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~~extreme environmental conditions

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Abstract. According to current experimental evidence, coral reefs could disappear within the century if CO_2 emissions remain unabated. However, recent discoveries of diverse and high cover reefs that already ~~thrive~~ live under extreme conditions ~~seem to contradict these projections~~suggest that some corals might thrive well under hot, high $p$$CO_2$, and deoxygenated seawater. Volcanic CO_2 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.~~Although they do not perfectly mimic future conditions, these natural laboratories offer unique opportunities to explore the mechanisms ~~how~~ that reef species could use to 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~~ing~~ the ecosystem response.

~~In t~~This study ~~we~~focus~~es~~ 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_T and 1.9 mg O_2 L^{-1} at Bouraké, vs 7.9 pH_T and 5.5 mg O_2 L^{-1} at reference reefs). Dissolved oxygen, temperature, and pH fluctuates according to the tide of up to 4.91 mg O_2 L^{-1}, 6.50 °C, and 0.69 pH_T units on a single day. Furthermore, the concentration of most of the chemical parameters was one- to five ~~5~~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 measured at Bouraké, 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~~extreme environmental conditions.

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1 Introduction

Atmospheric carbon dioxide (CO_2) 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 t~~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~~ laborator~~yies~~ ~~of future climatic conditions when~~ where at least one or more environmental parameters naturally mimic ~~climate change like~~extreme environmental 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 CO_2 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 pCO_2, or temperature, and eventually a decrease in dissolved oxygen (Camp et al., 2018). At these sites, ~~observations overall~~general observations suggest ecosystem-level consequences of life-long exposure to extreme conditions, such as reduced biological diversity, especially among calcifying organisms, ~~decreasing~~ decreased rates of coral calcification, and high rates of bioerosion (e.g., Hall-Spencer 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~~ laboratories can host ~~quite~~ very rich reef communities. ~~These~~ Examples of such sites have been documented in Palau (Golbuu et al., 2016; Barkley et al., 2017; Shamberger et al., 2018; ~~(~~Kurihara et al., 2021~~)~~), 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, have been argued to ~~may~~ bias the interpretation of the biological mechanisms that trigger the ~~organismal~~ responses of organisms (e.g., ~~(~~Vizzini et al., 2013~~; (~~Camp et al., 2018~~;)(~~Aiuppa et al., 2021). 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 CO_2 seeps, pH variability can unexpectedly go beyond projected future values (e.g., Hall-Spencer 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~~ crucial in shaping biological responses (Boyd et al., 2016; Rivest et al., 2017). For instance, early studies suggest that temperature

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84 fluctuations due to diel or tidal variations could expose corals to stressful temperatures long enough to induce acclimatization

85 or adaptation, but short enough to avoid coral mortality (Craig et al., 2001; Oliver and Palumbi, 2011; Castillo et al., 2012;

86 Palumbi et al., 2014; DeCarlo et al., 2019). Coral reef organisms from such thermally variable environments are expected to

87 respond positively to future heat events (Rivest et al., 2017). Besides, corals naturally subjected to high pCO$_2$ variability have

88 shown immune defences when experimentally exposed to high temperatures, thus buffering the magnitude of thermal stress

89 during heat waves (Wall et al., 2020). The extreme tidal range in the Kimberly region (Northwest of Australia) exposes corals

90 to short-term temperature maxima of up to 37 °C, and fluctuations of up to 7 °C daily. Despite the high temperature, also

91 combined with strong currents and turbid waters, diverse and probably resilient coral reefs have been described there (Dandan

92 et al., 2015; Schoepf et al., 2015).

93 Overall, ~~at natural analogues laboratories~~ only ~~a~~ part~~s~~ of these natural laboratories' ~~the~~ physical and biogeochemical

94 parameters have been quantified and only during short periods of fieldwork due to logistic constraints. Long-term monitoring

95 of seawater parameters and their fluctuation is essential to ~~understand~~ better understand the mechanisms used by resilient reef

96 organisms in these natural laboratories and interpret ~~predict~~ how marine taxa will respond to future biogeochemical changes

97 in the environment.

98 The semi-enclosed lagoon of Bouraké (New Caledonia, SW Pacific Ocean) has been ~~put forward to be as~~considered one of

99 the most suitable natural ~~analogues~~ laboratories ~~for~~of future extreme environmental conditions (Camp et al., 2019). In a

100 preliminary study, Camp et al., (2017) reported a series of compelling short-term data of seawater carbonate chemistry and a

101 general survey of the coral populations. In this first assessment of the Bouraké lagoon, the authors measured diel fluctuations

102 of temperature (ranging from 25.9-33.1 °C), pH (ranging from 7.24-7.91 pH$_T$ units) and dissolved oxygen (DO) (ranging from

103 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 the time

104 to a pH$_T$ of 7.7-7.8, and 71 % of the time to temperatures predicted for the end of the century under the IPCC scenario RCP4.5

105 (IPCC, 2014). These striking preliminary findings qualified the Bouraké lagoon as a unique site where potentially adapted

106 corals withstand extreme environmental conditions.

107 ~~These findings give hope to the future of coral reefs in the face of climate change, and suggest that Bouraké might play as a~~

108 ~~refuge for corals since it already hosts resistant reef species. However, the~~The extent to which the Bouraké species are exposed

109 to sub optimal conditions remains unclear~~. and W~~we believe that the ~~road map to test for such an~~best way to assess these very

110 encouraging ~~hypothesis~~ findings ~~is first~~ to start with fully characteriz~~ing~~e the main environmental parameters and the daily

111 and seasonal fluctuations to which reef species have been subjected during their entire life. Here we used a multi-scale

112 approach to map and describe the benthic community living in the Bouraké lagoon and report on new evidence based on three

113 years of data ~~collected at this remarkable natural laboratory~~. ~~B~~In particular, ~~b~~ecause of the size of the area, ~~vast area affected,~~

114 the close vicinity of a dense mangrove forest, and the demonstrated tide effect on the local environmental conditions, we

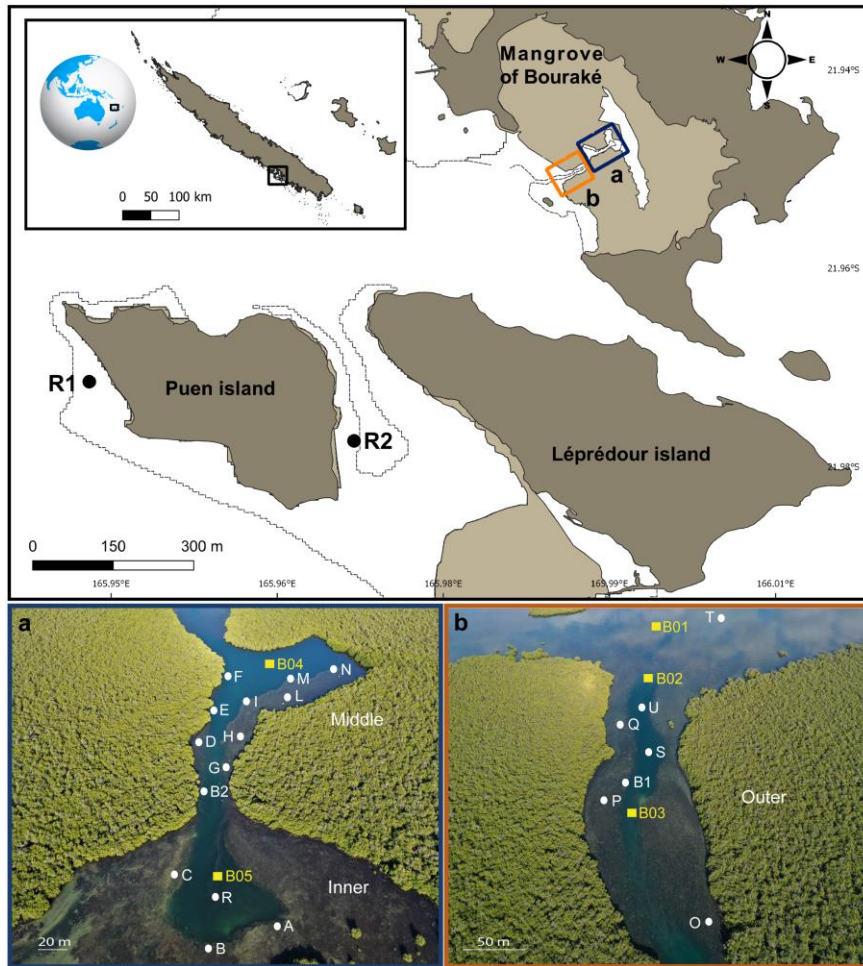
115 hypothesize~~d~~ that (1) environmental conditions fluctuate regularly but are spatially heterogeneous throughout ~~and differ~~

116 ~~spatially in~~the Bouraké lagoon, and (2) only a limited number of species ~~are able to~~can resist to the extreme physical and

117 chemical conditions at the study site, when compared to adjacent bay-sheltered reefs.

118

119 **2 Methods**

120 **2.1 Study sites**
121 ~~From~~ Starting in February 2016, we studied the semi-enclosed coral reef lagoon of Bouraké (South Province, Grande Terre,
122 New Caledonia) and adjacent reference reefs (Fig. 1). The mangrove of Bouraké is located in a semi-arid geographical area,
123 and it lacks rivers input typical of mangrove estuaries.

124

125 **Figure 1.** Map of the study site (top panel) showing the semi-enclosed mangrove lagoon of Bouraké and reference reefs (R1
126 and R2). Photos (a) and (b) (bottom panels) are aerial pictures (taken at 130 m above the Bouraké lagoon) of the inner (bottom)
127 and middle reefs **(a)** and the outer reef **(b)**. White dots and yellow squares indicate the sampling stations used for physical

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128 and chemical environmental monitoring, respectively. Georep New Caldonia database (https://georep.nc/) and QGis software

129 were used to build the figure (top panel).

131 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*

132 *marina* and *Rhizophora stylosa*. It expands into side pools and a large reservoir in the inner part of the mangrove system.

133 A preliminary calculation of its surface and seawater volume of the main area (i.e., without the large seawater reservoir

134 covered by the mangrove forest) using the 3ds Max Model gives underestimated values of 192,100 m^2 and 246,060 m^3,

135 respectively (Rodolfo-Metalpa et al., in prep.). Terraces extend from the mangrove, on both sides of the channel, and form

136 diverse and compact reefs at their ends. Coral species are less abundant and diverse near the mangrove roots, where the bottom

137 substrate is composed of fine sediment and mud. There, reefs are exposed to air only at low tide during the spring tides

138 (1.1 m maximum tidal range). We subdivided the lagoon into three main areas: an external, an intermediate, and

139 an inner reef (hereafter called outer, middle and inner reefs; panels a & b in Fig. 1). A series of sampling stations were selected,

140 and some of the main seawater chemical and physical environmental parameters were measured at the study site and two

141 adjacent reference reefs, namely R1, a typical fringing reef, and R2, a semi-enclosed shallow and relatively large bay. Both

142 reefs were located 4.8 and 3.2 km from the entrance of the Bouraké lagoon, respectively.

143 **2.2 Environmental monitoring**

144 **2.2.1. Oceanographic sensors deployment and short- to long-term measurements**

145 From February 2016 to December 2020 up to eight YSI 600 OMS-M, three Seabird SeaFET^{TM} pH loggers, and four

146 Hobo water temperature Pro V2, were set at 10-min logging intervals and used individually or in combination to assess short-

147 , medium-, or long-term variations across depth (as a proxy of the tide), temperature (°C), dissolved oxygen concentration

148 (DO, mg L^{-1}), seawater pH_T (total scale), and salinity. A summary of the deployments is given in Supplementary Table S1.

149 YSI dissolved oxygen optical sensors were calibrated against zero and 100 % saturated seawater at 25 °C. Two SeaFETs

150 were calibrated by the manufacturer, while the third was corrected before deployment by measuring its deviation from the

151 two others in the same seawater.

152 Short-term (i.e., 24-h) spatial and depth-related variations in pH and DO were simultaneously measured at several

153 stations in the Bouraké lagoon in March and April 2018 (Fig. 1). Spatial variations were assessed i) within the inner (St A-C

154 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

155 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

156 the Bouraké lagoon, we recorded differences between the surface (shallow) and the bottom water: i) at the outer reef (St S for

157 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

158 2019 (St R1, R2, B1 and B2) and December 2020 (St R1, R2, T and B2).

