The Bouraké semi-enclosed lagoon (New Caledonia). A natural laboratory to study the life-long adaptation of a coral reef ecosystem to climate change-like conditions

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Abstract. According to current experimental evidence, coral reefs could disappear within the century if CO2 emissions remain unabated. However, recent discoveries of diverse and high cover reefs that already thrive under extreme conditions seem to contradict these projections. Volcanic CO2 vents, semi-enclosed lagoons and mangrove estuaries are unique study sites where one or more ecologically relevant parameters for life in the oceans are close or even worse than currently projected for the year 2100. These natural analogues of future conditions hold new hope for the future of coral reefs and provide unique natural laboratories to explore how reef species could keep pace with climate change. To achieve this, it is essential to characterize their environment as a whole, and accurately consider all possible environmental factors that may differ from what is expected in the future and that may possibly alter the ecosystem response.

In this study, we focus on the semi-enclosed lagoon of Bouraké (New Caledonia, SW Pacific Ocean) where a healthy reef ecosystem thrives in warm, acidified and deoxygenated water. We used a multi-scale approach to characterize the main physical-chemical parameters and mapped the benthic community composition (i.e., corals, sponges, and macroalgae). The data revealed that most physical and chemical parameters are regulated by the tide, strongly fluctuate 3 to 4 times a day, and are entirely predictable. The seawater pH and dissolved oxygen decrease during falling tide and reach extreme low values at low tide (7.2 pH and 1.9 mg O2 L⁻¹ at Bouraké, vs 7.9 pH and 5.5 mg O2 L⁻¹ at reference reefs). Dissolved oxygen, temperature, and pH fluctuates according to the tide of up to 4.91 mg O2 L⁻¹, 6.50 °C, and 0.69 pH units on a single day. Furthermore, the concentration of most of the chemical parameters was one- to 10-times higher at the Bouraké lagoon, particularly for organic and inorganic carbon and nitrogen, but also for some nutrients, notably silicates. Surprisingly, despite extreme environmental conditions and altered seawater chemical composition, our results reveal a diverse and high cover community of macroalgae, sponges and corals accounting for 28, 11 and 66 species, respectively. Both environmental variability and nutrient imbalance might contribute to their survival under such extreme environmental conditions. We describe the natural dynamics of the Bouraké ecosystem and its relevance as a natural laboratory to investigate the benthic organism’s adaptive responses to multiple stressors like future climate change conditions.
1 Introduction

Atmospheric carbon dioxide (CO₂) has steadily increased over the industrial period (Gattuso et al., 2015), leading to ocean warming, acidification and deoxygenation. Although the extent to which these stressors will affect marine life is still debated, there is no doubt that their combination will negatively affect a range of marine organisms (e.g., Kroeker et al., 2011; Wittmann and Pörtner, 2013; Hughes et al., 2018). Coral reefs are among the most productive and biodiverse marine ecosystems on Earth, and their survival is expected to be compromised by climate change, whose impacts on reef structures and associated communities span from biodiversity loss to ecosystem change shift (e.g., Fabricius et al., 2013; Sunday et al., 2017; Agostini et al., 2018).

Marginal and extreme environments, where some species persist under sub-optimal environmental conditions, have become a precious tool to investigate the potential resilience of marine organisms in the face of climate change (Camp et al., 2017, 2018). These sites may be used as natural analogues of future climatic conditions when at least one or more environmental parameters naturally mimic climate change-like conditions over a large area of the ecosystem. They provide an opportunity to simultaneously investigate changes in species responses and their ability to acclimatize and adapt to global environmental changes (Soares, 2020; Kurihara et al., 2020). Shallow-water volcanic CO₂ seeps, low pH springs, semi-enclosed bays, mangrove habitats, shallow sheltered-bay reefs, macrotidal environments, and low-pH upwelling areas are all potential study systems where the surrounding seawater is subject to a localized or widespread increase in either ρCO₂, or temperature, and eventually a decrease in dissolved oxygen (Camp et al., 2018). At these sites, observations overall suggest ecosystem-level consequences of life-long exposure to extreme conditions, such as reduced biological diversity, especially among calcifying organisms, decreasing rates of coral calcification, and high rates of bioerosion (e.g., Hall-Špencer et al., 2008; Manzello et al., 2008; Fabricius et al., 2011; Crook et al., 2013; Kroeker et al., 2011; Iglesias-Prieto et al., 2014; Milazzo et al., 2014; Paytan et al., 2014). However, some natural analogues host quite rich reef communities. These have been documented in Palau (Golbu et al., 2016; Barkley et al., 2017; Shamberger et al., 2018), Papua New Guinea (Pichler et al., 2019), the Kimberly region, Australia (Dandan et al., 2015; Schoepf et al., 2015), and in mangrove lagoons of New Caledonia (Camp et al., 2017) and the US Virgin Islands (Yates et al., 2014).

These natural laboratories have become a common experimental asset in climate change research. However, it has been argued that the lack of empirical characterization of the physical and biogeochemical conditions, including diurnal and seasonal fluctuations, may bias the interpretation of the biological mechanisms that trigger the organisinal responses. Using limited environmental descriptors makes it difficult to unequivocally identify the main driver(s) of the biological response among the primary factors (i.e., acidification, warming and/or deoxygenation), the potential secondary factors (e.g., pollution, water flow, tide, seawater nutrients and organic content, turbidity, etc.), and their combination. For instance, at CO₂ seeps, pH variability can unexpectedly go beyond projected future values (e.g., Hall-Špencer et al., 2008; Kerrison et al., 2011) and the potential emission of toxic compounds, such as sulphur, arsenic, and metal trace elements (Vizzini et al., 2013) compromises the attribution of specific responses to ocean acidification. Water temperature, pH and dissolved oxygen can also co-vary negatively or positively and combine with other secondary factors, acting synergistically or antagonistically with unknown effects on benthic community responses. Their extreme values and the extent to which organisms are exposed are key in shaping biological responses (Boyd et al., 2016; Rivest et al., 2017). For instance, early studies suggest that temperature fluctuations due to diel or tidal variations could expose corals to stressful temperatures long enough to induce acclimatization or adaptation, but short enough to avoid coral mortality (Craig et al., 2001; Oliver and Palumbi, 2011; Castillo et al., 2012;
Palumbi et al., 2014; DeCarlo et al., 2019). Coral reef organisms from such thermally variable environments are expected to respond positively to future heat events (Rivest et al., 2017). Besides, corals naturally subject to high pCO₂ variability have shown immune defences when experimentally exposed to high temperatures, thus buffering the magnitude of thermal stress during heat waves (Wall et al., 2020). The extreme tidal range in the Kimberly region (Northwest of Australia) exposes corals to short-term temperature maxima of up to 37 °C, and fluctuations of up to 7 °C daily. Despite the high temperature, also combined with strong currents and turbid waters, diverse and probably resilient coral reefs have been described there (Dandante et al., 2015; Schoepf et al., 2015).

Overall, at natural analogues only a part of the physical and biogeochemical parameters have been quantified and only during short periods of fieldwork due to logistic constraints. Long-term monitoring of seawater parameters and their fluctuation is essential to understand better the mechanisms used by resilient reef organisms in these natural laboratories and predict how marine taxa will respond to future biogeochemical changes in the environment.

The semi-enclosed lagoon of Bouraké (New Caledonia, SW Pacific Ocean) has been put forward to be as one of the most suitable natural analogues of future extreme environmental conditions (Camp et al., 2019). In a preliminary study, Camp et al., (2017) reported a series of compelling short-term data of seawater carbonate chemistry and a general survey of the coral populations. In this first assessment of the Bouraké lagoon, the authors measured diel fluctuations of temperature (ranging from 25.9-33.1 °C), pH (ranging from 7.24-7.91 pH₇ units) and dissolved oxygen (DO) (ranging from 1.80-6.97 mg L⁻¹) regulated by a one-meter tide. They revealed that about 20 species of corals were exposed 44 % of time to a pH₇ of 7.7-7.8 and 71 % of time to temperatures predicted for the end of the century under the IPCC scenario RCP4.5 (IPCC, 2014). These striking preliminary findings qualified the Bouraké lagoon as a unique site where potentially adapted corals withstand extreme environmental conditions.

These findings give hope to the future of coral reefs in the face of climate change, and suggest that Bouraké might play as a refuge for corals since it already hosts resistant reef species. However, the extent to which the Bouraké species are exposed to sub optimal conditions remain unclear and we believe that the road-map to test for such an encouraging hypothesis is first to fully characterize the main environmental parameters and the daily and seasonal fluctuations to which reef species have been subjected during their entire life. Here we used a multi-scale approach to map and describe the benthic community living in the Bouraké lagoon and report on new evidence based on three years of data collected at this remarkable natural laboratory. In particular, because of the vast area affected, the close vicinity of a dense mangrove forest, and the demonstrated tide effect on the local environmental conditions, we hypothesized that (1) environmental conditions fluctuate regularly and differ spatially in Bouraké, (2) only a limited number of species are able to resist to the extreme physical and chemical conditions at the study site, when compared to adjacent bay-sheltered reefs.
2 Methods

2.1 Study sites
From February 2016, we studied the semi-enclosed coral reef lagoon of Bouraké (South Province, Grande Terre, New Caledonia) and adjacent reference reefs (Fig. 1).

