# 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

Federica Maggioni[1], Mireille Pujo-Pay[2], Jérome Aucan[1], Carlo Cerrano[3], Barbara Calcinai[3], Claude E. Payri[1],

Francesca Benzoni[4], Yves Letourneur[1], Riccardo Rodolfo-Metalpa[1]

[1] UMR ENTROPIE (UR-IRD-IFREMER-CNRS-UNC), Centre IRD, BP A5, 98848 Nouméa cedex, New Caledonia

[2] LOMIC, Laboratoire d'Océanographie Microbienne, Laboratoire Arago Banyuls sur Mer, France

[3] Department of Life and Environmental Sciences (DiSVA), Polytechnic University of Marche, Ancona, Italy

[4] Red Sea Research Center, Division of Biological and Environmental Science and Engineering, King Abdullah University of Science and Technology, 23955-6900 Thuwal, Saudi Arabia

**Correspondence:** Federica Maggioni (federica.maggioni@ird.fr)

**Key words:** natural analogues, extreme environments, climate change, ocean acidification, deoxygenation, benthic communities, coral reefs

15   **Abstract.** According to current experimental evidence, coral reefs could disappear within the century if $CO_2$ emissions remain

16   unabated. However, recent discoveries of diverse and high cover reefs that already thrive under extreme conditions seem to

17   contradict these projections. Volcanic $CO_2$ vents, semi-enclosed lagoons and mangrove estuaries are unique study sites where

18   one or more ecologically relevant parameters for life in the oceans are close or even worse than currently projected for the

19   year 2100. These natural analogues of future conditions hold new hope for the future of coral reefs and provide unique natural

20   laboratories to explore how reef species could keep pace with climate change. To achieve this, it is essential to characterize

21   their environment as a whole, and accurately consider all possible environmental factors that may differ from what is expected

22   in the future and that may possibly alter the ecosystem response.

23   In this study, we focus on the semi-enclosed lagoon of Bouraké (New Caledonia, SW Pacific Ocean) where a healthy reef

24   ecosystem thrives in warm, acidified and deoxygenated water. We used a multi-scale approach to characterize the main

25   physical-chemical parameters and mapped the benthic community composition (i.e., corals, sponges, and macroalgae). The

26   data revealed that most physical and chemical parameters are regulated by the tide, strongly fluctuate 3 to 4 times a day, and

27   are entirely predictable. The seawater pH and dissolved oxygen decrease during falling tide and reach extreme low values at

28   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,

29   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.

30   Furthermore, the concentration of most of the chemical parameters was one- to 10-times higher at the Bouraké lagoon,

31   particularly for organic and inorganic carbon and nitrogen, but also for some nutrients, notably silicates. Surprisingly, despite

32   extreme environmental conditions and altered seawater chemical composition, our results reveal a diverse and high cover

33   community of macroalgae, sponges and corals accounting for 28, 11 and 66 species, respectively. Both environmental

34   variability and nutrient imbalance might contribute to their survival under such extreme environmental conditions. We

35   describe the natural dynamics of the Bouraké ecosystem and its relevance as a natural laboratory to investigate the benthic

36   organism's adaptive responses to multiple stressors like future climate change conditions.

## 1 Introduction

41  Atmospheric carbon dioxide ($CO_2$) has steadily increased over the industrial period (Gattuso et al., 2015), leading to ocean

42  warming, acidification and deoxygenation. Although the extent to which these stressors will affect marine life is still debated,

43  there is no doubt that their combination will negatively affect a range of marine organisms (e.g., Kroeker et al., 2011;

44  Wittmann and Pörtner, 2013; Hughes et al., 2018). Coral reefs are among the most productive and biodiverse marine

45  ecosystems on Earth, and their survival is expected to be compromised by climate change, whose impacts on reef structures

46  and associated communities span from biodiversity loss to ecosystem change shift (e.g., Fabricius et al., 2013; Sunday et al.,

47  2017; Agostini et al., 2018).