159 Medium-term measurements (i.e., 2-3 weeks) of the DO and pH were recorded at the reference (St R1, R2) and

160 Bouraké reefs (St B1, B2) between 2016 and 2019.

161 Long-term measurements (>1 year) of seawater temperature were recorded at R1 and R2 starting from January

162 2019 and September 2017, respectively, and at B1 and B2 from October 2018 and September 2017, respectively.

163 Only temperature data between October 2018 to April 2020 were compared between sites.

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164   Short-term pH and DO data and long-term temperature data were compared between stations using General Linear

165 Modelling (GLM), and the Tukey' HSD *post hoc* test was used when significant factor effects were found. When data did not

166 conform to normality or homogeneity of variance, ~~we used~~ the Kruskal-Wallis test followed by the Dunn's multiple

167 comparisons test (Bonferroni-adjusted) or the Wilcoxon test were performed. Statistical analyses were ~~performed~~ carried out

168 using either Statistica® or R version 3.4.4 (R Core Team, 2018), the latter using "stats", "FSA", and "MASS" packages.

2.2.2. Phase averaged and tidal harmonic analyses for diurnal and semidiurnal oscillations

170 Medium-–term pH and DO changes were investigated by averaging time and tidal phases for diurnal and semi-diurnal

171 oscillations. To do this, all data were overlaid on a daily period and a tidal phase. First, we calculated a predicted tide for the

172 study area using the Nouméa harbour tide (50 km south of our study site) modified with coefficients from the Naval

173 Hydrographic and Oceanographic Service (SHOM; http://data.shom.fr). The predicted tide was used to assign a semidiurnal

174 tidal phase (12 h) to each sampling time, and the data were averaged for each of these tidal phases. Similarly, the data were

175 averaged for each hour of the day (24 h). Because tides at sea are a sequence of sinusoidal harmonic components that are

176 different for each location, we performed a harmonic tidal analysis on the DO and pH data. We used the "UTide"-ut_solv()

177 tidal analysis package (Codiga, 2011) ~~using~~ with the principal semidiurnal lunar constituent (M_2), principal semidiurnal solar

178 constituent (S_2), and solar diurnal constituent (S_1). For each parameter, the amplitudes of the tidal harmonics M_2 (12.4 h), S_2

179 (12 h), and S_1 (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

181 Surface water samples were collected across a diel ~~tide~~ cycles in June 2017, and July 2019 for pH, total alkalinity (A_T),

182 dissolved inorganic carbon (DIC), nutrients (orthosilicic acid [$Si(OH)_4$], nitrogen oxide [NO_x], ammonium [NH_4]$^+$, phosphate

183 [PO_4]$^{3-}$, dissolved organic carbon (DOC), particulate organic carbon (POC), and particulate organic nitrogen (PON). A

184 summary of the total sampling is given in Supplementary Table S2. Dissolved inorganic nitrogen (DIN) and total organic

185 carbon (TOC) were calculated as [NO_x] + [NH_4]$^+$, and DOC + POC, respectively. T~~t~~he most important ratios were calculated

186 (e.g., DOC:TOC; $Si(OH)_4$:DIN) and contrasted between stations .~~t~~To evaluate the availability of nutrients and organic matter

187 in the Bouraké lagoon (Jacquet et al., 2006; Leopold et al., 2017). ~~the most important ratios were calculated (e.g., DOC:TOC;~~

188 ~~Si(OH)₄:DIN) and contrasted between stations.~~

189   In 2017, during three consecutive days (from May 31~~st~~th to June 02nd), seawater was sampled six times: twice during

190 both high and low tide~~,~~ and once~~e time~~ at both rising and falling tide. In total, we sampled one reference station (R2), three

191 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

192 inner reef inside the lagoon (Inner: St B05) (Fig. 1). The whole collection lasted about 30 minutes.

193   In 2019, during three consecutive days (from July 16th to 18th), sampling was carried out every hour from 8 am to 3

194 pm. We sampled B1 and B2 on the first day, R1 on the second and R2 on the third day.

195 During diel cycles, a~~A~~t each station and sampling time, pH and temperature were measured at the surface (0.5 m deep) using

196 a portable pH-meter (913, Metrohm) calibrated with TRIS buffer (Dickson lab, batch #T28). A subsample (50 mL) was

197 filtered through 0.45 -µm Whatman^{TM} Puradisc CA filters using a syringe and poisoned with 20 µL saturated $HgCl_2$ to further

198 measure A_T. Two 20 mL subsamples were analysed using an auto titrator (EcoTitrator, Metrohm), and A_T was calculated from

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199   the Gran function. Results were corrected against A_T standards (A. Dickson, batch #155, Scripps, USA). The seawater

200   carbonate parameters pCO_2, CO_3^{2-}, and aragonite saturation state (Ω_{ara}) were then calculated from the pH_T, A_T, temperature,

201   and mean salinity (35) using the free-access CO_2SYS package (Pierrot et al., 2006).

202   Ammonium concentration was determined on a 40 mL subsample of unfiltered seawater, collected using a 60 mL

203   Schott bottle and stored in the dark. Samples were processed using a fluorimeter (Turner Designs) between six and 18 h after

204   two mL of OPA reagent (o-phthaldialdehyde) was added (Holmes et al., 1999).

205   The sampling of nutrients was performed using two replicate 20 mL polypropylene vials, rinsed three times using

206   filtered seawater (Whatman^{TM} Puradisc CA syringe filters 0.45 µm), filled with the sample and immediately poisoned with

207   20 µL saturated $HgCl_2$. Measurements of PO_4^{3-}, NO_x, and $Si(OH)_4$ nutrients were performed by colourimetry (Seal

208   Analytical).

209   Seawater samples for DIC were collected in two replicate glass vials (20 mL), filled with unfiltered water and

210   poisoned with 10 µL saturated $HgCl_2$. The vials were immediately closed, the absence of bubbles was visually checked, and

211   the samples were stored in the dark at room temperature for later analysis on a Shimadzu TOC-L analyser (Non-Dispersive

212   Infrared, NDIR). Typical analytical precision was less than $\pm$ 2 µmol kg^{-1}. The accuracy was verified using regular

213   measurements of reference material (CRM) from A. Dickson's laboratory.

214   Seawater samples for DOC were collected in two pre-combusted (4h at 450 °C) glass ampoules filled with water

215   filtered using a glass syringe filtration system (SGE^{TM}) with two pre-combusted 25-mm GF/F Whatman^{TM} filters. Samples

216   were then acidified with ultrapure orthophosphoric acid (H_3PO_4), sealed, and stored in the dark at room temperature for later

217   analysis by high-temperature catalytic oxidation (HTCO) (Sugimura and Suzuki, 1988; Cauwet, 1994) on a Shimadzu TOC-

218   L analyser. Typical analytical precision was $\pm$ 0.1-0.5 µM C (SD). Consensus reference materials

219   (http://www.rsmas.miami.edu/groups/biogeochem/CRM.html) were injected every 12 to 17 samples to ensure stable

220   operating conditions. DOC concentrations are only available for the 2017 sampling because of a sample's pollution in 2019.

221   Finally, one litre of unfiltered seawater was collected in a borosilicate glass bottle and stored on ice during sampling

222   for later measurement of POC and PON contents. In the lab, particulate matter was collected on pre-combusted (4h at 450

223   °C) Whatman^{TM} GF/F filters using a Nalgene® vacuum system. The filters were dried at 60 °C in the oven for 24 h and stored

224   in airtight glass vials at 4 °C in the dark until analysis on a CHN Perkin Elmer 2400.

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

226   Seawater chemistry data were pooled by sampling area (R1, R2, Outer, Middle, Inner), and differences were tested using the

227   Kruskal-Wallis test followed the Conover Multiple comparison test (Benjamini-Hochberg-adjusted). We focused on the effect

228   of the tidal phases (i.e., falling and rising tide) on the seawater chemical composition in the Bouraké lagoon only, by attributing

229   each sample a tidal phase between 0 (high tide) and 6 hours (low tide), and between 6 and 12 hours (high tide). Multiple linear

230   regression was used to assess the adjusted R^2 and significance ($p < 0.05$) of the data from 0 to 6 h (falling tide) and from 6 to

231   12 hours (rising tide) separately. Statistical analyses were performed using either Statistica® or R (version 3.2.4, R Core

232   Team, 2018), the latter using the "FSA", "stats", and "Conover.test" packages.

233   **2.3 Benthic community characterization and distribution**

234   The benthic community and bottom substrate of the Bouraké lagoon, referred hereafter as biotic and abiotic descriptors,

235   respectively, were assessed in April 2018. Twenty-four 30 m-long geo-referenced transects (T1-T24) were laid in the lagoon

236 along the terraces' edge at similar depths (i.e. ~ 1 m), targeting coral dominated benthic assemblages. On each transect, a 0.5

237 x 0.5 m PVC quadrat was placed every meter, and a picture was taken with a waterproof photo-camera (Nikon AW 130)

238 parallel to the substrate. W~~For each transect, w~~e made a general description of the bottom (i.e. the various substrates) and a

239 list of the most common and identifiable sessile species for each transect. For each of the 835 pictures collected, we estimated

240 the cover of abiotic (i.e., mud, sand, rock, rubble, dead corals and unreadable) and biotic descriptors (i.e., branching, massive

241 and soft corals, sponges, macroalgae and "others") with photoQuad software both by automatic multi-scale image

242 segmentation regions and manual grid cell counts when necessary.

243 We used the photos of quadrats, the many other pictures collected during fieldwork~~s~~, and laboratory morphological

244 observations on collected samples to produce a non-exhaustive species list of corals, macroalgae and sponges. Corals were

245 comprehensively sampled throughout the Bouraké lagoon and on the reference reef R2, while dominant macroalgal and

246 sponges species were collected in the Bouraké lagoon alone and only if they were encountered at least three times along a

247 transect, likely leading to an underestimation of their diversity. Coral diversity was assessed through photographic and

248 ~~destructive~~ sampling during time-based open search swims and SCUBA dives (Hill and Wilkinson, 2004). Whenever possible,

249 scleractinian corals were identified to species level *in situ* by photographic sampling only. ~~In case of doubtful~~When

250 identification was doubtful *in vivo*, or when ~~of~~ taxa were characterized by small corallite size (<1 mm in diameter) and

251 requir~~ing~~ed additional morphological examination of the skeleton ~~for positive~~to confirm identification (e.g. genera *Acropora*,

252 *Montipora* and *Porites*), a fragment of the colony was collected, tagged, cleaned in sodium hypochlorite overnight, rinsed in

253 freshwater and dried. The reference collection is housed at IRD Nouméa. Microscopic examination of the skeletal features

254 allowed species-level identification following the reference literature (Veron, and Wallace, 1984; Wallace, 1999; Veron,

255 2000). Sponges were identified ~~either~~ based on their spicules' morphological characteristics (i.e., shape, length and width), or

256 using a series of morphological descriptors (e.g., shape, size, colour, texture, surface ornamentations, fibres) for species

257 without spicules. In the lab, a subsample of the collected sponges ~~were~~ was immediately digested using HNO_3, and spicules

258 were measured with an optical stereomicroscope. For species without spicules, hand-cut sections of the choanosome and

259 ectosome were observed under a stereomicroscope. Species were identified using the taxonomical keys of Rützler (1978),

260 Hooper and Van Soest (2002), and Pons et al. (2017). Macroalgae and corals identification were based on morphological and

261 anatomical observations following the dedicated literature and ~~by~~ referring to ~~the collections of~~ specimens housed at IRD

262 Noumea.

263 Abiotic and biotic cover percentages~~,~~ averaged per transect, and species richness, calculated as the number of species

264 in the transect, were plotted using non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarities ("vegan"

265 package in R) of square-root transformed data. Finally, the best number of clusters for the whole Bouraké lagoon was

266 determined ~~by~~ using the gap statistic method ("cluster" and "factorextra" packages in R) and used for the hierarchical

267 clustering representation (Ward, 1963). The cluster separation was verified with a two-way analysis of similarity ANOSIM.