Figure 1. Map of the study site (top panel) showing the semi-enclosed mangrove lagoon of Bouraké and reference reefs (R1 and R2). Photos a and b (bottom panels) are aerial pictures (taken at 130 m above the Bouraké lagoon) of the inner (bottom) and middle reefs (a) and the outer reef (b). White dots and yellow squares indicate the sampling stations used for physical and chemical environmental monitoring, respectively.
In Bouraké, a channel of more than 80 m wide and 0.5 to 6 m deep penetrates a dense mangrove forest made by *Avicennia marina* and *Rhizophora stylosa*, and expands into side pools and a large reservoir in the inner part of the mangrove system. A preliminary calculation of its surface and seawater volume of the main area (i.e., without the large seawater reservoir covered by the mangrove forest) using the 3ds Max Model gives underestimated values of 192,100 m² and 246,060 m³, respectively (Rodolfo-Metalpa et al., in prep.). Terraces extend from the mangrove, on both sides of the channel, and form diverse and compact reefs at their ends. Coral species are less abundant and diverse near the mangrove roots where the bottom substrate is composed of fine sediment and mud. There, reefs are exposed to air only at low tide during the spring tidal cycle (1.1 m maximum tidal range). We subdivided the lagoon into three main areas: an external, an intermediate, and an inner reef (hereafter called outer, middle and inner reefs; panels a & b in Fig. 1). A series of sampling stations were selected and some of the main seawater chemical and physical environmental parameters were measured at the study site and at two adjacent reference reefs, namely R1 a typical fringing reef, and R2 a semi-enclosed shallow and relatively large bay. Both reefs were located 4.8 and 3.2 km from the entrance of the Bouraké lagoon, respectively.

2.2 Environmental monitoring

2.2.1. Oceanographic sensors deployment and short- to long-term measurements

From March 2016 to December 2020 up to eight YSI 600 OMS-M, three Seabird SeaFET™ pH loggers, and four Hobo water temperature Pro V2, were set at 10-min logging intervals and used individually or in combination to assess short-, medium-, or long-term variations across depth (as a proxy of the tide), temperature (°C), dissolved oxygen concentration (DO, mg L⁻¹), seawater pH (total scale), and salinity. A summary of the deployments is given in Supplementary Table S1. YSI dissolved oxygen optical sensors were calibrated against zero, and 100 % saturated seawater at 25 °C. Two SeaFETs were calibrated by the manufacturer, while the third was corrected before deployment by measuring its deviation from the two others in the same seawater.

Short-term (i.e., 24-h) spatial and depth-related variations in pH and DO were simultaneously measured at several stations in the Bouraké lagoon in March and April 2018 (Fig. 1). Spatial variations were assessed i) within the inner (St A-C for pH, and A-G for DO), the middle (St H-N for DO), and the outer (St O-Q for DO) reefs, ii) between the outer and the inner reefs (St B1, B2 for pH), and iii) between the outer and the reef outside the semi-enclosed lagoon (St U vs T for pH). In the Bouraké lagoon, we recorded differences between the surface (shallow) and the bottom water: i) at the outer reef (St S for pH), ii) at the middle reef (St I and N for DO), and iii) at the inner reef (St R for pH, and DO). Salinity was measured in July 2019 (St R1, R2, B1 and B2) and in December 2020 (St R1, R2, T and B2).

Medium-term measurements (i.e., 2-3 weeks) of the DO and pH were recorded at the reference (St R1, R2) and Bouraké reefs (St B1, B2) between 2017 and 2019.

Long-term measurements (>1 year) of seawater temperature were recorded at R1 and R2 starting in January 2019 and September 2017, respectively, and at B1 and B2 beginning in October 2018 and September 2017, respectively. Only temperature data from October 2018 to April 2020 were used to compare between sites.

Short-term pH and DO data and long-term temperature data were compared between stations using General Linear Modelling (GLM), and the Tukey’ HSD post hoc test was used when significant factor effects were found. When data did not conform to normality or homogeneity of variance, we used the Kruskal-Wallis test followed by the Dunn’s multiple
2.2.2. Phase averaged and tidal harmonic analyses for diurnal and semi-diurnal oscillations

Medium term pH and DO changes were investigated by averaging time and tidal phases for diurnal and semi-diurnal oscillations. To do this, all data were overlaid on a daily period and a tidal phase. First, we calculated a predicted tide for the study area using the Nouméa harbour tide (50 km south of our study site) modified with coefficients from the Naval Hydrographic and Oceanographic Service (SHOM; http://data.shom.fr). The predicted tide was used to assign a semi-diurnal tidal phase (12 h) to each sampling time, and the data were averaged for each of these tidal phases. Similarly, the data were averaged for each hour of the day (24 h). Because tides at sea are a sequence of sinusoidal harmonic components that are different for each location, we performed a harmonic tidal analysis on the DO and pH data. We used the "UTide"-ut_solv() tidal analysis package (Codiga, 2011) using the principal semi-diurnal lunar constituent (M2), principal semi-diurnal solar constituent (S2), and solar diurnal constituent (S1). For each parameter, the amplitudes of the tidal harmonics M2 (12.4 h), S2 (12 h), and S1 (24 h) were calculated with a 95% confidence interval based on the 200 Monte-Carlo simulations.

2.2.3. Diel cycles of carbonate chemistry and chemical parameters

Surface water samples were collected across diel tide cycles in June 2017, and July 2019 for pH, total alkalinity (A_T), dissolved inorganic carbon (DIC), nutrients (orthosilicic acid [Si(OH)₄], nitrogen oxide [NOₓ], ammonium [NH₄]⁺, phosphate [PO₄]³⁻, dissolved organic carbon (DOC), particulate organic carbon (POC), and particulate organic nitrogen (PON). A summary of the total sampling is given in Supplementary Table S2. Dissolved inorganic nitrogen (DIN) and total organic carbon (TOC) were calculated as [NOₓ] + [NH₄]⁺, and DOC + POC, respectively. To evaluate the availability of nutrients and organic matter in the Bouraké lagoon (Jacquet et al., 2006; Leopold et al., 2017) the most important ratios were calculated (e.g., DOC:TOC, Si(OH)₄:DIN) and contrasted between stations.

In 2017, during three consecutive days (from May 31st to June 2nd), seawater was sampled six times: twice during both high and low tide, and one time at both rising and falling tide. In total, we sampled one reference station (R2), three stations at the outer reef of the Bouraké lagoon (Outer: St B01-B03), one at the middle reef (Middle: St B04), and one at the inner reef inside the lagoon (Inner: St B05) (Fig. 1). The whole collection lasted about 30 minutes.

In 2019, during three consecutive days (from July 16th to 18th), sampling was carried out every hour from 8 am to 3 pm. We sampled B1 and B2 on the first day, R1 on the second and R2 on the third day.

At each station and sampling time, pH and temperature were measured at the surface (0.5 m deep) using a portable pH-meter (913, Metrohm) calibrated with TRIS buffer (Dickson lab, batch #T28). A subsample (50 mL) was filtered through 0.45-μm Whatman™ Puradisc CA filters using a syringe and poisoned with 20 μL saturated HgCl₂ to further measure A_T. Two 20 mL subsamples were analysed using an auto titrator (EcoTitrator, Metrohm), and A_T was calculated from the Gran function.

Results were corrected against A_T standards (A. Dickson, batch #155, Scripps, USA). The seawater carbonate parameters pCO₂, CO₃²⁻, and aragonite saturation state (Ωa) were then calculated from the pH_T, A_T, temperature, and mean salinity (35) using the free-access CO₂SYS package (Pierrot et al., 2006).
Ammonium concentration was determined on a 40 mL subsample of unfiltered seawater, collected using a 60 mL Schott bottle and stored in the dark. Samples were processed using a fluorimeter (Turner Designs) between six and 18 h after two mL of OPA reagent (o-phthalaldehyde) was added (Holmes et al., 1999).

The sampling of nutrients was performed using two replicate 20 mL polypropylene vials, rinsed three times using filtered seawater (Whatman™ Puradisc CA syringe filters 0.45 μm), filled with the sample and immediately poisoned with 20 μL saturated HgCl₂. Measurements of PO₄³⁻, NOₓ, and Si(OH)₄ nutrients were performed by colourimetry (Seal Analytical).

Seawater samples for DIC were collected in two replicate glass vials (20 mL), filled with unfiltered water and poisoned with 10 μL saturated HgCl₂. The vials were immediately closed, the absence of bubbles was visually checked, and the samples stored in the dark at room temperature for later analysis on a Shimadzu TOC-L analyser (Non-Dispersive Infrared, NDIR). Typical analytical precision was less than ± 2 μmol kg⁻¹. The accuracy was verified using regular measurements of reference material (CRM) from A. Dickson’s laboratory.