48  Marginal and extreme environments, where some species persist under sub-optimal environmental conditions, have become

49  a precious tool to investigate the potential resilience of marine organisms in the face of climate change (Camp et al., 2017,

50  2018). These sites may be used as natural analogues of future climatic conditions when at least one or more environmental

51  parameters naturally mimic climate change-like conditions over a large area of the ecosystem. They provide an opportunity

52  to simultaneously investigate changes in species responses and their ability to acclimatize and adapt to global environmental

53  changes (Soares, 2020; Kurihara et al., 2020). Shallow-water volcanic $CO_2$ seeps, low pH springs, semi-enclosed bays,

54  mangrove habitats, shallow sheltered-bay reefs, macrotidal environments, and low-pH upwelling areas are all potential study

55  systems where the surrounding seawater is subject to a localized or widespread increase in either $pCO_2$, or temperature, and

56  eventually a decrease in dissolved oxygen (Camp et al., 2018). At these sites, observations overall suggest ecosystem-level

57  consequences of life-long exposure to extreme conditions, such as reduced biological diversity, especially among calcifying

58  organisms, decreasing rates of coral calcification, and high rates of bioerosion (e.g., Hall-Spencer et al., 2008; Manzello et

59  al., 2008; Fabricius et al., 2011; Crook et al., 2013; Kroeker et al., 2011; Iglesias-Prieto et al., 2014; Milazzo et al., 2014;

60  Paytan et al., 2014). However, some natural analogues host quite rich reef communities. These have been documented in

61  Palau (Golbuu et al., 2016; Barkley et al., 2017; Shamberger et al., 2018), Papua New Guinea (Pichler et al., 2019), the

62  Kimberly region, Australia (Dandan et al., 2015; Schoepf et al., 2015), and in mangrove lagoons of New Caledonia (Camp et

63  al., 2017) and the US Virgin Islands (Yates et al., 2014).

64  These natural laboratories have become a common experimental asset in climate change research. However, it has been argued

65  that the lack of empirical characterization of the physical and biogeochemical conditions, including diurnal and seasonal

66  fluctuations, may bias the interpretation of the biological mechanisms that trigger the organismal responses. Using limited

67  environmental descriptors makes it difficult to unequivocally identify the main driver(s) of the biological response among the

68  primary factors (i.e., acidification, warming and/or deoxygenation), the potential secondary factors (e.g., pollution, water

69  flow, tide, seawater nutrients and organic content, turbidity, etc.), and their combination. For instance, at $CO_2$ seeps, pH

70  variability can unexpectedly go beyond projected future values (e.g., Hall-Spencer et al., 2008; Kerrison et al., 2011) and the

71  potential emission of toxic compounds, such as sulphur, arsenic, and metal trace elements (Vizzini et al., 2013) compromises

72  the attribution of specific responses to ocean acidification. Water temperature, pH and dissolved oxygen can also co-vary

73  negatively or positively and combine with other secondary factors, acting synergistically or antagonistically with unknown

74  effects on benthic community responses. Their extreme values and the extent to which organisms are exposed are key in

75  shaping biological responses (Boyd et al., 2016; Rivest et al., 2017). For instance, early studies suggest that temperature

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

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

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

79  respond positively to future heat events (Rivest et al., 2017). Besides, corals naturally subject to high $p$CO$_2$ variability have

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

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

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

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

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

85  Overall, at natural analogues only a part of the physical and biogeochemical parameters have been quantified and only during

86  short periods of fieldwork due to logistic constraints. Long-term monitoring of seawater parameters and their fluctuation is

87  essential to understand better the mechanisms used by resilient reef organisms in these natural laboratories and predict how

88  marine taxa will respond to future biogeochemical changes in the environment.

89  The semi-enclosed lagoon of Bouraké (New Caledonia, SW Pacific Ocean) has been put forward to be as one of the most

90  suitable natural analogues of future extreme environmental conditions (Camp et al., 2019). In a preliminary study, Camp et

91  al., (2017) reported a series of compelling short-term data of seawater carbonate chemistry and a general survey of the coral

92  populations. In this first assessment of the Bouraké lagoon, the authors measured diel fluctuations of temperature (ranging

93  from 25.9-33.1 °C), pH (ranging from 7.24-7.91 pH$_T$ units) and dissolved oxygen (DO) (ranging from 1.80-6.97 mg L$^{-1}$)

94  regulated by a one-meter tide. They revealed that about 20 species of corals were exposed 44 % of time to a pH$_T$ of 7.7-7.8

95  and 71 % of time to temperatures predicted for the end of the century under the IPCC scenario RCP4.5 (IPCC, 2014). These

96  striking preliminary findings qualified the Bouraké lagoon as a unique site where potentially adapted corals withstand extreme

97  environmental conditions.