268 Within each cluster, the benthic community and bottom substrate were averaged between transects, and the dominant biotic

269 and abiotic descriptors were selected and used to define the cluster.

270 Principal component analysis (PCA) was used to visualize the correlation between environmental parameters and

271 the ~~transects'~~ benthic descriptors of transects inside the Bouraké lagoon. The analysis was performed in R (package

272 "FactorMineR", version 3.2.4, R Core Team, 2018) using data of biotic descriptors (averaged per transect) and the seawater

273 parameters averaged for each sampling area (i.e., outer, middle and inner reefs).

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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).
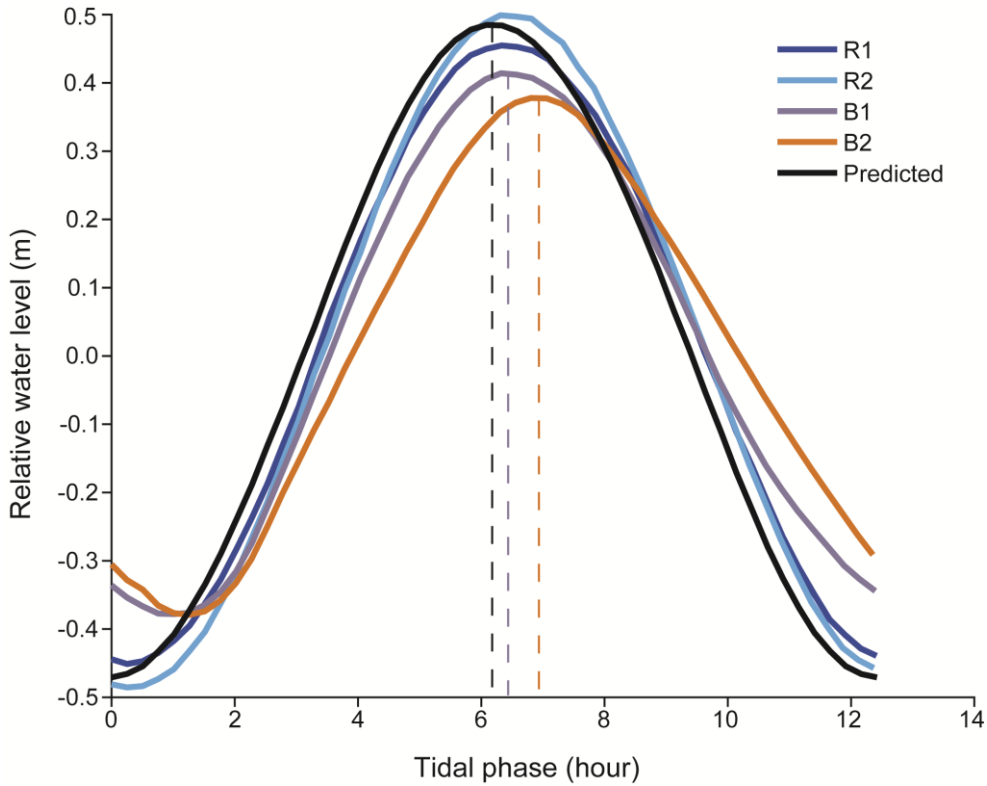
Figure 2. Temporal shift between the averaged tides recorded at the reference (St R1 and R2) and at the Bouraké reefs (St B1 and B2) and the predicted tide calculated for the study area (see SHOM: http://data.shom.fr for the Nouméa harbour).

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. ~~At B1 and B2, t~~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.

287   *Temperature.* Our results indicate that the water temperature has an annual cycle with lower values during ~~the austral~~
288   winter (May-October) and higher values in summer (November-April). Daily averaged temperatures at R2, B1 and B2 were
289   not significantly different, while the temperature at R1 was cooler in summer and warmer in winter (Fig. 3a; Tables 1)
290   compared to the other stations. On a weekly ba~~sisse~~, the averaged diel temperature variation was significantly different
291   between stations: 1.34 ± 0.39 °C at R1 and 3.73 ± 0.74 °C at B2 (Fig. 3b; Tables 1). In a single day, we recorded temperature
292   fluctuations of up to 3.4 °C at R1 and 6.5 °C at B2.
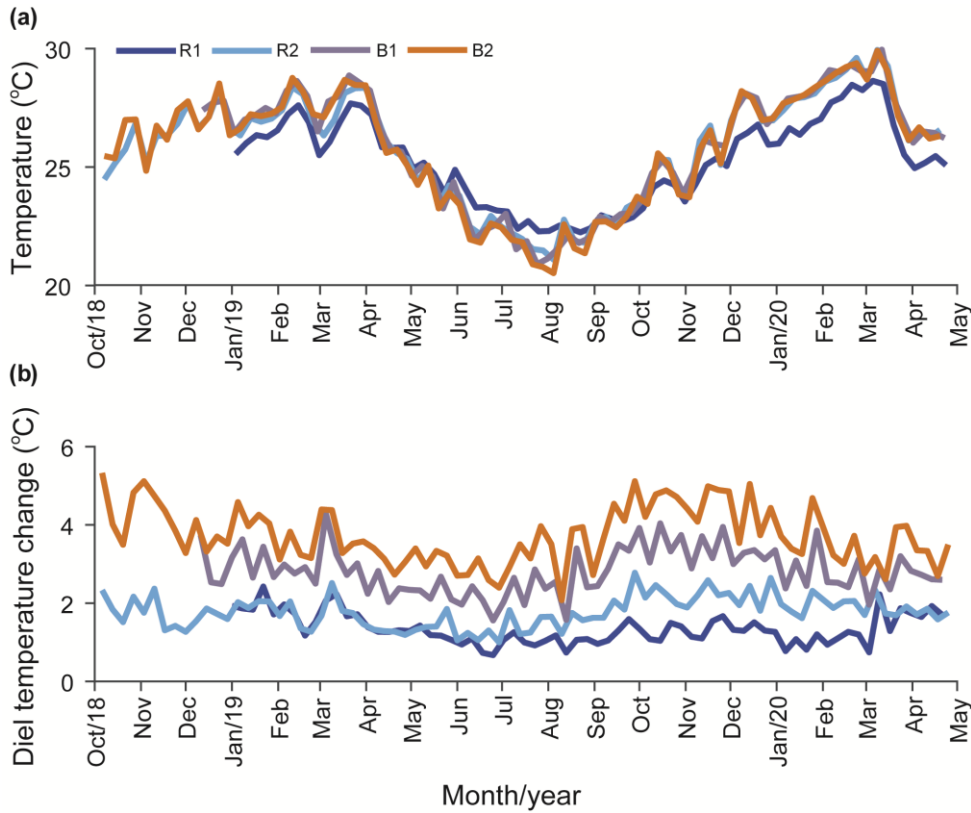
Figure 3. Long-term temperature monitoring from October 2018 to April 2020 at the reference (St R1 and R2) and Bouraké
reefs (St B1 and B2). Data are plotted using we~~ea~~kly averaged temperature **(a)** and ~~weakly~~ weekly averaged diel changes
(b).

301

302

303 **Table 1.** Summary of the statistical analyses applied to the seawater physical and chemical parameters collected between
304 2016 and 2020 ~~in~~ at the Bouraké lagoon (St B1, B2, St A-R, outer, middle and inner) and at reference reefs (St R1 and R2).
305 Differences in temperature, salinity and chemical parameters between the Bouraké lagoon and reference reefs and spatial and
306 vertical differences in pH and DO inside the Bouraké lagoon. **K-W:** Kruskal-Wallis's test; **W:** Wilcoxon test; **GLM:** General
307 Linear Model; **D:** Dunn's test; **T:** Tukey's test; **C:** Conover's test.

308

Parameters	(n)	K-W	W	GLM	*p*	post hoc (test)
Seawater temperature (St R1, R2, B1, B2)						
Daily means	2968	68.46			**< 0.001**	(D) *p*<0.001 R1<R2=B1=B2
~~Weakly~~ Weekly oscillations	305	234.63			**< 0.001**	(D) *p*<0.01 R1<R2<B1<B2
Seawater pH (Stations)						
Spatial INNER (A-C)	711			5.32	**0.005**	(T) *p*<0.01 A<C
Spatial (B1 vs B2)	1820			17.62	**< 0.001**	
Spatial (U vs T)	7280			189.8	**< 0.001**	
Surface vs deep (R)	664			26.88	**< 0.001**	
Surface vs deep (S)	692			41.48	**< 0.001**	
Seawater DO (Stations)						
Spatial INNER (A-G)	1031			1.145	0.330	
Spatial MIDDLE (H-N)	700			0.636	0.636	
Spatial OUTER (O-Q)	399			1.636	0.196	
Surface vs deep (I)	280			0.000	0.994	
Surface vs deep (N)	280			22.05	**< 0.001**	
Surface vs deep (R)	258			0.443	0.839	
Seawater Salinity (Stations)						
Winter (R1, R2, B1, B2)	1732			463.5	**< 0.001**	(T) *p*<0.01 R1<R2<B1<B2
Summer (R1, R2, T, B2)	5105			1583	**< 0.001**	(T) *p*<0.01 R1<R2<T<B2
Winter vs Summer (R1)	1872		287264		**< 0.001**	
Winter vs Summer (R2)	1728		253060		**< 0.001**	
Winter vs Summer (B2)	1872		150175		**< 0.001**	
Seawater carbonate chemistry (St R1, R2, outer, middle, and inner)						
pH_T	66	36.48			**< 0.001**	(C) *p*<0.05 R1>R2>Inn=Mid=Out
pCO_2	66	36.48			**< 0.001**	(C) *p*<0.01 R1=R2<Inn=Mid=Out
CO_3^{2-}	66	33.54			**< 0.001**	(C) *p*<0.05 R1>R2>Inn=Mid=Out
Ω_{ara}	66	33.27			**< 0.001**	(C) *p*<0.05 R1>R2>Inn=Mid=Out
DIC	66	25.95			**< 0.001**	(C) *p*<0.01 R1=R2<Inn=Mid=Out
A_T	66	20.94			**< 0.001**	(C) *p*<0.05 All≠; Mid=R1; Mid=R2; Out=Inn; R1=R2
Seawater chemical parameters (St R1, R2, outer, middle, inner)						
$SiOH_4$	66	45.37			**< 0.001**	(C) *p*<0.05 R1<R2<Out=Mid=Inn; Inn>Out
NO_x	66	26.46			**< 0.001**	(C) *p*<0.05; R1<R2=Inn=Mid; Inn<Out; Out >R1; Out>R2
NH_4^+	66	26.46			**< 0.001**	(C) *p*<0.01 R1<Inn=Mid=Out=R2
PO_4^{3-}	66	29.43			**< 0.001**	(C) *p*<0.05 All ≠; R2=Mid
DOC	36	16.12			**0.001**	(C) *p*<0.05 All ≠; Mid=Out
POC	66	52.46			**< 0.001**	(C) *p*<0.05 R1=R2<Out<Mid<Inn
PON	66	43.79			**< 0.001**	(C) *p*<0.05 R1=R2<Out<Mid<Inn
DIN	66	20.13			**< 0.001**	(C) *p*<0.01 R2<R1<Inn=Mid=Out
~~*Seawater chemical parameters (St R1, R2, outer, middle, inner)*~~						
TOC	36	19.48			**< 0.001**	(C) *p*<0.01 All ≠; Mid=Out

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DIC:DIN	66	17.40	< **0.001**	(C) $p<0.01$ R1>R2=Inn=Mid=Out
POC:PON	66	44.87	< **0.001**	(C) $p<0.01$ R1=R2<Inn=Mid=Out
POC:DOC	36	18.47	< **0.001**	(C) $p<0.05$ All ≠; Inn=Mid

DOC TOC	36	18.21	< **0.001**	(C) $p<0.01$ R2<Out<Inn<Mid; Inn=Mid; Inn=Out
Si(OH)$_4$:DIN	66	43.77	< **0.001**	(C) $p<0.01$ R2< Inn>Mid; Mid=Out; R1=R2
DIN:DIP	65	24.59	< **0.001**	(C) $p<0.05$ R1<R2>Inn; R2=Out=Mid; Inn=Mid
Si(OH)$_4$:DIP	65	36.62	< **0.001**	(C) $p<0.01$ R1<R2<Inn=Mid=Out;

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).