Seawater samples for DOC were collected in two pre-combusted (4h at 450 °C) glass ampoules filled with water filtered using a glass syringe filtration system (SGE™) with two pre-combusted 25-mm GF/F Whatman™ filters. Samples were then acidified with ultrapure orthophosphoric acid (H₃PO₄), sealed, and stored in the dark at room temperature for later analysis by high-temperature catalytic oxidation (HTCO) (Sugimura and Suzuki, 1988; Cauwet, 1994) on a Shimadzu TOC-L analyser. Typical analytical precision was ± 0.1-0.5 μM C (SD). Consensus reference materials (http://www.rsmas.miami.edu/groups/biogeochem/CRM.html) were injected every 12 to 17 samples to ensure stable operating conditions. DOC concentrations are only available for the 2017 sampling because of a sample's pollution in 2019.

Finally, one litre of unfiltered seawater was collected in a borosilicate glass bottle and stored on ice during sampling for later measurement of POC and PON contents. In the lab, particulate matter was collected on pre-combusted (4h at 450 °C) Whatman™ GF/F filters using a Nalgene® vacuum system. The filters were dried at 60°C in the oven for 24 h and stored in airtight glass vials at 4 °C in the dark until analysis on a CHN Perkin Elmer 2400.

All glass bottles and vials used were pre-combusted, washed with HCl solutions (10 %) and rinsed using milliQ water.

Seawater chemistry data were pooled by collected area (R1, R2, Outer, Middle, Inner), and differences were tested using the Kruskal-Wallis test followed by the Conover Multiple comparison test (Benjamini-Hochberg-adjusted). We focused on the effect of the tidal phases (i.e., falling and rising tide) on the seawater chemical composition in the Bouraké lagoon only, by attributing each sample a tidal phase between 0 (high tide) and 6 h (low tide), and between 6 and 12 h (high tide). Multiple linear regression was used to assess the adjusted R² and significance (p < 0.05) of the data from 0 to 6 h (falling tide) and from 6 to 12 h (rising tide) separately. Statistical analyses were performed using either Statistica® or R (version 3.2.4, R Core Team, 2018), the latter using the "FSA", "stats", and "Conover.test" packages.

2.3 Benthic community characterization and distribution

The benthic community and bottom substrate of the Bouraké lagoon, referred hereafter as biotic and abiotic descriptors, respectively, were assessed in April 2018. Twenty-four 30 m-long geo-referenced transects (T1-T24) were laid in the lagoon along the terraces’ edge at similar depths (i.e. ~ 1 m), targeting coral dominated benthic assemblages. On each transect, a 0.5 x 0.5 m PVC quadrat was placed every meter, and a picture was taken with a waterproof photo-camera (Nikon AW 130) parallel to the substrate. For each transect, we made a general description of the bottom (i.e. the various substrates) and a list...
of the most common and identifiable sessile species. For each of the 835 pictures collected, we estimated the cover of abiotic
(i.e., mud, sand, rock, rubble, dead corals and unreadable) and biotic descriptors (i.e., branching, massive and soft corals,
sponges, macroalgae and "others") with photoQuad software both by automatic multi-scale image segmentation regions and
manual grid cell counts when necessary.

We used the photos of quadrats, the many other pictures collected during fieldworks, and laboratory morphological
observations on collected samples to produce a non-exhaustive species list of corals, macroalgae and sponges. Corals were
comprehensively sampled throughout the Bouraké lagoon and on the reference reef R2, while dominant macroalgal and
sponges species were collected in the Bouraké lagoon alone and only if they were encountered at least three times along a
transect, likely leading to an underestimation of their diversity. Coral diversity was assessed through photographic and
destructive sampling during time-based open search swims and SCUBA dives (Hill and Wilkinson, 2004). Whenever possible,
scleractinian corals were identified to species level in situ by photographic sampling only. In case of doubtful identification
in vivo, or of taxa characterized by small corallite size (<1 mm in diameter) requiring morphological examination of the
skeleton for positive identification (e.g. genera Acropora, Montipora and Porites), a fragment of the colony was collected,
tagged, cleaned in sodium hypochlorite overnight, rinsed in freshwater and dried. The reference collection is housed at IRD
Noumea. Microscopic examination of the skeletal features allowed species level identification following the reference
literature (Veron, and Wallace, 1984; Wallace, 1999; Veron, 2000). Sponges were identified either based on their spicules’
morphological characteristics (i.e., length and width), or using a series of morphological descriptors (e.g., shape, size, colour,
texture, surface ornamentations, fibres) for species without spicules. In the lab, a subsample of the collected sponges were
immediately digested using HNO₃, and spicules were measured with an optical stereomicroscope. For species without
spicules, hand-cut sections of the choanosome and ectosome were observed under a stereomicroscope. Species were identified
using the taxonomical keys of Rützler (1978), Hooper and Van Soest (2002), and Pons et al. (2017). Macroalgae and corals
identification were based on morphological and anatomical observations following the dedicated literature and by referring
to the collections of specimens housed at IRD Noumea.

Abiotic and biotic cover percentages, averaged per transect, and species richness, calculated as the number of species
in the transect, were plotted using non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarities (vegan
package in R) of square-root transformed data. Finally, the best number of clusters for the whole Bouraké lagoon was
determined by using the gap statistic method (cluster and factorextra packages in R) and used for the hierarchical clustering
representation (Ward, 1963). The cluster separation was verified with a two-way analysis of similarity ANOSIM. Within each
cluster, the benthic community and bottom substrate were averaged between transects, and the dominant biotic and abiotic
descriptors were selected and used to define the cluster.

Principal component analysis (PCA) was used to visualize the correlation between environmental parameters and
the transects’ benthic descriptors of transects inside the Bouraké lagoon. The analysis was performed in R (package
FactorMineR, version 3.2.4, R Core Team, 2018) using data of biotic descriptors (averaged per transect) and the seawater
parameters averaged for each sampling area (i.e., outer, middle and inner reefs).
3 Results

3.1 Variability of physical environmental parameters

Tidal phases. The predicted tide in the study area (SHOM data) is close to what we measured at R1 and R2 (Fig. 2).

It is semidiurnal with a diurnal inequality ($M_2 = 0.44$ m, $S_2 = 0.16$ m) and has a small diurnal component ($S_1 = 0.15$ m). It varies between 0.4 and 1.7 m, depending on the phase of the moon, with a mean of 1.1 m. The tidal range inside the Bouraké lagoon is lower and varies between 0.4 and 1.2 m, with a mean of 0.9 m. The tidal signal at B1 and B2 lags both the predicted and the measured tide at the reference stations by an average of 1.5 h for low tide and up to 45 min for high tide.

Temperature. Our results indicate that the water temperature has an annual cycle with lower values during the austral winter (May-October) and higher values in summer (November-April). Daily averaged temperatures at R2, B1 and B2 were not significantly different, while the temperature at R1 was cooler in summer and warmer in winter (Fig. 3a; Tables 1)

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compared to the other stations. On a weekly base, the averaged diel temperature variation was significantly different between stations: $1.34 \pm 0.39 \, ^\circ\text{C}$ at R1 and $3.73 \pm 0.74 \, ^\circ\text{C}$ at B2 (Fig. 3b; Tables 1). In a single day, we recorded temperature fluctuations of up to $3.4 \, ^\circ\text{C}$ at R1 and $6.5 \, ^\circ\text{C}$ at B2.

Figure 3. Long-term temperature monitoring from October 2018 to April 2020 at the reference (St R1 and R2) and Bouraké reefs (St B1 and B2). Data are plotted using weakly averaged temperature (a) and weakly averaged diel changes (b).
Table 1. Summary of the statistical analyses applied to the seawater physical and chemical parameters collected between 2016 and 2020 in the Bouraké lagoon (St B1, B2, St A-R, outer, middle and inner) and at reference reefs (St R1 and R2).

<table>
<thead>
<tr>
<th>Parameters</th>
<th>(n)</th>
<th>K-W</th>
<th>W</th>
<th>GLM</th>
<th>p</th>
<th>post hoc (test)</th>
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<tr>
<td>Daily means</td>
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<td>68.46</td>
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<td>(D)</td>
<td>p &lt; 0.001 R1 &lt; R2 = B1 = B2</td>
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<td>Weakly oscillations</td>
<td>305</td>
<td>234.63</td>
<td></td>
<td>&lt; 0.001</td>
<td>(D)</td>
<td>p &lt; 0.01 R1 &lt; R2 &lt; B1 &lt; B2</td>
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<td><strong>Seawater pH (Stations)</strong></td>
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<td>Spatial INNER (A-C)</td>
<td>711</td>
<td>5.32</td>
<td></td>
<td>0.005</td>
<td>(T)</td>
<td>p &lt; 0.01 A &lt; C</td>
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<td>Surface vs deep (I)</td>
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<td>Surface vs deep (N)</td>
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<td>(T)</td>
<td>p &lt; 0.01 R1 &lt; R2 &lt; B1 &lt; B2</td>
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<td>p &lt; 0.01 R1 &lt; R2 &lt; T &lt; B2</td>
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<td>18.47</td>
<td></td>
<td>&lt; 0.001</td>
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Seawater pH. During the entire study period, pH was measured during 22, 72, 31, and 72 semidiurnal tidal cycles at R1, R2, B1, and B2, respectively. We overlaid all data on a single tidal phase of 12.4 h (Fig. 4a) and a 24-hours cycle (Fig. 4b).