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

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

100  to sub optimal conditions remain unclear and we believe that the road-map to test for such an encouraging hypothesis is first

101  to fully characterize the main environmental parameters and the daily and seasonal fluctuations to which reef species have

102  been subjected during their entire life. Here we used a multi-scale approach to map and describe the benthic community living

103  in the Bouraké lagoon and report on new evidence based on three years of data collected at this remarkable natural laboratory.

104  In particular, because of the vast area affected, the close vicinity of a dense mangrove forest, and the demonstrated tide effect

105  on the local environmental conditions, we hypothesized that (1) environmental conditions fluctuate regularly and differ

106  spatially in Bouraké, (2) only a limited number of species are able to resist to the extreme physical and chemical conditions

107  at the study site, when compared to adjacent bay-sheltered reefs.

108

## 2 Methods

### 2.1 Study sites

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

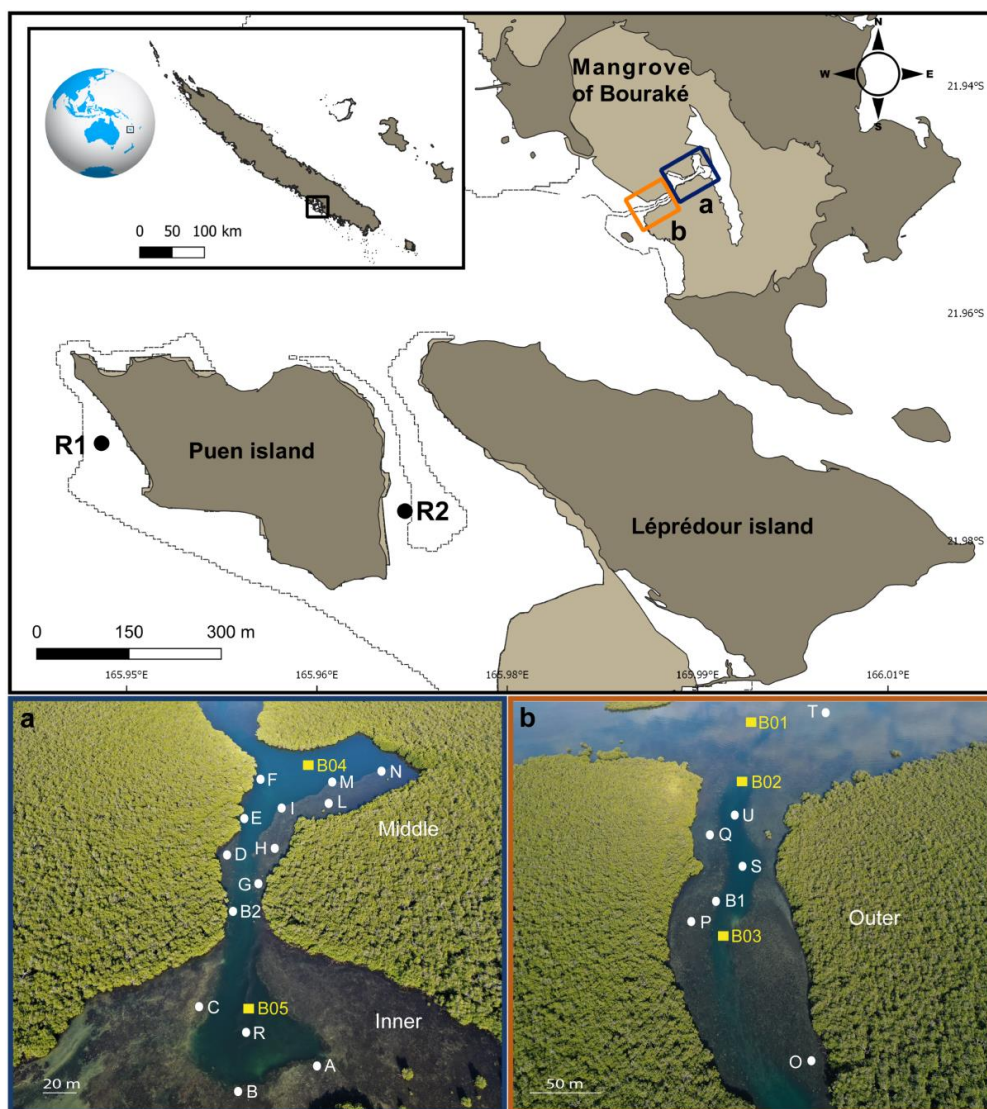



**Figure 1.** Map of the study site (top panel) showing the semi-enclosed mangrove lagoon of Bouraké and reference reefs (R1 and R2). Photos a and b (bottom panels) are aerial pictures (taken at 130 m above the Bouraké lagoon) of the inner (bottom) and middle reefs **(a)** and the outer reef **(b)**.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

119    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*
120    *marina* and *Rhizophora stylosa*, and expands into side pools and a large reservoir in the inner part of the mangrove system. A
121    preliminary calculation of its surface and seawater volume of the main area (i.e., without the large seawater reservoir covered
122    by the mangrove forest) using the 3ds Max Model gives underestimated values of 192,100 m$^2$ and 246,060 m$^3$, respectively
123    (Rodolfo-Metalpa et al., in prep.). Terraces extend from the mangrove, on both sides of the channel, and form diverse and
124    compact reefs at their ends. Coral species are less abundant and diverse near the mangrove roots where the bottom substrate
125    is composed of fine sediment and mud. There, reefs are exposed to air only at low tide during the spring tidal cycle (1.1 m
126    maximum tidal range). We subdivided the lagoon into three main areas: an external, an intermediate, and an inner reef
127    (hereafter called outer, middle and inner reefs; panels a & b in Fig. 1). A series of sampling stations were selected and some