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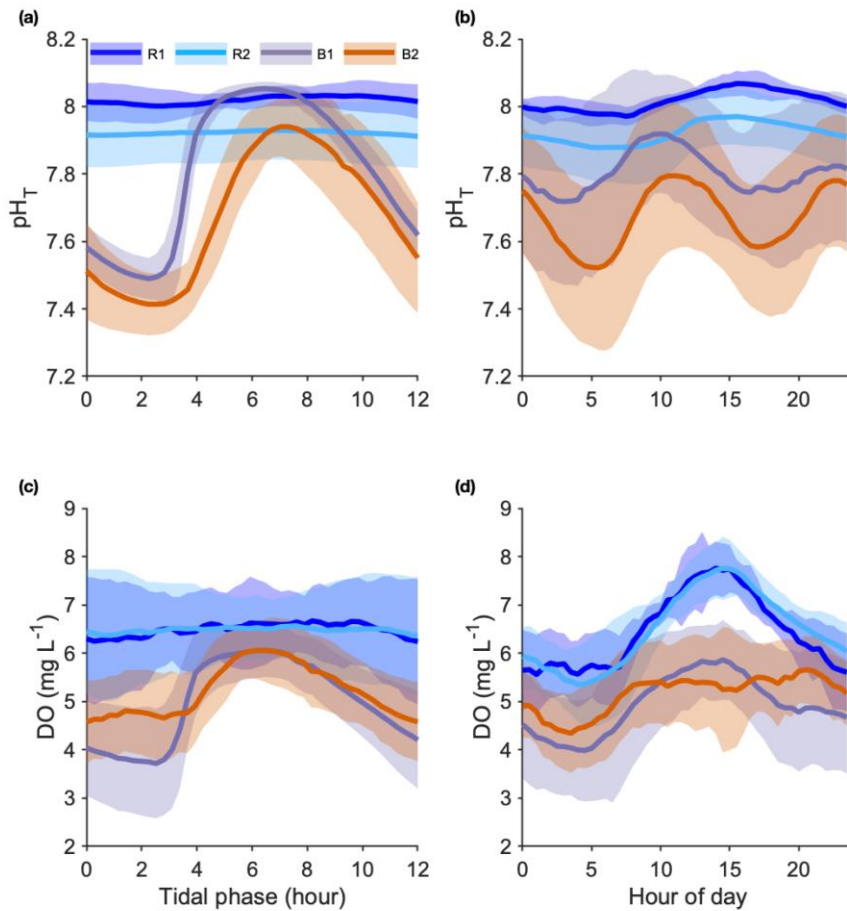
Figure 4. Seawater pH$_T$ **(a)**, **(b)** and dissolved oxygen (DO) **(c)**, **(d)** variations recorded at the reference (St R1 and R2) and Bouraké reefs (St B1 and B2). Data were ~~superimposed~~ overlaid in a single tidal phase (12 h) **(a)**, **(c)**; and in a 24-hour~~s~~ cycle **(b)**, **(d)**. 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. During the studied period, w~~W~~e recorded means of 8.01 ± 0.04 and 7.89 ± 0.08 pH$_T$ units at R1 and R2, and 7.80 ± 0.22 and 7.67 ± 0.23 pH$_T$ units at B1 and B2, respectively. At both B1 and B2, pH was strongly correlated with the tidal cycle (Fig. 4a, 82 and 73 % of the total variance were explained by the tidal harmonic analysis, respectively).~~,~~ In contrast, ~~while~~ it was ~~correlated~~ only marginally correlated with the 24-hour~~s~~ cycle (Fig. 4b).

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 (data not shown). The pH oscillations were mainly semidiurnal ($M_2 = 0.27 \pm 0.01$, $S_2 = 0.05 \pm 0.01$ pH_T units, for B1; $M_2 = 0.24 \pm 0.01$, $S_2 = 0.09 \pm 0.01$ 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 (Fig. 4b, $S_1 = 0.058 \pm 0.004$ and $S_1 = 0.049 \pm 0.007$ 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).

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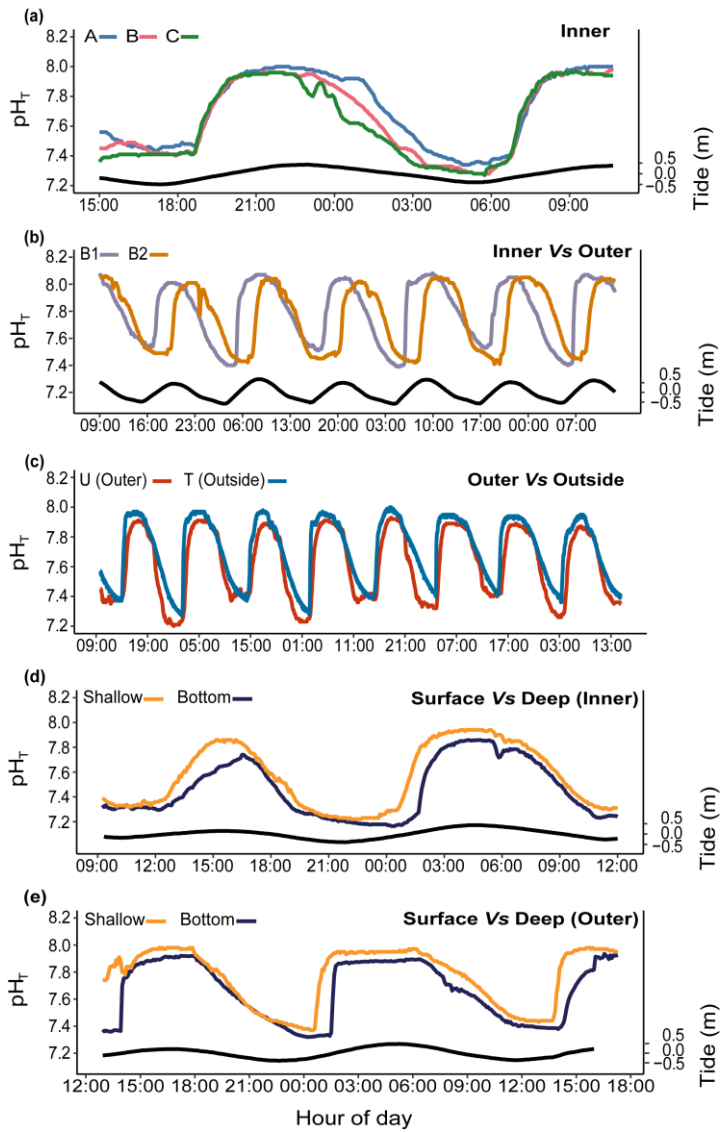
Figure 5. Spatial and depth-related short-term changes (24 h) in pH_T at stations in the Bouraké lagoon (see Figure 1 for the stations' location). Spatial variations were assessed: **(a)** within the inner reef (St A-C); **(b)** between the inner and the outer reefs (St B1, B2); **(c)** between the outer 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 inner reef (St R); and **(e)** at the outer reef (St S). Tide (black line) refers to St B2.

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402   *Dissolved oxygen (DO).* DO was measured during 36, 79, 34 and 42 semidiurnal tidal cycles at R1, R2, B1 and B2,

403 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

404 mean diel DO was higher at the reference reefs than in the Bouraké lagoon. During the studied period, mMean DO values

405 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,

406 respectively.

407 At stations B1 and B2, DO was strongly correlated with the tidal cycle (Fig. 4c, 82 and 72 % of the total DO variance were

408 explained by the tidal harmonic analysis, respectively), and only marginally with the 24-hour cycle (Fig. 4d). DO oscillations

409 were mainly semidiurnal ($M_2 = 1.17 \pm 0.08$ mg L^{-1}, and $M_2 = 0.83 \pm 0.09$ mg L^{-1} for B1 and B2, respectively) with a substantial

410 diurnal component ($S_1 = 1.12 \pm 0.04$ mg L^{-1}, and $S_1 = 0.681 \pm 0.04$ mg L^{-1} for B1 and B2, respectively). During a semidiurnal

411 tidal cycle, DO was lower at low tide (Fig. 4c, 3.7 mg L^{-1} and 4.6 mg L^{-1} at B1 and B2, respectively) and higher at high tide

412 (Fig. 4c, 6.0 mg L^{-1} and 6.1 mg L^{-1} at B1 and B2, respectively). The minimum (1.89 mg L^{-1}), and the maximum (7.24 mg L^{-1}

413) DO value were both measured at B1 during low and high tide, respectively (data not shown). During a 24-hours cycle, DO

414 was lower in the early morning (Fig. 4d, 4.0 and 4.3 mg L^{-1} at B1 and B2, respectively) and higher in the middle of the day

415 (Fig. 4d, 5.8 and 5.45 mg L^{-1} at B1 and B2, respectively). In a single day, we recorded DO fluctuations of up to 6.37 mg L^{-1}

416 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

417 value, 7.24 mg L^{-1}, was measured at B1during high tide (data not shown). At stations R1 and R2, DO was mainly diurnal

418 ($S_1 = 1.34 \pm 0.06$ mg L^{-1} and $S_1 = 1.53 \pm 0.09$ mg L^{-1} for R1 and R2, respectively) with lower values during the night (Fig. 4d,

419 5.5 mg L^{-1} at both stations), and higher values in the middle of the day (Fig. 4d, 7.8 mg L^{-1}, both stations). Simultaneous short-

420 term DO measurements (Fig. 6; Table 1) did not show significant differences over a 24-hours cycle at the inner (St A-G;

421 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

422 change on a vertical gradient at stations R and I, but the bottom DO was significantly lower at station N.

423
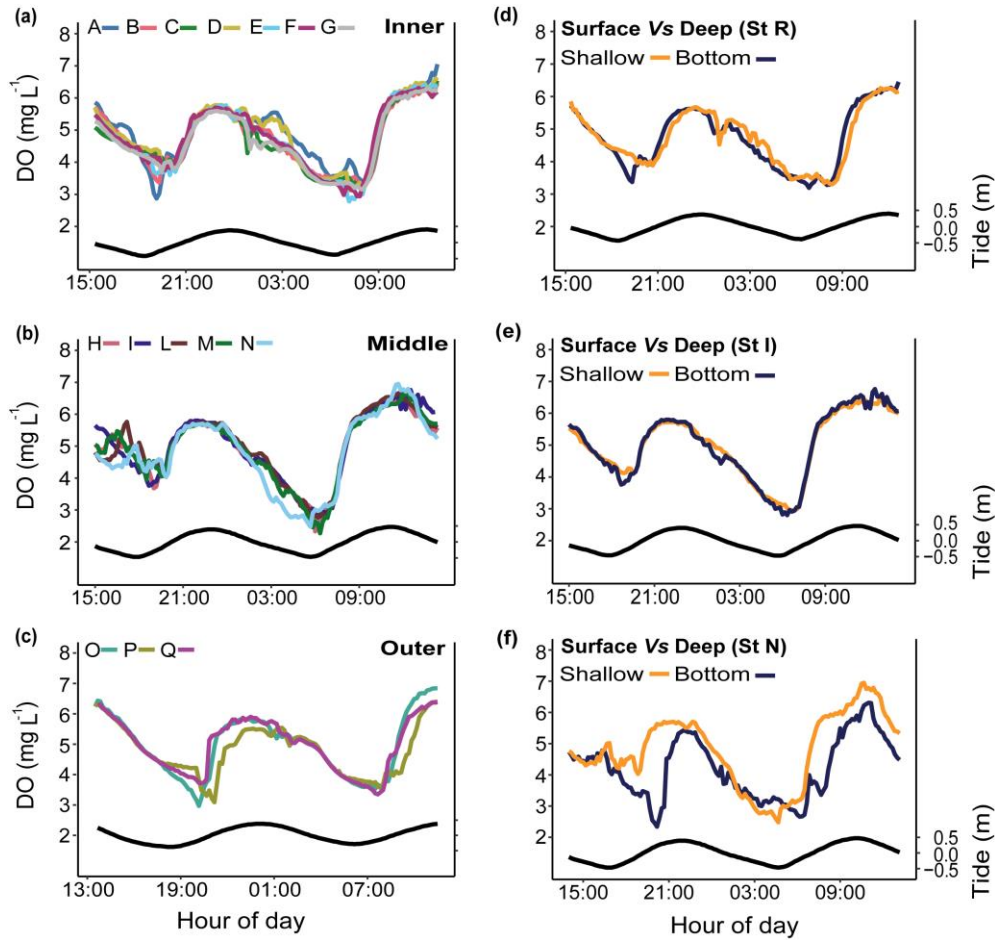
Figure 6. Spatial and depth-related short-term measurements (24 h) ~~in~~ of dissolved oxygen (DO) at stations in the Bouraké
lagoon (see Figure 1 for the location of the stations). Spatial variations were assessed on **(a)** the inner reef (St A-G), **(b)** the
middle reef (St H-N), and **(c)** the 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.

