Kristensen et al. 2008). Increased heterotrophy has previously been evidenced in turbid coastal environments (Anthony 2000) and has been shown to strengthen corals' symbiosis and help to maintain chlorophyll contents and high symbiont

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Table 3 Results from non-parametric Kruskal–Wallis test on the corals' chlorophyll (chl) and symbiont contents

Species	Parameters	*df*	H	*p*-value
A. samoensis	chl *a*	1,13	3.50	0.063
	chl c_2	1,13	2.94	0.086
	Symbionts	1,13	5.90	**0.015**
	chl *a* cell^{-1}	1,13	0.51	0.475
A. tenuis	chl *a*	1,24	13.53	**0.000**
	chl c_2	1,24	11.49	**0.000**
	Symbionts	1,24	6.06	**0.014**
	chl *a* cell^{-1}	1,24	15.30	**0.000**
Echinopora spp.	chl *a*	1,13	2.47	0.116
	chl c_2	1,13	0.18	0.668
	Symbionts	1,13	2.04	0.153
	chl *a* cell^{-1}	1,13	0.31	0.574
M. digitata	chl *a*	1,11	0.13	0.715
	chl c_2	1,11	1.63	0.201
	Symbionts	1,11	2.13	0.144
	chl *a* cell^{-1}	1,11	2.70	0.100
M. stellata	chl *a*	1,13	4.60	**0.032**
	chl c_2	1,13	4.00	**0.045**
	Symbionts	1,13	2.94	0.086
	chl *a* cell^{-1}	1,13	4.00	**0.045**
P. cylindrica	chl *a*	1,15	8.37	**0.004**
	chl c_2	1,15	0.12	0.728
	Symbionts	1,15	4.34	**0.037**
	chl *a* cell^{-1}	1,15	1.77	0.183
P. damicornis	chl *a*	1,12	7.41	**0.006**
	chl c_2	1,12	1.25	0.262
	Symbionts	1,12	3.10	0.078
	chl *a* cell^{-1}	1,12	0	1

Statistically significant values are in bold

densities under warm and acidified conditions (Edmunds 2011; Ferrier-Pagès et al. 2010; Houlbrèque et al. 2015). The combination of attenuated solar radiations and increased heterotrophy could be an explanation for how corals can maintain unchanged densities of symbionts despite developing in extreme environmental conditions. Isotopic analyses in both Symbiodiniaceae and tissues as well as measurements of nutrients, dissolved and particulate organic carbon, and different plankton populations are currently being carried out in the Bouraké lagoon to confirm whether increased heterotrophy could indeed support both hosts and symbionts in this extreme environment. A last specificity of the Bouraké lagoon that could influence the chlorophyll and symbiont content of corals is its high salinity, with daily fluctuations in the summer ranging from normal values to 40 in relation to the tide (Maggioni et al. 2021). Indeed, higher thermotolerance and reduced sensitivity to bleaching were found on Aiptasia from the hypersaline Red Sea, partially explaining the strong heat tolerance of corals from the northern Red Sea, and the Gulf of Aqaba (Gegner et al. 2017). Although corals from the Bouraké lagoon are not constantly exposed to high salinity as in the above-mentioned seas, they experience extreme levels which are comparable, therefore the same unknown mechanisms might have improved the persistence of symbionts in the corals from Bouraké, an interesting hypothesis that should be experimentally tested. Lastly, previous studies showed no effect of acidification on chlorophyll and symbiont contents in both short-time tank experiments (Godinot et al. 2011; Schoepf et al. 2013) and experiments using corals from volcanic CO_2 seeps (Noonan et al. 2013; Biscéré et al. 2019), which suggests that acidity is not a key factor in their determination.

Although this study mostly focused on the symbionts' responses to an extreme environment, the holobiont response as a whole was also investigated by characterizing the photosynthesis and day respiration of corals. By incubating corals from an extreme and a reference site under both future and present-day conditions, we obtained information on (1) the respiration and photosynthesis responses of corals to a short-term exposure to future conditions; (2) the endosymbiont specificities of corals originating from two contrasting environments. Photosynthesis and respiration rates measured during the incubations were in the same ranges as those measured in previous studies carried out in the Bouraké lagoon (Camp et al. 2017, 2020) and in other sites in New Caledonia (Biscéré et al. 2017, 2018). As hypothesized, a short-term exposure to future conditions (i.e. increased temperatures of 2 ± 0.2 °C, decreased pH_T of 0.3 ± 0.03 and decreased DO of 1.3 ± 0.02 mg L^{-1}) did not significantly modify corals' photosynthesis and respiration in comparison to present-day conditions. To the best of our knowledge, this is the first time that the effects of a short-term exposure to this trio of stressors is investigated. Previous studies that examined the effects of a short-term exposure to combined low pH and high temperature on corals' P and R rates have shown conflicting and non-linear results (e.g., Brown et al. 2019; Godinot et al. 2011; Hoadley et al. 2015). Overall, past results showed that temperature was the most impacting factor on corals' P and R rates, while the little effect of short-term exposure to acidified conditions was observed (e.g., Rodolfo-Metalpa et al. 2011; Comeau et al. 2017). The absence of detected effects on corals' *P* and *R* rates in this study could come from the length of the incubations used in this study, which was shorter than in the aforementioned studies (hour long vs. 10 days to a month in previous studies) and might not allow for plasticity or inhibition processes to occur. The unchanged P and R rates could also result from offsetting effects between increased T and decreased pH and DO. Longer exposure of adapted and non-adapted corals to low pH, DO and high T would allow to assess whether the absence of changes observed in this study is due to the