(continue Table 1)

<p>| | | | | |</p>
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<tr>
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<td>(C) p &lt; 0.05 R1 &lt; R2 &lt; Inn; R2 = Out = Mid; Inn = Mid</td>
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<td>&lt; 0.001</td>
<td>(C) p &lt; 0.01 R1 &lt; R2 &lt; Inn &lt; Mid = Out;</td>
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We overlaid all data on a single tidal phase of 12.4 h (Fig. 4a) and a 24-hours cycle (Fig. 4b).
Figure 4. Seawater pH (a), (b) and dissolved oxygen (DO) (c), (d) variations recorded at the reference (St R1 and R2) and Bouraké reefs (St B1 and B2). Data were superimposed in single tidal phase (a), (c); and in a 24-hours cycle (b), (d). Data are 22, 72, 31, and 72 semidiurnal tidal cycles for pH, and 36, 79, 34 and 42 semidiurnal tidal cycles for DO, for R1, R2, B1 and B2, respectively.

The pH differed significantly between stations. We recorded means of $8.01 \pm 0.04$ and $7.89 \pm 0.08$ pH units at R1 and R2, and $7.80 \pm 0.22$ and $7.67 \pm 0.23$ pH units at B1 and B2, respectively. At both B1 and B2, pH was strongly correlated with the tidal cycle (82 and 73% of the total variance were explained by the tidal harmonic analysis, respectively), while it correlated only marginally with the 24-hours cycle. During each tidal phase, the pH changed on average by about 0.6 units.
and reached a minimum of 7.23 and a maximum of 8.06 at B2 at low and high tide, respectively. The pH oscillations were mainly semidiurnal (M$_2$ = 0.27 ± 0.01, S$_2$ = 0.05 ± 0.01 pH$_{T}$ units, for B1; M$_2$ = 0.24 ± 0.01, S$_2$=0.09 ± 0.01 pH$_{T}$ units for B2). At stations R1 and R2, pH was closely linked to tidal oscillations. It changed on average by about 0.1 pH$_{T}$ units and was mostly dependent on the 24-hours cycle (S$_1$ = 0.058 ± 0.004 and S$_1$= 0.049 ± 0.007 pH$_{T}$ units for R1 and R2, respectively). Simultaneous short-term pH measurements showed significant spatial differences (Fig. 5; Tables 1), between i) stations A and C, ii) stations B1 and B2, and iii) the outer reef in the Bouraké lagoon (St U) and the station outside the system (St T). There were also significant depth-related differences between shallow reefs and bottom water at stations R and S. In both spatial and depth-related analyses, differences were approximately 0.05 to 0.1 pH$_{T}$ units, and we found the lowest values at stations C and B2, and at the bottom of the channel (St R and S).
Figure 5. Spatial and depth-related short-term changes (24 h) in pH\textsubscript{T} at stations in the Bouraké lagoon (see Figure 1 for the stations’ location). Spatial variations were assessed: (a) within the inner reef (St A-C); (b) between the inner and the outer reefs (St B1, B2); (c) between the outer reef (but still inside the Bouraké lagoon), and the reef outside the semi-enclosed lagoon (St U vs T). Depth-related variations were assessed between shallow reefs and the bottom of the channel: (d) at the outer reef (St S); and (e) at the inner reef (St R). Tide (black line) refers to St B2.
Dissolved oxygen (DO). DO was measured during 36, 79, 34 and 42 semidiurnal tidal cycles at R1, R2, B1 and B2, respectively. We overlaid all data on a single tidal phase of 12.4 h (Fig. 4c) and a 24-hours cycle (Fig. 4d). As with pH, the mean diel DO was higher at the reference reefs than in the Bouraké lagoon. Mean DO values were 4.89 ± 1.18 and 5.23 ± 0.89 mg L⁻¹ at B1 and B2, respectively, and 6.45 ± 0.95 and 6.48 ± 1.05 mg L⁻¹ at R1 and R2, respectively.

At stations B1 and B2, DO was strongly correlated with the tidal cycle (82 and 72 % of the total DO variance were explained by the tidal harmonic analysis, respectively). DO oscillations were mainly semidiurnal (M2 = 1.17 ± 0.08 mg L⁻¹, and M2 = 0.83 ± 0.09 mg L⁻¹ for B1 and B2, respectively) with a substantial diurnal component (S1 = 1.12 ± 0.04 mg L⁻¹, and S1 = 0.681 ± 0.04 mg L⁻¹ for B1 and B2, respectively). During a semidiurnal tidal cycle, DO was lower at low tide (3.7 mg L⁻¹ and 4.6 mg L⁻¹ at B1 and B2, respectively). During a 24-hours cycle, DO was lower in the early morning (4.0 and 4.3 mg L⁻¹ at B1 and B2, respectively) and higher in the middle of the day (5.8 and 5.5 mg L⁻¹ at B1 and B2, respectively). In a single day, we recorded DO fluctuations of up to 6.37 mg L⁻¹ at R1 and 4.91 mg L⁻¹ at B2. The minimum DO value, 1.89 mg L⁻¹, was measured during low tide, and the maximum DO value, 7.24 mg L⁻¹, was measured at B1 during high tide (data not shown).

At stations R1 and R2, DO was mainly diurnal (S1=1.34 ± 0.06 mg L⁻¹ and S1 = 1.53 ± 0.09 mg L⁻¹ for R1 and R2, respectively) with lower values during the night (5.5 mg L⁻¹ at both stations), and higher values in the middle of the day (7.8 mg L⁻¹, both stations). Simultaneous short-term DO measurements (Fig. 6; Table 1) did not show significant differences over a 24-hours cycle at the inner (St A-G; except for some specific deviations, e.g., St A), the middle (St H-N) or the outer reef (St O-Q). Dissolved oxygen did not change on a vertical gradient at stations R and I, but the bottom DO was significantly lower at station N.
Figure 6. Spatial and depth-related short-term measurements (24 h) in dissolved oxygen (DO) at stations in the Bouraké lagoon (see Figure 1 for the location of the stations). Spatial variations were assessed on (a) the inner reef (St A-G), (b) the middle reef (St H-N), and (c) the outer reef (St O-Q). Depth-related variations between shallow reefs and bottom water within the Bouraké lagoon were assessed (d) at the inner reef (St R), and (e, f) at the middle reef (St I and N). Tide (black line) refers to St B2.
Salinity (S). Salinity was measured only during two short-term periods in winter 2019 and summer 2020 (Fig. 7).

Figure 7. Short-term salinity monitoring during (a) the winter of 2019 (from 15/07/2019 to 18/07/2019) at the reference (St R1 and R2) and Bouraké reefs (St B1 and B2); (b) the summer of 2020 (from 29/11/2020 to 04/12/2020) at the reference (St R1 and R2) and Bouraké reefs (St T and B2). Tide (black line) refers to St B2.

Its variations in the Bouraké lagoon was strongly correlated with the tidal cycle, and the highest mean values were measured during both winter and summer. Salinity was lower at reference reefs. The mean salinity during the winter of 2019 was 35.49 ± 0.04 at R1, 35.67 ± 0.10 at R2, 36.00 ± 0.35 at B1, and 36.17 ± 0.47 at B2 with significant differences between stations (Tables 1). Salinity in the Bouraké lagoon peaked at 37.22 at B2 during low tide, while it was 35.65 at R1. During the summer of 2020, the mean salinity increased significantly in the Bouraké lagoon with 37.22 ± 0.53 at B2, reaching up to 39.37, while it remained lower at R1 with 35.42 ± 0.10 and at R2 with 35.71 ± 0.16. In the summer of 2020 we also measured short-term variations in salinity at station T, which is outside the Bouraké system. Although its distance from the entrance of the lagoon, the water mass discharged during falling tide increased seawater salinity also at this station where we measured a maximum value of 37.33 during low tide.

3.2 Diel cycles of carbonate chemistry and chemical parameters

We monitored diel cycles in June 2017 and July 2019 at two reference reefs and three reefs within the semi-enclosed lagoon of Bouraké (i.e., the outer, the middle and the inner reefs). The seawater carbonate chemistry differed significantly between the reference and the Bouraké lagoon reefs (Fig. 8a-c; Supplementary Fig. S1; Tables 1, 2).
Figure 8. Seawater carbonate chemistry measured (\(pH_T\)) and calculated (DIC and \(\Omega_{\text{ara}}\)) during diel cycles in 2017 and 2019 (pooled data, see also Supplementary Figure S1) at R1, R2 and the Bouraké reefs (outer, middle and inner) (a-c). Boxes (n = 6-14) represent the interquartile range (25\(^{\text{th}}\) and 75\(^{\text{th}}\) percentile); the horizontal line is the median, and the whiskers represent the data range (i.e., minimum and maximum). Changes are illustrated across a 12-h tidal phase in the Bouraké lagoon (d-f). Linear regression lines are plotted for each falling (HT to LT) and rising tide (LT to HT). Shaded boxes have only a graphical significance and only suggest the tide changes during measurements.
Table 2. Summary of the seawater physical and chemical data (mean ± SD) measured in July 2017 and June 2019 and calculated using the CO₂SYS package. Data were pooled and averaged per station. nd = not determined. Reference reefs: St R1 and R2; Bouraké lagoon stations: outer, middle and inner.