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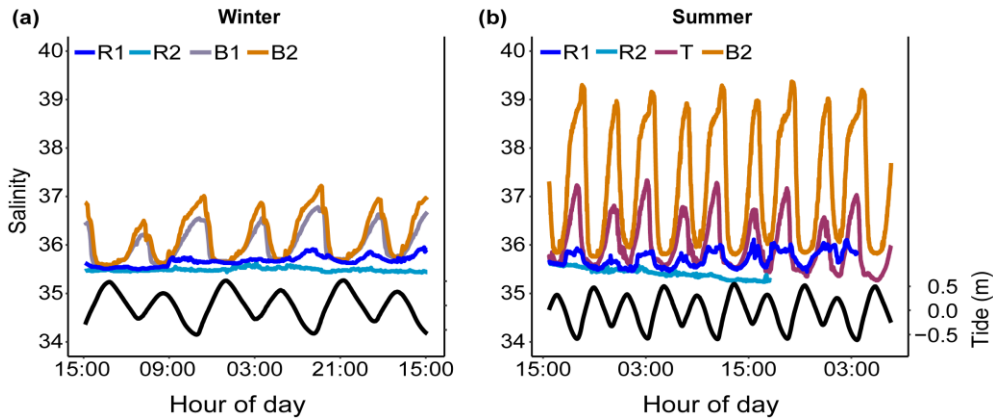
433   *Salinity (S)*. Salinity was measured only during two short-term periods in winter 2019 and summer 2020 (Fig. 7).

434

435   **Figure 7.** Short-term salinity monitoring during **(a)** the winter of 2019 (from 15/07/2019 to 18/07/2019) at the reference (St
436   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
437   R1 and R2) and Bouraké reefs (St T and B2). Tide (black line) refers to St B2.

438   ~~Its~~ Salinity variations in the Bouraké lagoon ~~was~~ were strongly correlated with the tidal cycle, and the highest mean values
439   were measured during both winter and summer. Salinity was lower at reference reefs during both the winter and summer
440   seasons (Fig. 7a-b). 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
441   B1, and 36.17 ± 0.47 at B2 with significant differences between stations (Tables 1). Salinity in the Bouraké lagoon peaked at
442   37.22 at B2 during low tide, while it was 35.65 at R1. During the summer of 2020, the mean salinity increased significantly
443   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
444   ~~at~~ R2 with 35.71 ± 0.16. ~~In the~~During summer ~~of~~ 2020, we also measured short-term variations in salinity at station T, which
445   is outside the Bouraké system. Although its distance from the ~~entrance of the lagoon~~lagoon entrance, the water mass
446   discharged during falling tide increased seawater salinity also at this station where we measured a maximum value of 37.33
447   during low tide.

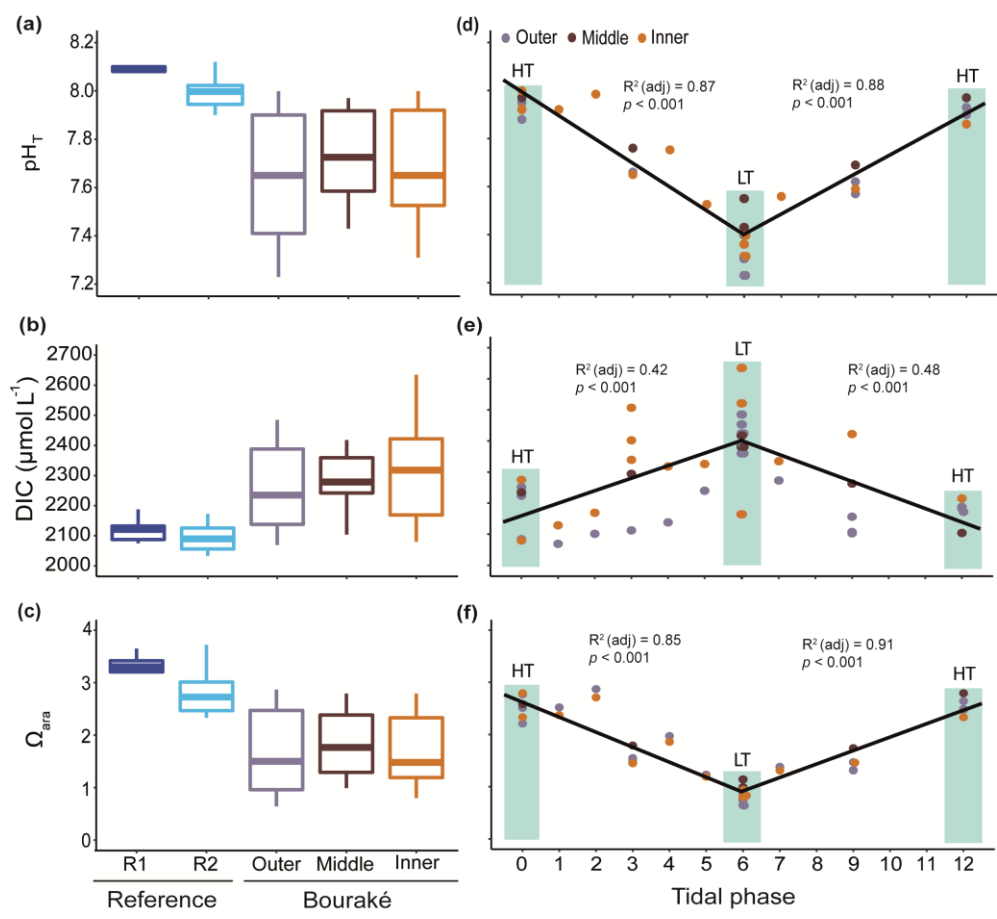
448   **3.2 Diel cycles of carbonate chemistry and chemical parameters**
449   We monitored diel cycles in June 2017 and July 2019 at two reference reefs and three reefs within the semi-enclosed lagoon
450   of Bouraké (i.e., the outer, the middle and the inner reefs). The seawater carbonate chemistry differed significantly between
451   the reference and the Bouraké lagoon reefs (Fig. 8a-c; Supplementary Fig. S1; Tables 1, 2).

452
453 **Figure 8.** Seawater carbonate chemistry measured (pH$_T$) and calculated (DIC and Ω_{ara}) during diel cycles in 2017 and 2019
454 (pooled data, see also Supplementary Figure S1) at R1, R2 and the Bouraké reefs (outer, middle and inner) **(a-c)**. Boxes (n =
455 6-14) represent the interquartile range (25th and 75th percentile); the horizontal line is the median, and the whiskers represent
456 the data range (i.e., minimum and maximum). Changes are illustrated across a 12-hour tidal phase in the Bouraké lagoon **(d-**
457 **f)**. Linear regression lines are plotted for each falling (HT to LT) and rising tide (LT to HT). Shaded boxes have only a
458 graphical significance and only suggest the tide changes during measurements.

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Table 2. Summary of the seawater physical and chemical data (mean ± SD) measured in July 2017 and June 2019 and calculated using the CO_2SYS package. Data were pooled and averaged per station. nd = not determined. Reference reefs: St R1 and R2; Bouraké lagoon stations: outer, middle and inner.

	R1	R2	Outer	Middle	Inner
Measured					
Temp (°C)	22.54 ± 0.31	22.69 ± 1.50	23.57 ± 1.31	24.05 ± 1.20	23.00 ± 1.46
pH_T	8.09 ± 0.01	8.02 ± 0.07	7.66 ± 0.25	7.73 ± 0.22	7.68 ± 0.24
DO (mg L^{-1})	7.20 ± 0.64	6.91 ± 1.01	6.11 ± 0.68	nd	5.98 ± 0.67
A_T (µmol kg^{-1})	2294.1 ± 0.3	2261.2 ± 0.04	2357.8 ± 0.1	2256.3 ± 0.06	2393.7 ± 0.08
$Si(OH)_4$ (µmol L^{-1})	0.71 ± 0.42	2.86 ± 1.41	8.22 ± 3.14	8.88 ± 2.72	11.93 ± 4.27
No_x (µmol L^{-1})	0.21 ± 0.05	0.51 ± 0.16	0.65 ± 0.20	0.54 ± 0.09	0.54 ± 0.12
PO_4^{3-} (µmol L^{-1})	0.63 ± 0.08	0.19 ± 0.05	0.26 ± 0.13	0.19 ± 0.01	0.42 ± 0.23
NH_4^+ (µmol L^{-1})	0.08 ± 0.06	0.23 ± 0.09	0.27 ± 0.12	0.34 ± 0.12	0.23 ± 0.14
DOC (µmol L^{-1})	nd	81.15 ± 5.49	96.89 ± 10.78	95.70 ± 8.38	112.82 ± 14.41
DIC (µmol L^{-1})	2117.7 ± 39.4	2092.4 ± 42.9	2251.1 ± 132.2	2282.5 ± 112.0	2315.1 ± 168.1
POC (µmol L^{-1})	9.28 ± 1.47	11.15 ± 1.97	24.07 ± 5.31	29.37 ± 7.03	38.11 ± 10.43
PON (µmol L^{-1})	1.24 ± 0.46	1.21 ± 0.22	1.64 ± 0.22	1.98 ± 0.35	2.43 ± 0.52
Calculated					
pCO_2 (µatm)	353.42 ± 7.24	467.76 ± 112.03	1402.92 ± 896.42	1047.06 ± 599.07	1318.95 ± 819.79
CO_3^{2-} (µmol kg^{-1})	211.92 ± 9.79	176.80 ± 30.05	105.84 ± 46.46	115.57± 46.18	109.02 ± 45.59
$\Omega_{aragonite}$	3.35 ± 0.16	2.80 ± 0.49	1.68 ± 0.73	1.84 ± 0.73	1.72 ± 0.71
TOC (µmol L^{-1})	nd	93.22 ± 6.18	121.63 ± 14.07	125.07 ± 13.32	144.72 ± 17.5
DIN (µmol L^{-1})	0.29 ± 0.07	0.74 ± 0.24	0.85 ± 0.33	0.88 ± 0.12	0.77 ± 0.24
DIC:DIN	7371.9 ± 1940.8	3132.9 ± 999.1	4068.5 ± 4621.8	2625.3 ± 318.8	3276.9 ± 1031.0
POC:PON	8.10 ± 2.41	9.26 ± 1.07	14.64 ± 2.04	14.70 ± 1.42	15.55 ± 1.33
POC:DOC	nd	0.15 ± 0.02	0.26 ± 0.06	0.31 ± 0.06	0.28 ± 0.05
DOC:TOC	nd	0.87 ± 0.01	0.80 ± 0.03	0.77 ± 0.02	0.78 ± 0.03
$Si(OH)_4$:DIN	2.43 ± 1.31	4.14 ± 2.18	12.17 ± 8.99	9.90 ± 2.10	16.34 ± 6.38
DIN:DIP	0.47 ± 0.12	4.22 ± 1.28	nd	4.65 ± 0.52	2.78 ± 1.21
$Si(OH)_4$:DIP	1.11 ± 0.63	15.11 ± 6.36	37.01 ± 17.16	46.79 ± 14.23	37.51 ± 24.46

The reference reefs R1 and R2 had higher pH, CO_3^{2-} and Ω_{ara}, and ~~consequently,~~ lower DIC and pCO_2 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 $pCO_2 > 2,000$ µatm and levels of $\Omega_{ara} < 1$. 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 CO_3^{2-} reached the lowest value of 50.10 µmol kg^{-1} during low tide on the inner reef with an average of 109.02 ± 45.59 µmol kg^{-1}.