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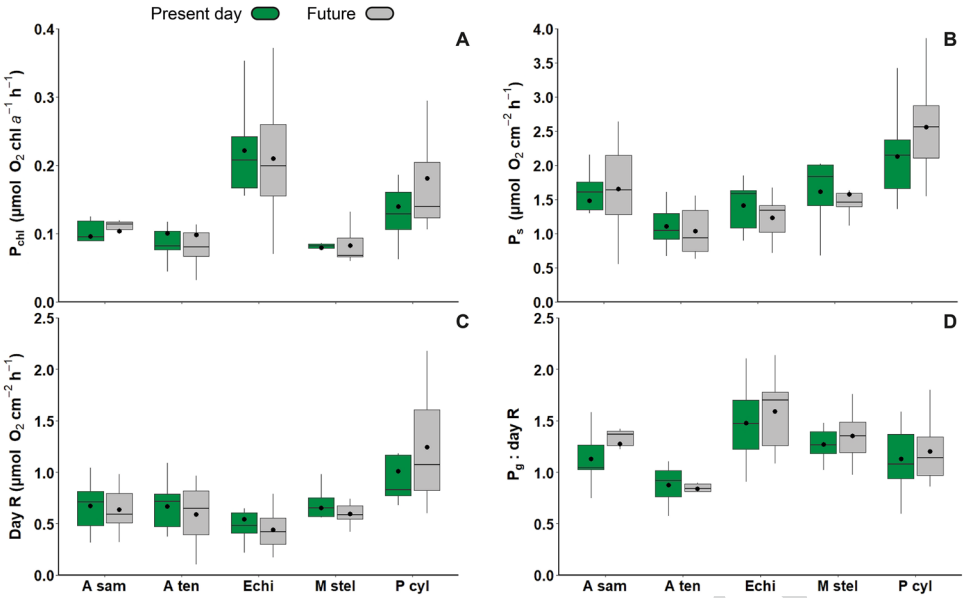

Fig. 3 Photosynthesis and respiration rates of fragments from Bouraké ($n = 5$–7 depending on species) incubated either under present-day (green) or future conditions (grey). See Table 2 for seawater conditions. **A** Gross photosynthesis rates normalized by chl *a* content (P_{chl}, µmol O_2 chl a^{-1} h^{-1}); **B** gross photosynthesis rates normalized by surface (P_S, µmol O_2 cm^{-2} h^{-1}); **C** day respiration rates normalized by surface (Day R, µmol O_2 cm^{-2} h^{-1}), and **D** their P_g: day *R* ratios. Data are represented as median values (lines) ± 25th and 75th percentiles (box), minimum and maximum values (whiskers) and mean values (dots). No significant differences between incubation conditions were found (see Table 4)

Table 4 Results of a two x two-way ANOVA testing the effect of colonies' origin (Bouraké and reference); seawater condition during incubations (HT: present-day and LT: future), and their interaction on the gross photosynthesis rates per chlorophylent (P_{chl}), and per surface area (P_S), day respiration (day R), and photosynthesis to day respiration ratio (P_g: day R) of colonies from five coral species

Species	Factor	Pchl				Ps				day R				Ps: day R			
		df	SS	F	P	df	SS	F	P	df	SS	F	P	df	SS	F	P
A. samoensis	Origin	1	0.035	26.38	**0.000**	1	0.005	0.02	0.898	1	0.109	1.52	0.230	1	0.035	0.257	0.617
	Condition	1	0	0.33	0.568	1	0.126	0.40	0.535	1	0.001	0.02	0.887	1	0.201	1.49	0.235
	Origin × cond	1	0	0	0.983	1	0.006	0.02	0.889	1	0.002	0.03	0.853	1	0.005	0.03	0.856
	Error	22	0.029			22	6.979			22	1.584			19	2.966		
A. tenuis	Origin	1	0.471	14.70	**0.001**	1	1.107	6.90	**0.017**	1	0.013	0.24	0.631	1	0.229	0.38	0.544
	Condition	1	0.011	0.35	0.563	1	0.007	0.04	0.838	1	0.184	3.26	0.088	1	1.982	3.31	0.085
	Origin × cond	1	0.021	0.66	0.426	1	0.107	0.66	0.425	1	0.105	1.87	0.188	1	0.319	0.53	0.475
	Error	18	0.577			18	2.892			18	1.014			18	10.768		
Echinopora spp.	Origin	1	0.439	13.33	**0.001**	1	1.892	5.70	**0.026**	1	0.760	8.71	**0.007**	1	0.622	3.04	0.095
	Condition	1	0.006	0.18	0.674	1	0.186	0.56	0.462	1	0.091	1.04	0.318	1	0.161	0.78	0.385
	Origin × cond	1	0.002	0.06	0.808	1	0.001	0.002	0.965	1	0.002	0.02	0.886	1	0.012	0.06	0.809
	Error	22	0.724			22	7.298			22	1.919			22	4.502		
M. stellata	Origin	1	0.012	10.39	**0.004**	1	0.378	1.97	0.175	1	0.092	2.53	0.126	1	0.714	9.45	**0.006**
	Condition	1	0	0.35	0.557	1	0.077	0.40	0.532	1	0.001	0.03	0.853	1	0.003	0.04	0.843
	Origin × cond	1	0.001	0.58	0.455	1	0.025	0.13	0.723	1	0.010	0.26	0.612	1	0.020	0.27	0.610
	Error	22	0.025			22	4.223			22	0.805			22	1.663		
P. cylindrica	Origin	1	0.030	6.36	**0.018**	1	4.399	9.25	**0.005**	1	0.123	0.88	0.357	1	0.796	10.02	**0.004**
	Condition	1	0	0.10	0.759	1	0.413	0.87	0.359	1	0.057	0.40	0.531	1	0.001	0.02	0.880
	Origin × cond	1	0.010	2.08	0.161	1	1.249	2.63	0.117	1	0.195	1.39	0.250	1	0.025	0.31	0.583
	Error	26	0.121			26	12.358			26	3.651			26	2.066		