128    of the main seawater chemical and physical environmental parameters were measured at the study site and at two adjacent
129    reference reefs, namely R1 a typical fringing reef, and R2 a semi-enclosed shallow and relatively large bay. Both reefs were
130    located 4.8 and 3.2 km from the entrance of the Bouraké lagoon, respectively.

131    **2.2 Environmental monitoring**

132    **2.2.1. Oceanographic sensors deployment and short- to long-term measurements**

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

140         Short-term (i.e., 24-h) spatial and depth-related variations in pH and DO were simultaneously measured at several
141    stations in the Bouraké lagoon in March and April 2018 (Fig. 1). Spatial variations were assessed i) within the inner (St A-C
142    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
143    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
144    the Bouraké lagoon, we recorded differences between the surface (shallow) and the bottom water: i) at the outer reef (St S for
145    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
146    2019 (St R1, R2, B1 and B2) and in December 2020 (St R1, R2, T and B2).

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

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

152         Short-term pH and DO data and long-term temperature data were compared between stations using General Linear
153    Modelling (GLM), and the Tukey' HSD *post hoc* test was used when significant factor effects were found. When data did not
154    conform to normality or homogeneity of variance, we used the Kruskal-Wallis test followed by the Dunn's multiple

155   comparisons test (Bonferroni-adjusted) or the Wilcoxon test. Statistical analyses were performed using either Statistica® or

156   R version 3.4.4 (R Core Team, 2018), the latter using "stats", "FSA", and "MASS" packages.

157   **2.2.2. Phase averaged and tidal harmonic analyses for diurnal and semidiurnal oscillations**

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

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

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

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

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

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

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

165   tidal analysis package (Codiga, 2011) using the principal semidiurnal lunar constituent ($M_2$), principal semidiurnal solar

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

167   (12 h), and $S_1$ (24 h) were calculated with a 95% confidence interval based on the 200 Monte-Carlo simulations.