Most of the chemical parameters were, in general, more concentrated (up to 5-times) in the Bouraké lagoon than ~~on~~ at the reference reefs R1 and R2, and increased from the outer to the inner reef (Fig. 9a-d; Supplementary Fig. S2; Tables 1, 2).

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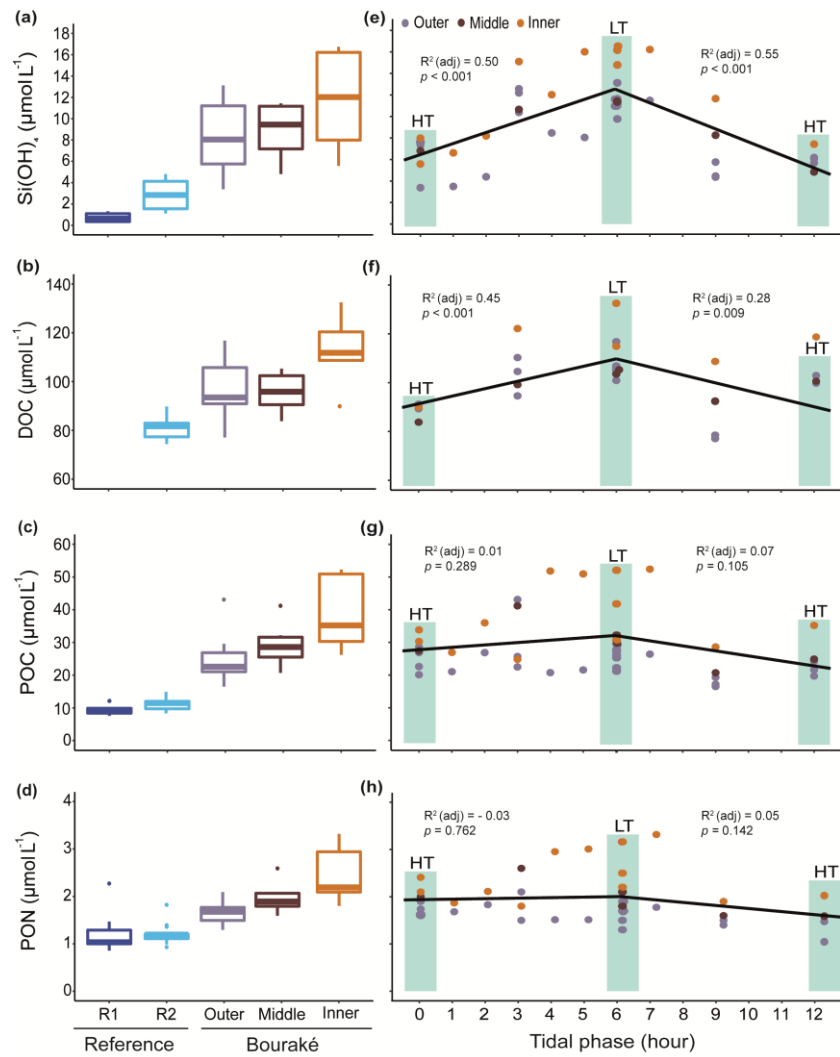
504

505 **Figure 9.** Orthosilicic acid, organic carbon and nitrogen parameters measured during diel cycles in 2017 and 2019 (pooled

506 data, see also Supplementary Figure S2) at R1, R2 and the Bouraké reefs (outer, middle and inner) **(a-d)**. Boxes (n = 6-14)

507 represent the interquartile range (25th and 75th percentile); the horizontal line is the median, and the whiskers represent the

508 data range (i.e., minimum and maximum). Changes are illustrated across a 12-h tidal phase in Bouraké **(e-h)**. Linear regression

509 lines are plotted for each falling (HT to LT) and rising tide (LT to HT). Shaded boxes have only a graphical significance and

510 only suggest the tide changes during measurements.

511   In addition, despite the Bouraké lagoon receives new seawater during the rising tide, only $Si(OH)_4$ had a decent regression

512   coefficient showing either positive and negative correlation with the falling and the rising tide (Fig. 9e-h; Supplementary Fig.

513   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

514   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 $8.22 \pm$

515   3.14 μmol L^{-1}, 3- to 6-time higher than at the reference stations R2 and R1. The lack of a clear effect of the tide for the other

516   chemicals causes their accumulation inside the lagoon system. Ratios of organic and inorganic carbon, nitrogen, and nutrients

517   showed significant differences between the Bouraké lagoon and the reference reefs (Tables 1, 2) with higher average

518   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

519   Bouraké lagoon compared to reference reefs.

520   **3.3 Benthic community distribution and species identification**

521   *Benthic community distribution.* The cluster analysis and nMDS allowed grouping the 24 transects in the Bouraké lagoon in

522   six clusters corresponding to habitat descriptors, namely clusters A, B1, B2, C1, C2, and C3 (Fig. 10a; see Supplementary

523   Fig. S3 for details of the community descriptors, and Table S4 for transect averaged data). The nMDS produced an exhaustive

524   representation of the Bouraké lagoon benthic communities and abiotic features (2-dimensional stress = 0.136) confirmed by

525   ANOSIM (Global R = 0.948, p = 0.001). For the benthic community distribution, a clear separation (95% of confidence

526   interval represented by the ellipse in Fig. 10a) was found for cluster A and B2, including most of the transects located on the

527   middle and inner reefs (Fig. 10b).

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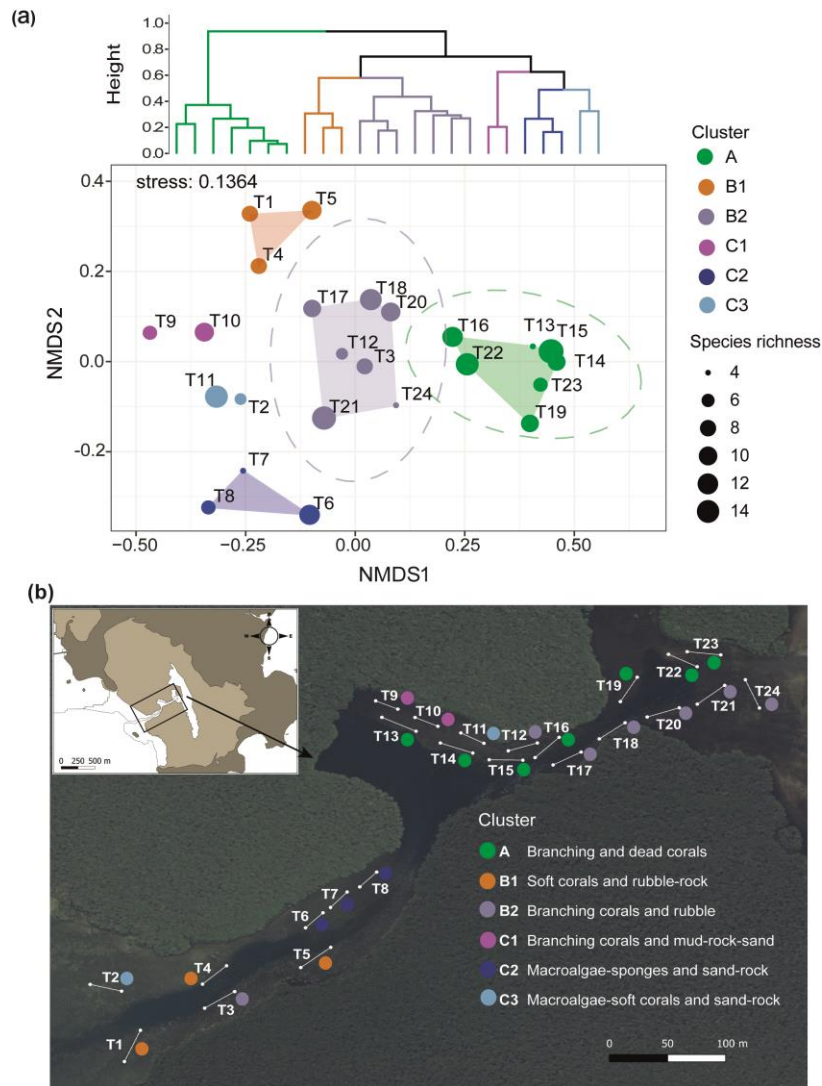
528
529 **Figure 10.** Benthic community and bottom substrate characterization in the Bouraké lagoon. Hierarchical Ward's method
530 cluster dendrogram (top) and non-metric multidimensional scaling (nMDS) of abiotic and biotic percent cover and species
531 richness per transect (T1-T24) **(a)**. Colored circles represent clusters of transects identified in the dendrogram; circle size
532 corresponds to species richness. Ellipses represent 95% confidence intervals. Dominant biotic and abiotic descriptors were
533 used to describe the benthic community and bottom substrate for each cluster in **(b)**. The satellite image is from georep New
534 Caledonia database (https://georep.nc/), and the QGis software was used for transect georeferencing.

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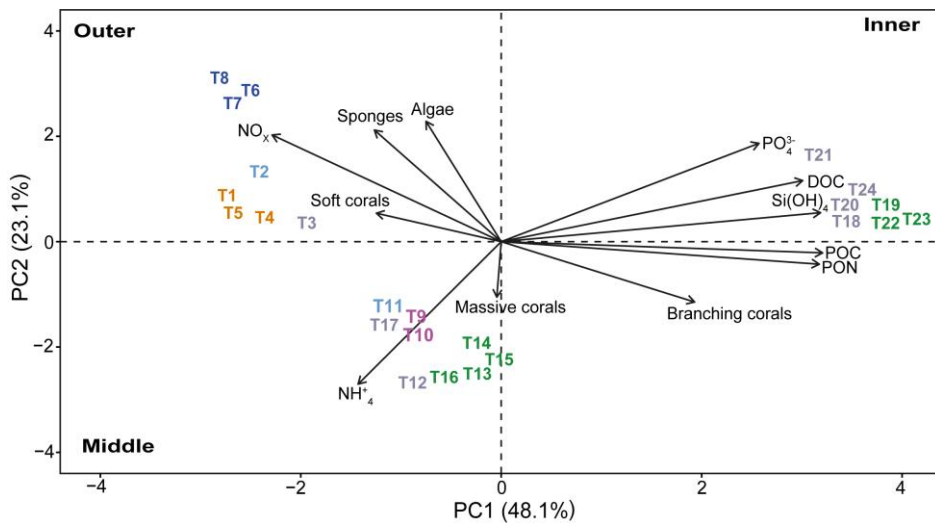
535 For both, branching corals were the dominant biotic descriptor with 81 % and 31 % cover~~age~~, respectively~~)~~ (Supplementary
536 Fig. S3), with a maximum of 96 % in cluster A (T23, Supplementary Table S4). Among branching corals, the two most
537 abundant genera were *Acropora* and *Montipora* (data not shown). For the abiotic features of the substrate, dead corals and
538 rubbles characterized transects in clusters A and B2, respectively. Species richness (Fig. 10a) was high in all transects of the
539 Bouraké lagoon, except T13 and T24, both found at the middle and inner reefs' limits. The abiotic substrate of cluster C1 was
540 characterized by 66 % mud, 12 % rocks and 10 % sand (see Supplementary Table S4 for detailed cover data per transect).
541 Only a few branching corals (<10 %) were found, but species richness was relatively high (6 at T9 and 10 at T10). Cluster C2
542 was distinct, which is not surprising due to its location in a relatively shallow convergence zone that divides the lagoon into
543 two parts. There, the substrate is made of coarse sand (13 %) and rocks (12 %) and is mainly colonized by macroalgae and
544 sponges (31 % and 32 %, respectively). Species richness in the area was heterogeneous and ranged from 4 to 12. *Dictyota*
545 spp. and *Halimeda discoidea* were the main macroalgal species, while *Rhabdastrella globostellata* was the dominant sponge
546 species in the area. Cluster B1, located on the outer reef, is characterized by an abundance of soft corals (48 %) and rubbles
547 (21 %), and high biological richness (Fig. 10a). Cluster C3 is characterized by coarse sand (49 %), rocks (17 %) and a few
548 benthic organisms such as macroalgae (10 %) and soft corals (8 %).
549   Principal component analysis (PCA) reduced the multicollinearity problem and the first two Principal Components
550 accounted for a cumulative 71.2 % of the dataset variance. In particular. The PCA plot (Fig. 11) allowed us to assign the
551 transects to three distinct groups depending on their position in the study area.