Significant values are in bold

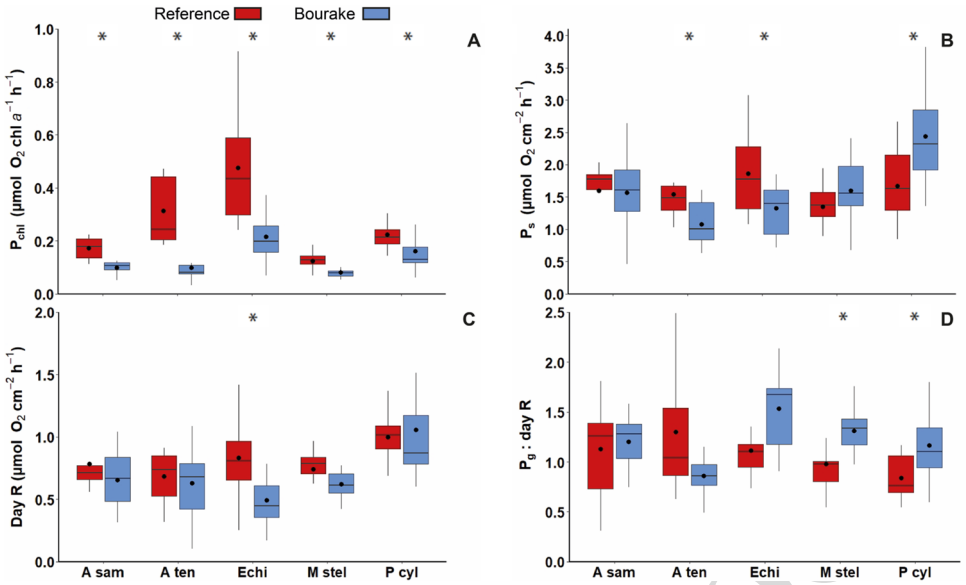

Fig. 4 Photosynthesis and respiration rates of fragments from the reference and the Bouraké site pooled between incubation conditions ($n = 5$–7 depending on species). **A** Gross photosynthesis rates normalized by chl *a* content (P_{chl}, µmol O_2 chl a^{-1} h^{-1}); **B** gross photosynthesis rates normalized by surface (P_S, µmol O_2 cm^{-2} h^{-1}); **C** day respiration rates normalized by surface (Day R, µmol O_2 cm^{-2} h^{-1}), and **D** P_g: day R ratios. Data are represented as median values (lines) ± 25th and 75th percentiles (box), minimum and maximum values (whiskers) and mean values (dots). Asterisks indicate statistical differences between sites of origin (see Table 4)

incubation length used or to compensating effects between the three stressors.

Conversely, corals' origin had a significant and species-specific effect on respiration and photosynthetic rates. While the incubation conditions were identical for both groups of corals, the rate of P_{chl} was significantly lower for all species from the Bouraké site. This could result from the higher density of chl *a* in Bouraké corals, which can lead to self-shading and lower the absorption efficiency of pigments (Enríquez et al. 2005). Symbionts from Bouraké could also have adapted to the lower light intensity in the lagoon by displaying lower light intensity saturation points, leading to lower productivity compared to reference symbionts. The differences in the measured P_{chl} rates could also be caused by a change in symbiont types between Bouraké and the reference site, which has been shown to be a common adaptive feature in extreme environments (Howells et al. 2016). Camp et al. (2020) found differences in symbiont types between Bouraké corals and nearby reference corals. These changes were species-specific, which is consistent with the species-specific results found for P_{chl} rates. Adaptation of symbionts to acidified environments could for example take the form of the ability to enhance *P* rates by taking advantage of increased pCO_2. This adaptation has been shown to occur for some, but not all, host + symbiont assemblages (Biscéré et al. 2019; Inoue et al. 2013; Langdon and Atkinson 2005). However, the decrease in photosynthetic rates per chl *a* of Bouraké corals was counterbalanced by the increase in the chl *a* content of these corals per surface area. These two compensating factors resulted in *P* rates per surface area (P_S) lower for *A. tenuis* and *Echinopora* spp., higher for *P. cylindrica* and comparable for the two other species at the Bouraké site. Furthermore, the differences observed between sites in the P_s rates were less pronounced than those observed for P_{chl}. In previous studies conducted at the Bouraké site, Camp et al. (2017) found no changes in P_S rates for fragments of *A. pulchra*, *A. muricata* and *P. lutea*. Collectively, these results suggest that P_S rates of the Bouraké corals are either comparable or slightly lower than those of corals from adjacent reference reefs.

Corals' origin also had a significant effect on respiration rates, which were lower for two out of five species from the Bouraké site. It is established that water acidification increases energy demands to maintain calcification rates, although marginally (McCulloch et al. 2012). In an acidified environment like the Bouraké lagoon, unchanged or lower R rates of corals as observed in this study suggest either lower growth rates or reallocation of the energy budget. The former outcome seems likely, as Camp et al. (2017) reported lower calcification rates of Bouraké corals compared to reference corals. A study conducted at another mangrove site in Sulawesi, Indonesia also found that corals did not increase their R rates compared to control fragments (Camp et al. 2016). Low pO_2 characteristic of mangrove habitats (Kristensen et al. 2008) could be a limiting factor in the ability of corals to increase their day *R* rates, especially at night when O_2 is not being produced by symbionts. It is to be noted that previous studies carried out in Bouraké found that day R

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rates of Bouraké corals were higher than those of reference corals (Camp et al. 2017, 2020). The discrepancy in results could come from the differences in experimental design, as well as differences in the species studied. Indeed, these previous studies incubated Bouraké and reference corals using seawater from their respective sites, while we compared P and R rates of both groups using seawater collected only in Bouraké.