168   **2.2.3. Diel cycles of carbonate chemistry and chemical parameters**

169   Surface water samples were collected across diel tide cycles in June 2017, and July 2019 for pH, total alkalinity ($A_T$), dissolved

170   inorganic carbon (DIC), nutrients (orthosilicic acid [$Si(OH)_4$], nitrogen oxide [$NO_x$], ammonium [$NH_4]^+$, phosphate [$PO_4]^{3-}$),

171   dissolved organic carbon (DOC), particulate organic carbon (POC), and particulate organic nitrogen (PON).  A summary of

172   the total sampling is given in Supplementary Table S2. Dissolved inorganic nitrogen (DIN) and total organic carbon (TOC)

173   were calculated as [$NO_x$] + [$NH_4]^+$, and DOC + POC, respectively. To evaluate the availability of nutrients and organic matter

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

175   $Si(OH)_4$:DIN) and contrasted between stations.

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

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

178   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

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

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

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

182   At each station and sampling time, pH and temperature were measured at the surface (0.5 m deep) using a portable pH-meter

183   (913, Metrohm) calibrated with TRIS buffer (Dickson lab, batch #T28). A subsample (50 mL) was filtered through 0.45-μm

184   Whatman™ Puradisc CA filters using a syringe and poisoned with 20 μL saturated $HgCl_2$ to further measure $A_T$. Two 20 mL

185   subsamples were analysed using an auto titrator (EcoTitrator, Metrohm), and $A_T$ was calculated from the Gran function.

186   Results were corrected against $A_T$ standards (A. Dickson, batch #155, Scripps, USA). The seawater carbonate parameters

187   $pCO_2$, $CO_3^{2-}$, and aragonite saturation state ($\Omega_{ara}$) were then calculated from the $pH_T$, $A_T$, temperature, and mean salinity (35)

188   using the free-access $CO_2SYS$ package (Pierrot et al., 2006).

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

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

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

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

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

194    20 μL saturated HgCl$_2$. Measurements of PO$_4^{3-}$, NO$_x$, and Si(OH)$_4$ nutrients were performed by colourimetry (Seal

195    Analytical).

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

197    poisoned with 10 μL saturated HgCl$_2$. The vials were immediately closed, the absence of bubbles was visually checked, and

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

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

200    reference material (CRM) from A. Dickson's laboratory.

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

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

203    were then acidified with ultrapure orthophosphoric acid (H$_3$PO$_4$), sealed, and stored in the dark at room temperature for later

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

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

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

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

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

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

210    °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

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

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

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

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

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

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

217    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

218    12 h (rising tide) separately. Statistical analyses were performed using either Statistica® or R (version 3.2.4, R Core Team,

219    2018), the latter using the "FSA", "stats", and "Conover.test" packages.

### 2.3 Benthic community characterization and distribution

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

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

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

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

225    parallel to the substrate. For each transect, we made a general description of the bottom (i.e. the various substrates) and a list

226  of the most common and identifiable sessile species. For each of the 835 pictures collected, we estimated the cover of abiotic

227  (i.e., mud, sand, rock, rubble, dead corals and unreadable) and biotic descriptors (i.e., branching, massive and soft corals,

228  sponges, macroalgae and "others") with photoQuad software both by automatic multi-scale image segmentation regions and

229  manual grid cell counts when necessary.

230  We used the photos of quadrats, the many other pictures collected during fieldworks, and laboratory morphological

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

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

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

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

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

236  scleractinian corals were identified to species level in situ by photographic sampling only. In case of doubtful identification

237  in vivo, or of taxa characterized by small corallite size (<1 mm in diameter) requiring morphological examination of the

238  skeleton for positive identification (e.g. genera *Acropora*, *Montipora* and *Porites*), a fragment of the colony was collected,

239  tagged, cleaned in sodium hypochlorite overnight, rinsed in freshwater and dried. The reference collection is housed at IRD

240  Noumea. Microscopic examination of the skeletal features allowed species level identification following the reference

241  literature (Veron, and Wallace, 1984; Wallace, 1999; Veron, 2000). Sponges were identified either based on their spicules'

242  morphological characteristics (i.e., length and width), or using a series of morphological descriptors (e.g., shape, size, colour,

243  texture, surface ornamentations, fibres) for species without spicules. In the lab, a subsample of the collected sponges were

244  immediately digested using $HNO_3$, and spicules were measured with an optical stereomicroscope. For species without

245  spicules, hand-cut sections of the choanosome and ectosome were observed under a stereomicroscope. Species were identified

246  using the taxonomical keys of Rützler (1978), Hooper and Van Soest (2002), and Pons et al. (2017). Macroalgae and corals

247  identification were based on morphological and anatomical observations following the dedicated literature and by referring

248  to the collections of specimens housed at IRD Noumea.