552
553 **Figure 11.** Principal component analysis (PCA) between benthic community (macroalgae, sponges, corals, branching corals
554 and massive corals) data and environmental parameters (PON, POC, DOC, Si(OH)$_4$, PO$_4^{3-}$, NOx, and NH$_4^+$) measured for
555 each transect (n = 24). The length of the vectors indicates the contribution of each parameter. The first dimension explains
556 48.1 % of the variance, and the second dimension explains 23.1 % of the variance. ~~Red dots indicate the transects.~~ Colors
557 refer to the cluster subdivision (Fig. 10).

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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. However, t~~T~~hese two reef groups ~~, however,~~ differ in their major correlation to NH_4^+ for middle reef sites and POC, DOC, $Si(OH)_4$, and PO_4^{3-} 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~~ In 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~~s~~ (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.

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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 that are 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 and extreme, ~~climate change like~~ conditions (Kurihara et al., 2021). When using these natural laboratories to predict species responses to future environmental conditions, it is essential to ~~assess~~ take a multi-scale approach that incorporates the spatial and temporal variability of the key physical and chemical parameters characterizing the study site (e.g., Vizzini et al., 2013; Camp et al., 2018; Aiuppa et al., 2021). ~~In this study~~Here, we mapped the spatial and temporal variability of the~~se~~ physical and ~~-~~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 1~~7.5~~7 — 33.8~~3~~ °C), deoxygenated (ranging from 1.87~~--~~-7.24 mg L^{-1}), and acid (ranging from 7.23~~--~~-7.92 pH$_T$ units) when compared to neighboring reefs. Besides, we found that salinity was significantly higher than at the reference reefs ~~in~~ during 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, both in the absolute range, and in the variability of the measured environmental parameters.

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~~resulting in an annual temperature range of 17.5-33.8 °C. W~~If we~~ compare~~d~~ temperature~~s~~ recorded at Bouraké lagoon to those of 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)~~.~~, W~~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

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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~~ large fluctuations in the main environmental parameters, toward sub-optimal values. ~~and S~~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. According to the organisms tolerance to DO fluctuation, which is quite unknown in corals, low DO concentrations can change fish tidal migration in the mangrove (Dubuc et al., 2019). 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 finding 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~~linked to ~~the~~ its unique topographical and geomorphological characteristics~~, of this unique site,~~ the resulting water circulation and the direction of the tide. New water from the lagoon enters through the channel at each rising tide and flows into the semi-enclosed lagoon towards the large mangrove area behind it. This water ~~originally~~initially had ambient values of pH, temperature and dissolved oxygen, but, during the trip, it mixes with the acidic, warm and deoxygenated water in the system and the mangrove area, therefore gradually changing from its original values. ~~At~~Inside the mangrove ~~area~~forest, we hypothesize that the water chemistry further changes due to the metabolic reactions in the sediments, ~~coral reefs~~ and mangrove roots (e.g., (Alongi et al., 2004); (Bouillon et al., 2007); (Gleeson et al., 2013); (Call et al., 2015)). 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 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 t~~he species living in this area have likely developed specific mechanisms to withstand the very fluctuating environmental conditions, and as such, they warrant further attention.

~~It could be argued that because~~Since the fluctuations are linked to tidal phases, it could be argued that 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 (e.g., (Rivest et al., 2017). 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~~ as the low tide is delayed by 1.5 h compared to the reference reef (Fig. 2).

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651 Preliminary results from a hydrodynamic model of the study site ~~also~~ suggest that tide-associated water mass movements are

652 spatially heterogeneous and likely to play an essential role in shaping coral resilience to extreme conditions (see discussion

653 below). Indeed, one can imagine a single water mass moving with the same physical characteristics from the mangrove area

654 towards the outer reefs or in the opposite direction depending on the tide. However, the complex geomorphology of the

655 Bouraké lagoon, its bottom topography and the complex web of coral reefs and ~~of~~ mangrove trees on the edges deviate and

656 probably change the seawater physical and chemical properties. We measured significant spatial differences in pH within

657 each reef area (inner, middle and outer reefs; Fig. 5a, b), as well as throughout the water column (i.e., between the surface

658 and the bottom; Fig. 5d,e). In general, bottom seawater was 0.1-0.2 pH_T units lower than the surface, probably due to a

659 pumping mechanism by the water mass of more acidic pore water from the sediments. The pH also differed spatially within

660 the inner reef, by up to 0.3 pH_T units (for instance St. A *vs* St. C; Fig. 5a), perhaps due to the influence of stagnant water on

661 the mangrove edges ~~of the mangrove~~ or a more intense metabolic activity by the local benthic community. Dissolved oxygen

662 concentrations between the surface and the bottom were only significantly different ~~on~~ at St. N on the middle reef (Fig. 6f).~~,~~

663 ~~and only at St. N~~ This station ~~which~~ is mainly characterized by mud as the current ~~there~~ is lower than anywhere else in the

664 Bouraké lagoon. Here, the sediment's biological activity possibly traps the oxygen making it less available to the water

665 column.

666 We can assume that, throughout the Bouraké lagoon, organisms are exposed to extreme and fluctuating suboptimal physical

667 parameters, such as pH, and DO which are more pronounced on the bottom and last longer, and with more extreme values,

668 on the inner reefs. It is also true for~~-~~ some of the seawater ~~chemistry~~ chemical parameters we measured, which~~with~~ show

669 higher concentrations in the Bouraké lagoon than on the reference reefs (see Table 2). For instance, we found that orthosilicic

670 acid, phosphate, dissolved and particulate organic carbon, and particulate organic nitrogen were 1.4 to 4.2-fold more

671 concentrated on the inner reef than at station R2. Within the Bouraké lagoon in general, chemicals increased from the outer

672 to the inner reef, and ~~with the exception of~~ except for $[NO_x]$, $[NH_4]^+$, $[PO_4]^{3-}$, they never return to "normal" values despite the

673 Bouraké system receives new seawater during the rising tide. The high concentrations in orthosilicic acid and organic

674 compounds, both dissolved and particulate are due to the combined effect of more acidic and organic-rich water coming out

675 of the mangrove forest during a falling tide (Fig. 9) and the ~~particular~~ system's particular morphology, ~~of the system which~~

676 limiting the ~~full~~ complete renewal of the seawater~~ renew~~, especially at the inner reefs.

677 **4.2 Effects of physical and chemical conditions on species distribution**

678 Extreme environmental conditions, such as those measured in the Bouraké lagoon, are known to strongly affect the

679 metabolism, growth and even survival of several marine organisms, particularly those ~~that~~ tolerating only a narrow range of

680 environmental changes ~~are commonly considered stenotopic like~~ such as scleractinian corals (e.g., Coles and Jokiel, 1977;

681 Hoegh-Guldberg and Smith, 1989; Hoegh-Guldberg, 1999; Fitt et al., 2001). For instance, *in situ* studies at volcanic CO_2

682 seeps have shown that chronic exposure to ocean acidification (near-future pCO_2 levels) can cause a reduction in coral

683 diversity and lower the~~, lower~~ recruitment and abundances of structurally complex hermatypic corals. Moreover, shifts in

684 competitive interactions between taxa and a decrease in cover and richness of soft corals and sponges were also observed

685 (e.g., Fabricius et al., 2011; ~~(~~Enochs et al., 2015~~;)~~ Sunday et al., 2017; Agostini et al., 2018~~; Teixidó et al., 2018~~). However,

686 the Bouraké lagoon features high coral, sponge, macroalgae and CCA cover and species richness, adding at the check-list

687 proposed by Camp et al.~~,~~ (2017) an additional 46 coral species (totaling 66 species and 33 genera), 28~~3~~ species of macroalgae

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688 and 11 species of sponges (Supplementary Table S5). Such a high number of species has never been reported for mangrove

689 systems characterized by marginal conditions, at least ~~with regard to~~concerning the three major benthic groups taxa

690 investigated here (e.g., Yates et al., 2014; Camp et al., 2019). In general, given the extensive literature demonstrating the

691 negative effects of suboptimal abiotic conditions on corals, our findings are unexpected and suggest that corals in the Bouraké

692 lagoon may have developed unique survival and adaptive mechanisms. Some studies have reported similar findings, but none

693 has ever reported such ~~a~~ high coral species diversity (e.g., Yates et al., 2014; Schoepf et al., 2015; Shamberger et al., 2018;

694 Camp et al., 2019). For instance, in Palau (Micronesia), the highest coral cover (> 60%) and species diversity (21 scleractinian

695 genera) were found at the lowest pH study site of the Nikko Bay station (Barkley et al., 2015). Studies in the Virgin Islands'

696 mangrove system have reported over 30 coral species growing in marginal conditions (Yates et al., 2014; Rogers, 2017).

697 Similarly, in a recent study of two Australian mangrove lagoons, ~~both~~ characterized by relatively extreme environmental

698 conditions (low pH, low oxygen and high temperature), Camp et al., (2019) identified 12 and 29 scleractinian coral species

699 in the Woody Isles and at Howick Island, respectively. Among the 66 species we identified, ~~a total of~~ 29 of the most abundant

700 coral species in New Caledonia ~~are shared between~~were found at both the reference reef and in the Bouraké lagoon, indicating

701 that species living at our study site are not very different ~~than on~~from a typical bay-sheltered fringing reef. There is not an

702 apparent selection in the coral form~~,~~ since massive (e.g., *Porites* spp.), corymbose (e.g., *Pocillopora digitata*), phaceloid

703 (*Galaxea fascicularis*) and branching (*Acropora* spp.) species are equally abundant, as well as in their thermal and pH

704 tolerance. Further experiments are underway at both the molecular and phenotypic level to better understand the mechanisms

705 of resilience used by the corals from Bouraké.

706 Remarkably, the two coral species, currently considered New Caledonia endemics, thrive in the innermost benthic

707 assemblages of the Bouraké lagoon, making it not only a unique natural laboratory ~~but also~~as well as a potential conservation

708 priority site ~~in light of its overall uniqueness characterized in this study~~. In the Bouraké lagoon, benthos species richness was

709 very high throughout the system and the distribution of branching and massive corals was spatially heterogeneous (Fig. 10b;

710 Supplementary Fig. S3). Coral cover decreased near the mangrove, where the accumulation of fine sediments and exposure

711 to air during low tide do not allow corals' survival~~, but the percent cover reached up to 90 % on the reef margin~~ (Supplementary

712 Fig. S3). Branching corals were particularly abundant on the inner and middle reefs, with the highest cover of 96 % in the

713 inner reef (T23, Supplementary Table S4). They became sparse on the outer reef, even absent at the system's entrance where

714 soft and massive corals dominated. Macroalgae and sponges, including CCA (data not shown), were quite cryptic throughout

715 the Bouraké lagoon~~,~~ but found almost everywhere ~~both~~ in the coral matrix and buried in the sediment. They are particularly

716 abundant ~~only~~ in a shallow area that divides the lagoon into two parts (transects T6-T8). There, a Venturi effect generates a

717 strong current, and the substrate ~~is made~~consists of coarse sand and rocks. ~~T~~Both ~~t~~he high flow and the bottom characteristics

718 are both likely to promote macroalgae and sponge occurrences (averaged 30 % and 32 % cover, respectively). The~~re, the~~

719 sponge *Rhabdastrella globostellata* is particularly abundant (up to 40 % cover) and form~~s~~ massive banks embedding adjacent

720 coral colonies. In general, macroalgae and sponges diversity wa~~s~~is not particularly rich, with ~~respectively~~ only 28 and 11

721 species ~~have been detected~~, respectively, likely due to the sampling method. However, ~~sponge diversity,~~ in the Indo-pacific

722 mangrove systems, sponge diversity is, in general, not extremely high, especially if compared to the Caribbean (Nagelkerken

723 et al., 2008). Few studies are available from Indo-Pacific mangrove sponges. ~~T~~and ~~t~~he highest diversity was reported in a

724 study in the mangrove of Banka Island (North Sulawesi, Indonesia), where 19 species ~~of sponges~~ were found (Calcinai et al.,