Altogether, our results show that corals that have been chronically exposed to extreme conditions display different P and R rates than corals from an adjacent reference site. These differences persisted even when corals were exposed during short-term periods to contrasting incubation conditions, suggesting that they originate from intrinsic traits rather than differing environmental conditions. This study does not allow to discriminate the role played by acclimatization (resulting from corals' plasticity) and adaptation (resulting from genetic modifications) in the differences observed between both sites. As acclimation occurs at a faster rate than adaptation, knowing which process is prevalent is important to assess if corals' have the potential to keep up with climate change (Palumbi et al. 2014). Transplantation experiments and metatranscriptomic approaches would be necessary to assess the respective roles of adaptation and acclimation, which have never been carried out yet in an environment combining this trio of stressors.

The Bouraké site is the first site displaying multiple and fluctuating stressors where corals' endosymbiont functions, photosynthesis and respiration have been investigated. This study consolidates previous results from single-stressor sites, such as CO_2 seeps, showing that corals' responses to extreme conditions are largely species-specific. Indeed, variations of P and day R rates between Bouraké and reference corals were heterogeneous among species, and both increases and decreases in these values were observed. This is consistent with findings from coral communities developing around volcanic CO_2 seeps in Papua New Guinea (Biscéré et al. 2019; Strahl et al. 2015), which showed species-specific rather than stereotyped responses of *P* and *R* rates to their acidified environment. While Strahl et al. (2015) found no effect of pCO_2 on *R* rates and heterogeneous effects on P_g rates, Biscéré et al. (2019) found increased P_g, day *R* and P_g: day R under elevated pCO_2. This suggests that corals' adjustments to extreme environments can take diverse forms and that responses are species- and site-dependent rather than stereotyped (Hoadley et al. 2015). This study also highlights that some coral species might have more limited abilities to adjust to unfavorable conditions. For example, we found that the two Acroporidae species (*A. tenuis* and *A. samoensis*) displayed the lowest P_g: day *R* rates and were the only species for which this value was not higher than that of the reference colonies. Increased *P* rates and P_g: day *R* ratios have been linked to higher productivity, which is thought to play an important role in corals' tolerance to acidified conditions (Fabricius et al. 2011). This suggests that Acroporidae species are undergoing higher energetic stress, and could thus be more vulnerable to any additional stressor occurring in the Bouraké lagoon. Past studies have also evidenced a lower resistance of Acroporidae to extreme conditions, suggesting they could be potential losers in our world's future oceans (Loya et al. 2001; Schoepf et al. 2013). The vulnerability of Acroporidae could be further exacerbated by their typically low heterotrophic intakes and low heterotrophic plasticity compared to other genera such as Montiporidae or Pocilloporidae (Palardy et al. 2008; Conti-Jerpe et al. 2020; Sangmanee et al. 2020). However, comparison of results between species is limited because tissue extraction and wax surface measurement is known to vary depending on each species' structure and geometry (Edmunds and Gates 2002), leading to a species bias for chlorophyll contents, symbiont contents and surface area. As our results for photosynthesis and respiration rates were normalized by chlorophyll and area values, species comparison for any of our studied variables is to be considered cautiously, which is why it was not further developed in this study.

The persistence of knowledge gaps on how single environmental stressors affect corals' metabolism obscures the interpretation of how these stressors could affect photosynthesis and respiration when combined. While the effects of acidification and warming have been largely investigated, at least separately and on non-adapted corals, the effects of low DO on corals' physiology are poorly understood. Deoxygenation is predicted to increasingly affect marine ecosystems as a result of global warming and eutrophication (Hughes et al. 2020). The few studies conducted on coral reefs (Altieri et al. 2017; Haas et al. 2014; Hughes et al. 2020) reported hypoxic thresholds around 3–4.0 mg L^{-1}, although this value is likely to vary according to species and site. As DO reach a minimum of 2.28 mg L^{-1} in the Bouraké lagoon, it likely acts as a stressor on corals' metabolism. Additionally, as low DO limits aerobic metabolism, it is thought to be even more harmful when combined with other stressors such as high temperatures or acidification, which tend to increase the energy requirements of marine organisms (Breitburg et al. 2018). While hyposalinity has been shown to be detrimental to corals' metabolism (Moberg et al. 1997; Ferrier-Pages et al. 1999; Alutoin et al. 2001; Gardner et al. 2016), the effects of high salinity have received little attention, although some evidence suggests it could convey thermotolerance to coral species (Gegner et al., 2017). The numerous and concomitant stressors occurring in the Bouraké lagoon are thus both what make it a unique and valuable natural laboratory and what limit the interpretation of our results.

We recognise that our experimental approach has limitations and that several caveats might interfere with our results

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reporting low metabolic "stress" in corals that have developed in the extreme conditions of the lagoon of Bouraké. First of all, we compared only two sites: one within the Bouraké lagoon and one adjacent reference fringing reef, which does not allow us to investigate whether spatial variations occur in our studied system. Although environmental conditions are quite homogeneous within the Bouraké lagoon, which is why we based our experiment on a single site, we would recommend future studies to sample corals from several sites both within the lagoon of Bouraké and in adjacent fringing reefs. Furthermore, this experiment measured the photosynthesis and respiration of corals during the morning low tide and during the afternoon high tide. This could introduce a bias in the comparison of photosynthesis and respiration under low tide and high tide conditions because metabolism is known to change in relation to the time of the day. Ideally, our experiment should also be repeated during the night to test both low and high tide conditions on corals fully dark adapted, although such an experiment would come with logistic and security constraints on a research vessel.