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</tbody>
</table>

The reference reefs R1 and R2 had higher pH, CO₂⁻ and Ωaragonite and consequently, lower DIC and pCO₂ than the outer, middle or inner reefs in the Bouraké lagoon. The range of values in the lagoon was similar to our previous measurements (see above), with levels of pCO₂ > 2,000 µatm and Ωaragonite < 1. By assigning a tidal phase (from 0 to 12 h) to each sample taken in the Bouraké lagoon (all reefs combined), our diel measurements showed significant regressions, either positive or negative, depending on the seawater carbonate parameter and the tide phase (Fig. 8d-f; Supplementary Fig. S1; Supplementary Table S3). For example, the DIC reached the highest value of 2,635 µmol L⁻¹ during low tide on the inner reef with an average of 2,315.1 ± 168.1 µmol L⁻¹, while CO₂⁻ reached the lowest value of 50.10 µmol L⁻¹ during low tide on the inner reef with an average of 109.02 ± 45.59.

Most of chemical parameters were in general more concentrated (up to 5-times) in the Bouraké lagoon than on the reference reefs R1 and R2, and increased from the outer to the inner reef (Fig. 9a-d; Supplementary Fig. S2; Tables 1, 2).
Figure 9. Orthosilicic acid, organic carbon and nitrogen parameters measured during diel cycles in 2017 and 2019 (pooled data, see also Supplementary Figure S2) at R1, R2 and the Bouraké reefs (outer, middle and inner) (a-d). Boxes (n = 6-14) represent the interquartile range (25th and 75th percentile); the horizontal line is the median, and the whiskers represent the data range (i.e., minimum and maximum). Changes are illustrated across a 12-h tidal phase in Bouraké (e-h). Linear regression lines are plotted for each falling (HT to LT) and rising tide (LT to HT). Shaded boxes have only a graphical significance and only suggest the tide changes during measurements.
In addition, despite the Bouraké lagoon receives new seawater during the rising tide, only Si(OH)$_4$ had a decent regression coefficient showing either positive and negative correlation with the falling and the rising tide (Fig. 9e-h; Supplementary Fig. S2; Supplementary Table S3). It reached the highest value of 16.74 µmol L$^{-1}$ during low tide on the inner reef with an average of 11.93 ± 4.27 µmol L$^{-1}$, and the lowest value of 3.38 µmol L$^{-1}$ during high tide on the outer reef with an average of 8.22 ± 3.14 µmol L$^{-1}$. The lack of a clear effect of the tide for the other chemicals cause their accumulation inside the lagoon system. Ratios of organic and inorganic carbon, nitrogen, and nutrients showed significant differences between the Bouraké lagoon and the reference reefs (Tables 1, 2) with higher average POC:PON, POC:DOC, Si(OH)$_4$:DIN, Si(OH)$_4$:DIP and DIN:DIP (PO$_4^{3-}$), and lower average DIC:DIN and DOC:TOC in the Bouraké lagoon compared to reference reefs.

### 3.3 Benthic community distribution and species identification

**Benthic community distribution.** The cluster analysis and nMDS allowed grouping the 24 transects in the Bouraké lagoon in six clusters corresponding to habitat descriptors, namely clusters A, B1, B2, C1, C2, and C3 (Fig. 10a; see Supplementary Fig. S3 for details of the community descriptors, and Table S4 for transect averaged data). The nMDS produced an exhaustive representation of the Bouraké lagoon benthic communities and abiotic features (2-dimensional stress = 0.136) confirmed by ANOSIM (Global R = 0.948, p = 0.001). For the benthic community distribution, a clear separation (95% of confidence interval represented by the ellipse in Fig. 10a) was found for cluster A and B2, including most of the transects located on the middle and inner reefs (Fig. 10b).
Figure 10. Benthic community and bottom substrate characterization in the Bouraké lagoon. Hierarchical Ward's method cluster dendrogram (top) and non-metric multidimensional scaling (nMDS) of abiotic and biotic percent cover and species richness per transect (T1-T24) (a). Colored circles represent clusters of transects identified in the dendrogram; circle size corresponds to species richness. Ellipses represent 95% confidence intervals. Dominant biotic and abiotic descriptors were used to describe the benthic community and bottom substrate for each cluster in (b). The satellite image is from georep New Caledonia database (https://georep.nc/), and the QGIS software was used for transect georeferencing.
For both branching corals were the dominant biotic descriptor with 81% and 31% cover, respectively (Supplementary Fig. S3). Among branching corals, the two most abundant genera were Acropora and Montipora (data not shown). For the abiotic features of the substrate, dead corals and rubbles characterized transects in clusters A and B2, respectively. Species richness (Fig. 10a) was high in all transects of the Bouraké lagoon, except T13 and T24, both found at the middle and inner reefs' limits. The abiotic substrate of cluster C1 was characterized by 66% mud, 12% rocks and 10% sand (see Supplementary Table S4 for detailed cover data per transect). Only a few branching corals (<10%) were found, but species richness was relatively high (6 at T9 and 10 at T10). Cluster C2 was distinct, which is not surprising due to its location in a relatively shallow convergence zone that divides the lagoon into two parts. There, the substrate is made of coarse sand (13%) and rocks (12%) and is mainly colonized by macroalgae and sponges (31% and 32%, respectively). Species richness in the area was heterogeneous and ranged from 4 to 12. Dictyota spp. and Halimeda discoides were the main macroalgal species, while Rhabdastrella globostellata was the dominant sponge species in the area. Cluster B1, located on the outer reef, is characterized by an abundance of soft corals (48%) and rubbles (21%), and high biological richness (Fig. 10a). Cluster C3 is characterized by coarse sand (49%), rocks (17%) and a few benthic organisms such as macroalgae (10%) and soft corals (8%).

Principal component analysis (PCA) reduced multicollinearity problem and the first two Principal Components accounted for a cumulative 71.2% of the dataset variance. In particular, the PCA plot (Fig. 11) allowed us to assign the transects to three distinct groups depending on their position in the study area.  

Figure 11. Principal component analysis (PCA) between benthic community (macroalgae, sponges, corals, branching corals and massive corals) data and environmental parameters (PON, POC, DOC, Si(OH)₄, PO₄³⁻, NOₓ, and NH₄⁺) measured for each transect (n = 24). The length of the vectors indicates the contribution of each parameter. The first dimension explains 48.1% of the variance, and the second dimension explains 23.1% of the variance. Red dots indicate the transects. Colors refer to the cluster subdivision (Fig. 10).
The distinction among transects groups in the biplot is clear and they are grouped based on their location in the outer, middle or inner lagoon reefs. The outer reef sites are characterized by the presence of sponges, macroalgae and soft corals, which appear to correlate with NOx. Conversely, branching corals are the shared and characteristic feature of the middle and inner reef sites. These two reef groups, however, differ in their major correlation to NH₄⁺ for middle reef sites and POC, DOC, Si(OH)₄, and PO₄³⁻ for the inner sites.

Species identification. A total of 66 coral species were identified from the Bouraké lagoon (Supplementary Table S5). Most of the species belong to the family Acroporidae (17 Acropora species, 2 Anacropora and 4 Montipora) and Merulinidae (15 species). A total of 58 species were identified from the reference reef R2, 29 of which were also found in the Bouraké lagoon. Overall, the hard coral fauna within the lagoon was characterized by species commonly found around the Grande Terre, with some of them typically found in turbid coastal environments such as Pseudosiderastrea tayamai and Heliofungia actiniformis. They were not encountered at the reference site. Remarkably, two New Caledonia endemic coral species, namely Cantharellus noumeae and Polycyathus fulvus, both described from coastal habitats characterized by terrigenous sediment input (Noumea lagoon and Prony Bay, respectively), were common in the innermost reef of the Bouraké lagoon. The Bouraké lagoon also had 28 species of macroalgae (14 Phaeophyceae, 9 Chlorophyta and 5 Rhodophyta), including the crustose coralline algae Lithothamnium sp., Lithophyllum sp., and Hydrolithon reinboldii, and 11 sponge species belonging to eight families of the class Demospongiae (Supplementary Tables S5 and S6), which were found mainly in the coral matrix and sediment.
4 Discussion

Marginal and extreme natural environments are increasingly used to predict the future of reefs in a changing world (Camp et al., 2018). In these environments, one or the combination of more environmental conditions differ from present-day values, providing an opportunity to assess the resilience of organisms and to study their adaptive mechanisms in a natural environment. Coral reefs, that are exposed to seawater pH and temperature values close to or even worse than those expected for the future, have likely developed physiological trade-offs and expressed molecular changes that allow them to survive sub-optimal, climate change-like conditions. When using these natural laboratories to predict species responses to future environmental conditions, it is essential to assess a multi-scale approach that incorporates the spatial and temporal variability of the key physical and chemical parameters characterizing the study site. In this study, we mapped the spatial and temporal variability of these physical-chemical parameters in the semi-enclosed lagoon of Bouraké, which is likely one of the most suitable natural laboratories known to date to study the adaptation of corals to the combination of acidification, warming and deoxygenation (Camp et al., 2017). There, we found an unprecedented number of benthic species, including two New Caledonia endemics, thriving under chronic suboptimal conditions that fluctuate with the tide. While the exact mechanism/s explaining their resilience remains to be discovered, our study provides a compelling basis and fundamental baseline for using this site as a natural laboratory to investigate species’ responses to a combination of stresses in their natural environment.