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725 2017). Our findings on mangrove sponges in such a unique mangrove area in New Caledonia ~~improve~~ add to the limited
726 knowledge ~~on the~~of sponge species diversity in Pacific mangrove systems.
727 Water flow may play a critical role in the response of organisms to acidification (Cornwall et al., 2014; Hurd, 2015; Comeau
728 et al., 2019), warming (Schoepf et al., 2018) and deoxygenation (Hughes et al., 2020). It has been reported to affect the
729 diffusion boundary layer (i.e., a thin layer of stagnant water located around aquatic organisms) of corals, CCA and other
730 calcareous macroalgae, altering their ability to calcify at low pH and to excrete metabolic wastes (reviewed in Nelson and
731 Altieri, 2019). Knowing that flow speed could play a ~~key~~ critical role ~~which~~ and that deserves further investigations and
732 measurements at the study site, we found two hypotheses to explain the high diversity of the Bouraké species and their
733 resilience to suboptimal parameters: i) the species may benefit from the constant fluctuations of the ~~physico-chemical~~physical
734 and chemical parameters, ii) the species may benefit from heterotrophic inputs of the mangrove (in term of nutrients and
735 organic matter).
736 ~~With regards to~~Regarding environmental fluctuations, we measured averaged daily variations in temperature, DO, and pH of
737 about 3.79 °C, 3.80 mg L^{-1}, and 0.63 pH$_T$ units, respectively. The t~~T~~emperature ~~changed of~~fluctuated by up to 6.55 °C ~~on~~ in
738 a single day. Frequent exposure to stressful temperatures can induce acclimatization or adaptation in corals if the period of
739 exposure is short enough to avoid mortality (Oliver and Palumbi, 2011; Palumbi et al., 2014; Schoepf et al., 2015; Rivest et
740 al., 2017; Safaie et al., 2018). For example, in the Kimberly region (Australia), corals regularly exposed to temperatures up
741 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~~
742 ~~corals~~ in more thermally stable environments (Dandan et al., 2015; Schoepf et al., 2015; 2020). However, ~~although~~ they are
743 not immune to extreme heat stress event s (Le Nohaïc et al., 2017). Another example is the corals in the back reef and shallow
744 pools around the island of Ofu (American Samoa), which despite occasional daily fluctuations of up to 6 °C, and an average
745 daily temperature of 29 °C in summer (Piniak and Brown, 2009; Oliver and Palumbi, 2011) sustain reasonable levels of coral
746 cover (25–26 %) and high diversity (Craig et al., 2001). Some studies tend to indicate that corals depended on the *a priori*
747 'frontloading' of genes involved in heat resistance in the coral host and/or the host's ability to adjust its physiology during
748 short-term (weeks) environmental changes (Barshis et al., 2013; Palumbi et al., 2014). However, physiological adjustments
749 have an energetic cost that corals cannot sustain in the long term, affecting other metabolic functions such as calcification. It
750 could explain in part the lower calcification rates observed in some coral species, as seems to be the case for corals in the
751 Bouraké lagoon (e.g., Camp et al., 2017). There is also evidence that exposure to short-term oscillations in low pH, alone or
752 in combination with high temperature, can mitigate the impact of extreme environmental stressors on corals (Warner et al.,
753 1996; Oliver and Palumbi, 2011; Dufault et al., 2012; Schoepf et al., 2015; Safaie et al., 2018). Species in the Bouraké lagoon
754 appear to be thriving despite ~~With regard to~~ the large seawater pH variability (up to 0.6 pH$_T$ units). ~~variability, species in the~~
755 ~~Bouraké lagoon appear to be thriving.~~ In general, species exposed to pCO$_2$ fluctuations above 500 µatm in their natural
756 environment display enhanced plasticity to future ocean acidification scenarios (Vargas et al., 2017; Carstensen and Duarte,
757 2019). For example, fluctuations in pH could increase CCA tolerance to ocean acidification by providing respite periods at
758 ambient ~~low~~ pH (Rivest et al., 2017), during which organisms can calcify at a standard rate, compensating for decreased
759 calcification during periods of lower pH (Comeau et al., 2013; Cornwall et al., 2018). Diurnal variability in pH, typical of
760 more variable pH habitats, may confer tolerance to resident calcifying species via the selection of individuals better adapted
761 to survive in these environments (Rivest et al., 2017; Kapsenberg and Cyronak, 2019), although transgenerational
762 acclimatization is required (Cornwall et al., 2020).

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763 In addition to changes in temperature and pH, which are the two most commonly tested environmental parameters, oxygen

764 must also be considered. ~~Although~~ Despite the impact of reduced oxygen levels and its natural fluctuations on coral reefs ~~have~~

765 has yet to be established, ~~it appears that~~ low DO (2-4 mg L^{-1}) seems to increase~~s~~ the sensitivity of branching corals, resulting

766 in a decline in coral health, bleaching, and tissue loss (Haas et al., 2014; Hughes et al., 2020; Alderdice et al., 2021). ~~However,~~

767 ~~o~~Our study shows that although the Bouraké system can reach conditions close to hypoxia for several coral species (< 3 mg

768 L^{-1}; Fig. 4), ~~species~~ these latter seem to have promoted compensation mechanisms that allow them to survive in these

769 conditions. The natural laboratory of Bouraké, where DO fluctuates with the tide, in combination with other environmental

770 stressors, offers a perfect setting to test the practically unknown effects of deoxygenation ~~and hypoxia thresholds~~ in reef-

771 building corals exposed to acid and hot conditions (Nelson and Altieri, 2019; Hughes et al., 2020).

772 ~~A~~Although corals ~~seem~~appear to possess cellular mechanisms to counteract short-term osmotic changes (Mayfield and Gates,

773 2007), high and fluctuating salinity is possible additional stress that corals living in the Bouraké lagoon have to face daily,

774 adding up to the already long list of suboptimal environmental parameters. *In situ* studies have demonstrated that acute ~~acute,~~

775 ~~rapid~~and prolonged ~~changes~~decrease in salinity can ~~induce coral death (e.g.,~~(Jokiel et al., 1993). ~~Such death is attributed to~~

776 ~~the effects of salinity on the~~affect the coral photosynthe~~t~~sic~~s of zooxanthellae~~efficiency, resulting in a reduction of the amount

777 of energy transferred to corals (Muthiga and Szmant, 1987~~);~~ ~~(~~Manzello and Lirman, 2003)~~,~~ and induce coral death (e.g., Jokiel

778 et al., 1993). The response of corals to a change in salinity is related to the strength and duration of the hypo-hypersaline

779 exposure and the species tolerance~~considered~~. For example, *Stylophora pistillata* seems able to acclimate more effectively to

780 hypo- rather than to hyper-saline conditions (Ferrier-Pagès et al., 1999). Further experiments are needed to assess the effect

781 of high and fluctuating salinity on the ~~corals~~their physiology of corals in Bouraké~~.~~

782 Besides the hypothesis that environmental variability improves the metabolism of organisms, particularly their resilience to

783 extreme conditions, a series of other physical (e.g., current flow) and chemical parameters (e.g., organic matter) in the Bouraké

784 lagoon may work in combination to offset or enhance these effects. Mangrove habitats are highly productive ecosystems and

785 are sites of intense carbon processing, with a high potential impact on the global carbon budget (e.g., Borges et al., 2003;

786 Dittmar et al., 2006; Bouillon et al., 2014). In the Bouraké lagoon, benthic communities might have access to a range of

787 heterotrophic inputs, nutrients, carbon, and nitrogen sources. These sources can be metabolized by the species to increase

788 their energy budget and cope with the suboptimal parameters, but they can also become toxic~~,~~ if too concentrated~~,~~ or depleted,

789 leading to functional limitations. We measured ~~particularly~~exceptionally high concentrations of organic and inorganic carbon

790 and nitrogen, but also of some nutrients, notably silicates and phosphorus, and we confirmed the potential contribution of the

791 mangrove in those inputs, especially during the falling tide (Fig. 8 and 9; Supplementary Fig. S1 and S2; Table 2). We found

792 that dissolved organic carbon contributes significantly to the TOC pool (POC+DOC), with a~~n increasing~~ concentration

793 increase between the reference sites and the Bouraké lagoon, reaching maximum values on the inner reef. High organic matter

794 content can increase DOC availability to corals, providing the ~~with~~ sustainable energy to withstand extreme environmental

795 conditions (Levas et al., 2015). Some studies showed that the high organic matter of turbid reefs can support elevated coral

796 heterotrophy that can facilitate energy maintenance during periods of stress (Anthony and Fabricius, 2000).

797 We also found that nutrients could partially explain the distribution of organisms throughout the Bouraké lagoon (Fig. 11).

798 Indeed, NO$_x$ concentrations were higher on the outer reef, dominated by sponges, macroalgae and soft corals, while NH$_4^+$ was

799 high on the middle reef and POC, DOC, Si(OH)$_4$, and PO$_4^{3-}$ were higher on the inner reef. Both the middle and inner reefs are

800 characterized by the highest branching coral cover. Nitrates can accumulate inside the host cells, ~~which could be in favor~~

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ofpossibly favoring sponges and macroalgae, while ammonium is the preferred source used by coral symbionts (Raven et al., 1992). While it is not obvious to demonstrate experimentallyHowever, the nutrient negative or positive effect on corals' physiology is difficult to demonstrate experimentally (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 dependss on concentrations of of, and, 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 Justić et al. (1995) and is similar to the conditions observed in other New Caledonian mangroves (Jacquet et al., 2006). On the other hand, itNutrients limitation has been experimentally demonstrated that nutrient limitationto lowers the temperature effect at which coral bleaching occurs (Wiedenmann et al., 2013; Ezzat et al., 2016a; 2019), which is in contrastss with to the resilience of Bouraké coral's resilience to the warming of in the summer of 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 at 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 cautioncautiously, they suggest that the Bouraké lagoon seawater is not limited in phosphorus, a keyan essential nutrient in coral resilience to bleaching (Ezzat et al., 2016b; Rosset et al., 2017). Seawater in the Bouraké lagoon was not limited in Si (Si(OH)$_4$:DIP > 10 and Si(OH)$_4$:DIN >1; (Justić 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 one can be expected that orthosilicic acid would rise during the 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 communitythis complex and dynamic coral ecosystem. However, we our data already recognize demonstrate 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, to some extent, 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 certainly longer. With this in mind, we assume that, at least in the previous century, the situation is similar for environmental conditions remained unchanged, 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.; Tthey are common throughout New Caledonia as well as inand the SW Pacific region, suggesting that they have used specific strategies to cope with the suboptimal environmental conditions.

839 We are also unsure how the different parameters will fluctuate at bay-sheltered reefs over time and under future climate
840 change conditions and if the variability measured in the Bouraké lagoon is representative of the natural fluctuations expected
841 for coastal habitats in the future. Indeed, earth system model simulations, which are ~~mostly~~ mainly based on open-ocean
842 system models, project that the seasonal amplitude ~~for~~ of pH and pCO$_2$ ~~in the future climate~~ will increase by 81 % in the
843 future climate (Kwiatkowski and Orr, 2018). Projections also indicate that ~~and~~ ocean acidity extremes will be more frequent
844 (Burger et al., 2020), which could mean that future diel pH variability will increase even more at sites with the most significant
845 variability today. The situation could be similar for seawater temperature, a parameter that is already high in Bouraké, and
846 likely close to the coral's thermal tolerance threshold. If this were to happen in the following decades, the ~~is the case,~~ coral
847 reef ~~in~~ of Bouraké ~~will~~ would face ~~in the next decades~~ incredibl~~e~~y harsh environmental conditions since physical and
848 biogeochemical parameters measured ~~in~~ during this study already exceed future climatic simulations.
849

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5 Conclusion

We used a multi-scale approach to characterize the physical and chemical environmental parameters of one of the most ~~suitable~~ realistic natural ~~analogue~~ laboratory for ~~extreme~~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~~physical and 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 (i.e., pH, DO, temperature and salinity); 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' 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~~ in ~~future-like~~ extreme environmental conditions. Our study provides evidence that this is possible in existing natural habitat~~se~~, 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~~future extreme conditions. ~~However~~Finally, we ~~also~~ provide~~s~~ the compelling basis for using this site as a natural laboratory and ~~to better~~ study better 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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