Although some limitations exist, corals from naturally extreme environments are an invaluable tool to understand the mechanisms supporting higher tolerance to future climatic conditions. This study showed that corals that have been exposed their whole life, and possibly across generations, to extreme and fluctuating T, pH and DO, are able to maintain unaltered levels of symbionts and chlorophylls, as well as sustained photosynthesis and respiration rates. As such, the lagoon of Bouraké provides evidence that corals are able to maintain their autotrophic source of energy even under the combined effects of warming, acidification and deoxygenation, which have been feared to impair the physiological mechanisms necessary for corals' survival (Breitburg et al. 2018; Hughes et al. 2020). The variability of T, pH and DO occurring in the Bouraké lagoon could play a significant role in the ability of corals to cope with extreme conditions. Although research on the role of environmental variability is in its prime, it has been suggested to enhance corals' plasticity and possibly their tolerance to future projected conditions (Oliver and Palumbi 2011; Rivest et al. 2017; Schoepf et al. 2015). Undergoing chronic varying conditions could have helped the Bouraké corals to survive the 2016 bleaching episode that impacted most reefs of New Caledonia (Benzoni et al. 2017; Camp et al. 2017). Other specificities of the Bouraké lagoon, such as higher turbidity levels and potentially higher nutrient concentrations, could also play a role in the survival of the documented coral species by counterbalancing the negative effects of local stressors. The combination of these specificities could explain why the lagoon of Bouraké is one of the only sites where corals developing under warm, acidified and deoxygenated conditions have been observed. While providing evidence for the ability of corals to develop under such stressors, it does not ensure that this ability could be generalized to other sites displaying a different set of unique environmental conditions and that this ability will be maintained in a warmer future (Grottoli et al. 2014; Schoepf et al. 2015; Nohaïc et al. 2017).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-022-04063-6.

Acknowledgements We thank the whole crew on board of the Alis vessel to have enabled us to conduct this fieldwork. We thank the IRD of Nouméa for having provided facilities and the equipment necessary to conduct this study. We are grateful to Federica Maggioni for her help during fieldwork and for data sharing. We thank Saki Harii for his help throughout the reviewing and editing process of this article, and Kaleb Trunnell for English proofreading. The base data to drawn Figure 1 were collected from map tiles at www.georep.nc (©Georep contributors).

Author contributions The study conception and design were performed by RRM. Material preparation and data collection were performed by JJ and CT, under the supervision of RRM and FH. Data analysis and writing of the first draft were performed by JJt. All authors read and approved the final manuscript.

Funding This work was partially funded by the LabEx-Corail (project SURF to F.H.), and the Ministère des Affaires étrangères et du développement international (MAEDI) Fonds Pacifique (project Super Coraux to R.R.-M.). Data were collected during the cruise SuperNatural 2 (https://doi.org/10.17600/18001102) onboard the R/V Alis (Flotte Océanographique Francaise).

Availability of data The datasets generated and analysed during the current study are available from the corresponding author on reasonable request

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no competing interests.

Ethics approval All corals were collected under permits issued by the Province Sud of New Caledonia (# 3413–2019)).

References

Altieri AH, Harrison SB, Seemann J, Collin R, Diaz RJ, Knowlton N (2017) Tropical dead zones and mass mortalities on coral reefs. Proc Natl Acad Sci USA 114:3660–3665. https://doi.org/10.1073/pnas.1621517114

Alutoin S, Boberg J, Nyström M, Tedengren M (2001) Effects of the multiple stressors copper and reduced salinity on the metabolism of the hermatypic coral *Porites lutea*. Mar Env Res 52:289–299. https://doi.org/10.1016/S0141-1136(01)00105-2

Anthony KRN (2000) Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). Coral Reefs 19:59–67. https://doi.org/10.1007/s003380050227

Anthony K, Kline D, Diaz-Pulido G, Dove S, Hoegh-Guldberg O (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. Proc Natl Acad Sci USA 105:17442–6. https://doi.org/10.1073/pnas.0804478105

Benzoni F, Houlbreque F, Andre L, Payri C (2017) Plan d'action rapide et adaptatif, en cas de blanchissement corallien : le cas de la Nouvelle-Calédonie, épisode 2016: synthèse

Biscéré T, Lorrain A, Rodolfo-Metalpa R, Gilbert A, Wright A, Devissi C, Peignon C, Farman R, Duvieilbourg E, Payri C, Houlbrèque F (2017) Nickel and ocean warming affect scleractinian coral growth. Mar Pollut Bull 120:250–258. https://doi.org/10.1016/j.marpolbul.2017.05.025

Biscéré T, Zampighi M, Lorrain A, Jurriaans S, Foggo A, Houlbrèque F, Rodolfo-Metalpa R (2019) High pCO_2 promotes coral primary production. Biol Lett 15:20180777. https://doi.org/10.1098/rsbl.2018.0777

Biscéré T, Ferrier-Pagès C, Gilbert A, Pichler T, Houlbrèque F (2018) Evidence for mitigation of coral bleaching by manganese. Sci Rep 8:16789. https://doi.org/10.1038/s41598-018-34994-4

Bopp L, Resplandy L, Orr JC, Doney SC, Dunne JP, Gehlen M, Halloran P, Heinze C, Ilyina T, Seferian R, Tjiputra J (2013) Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. Biogeosciences 10:6225–6245. https://doi.org/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. https://doi.org/10.1126/science.aam7240

Brown KT, Bender-Champ D, Kenyon TM, Rémond C, Hoegh-Guldberg O, Dove S (2019) Temporal effects of ocean warming and acidification on coral–algal competition. Coral Reefs 38:297–309. https://doi.org/10.1007/s00338-019-01775-y

Camp EF, Suggett DJ, Gendron G, Jompa J, Manfrino C, Smith DJ (2016) Mangrove and seagrass beds provide different biogeochemical services for corals threatened by climate change. Front Mar Sci 3:52. https://doi.org/10.3389/fmars.2016.00052