4.1 Physical and chemical characteristics of the Bouraké lagoon

The Bouraké lagoon covers an estimated area of ca. 20 ha that penetrates a mangrove forest, large enough to assess the combined effects of extreme environmental conditions on an established coral reef ecosystem. Our multi-scale approach confirmed previous findings (Camp et al., 2017), showing that the Bouraké lagoon is hottest (ranging from 17 - 33 °C), deoxygenated (ranging from 1.87 - 7.24 mg L⁻¹), and acid (ranging from 7.23 - 7.92 pH units) when compared to neighboring reefs. Besides, we found that salinity was significantly higher than at the reference reefs in both winter and summer (with maxima of 37.22 and 39.37, respectively). Although corals seem to possess cellular mechanisms to counteract short-term osmotic changes (Mayfield and Gates, 2007), high and fluctuating salinity is possible additional stress that corals living in the Bouraké lagoon have to face daily, adding up to the already long list of suboptimal environmental parameters. Further experiments are needed to assess the effect of high and fluctuating salinity on their physiology.

We found several marked differences in the environmental conditions between the Bouraké lagoon and the reference reefs. First, the seawater temperature is higher in summer in the Bouraké lagoon (Fig. 3), but it is also colder during winter, occasionally more than 25 °C. If we compare temperature recorded at the reference St R2, which showed the most typical temperature range for shallow water temperatures in the south of New Caledonia (i.e., 22 - 28 °C, (Varillon et al., 2021), we notice that in Bouraké temperatures were 40% of the time above 28°C during the summer of 2020, while winter temperatures were on average 46.5 % of the time lower than 22 °C. While warming is considered the main threat for coral reefs, low temperatures (< 20 °C) can cause coral bleaching by inducing responses similar to high temperatures, including a reduction in the Symbiodiniaceae cell density and chlorophyll a content (e.g., Saxby et al., 2003; Hoegh-Guldberg and Fine, 2004; Hoegh-Guldberg et al., 2005; Kemp et al., 2011; (Bellworthy and Fine, 2021). The negative effect of cold temperatures is even more substantial during neap tides when colonies on the reef crest are exposed to air for hours at low temperatures during cold winters. For example, Porter et al. (1982) and Davis (1982) reported > 90 % coral mortality in shallow (< 2 m) reefs of the Dry Tortugas following the winter of 1976 - 1977 when temperatures reached 14 °C. This is consistent with our
observations (data not shown) during the cold winter of 2019 when we found that the upper 12 - 20 cm of several massive and branching corals had died.

Second, in the Bouraké lagoon, benthic assemblages are continuously exposed to suboptimal fluctuations in the main environmental parameters, and some of these environmental fluctuations are entirely predictable. For instance, marine organisms are exposed to a temperature fluctuation of about twice the reference reefs’ amplitude (up to 6.5 °C vs 3.5 °C) in a single day. Dissolved oxygen fluctuations were similar between stations but in a significantly different range: 3.7 to 6.8 mg L\(^{-1}\) at B2 and 5.4 to 7.8 mg L\(^{-1}\) at the reference stations. Besides, our tidal modelling revealed that, at the reference reefs, pH, DO (Fig. 4), and temperatures (data not shown) slightly increased in the afternoon and decreased during the night. This agrees with what should be expected from reef metabolic activities and daily cycles but, in the Bouraké lagoon, these parameters, including salinity (Fig. 7), are entirely driven by tides. Here, seawater pH and DO varied between extremely low values at low tide and close-to-normal values during high tide (see also Fig. 8a-c for pH). Finally, we found that the timing of the tide was out of phase between sites, with a delay of about 45 minutes at high tide and 1.5 h at low tide in the Bouraké lagoon (Fig. 2).

The unique environmental conditions measured in the Bouraké lagoon are mainly due to the topographical and geomorphological characteristics of this unique site, the resulting water circulation and the direction of the tide. At each rising tide, new water enters through the channel, flows into the semi-enclosed lagoon towards the large mangrove area behind it, and mixes with the acidic, warm and deoxygenated water that was already in the system and the mangrove area. There, we hypothesize that the water chemistry changes due to the metabolic reactions in the sediments, coral reefs and mangrove roots. Conversely, on a falling tide, the seawater becomes gradually more acidic, hot and oxygen-depleted because the water that resided in the mangrove area gradually drains out of the system. This takes about 6 hours, during which the vast reservoir of shallow mangrove water continues to be chemically altered, becoming increasingly acidic, oxygen-depleted and hot. As a result, we measured a significant spatial differences in pH between the outer reef (the entry of the lagoon) and the inner reef (near the mangrove forest), as well as a considerable delay in the synchronization of the tidal shift (Fig. 5b). Interestingly, because the volume of seawater discharged in 6 hours is so large, it affects also the area outside the system where we measured similar seawater conditions as inside, even if it mixes with the main lagoon’s water (see Fig. 5c, St U vs St T). It means that the area (and the organisms) affected by the suboptimal parameters is larger than previously thought. It is likely that the species living in this area have developed specific mechanisms to withstand the very fluctuating environmental conditions, and as such, they warrant further attention.

It could be argued that because the fluctuations are linked to tidal phases, organisms living in the Bouraké lagoon may benefit from periods of normal conditions at high tide during which they can recover from the stress they have experienced at low tide. While this could be partially the case for species living on the outer reef, close to the main lagoon, the environmental conditions inside the Bouraké lagoon rarely reach normal values (Fig. 8a-c), and also persist longer since the low tide is delayed by 1.5 h compared to the reference reef (Fig. 2).

Preliminary results from a hydrodynamic model of the study site also suggest that tide-associated water mass movements are spatially heterogeneous and likely to play an essential role in shaping coral resilience to extreme conditions (see discussion below). Indeed, one can imagine a single water mass moving with the same physical characteristics from the mangrove area towards the outer reefs or in the opposite direction depending on the tide. However, the complex geomorphology of the Bouraké lagoon, its bottom topography and the complex web coral reefs and of mangrove trees on the edges deviate and
probably change the seawater physical and chemical properties. We measured significant spatial differences in pH within each reef area (inner, middle and outer reefs; Fig. 5a, b), as well as throughout the water column (i.e., between the surface and the bottom; Fig. 5d,e). In general, bottom seawater was 0.1-0.2 pH units lower than the surface, probably due to a pumping mechanism by the water mass of more acidic pore water from the sediments. The pH also differed spatially within the inner reef, by up to 0.3 pH units (for instance St. A vs St. C; Fig. 5a), perhaps due to the influence of stagnant water on the edges of the mangrove or a more intense metabolic activity by the local benthic community. Dissolved oxygen concentrations between the surface and the bottom were only significantly different on the middle reef (Fig. 6f), and only at St. N which is mainly characterized by mud as the current there is lower than anywhere else in the Bouraké lagoon. Here, the sediment's biological activity possibly traps the oxygen making it less available to the water column.

We can assume that, throughout the Bouraké lagoon, organisms are exposed to extreme and fluctuating suboptimal physical parameters, such as pH, and DO which are more pronounced on the bottom and last longer, and with more extreme values, on the inner reefs. It is also true for the seawater chemistry with higher concentrations in the Bouraké lagoon than on the reference reefs (see Table 2). For instance, we found that orthosilicic acid, phosphate, dissolved and particulate organic carbon, and particulate organic nitrogen were 1.4 to 4.2-fold more concentrated on the inner reef than at station R2. Within the Bouraké lagoon in general, chemicals increased from the outer to the inner reef and with the exception of [NO$_3$]$_i$, [NH$_4$]$^+$, [PO$_4$]$^{3-}$, they never return to “normal” values despite the Bouraké system receives new seawater during the rising tide. The high concentrations in orthosilicic acid and organic compounds, both dissolved and particulate are due to the combined effect of more acidic and organic rich water coming out of the mangrove forest during a falling tide (Fig. 9) and the particular morphology of the system which limits the full seawater renew, especially at the inner reefs.