Camp EF, Nitschke MR, Rodolfo-Metalpa R, Houlbreque F, Gardner SG, Smith DJ, Zampighi M, Suggett DJ (2017) Reef-building corals thrive within hot-acidified and deoxygenated waters. Sci Rep 7:2434. https://doi.org/10.1038/s41598-017-02383-y

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. Front Mar Sci 5:4. https://doi.org/10.3389/fmars.2018a.00004

Camp EF, Schoepf V, Suggett DJ (2018b) How can "Super Corals" facilitate global coral reef survival under rapid environmental and climatic change? Glob Change Biol 24:2755–2757. https://doi.org/10.1111/gcb.14153

Camp EF, Suggett DJ, Pogoreutz C, Nitschke MR, Houlbreque F, Hume BCC, Gardner SG, Zampighi M, Rodolfo-Metalpa R, Voolstra CR (2020) Corals exhibit distinct patterns of microbial reorganisation to thrive in an extreme inshore environment. Coral Reefs 39:701–716. https://doi.org/10.1007/s00338-019-01889-3

Comeau S, Carpenter RC, Edmunds PJ (2017) Effects of pCO_2 on photosynthesis and respiration of tropical scleractinian corals and calcified algae. ICES J Mar Sci 74:1092–1102. https://doi.org/10.1093/icesjms/fsv267

Connolly SR, Lopez-Yglesias MA, Anthony KRN (2012) Food availability promotes rapid recovery from thermal stress in a scleractinian coral. Coral Reefs 31:951–960. https://doi.org/10.1007/s00338-012-0925-9

Conti-Jerpe IE, Thompson PD, Wong CWM, Oliveira NL, Duprey NN, Moynihan MA, Baker DM (2020) Trophic strategy and bleaching resistance in reef-building corals. Sci Adv. https://doi.org/10.1126/sciadv.aaz5443

Crawley A, Kline D, Dunn S, Anthony K, Dove S (2010) The effect of ocean acidification on symbiont photorespiration and productivity in *Acropora formosa*. Glob Change Biol 16:851–863. https://doi.org/10.1111/j.1365-2486.2009.01943.x

Edmunds PJ (2011) Zooplanktivory ameliorates the effects of ocean acidification on the reef coral *Porites* spp. Limnol Oceanogr 56:2402–2410. https://doi.org/10.4319/lo.2011.56.6.2402

Edmunds P (2012) Effect of pCO_2 on the growth, respiration, and photophysiology of massive *Porites* spp. in Moorea. French Polynesia Mar Biol 159:2149–2160. https://doi.org/10.1007/s00227-012-2001-y

Edmunds PJ, Davies PS (1988) Post-illumination stimulation of respiration rate in the coral *Porites porites*. Coral Reefs 7:7–9. https://doi.org/10.1007/BF00301975

Edmunds P, Gates R (2002) Normalizing physiological data for scleractinian corals. Coral Reefs 21:193–197. https://doi.org/10.1007/s00338-002-0214-0

Enríquez S, Méndez ER, Iglesias-Prieto R (2005) Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. Limnol Oceanogr 50:1025–1032. https://doi.org/10.4319/lo.2005.50.4.1025

Fabricius KE, Langdon C, Uthicke S, Humphrey C, Noonan S, De'ath G, Okazaki R, Muehllehner N, Glas MS, Lough JM (2011) Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. Nat Clim Change 1:165–169. https://doi.org/10.1038/nclimate1122

Ferrier-Pages C, Gattuso J, Jaubert J (1999) Effect of small variations in salinity on the rates of photosynthesis and respiration of the zooxanthellate coral *Stylophora pistillata*. Mar Ecol Prog Ser 181:309–314. https://doi.org/10.3354/meps181309

Ferrier-Pagès C, Rottier C, Beraud E, Levy O (2010) Experimental assessment of the feeding effort of three scleractinian coral species during a thermal stress: Effect on the rates of photosynthesis. J Exp Mar Biol Ecol 390:118–124. https://doi.org/10.1016/j.jembe.2010.05.007

Gardner SG, Nielsen DA, Laczka O, Shimmon R, Beltran VH, Ralph PJ, Petrou K (2016) Dimethylsulfoniopropionate, superoxide dismutase and glutathione as stress response indicators in three corals under short-term hyposalinity stress. Proc R Soc B-Biol Sci 283:20152418. https://doi.org/10.1098/rspb.2015.2418

Gegner HM, Ziegler M, Rädecker N, Buitrago-López C, Aranda M, Voolstra CR (2017) High salinity conveys thermotolerance in the coral model *Aiptasia*. Biology Open 6:1943–1948. https://doi.org/10.1242/bio.028878

Godinot C, Houlbrèque F, Grover R, Ferrier-Pagès C (2011) Coral uptake of inorganic phosphorus and nitrogen negatively affected by simultaneous changes in temperature and pH. PLoS ONE 6:e25024. https://doi.org/10.1371/journal.pone.0025024

Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440:1186–1189. https://doi.org/10.1038/nature04565

Grottoli AG, Warner ME, Levas SJ, Aschaffenburg MD, Schoepf V, McGinley M, Baumann J, Matsui Y (2014) The cumulative impact of annual coral bleaching can turn some coral species winners into losers. Glob Change Biol 20:3823–3833. https://doi.org/10.1111/gcb.12658

Grottoli A, Tchernov D, Winters G (2017) Physiological and biogeochemical responses of super-corals to thermal stress from the Northern Gulf of aqaba. Red Sea Front Mar Sci 4:215. https://doi.org/10.1038/srep18371

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

Hoadley KD, Pettay DT, Grottoli AG, Cai WJ, Melman TF, Schoepf V, Hu X, Li Q, Xu H, Wang Y, Matsui Y, Baumann JH, Warner ME (2015) Physiological response to elevated temperature and pCO_2 varies across four Pacific coral species: Understanding the unique host+symbiont response. Sci Rep 5:18371. https://doi.org/10.1038/srep18371

Hoegh-Guldberg O, Mumby P, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell C, Sale P, Edwards A, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury R, Dubi A, Hatziolos M (2008) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742. https://doi.org/10.1126/science.1152509

Hoegh-Guldberg O, Poloczanska E, Skirving W, Dove S (2017) Coral reef ecosystems under climate change and ocean acidification. Front Mar Sci 4:158. https://doi.org/10.3389/fmars.2017.00158

Hoegh-Guldberg O, Jacob DM, Taylor M, Bindi S, Brown I, Camilloni A, Diedhiou R, Djalante KL, Ebi F, Engelbrecht J, Guiot Y, Hijioka S, Mehrotra A, Payne SI, Seneviratne A, Thomas R, Zhou G (2018) Impacts of 1.5ºC Global Warming on Natural and Human Systems. In: Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty (In Press)

Houlbrèque F, Tambutté E, Ferrier-Pagès C (2003) Effect of zooplankton availability on the rates of photosynthesis, and tissue and skeletal growth in the scleractinian coral *Stylophora pistillata*. J Exp Mar Biol Ecol 296:145–166. https://doi.org/10.1016/S0022-0981(03)00259-4

Houlbrèque F, Reynaud S, Godinot C, Oberhänsli F, Rodolfo-Metalpa R, Ferrier-Pagès C (2015) Ocean acidification reduces feeding rates in the scleractinian coral *Stylophora pistillata*. Limnol Oceanogr 60:89–99. https://doi.org/10.1002/lno.10003

Howells EJ, Abrego D, Meyer E, Kirk NL, Burt JA (2016) Host adaptation and unexpected symbiont partners enable reef-building corals to tolerate extreme temperatures. Glob Change Biol 22:2702–2714. https://doi.org/10.1111/gcb.13250

Hughes DJ, Alderdice R, Cooney C, Kühl M, Pernice M, Voolstra CR, Suggett DJ (2020) Coral reef survival under accelerating ocean deoxygenation. Nat Clim Change 10:296–307. https://doi.org/10.1038/s41558-020-0737-9

Inoue S, Kayanne H, Yamamoto S, Kurihara H (2013) Spatial community shift from hard to soft corals in acidified water. Nat Clim Change 3:683–687. https://doi.org/10.1038/nclimate1855

IPCC (2019) Summary for policymakers. In: Pörtner HO, Roberts DC, Masson-Delmotte V, Zhai P, Tignor M, Poloczanska E, Mintenbeck K, Alegría A, Nicolai M, Okem A, Petzold J, Rama B, Weyer NM (eds) IPCC Special Report on the Ocean and Cryosphere in a Changing Climate (In press)

Jeffrey SW, Humphrey GF (1975) New spectrophotometric equations for determining chlorophylls a, b, c_1 and c_2 in higher plants, algae and natural phytoplankton. Biochem Physiol Pflanz 167:191–194. https://doi.org/10.1016/S0015-3796(17)30778-3

Kenkel CD, Moya A, Strahl J, Humphrey C, Bay LK (2018) Functional genomic analysis of corals from natural CO_2 -seeps reveals core molecular responses involved in acclimatization to ocean acidification. Glob Change Biol 24:158–171. https://doi.org/10.1111/gcb.13833

Kleypas JA, McManus JW, Menez LA (1999) Environmental limits to coral reef development: where do we draw the line? Am Zool 39:146–159. https://doi.org/10.1093/icb/39.1.146

Kristensen E, Bouillon S, Dittmar T, Marchand C (2008) Organic carbon dynamics in mangrove ecosystems: A review. Aquatic Botany Mangrove Ecol Applic Forestry Coastal Zone Manag 89:201–219. https://doi.org/10.1016/j.aquabot.2007.12.005

Kroeker KJ, Kordas RL, Crim RN, Singh GG (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecol Lett 13:1419–1434. https://doi.org/10.1111/j.1461-0248.2010.01518.x

Kroeker KJ, Kordas RL, Crim R, Hendriks IE, Ramajo L, Singh GS, Duarte CM, Gattuso JP (2013) Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. Glob Change Biol 19:1884–1896. https://doi.org/10.1111/gcb.12179

Langdon C, Atkinson M (2005) Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. J Geophysical Res. https://doi.org/10.1029/2004JC002576

Le Nohaïc M, Ross CL, Cornwall CE, Comeau S, Lowe R, McCulloch MT, Schoepf V (2017) Marine heatwave causes unprecedented regional mass bleaching of thermally resistant corals in northwestern Australia. Sci Rep 7:111. https://doi.org/10.1038/s41598-017-14794-y

Lesser MP, Farrell JH (2004) Exposure to solar radiation increases damage to both host tissues and algal symbionts of corals during thermal stress. Coral Reefs 23:367–377. https://doi.org/10.1007/s00338-004-0392-z

Logan CA, Dunne JP, Eakin CM, Donner SD (2014) Incorporating adaptive responses into future projections of coral bleaching. Glob Change Biol 20:125–139. https://doi.org/10.1111/gcb.12390

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. Ecol Lett 4:122–131. https://doi.org/10.1046/j.1461-0248.2001.00203.x

Maggioni F, Pujo-Pay M, Aucan J, Cerrano C, Calcinai B, Payri C, Benzoni F, Letourneur Y, Rodolfo-Metalpa R (2021) The Bouraké semi-enclosed lagoon (New Caledonia)–a natural laboratory to study the lifelong adaptation of a coral reef ecosystem to extreme environmental conditions. Biogeosciences 18:5117–5514. https://doi.org/10.5194/bg-18-5117-2021