### 4.2 Effects of physical and chemical conditions on species distribution

Extreme environmental conditions, such as those measured in the Bouraké lagoon, are known to strongly affect the metabolism, growth and even survival of several marine organisms, particularly those that are commonly considered stenotopic like scleractinian corals. For instance, in situ studies at volcanic CO$_2$ seeps have shown that chronic exposure to ocean acidification (near-future pCO$_2$ levels) can cause a reduction in coral diversity, lower recruitment and abundances of structurally complex hermatypic corals. Moreover, shifts in competitive interactions between taxa and a decrease in cover and richness of soft corals and sponges were also observed (e.g., Fabricius et al., 2011; Sunday et al., 2017; Agostini et al., 2018; Teixidó et al., 2018). However, the Bouraké lagoon features high coral, sponge, macroalgae and CCA cover and species richness, adding at the check-list proposed by Camp et al., (2017) an additional 46 coral species (totaling 66 species and 33 genera), 23 species of macroalgae and 11 species of sponges (Supplementary Table S5). Such a high number of species has never been reported for mangrove systems characterized by marginal conditions, at least with regard to the three major benthic groups taxa investigated here (e.g., Yates et al., 2014; Camp et al., 2019). In general, given the extensive literature demonstrating the negative effects of suboptimal abiotic conditions on corals, our findings are unexpected and suggest that corals in the Bouraké lagoon may have developed unique survival and adaptive mechanisms. Some studies have reported similar findings, but none has ever reported such a high coral species diversity (e.g., Yates et al., 2014; Schoepf et al., 2015; Shamberger et al., 2018; Camp et al., 2019). For instance, in Palau (Micronesia), the highest coral cover (> 60%) and species diversity (21 scleractinian genera) were found at the lowest pH study site of the Nikko Bay station (Barkley et al., 2015). Studies in the Virgin Islands’ mangrove system have reported over 30 coral species growing in marginal conditions (Yates et
al., 2014; Rogers, 2017). Similarly, in a recent study of two Australian mangrove lagoons, both characterized by relatively extreme environmental conditions (low pH, low oxygen and high temperature), Camp et al., (2019) identified 12 and 29 scleractinian coral species in the Woody Isles and at Howick Island, respectively. Among the 66 species we identified, a total of 29 of the most abundant coral species in New Caledonia are shared between the reference reef and the Bouraké lagoon, indicating that species living at our study site are not very different than on a typical bay-sheltered fringing reef. There is not an apparent selection in the coral form, since massive (e.g., *Porites* spp.), corymbose (e.g., *Pocillopora digitata*), phaceloid (*Galaxea fascicularis*) and branching (*Acropora* spp.) species are equally abundant, as well as in their thermal and pH tolerance. Further experiments are underway at both the molecular and phenotypic level to better understand the mechanisms of resilience used by the corals from Bouraké.

Remarkably, the two coral species currently considered New Caledonia endemics thrive in the innermost benthic assemblages of the Bouraké lagoon, making it not only a unique natural laboratory but also a potential conservation priority site in light of its overall uniqueness characterized in this study. In the Bouraké lagoon, benthos species richness was very high throughout the system and the distribution of branching and massive corals was spatially heterogeneous (Fig. 10b; Supplementary Fig. S3). Coral cover decreased near the mangrove, where the accumulation of fine sediments and exposure to air during low tide do not allow corals’ survival, but the percent cover reached up to 90% on the reef margin (Supplementary Fig. S3). Branching corals were particularly abundant on the inner and middle reefs. They became sparse on the outer reef, even absent at the system’s entrance where soft and massive corals dominated. Macroalgae and sponges, including CCA (data not shown), were quite cryptic throughout the Bouraké lagoon, but found almost everywhere both in the coral matrix and buried in the sediment.

They are particularly abundant only in a shallow area that divides the lagoon into two parts (transects T6-T8). There, a Venturi effect generates a strong current and the substrate is made of coarse sand and rocks. Both the high flow and the bottom characteristics likely promote macroalgae and sponge occurrences (averaged 30% and 32% cover, respectively). There, the sponge *Rhabdastrella globostellata* is particularly abundant (up to 40% cover) and form massive banks embedding adjacent coral colonies. In general, macroalgae and sponges diversity is not particularly rich with respectively only 28 and 11 species have been detected, likely due to the sampling method. However, sponge diversity, in the Indo-pacific mangrove systems, is in general not extremely high especially if compared to the Caribbean (Nagelkerken et al., 2008). Few studies are available from Indo-Pacific mangrove sponges and the highest diversity was reported in a study in the mangrove of Banka Island (North Sulawesi, Indonesia), where 19 species of sponges were found (Calcinaï et al., 2017). Our findings on mangrove sponges in such a unique mangrove area in New Caledonia improve the limited knowledge on the sponge species diversity in Pacific mangrove systems.

Water flow may play a critical role in the response of organisms to acidification (Hurd, 2015; Comeau et al., 2019), warming (Schoepf et al., 2018) and deoxygenation (Hughes et al., 2020). It has been reported to affect the diffusion boundary layer (i.e., a thin layer of stagnant water located around aquatic organisms) of corals, CCA and other calcareous macroalgae, altering their ability to calcify at low pH and to excrete metabolic wastes (reviewed in Nelson and Altieri, 2019). Knowing that flow speed could play a key role which deserves further investigations and measurements at the study site, we found two hypotheses to explain the high diversity of the Bouraké species and their resilience to suboptimal parameters: i) the species may benefit from the constant fluctuations of the physico-chemical parameters, ii) the species may benefit from heterotrophic inputs of the mangrove (in term of nutrients and organic matter).
With regards to environmental fluctuations, we measured averaged daily variations in temperature, DO, and pH of about 3.79 °C, 3.80 mg L⁻¹, and 0.63 pH units, respectively. Temperature changed up to 6.55 °C on a single day. Frequent exposure to stressful temperatures can induce acclimatization or adaptation in corals if the period of exposure is short enough to avoid mortality (Oliver and Palumbi, 2011; Palumbi et al., 2014; Schoepf et al., 2015; Rivest et al., 2017; Safaie et al., 2018). For example, in the Kimberly region (Australia), corals exposed to temperatures up to 37 °C with daily variations of up to 7 °C appear less prone to bleaching and grow and calcify at rates comparable to those in more thermally stable environments (Dandan et al., 2015; Schoepf et al., 2015; 2020), although they are not immune to extreme heat stress event (Le Nohaïc et al., 2017). Another example is the corals in the back reef and shallow pools around the island of Ofu (American Samoa), which despite occasional daily fluctuations of up to 6 °C, and an average daily temperature of 29 °C in summer (Piniak and Brown, 2009; Oliver and Palumbi, 2011) sustain reasonable levels of coral cover (25 - 26 %) and high diversity (Craig et al., 2001). Some studies tend to indicate that corals depended on the a priori 'frontloading' of genes involved in heat resistance in the coral host and/or the host's ability to adjust its physiology during short-term (weeks) environmental changes (Barshi et al., 2013; Palumbi et al., 2014). However, physiological adjustments have an energetic cost that corals cannot sustain in the long term, affecting other metabolic functions such as calcification. It could explain in part the lower calcification rates observed in some coral species, as seems to be the case for corals in the Bouraké lagoon (e.g., Camp et al., 2017). There is also evidence that exposure to short-term oscillations in low pH, alone or in combination with high temperature, can mitigate the impact of extreme environmental stressors on corals ( Warner et al., 1996; Oliver and Palumbi, 2011; Dufault et al., 2012; Schoepf et al., 2015; Safaie et al., 2018). With regard to the large seawater pH (up to 0.6 pH units) variability, species in the Bouraké lagoon appear to be thriving. In general, species exposed to pCO₂ fluctuations above 500 µatm in their natural environment display enhanced plasticity to future ocean acidification scenarios (Vargas et al., 2017; Carstensen and Duarte, 2019). For example, fluctuations in pH could increase CCA tolerance to ocean acidification by providing respite periods at low pH (Rivest et al., 2017) during which organisms can calcify at a standard rate, compensating for decreased calcification during periods of lower pH (Comeau et al., 2013; Cornwall et al., 2018). Diurnal variability in pH, typical of more variable pH habitats, may confer tolerance to resident calcifying species via the selection of individuals better adapted to survive in these environments (Rivest et al., 2017; Kapsenberg and Cyronak, 2019), although transgenerational acclimatization is required (Cornwall et al., 2020). In addition to changes in temperature and pH, which are the two most commonly tested environmental parameters, oxygen must also be considered. Although the impact of reduced oxygen levels and its natural fluctuations on coral reefs have yet to be established, it appears that low DO (2-4 mg L⁻¹) increases the sensitivity of branching corals, resulting in a decline in coral health, bleaching, and tissue loss (Haas et al., 2014; Hughes et al., 2020; Alderdice et al., 2021). However, our study shows that although the Bouraké system can reach conditions close to hypoxia (< 3 mg L⁻¹; Fig. 4), species seem to have promoted compensation mechanisms that allow them to survive in these conditions. The natural laboratory of Bouraké, where DO fluctuates with the tide, in combination with other environmental stressors, offers a perfect setting to test the practically unknown effects of deoxygenation and hypoxia thresholds in reef-building corals exposed to acid and hot conditions (Nelson and Altieri, 2019; Hughes et al., 2020).