McCulloch M, Falter J, Trotter J, Montagna P (2012) Coral resilience to ocean acidification and global warming through pH up-regulation. Nat Clim Change 2:623–627. https://doi.org/10.1038/nclimate1473

McLachlan RH, Price JT, Solomon SL, Grottoli AG (2020) Thirty years of coral heat-stress experiments: a review of methods. Coral Reefs 39(4):885–902. https://doi.org/10.1007/s00338-020-01931-9

Moberg F, Nyström M, Kautsky N, Tedengren M, Jarayabhand P (1997) Effects of reduced salinity on the rates of photosynthesis and respiration in the hermatypic corals *Porites lutea* and *Pocillopora damicornis*. Mar Ecol Prog Ser 157:53–59. https://doi.org/10.3354/meps157053

Morgan KM, Perry CT, Johnson JA, Smithers SG (2017) Nearshore turbid-zone corals exhibit high bleaching tolerance on the Great barrier reef following the 2016 ocean warming event. Front Mar Sci 4:224. https://doi.org/10.3389/fmars.2017.00224

Muscatine L (1990) The role of symbiotic algae in carbon and energy flux in reef corals. Ecosyst World 25:75–87

Noonan SHC, Fabricius KE, Humphrey C (2013) Symbiodinium community composition in scleractinian corals is not affected by lifelong exposure to elevated carbon dioxide. PLoS ONE 8:e63985. https://doi.org/10.1371/journal.pone.0063985

Oliver TA, Palumbi SR (2011) Do fluctuating temperature environments elevate coral thermal tolerance? Coral Reefs 30:429–440. https://doi.org/10.1007/s00338-011-0721-y

Palardy JE, Rodrigues LJ, Grottoli AG (2008) The importance of zooplankton to the daily metabolic carbon requirements of healthy and bleached corals at two depths. J Exp Mar Biol Ecol 367:180–188. https://doi.org/10.1016/j.jembe.2008.09.015

Palumbi S, Barshis D, Traylor-Knowles N, Bay R (2014) Mechanisms of reef coral resistance to future climate change. Science 344:895–898. https://doi.org/10.1126/science.1251336

Rees TV, Smith D (1991) Are symbiotic algae nutrient deficient? Proc R Soc B-Biol Sci 243:227–233. https://doi.org/10.1098/rspb.1991.0036

Rivest EB, Comea S, Cornwall CE (2017) The role of natural variability in shaping the response of coral reef organisms to climate change. Curr Clim Change Rep 3:271–281. https://doi.org/10.1007/s40641-017-0082-x

Rodolfo-Metalpa R, Houlbrèque F, Tambutté É, Boisson F, Baggini C, Patti FP, Jeffree R, Fine M, Foggo A, Gattuso JP, Hall-Spencer JM (2011) Coral and mollusc resistance to ocean acidification adversely affected by warming. Nat Clim Change 1:308–312. https://doi.org/10.1038/nclimate1200

RStudio Team (2019) RStudio: Integrated Development for R. RStudio Inc., Boston. https://www.rstudio.com

Sangmanee K, Casareto BE, Nguyen TD, Sangsawang L, Toyoda K, Suzuki T, Suzuki Y (2020) Influence of thermal stress and bleaching on heterotrophic feeding of two scleractinian corals on pico-nanoplankton. Mar Pollut Bull 158:111405. https://doi.org/10.1016/j.marpolbul.2020.111405

Schoepf V, Grottoli A, Warner M, Cai WJ, Melman T, Hoadley K, Pettay D, Hu X, Li Q, Xu H, Wang Y, Matsui Y, Baumann J (2013) Coral energy reserves and calcification in a high-CO_2 world at two temperatures. PLoS One 8:e75049. https://doi.org/10.1371/journal.pone.0075049

Schoepf V, Sta M, Falter JL, McCulloch MT (2015) Limits to the thermal tolerance of corals adapted to a highly fluctuating, naturally extreme temperature environment. Sci Rep 5:17639. https://doi.org/10.1038/srep17639

Strahl J, Stolz I, Uthicke S, Vogel N, Noonan SHC, Fabricius KE (2015) Physiological and ecological performance differs in four coral taxa at a volcanic carbon dioxide seep. Comp Biochem Phys A 184:179–186. https://doi.org/10.1016/j.cbpa.2015.02.018

Sully S, van Woesik R (2020) Turbid reefs moderate coral bleaching under climate-related temperature stress. Glob Change Biol 26:1367–1373. https://doi.org/10.1111/gcb.14948

Titlyanov EA, Titlyanova TV, Yamazato K, van Woesik R (2001) Photo-acclimation dynamics of the coral *Stylophora pistillata* to low and extremely low light. J Exp Mar Biol Ecol 263:211–225. https://doi.org/10.1016/S0022-0981(01)00309-4

Torda G, Donelson JM, Aranda M, Barshis DJ, Bay L, Berumen ML, Bourne DG, Cantin N, Foret S, Matz M, Miller DJ, Moya A, Putnam HM, Ravasi T, van Oppen MJH, Thurber RV, Vidal-Dupiol J, Voolstra CR, Watson SA, Whitelaw E, Willis BL, Munday PL (2017) Rapid adaptive responses to climate change in corals. Nat Clim Change 7:627–636. https://doi.org/10.1038/nclimate3374

Van Woesik R, Houk P, Isechal AL, Idechong JW, Victor S, Golbuu Y (2012) Climate-change refugia in the sheltered bays of Palau: analogs of future reefs. Ecol Evol 2:2474–2484. https://doi.org/10.1002/ece3.363

Veal CJ, Carmi M, Fine M, Hoegh-Guldberg O (2010) Increasing the accuracy of surface area estimation using single wax dipping of coral fragments. Coral Reefs 29:893–897. https://doi.org/10.1007/s00338-010-0647-9