Besides the hypothesis that environmental variability improves the metabolism of organisms, particularly their resilience to extreme conditions, a series of other physical and chemical parameters in the Bouraké lagoon may work in combination to offset or enhance these effects. Mangrove habitats are highly productive ecosystems and are sites of intense carbon processing, with a high potential impact on the global carbon budget (e.g., Borges et al., 2003; Dittmar et al., 2006; Bouillon et al., 2014).
In the Bouraké lagoon, benthic communities might have access to a range of heterotrophic inputs, nutrients, carbon and nitrogen sources. These sources can be metabolized by the species to increase their energy budget and cope with the suboptimal parameters, but they can also become toxic, if too concentrated, or depleted, leading to functional limitations. We measured particularly high concentrations of organic and inorganic carbon and nitrogen, but also of some nutrients, notably silicates and phosphorus, and we confirmed the potential contribution of the mangrove in those inputs, especially during the falling tide (Fig. 8 and 9; Supplementary Fig. S1 and S2; Table 2). We found that dissolved organic carbon contributes significantly to the TOC pool (POC + DOC), with an increasing concentration between the reference sites and the Bouraké lagoon, reaching maximum values on the inner reef. High organic matter content can increase DOC availability to corals, providing the with sustainable energy to withstand extreme environmental conditions (Levas et al., 2015). Some studies showed that the high organic matter of turbid reefs can support elevated coral heterotrophy that can facilitate energy maintenance during periods of stress (Anthony and Fabricius, 2000).

We also found that nutrients could partially explain the distribution of organisms throughout the Bouraké lagoon (Fig. 11). Indeed, NO₃ concentrations were higher on the outer reef, dominated by sponges, macroalgae and soft corals, while NH₄⁺ was high on the middle reef and POC, DOC, Si(OH)₄, and PO₄³⁻ were higher on the inner reef. Both the middle and inner reefs are characterized by the highest branching coral cover. Nitrates can accumulate inside the host cells, which could be in favor of sponges and macroalgae, while ammonium is the preferred source used by coral symbionts (Raven et al., 1992). While it is not obvious to demonstrate experimentally the nutrient negative or positive effect on corals' physiology (Atkinson et al., 1995; Szmant, 2002; Bongiorni et al., 2003). Van De Waal et al., (2009) have shown that the performance of organisms does not only depend on concentrations, but also on the ratios between different nutrients, and between organic and inorganic matter/components and the possible imbalance due to environmental changes. We found that the Bouraké lagoon is mostly N-limited (DIN:DIP < 10 and Si(OH)₄:DIN > 1), which confirms the findings of Justič et al. (1995) and is similar to the conditions observed in other New Caledonian mangroves (Jacquet et al., 2006). On the other hand, it has been experimentally demonstrated that nutrient limitation lowers the temperature effect at which coral bleaching occurs (Wiedenmann et al., 2013; Ezzat et al., 2016a; 2019), which is in contrast to the Bouraké coral’s resilience to the warming of summer 2016 (10-20 % bleaching only) compared to other reefs in New Caledonia (up to 90 % bleaching) (Benzoni et al., 2017). Corals symbionts recycle their host's metabolic wastes and take up dissolved inorganic nitrogen (DIN) and phosphorus (DIP) from seawater (Grover et al., 2003; Pernice et al., 2012; Rosset et al., 2015), both of which are used to produce vital organic molecules.

Nutrient starvation can occur when the availability of one type of essential nutrient decreases, resulting in an imbalanced N:P ratio of inorganic nutrients in seawater (Wiedenmann et al., 2013; D'Angelo and Wiedenmann, 2014). Based on our measurements, the N:P ratio in the Bouraké lagoon was 2.8:1 and 4.6:1 on the middle and the reference reefs, respectively, which is lower than the range calculated for average reef waters of 4.3:1 to 7.2:1 (Crossland et al., 1984, Furnas et al., 1995).

Although these data should be considered with caution, they suggest that the Bouraké lagoon seawater is not limited in phosphorus, a key nutrient in coral resilience to bleaching (Rosset et al., 2017; Ezzat et al., 2016a).

Seawater in the Bouraké lagoon was not limited in Si (Si(OH)₄:DIP > 10 and Si(OH)₄:DIN > 1; Justič et al., 1995), and Si was six times more abundant on the inner reef than elsewhere in the system (Fig. 9; Table 2). Silicates are an important source of nutrition and skeletal construction for primary producers such as sponges. Orthosilicic acid is a biologically available form of silicon that is poorly soluble at a very low pH. In the Bouraké lagoon, pH fluctuates with the tide, and it can be expected that orthosilicic acid would rise during falling tide. This elevated concentration of orthosilicic acid could be involved in the
growth and persistence of the Bouraké large banks of *Rhabdastrella globostellata*, as previously reported for other sponges in the shallow hydrothermal vents in the Pacific Ocean (Maldonado et al., 1999; Cárdenas and Rapp, 2013; Bertolino et al., 2017).

We are still missing information about light, turbidity, current, bacteria biomass and phytoplankton sources as well as other biological communities (e.g., fish) to fully understand this complex and dynamic system and the functioning of its coral community. However, we recognize the Bouraké lagoon's uniqueness as a natural laboratory for studying the adaptive responses of corals and other reef species to the combination of multiple suboptimal environmental parameters, which are similar to or perhaps worse than those projected for the future. Our investigations indicate that the geomorphology of this unique site has not changed for the last 80 to 100 years probably longer. With this in mind, we assume that the situation is similar for environmental conditions and that the corals of the Bouraké lagoon have experienced the current extreme conditions for several generations. Most importantly, the species found in the Bouraké lagoon are not unique to the mangrove habitat; they are common throughout New Caledonia as well as in the SW Pacific region, suggesting that they have used specific strategies to cope with the suboptimal environmental conditions.

We are also unsure how the different parameters will fluctuate at bay-sheltered reefs over time and under future climate change conditions and if the variability measured in the Bouraké lagoon is representative of the natural fluctuations expected for coastal habitats in the future. Indeed, earth system model simulations, which are mostly based on open-ocean system models, project that the seasonal amplitude for pH and \( \rho \text{CO}_2 \) in the future climate will increase by 81\% (Landschützer and Orr, 2018) and ocean acidity extremes will be more frequent (Burger et al., 2020), which could mean that future diel pH variability will increase even more at sites with the most significant variability today. If this is the case, coral reef in Bouraké will face in the next decades incredible harsh environmental conditions since physical and biogeochemical parameters measured in this study already exceed future climatic simulations.
5 Conclusion

We used a multi-scale approach to characterize the physical and chemical environmental parameters of one of the most suitable natural analogue for future environmental conditions, the semi-enclosed lagoon of Bouraké (New Caledonia), and accurately map its benthic community for the first time. We studied several physico-chemical parameters such as pH, dissolved oxygen, temperature, and salinity, but also nutrients and organic matter and we found that: i) they fluctuate between low and high tides, ranging from suboptimal-extreme to near normal values; ii) although predictable according to the tide, they differed spatially, and iii) suboptimal values persisted longer and were more acute on the inner reef. Our data clearly show that fluctuations are: i) predictable, at least for some (pH, DO, temperature and salinity) of the physical parameters for which we have enough data; ii) mainly driven by the tide; and iii) that seawater nutrient imbalance and organic inputs increase during the falling tide and originate from the mangrove forest and associated sediments. Although several studies suggest that ocean acidification, warming and, to some extent, deoxygenation will lead to a reduction in biodiversity, increase in bleaching and reef dissolution, in the Bouraké lagoon, we found a rich and healthy reef with high coral cover and species richness, but also sponges and macroalgae (including CCA). It was beyond the scope of this already multidisciplinary study to assess the contribution of environmental variability and nutrient imbalance to the organism’s stress tolerance under extreme conditions. However, both coexist in the Bouraké lagoon, and we believe there is evidence of their contribution to the survival of organisms to future-like environmental conditions. Our study provides evidence that this is possible in nature, giving a glimmer of hope for the future of coral reefs. Further experiments are needed to reveal the mechanisms involved in the organisms’ resilience to such conditions and the potential role of this unique site as a refuge for organisms threatened by climate change. However, we also provides the compelling basis for using this site as a natural laboratory and to better study the multitude of complex stressors acting together on life-long adapted coral reefs.
Author contribution. R.R-M. conceived and designed the project with input from F.M. for the benthic community distribution study. F.M. and R.R.M. collected the data. F.B., C.P., C.C. and B.C. identified the corals, macroalgae and sponges, respectively. M.P.-P. performed all the chemical analyses. F.M. conducted the data analysis with the help of J.A. and R.R-M. F.M. drafted the manuscript in collaboration with R.R-M. All co-authors read and edited the final version of the manuscript.

Competing interests. The authors declare that they have no conflict of interest.

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