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

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

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

252  determined by using the gap statistic method (cluster and factorextra packages in R) and used for the hierarchical clustering

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

254  cluster, the benthic community and bottom substrate were averaged between transects, and the dominant biotic and abiotic

255  descriptors were selected and used to define the cluster.

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

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

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

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

260

# 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).

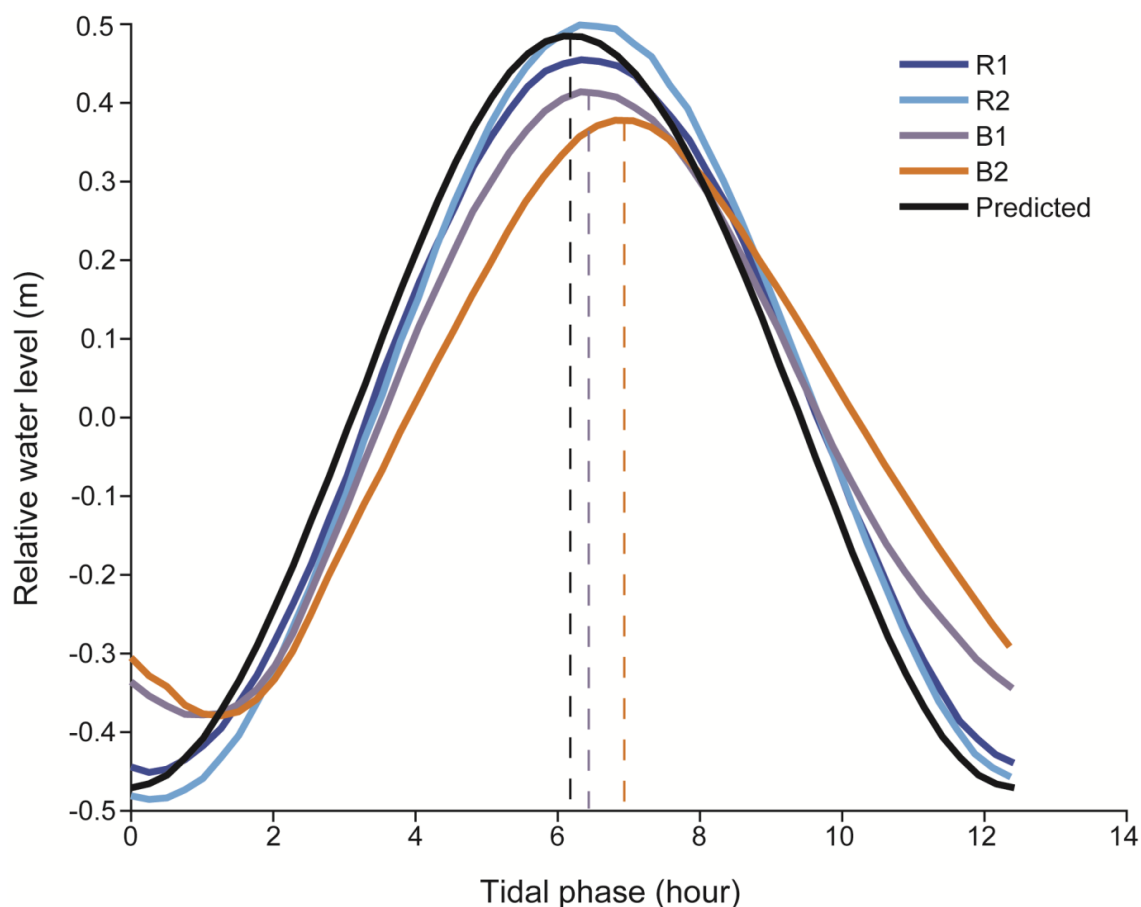



**Figure 2.** Temporal shift between the averaged tides recorded at the reference (St R1 and R2) and at the Bouraké reefs (St B1 and B2) and the predicted tide calculated for the study area (see SHOM: http://data.shom.fr for the Nouméa harbour).

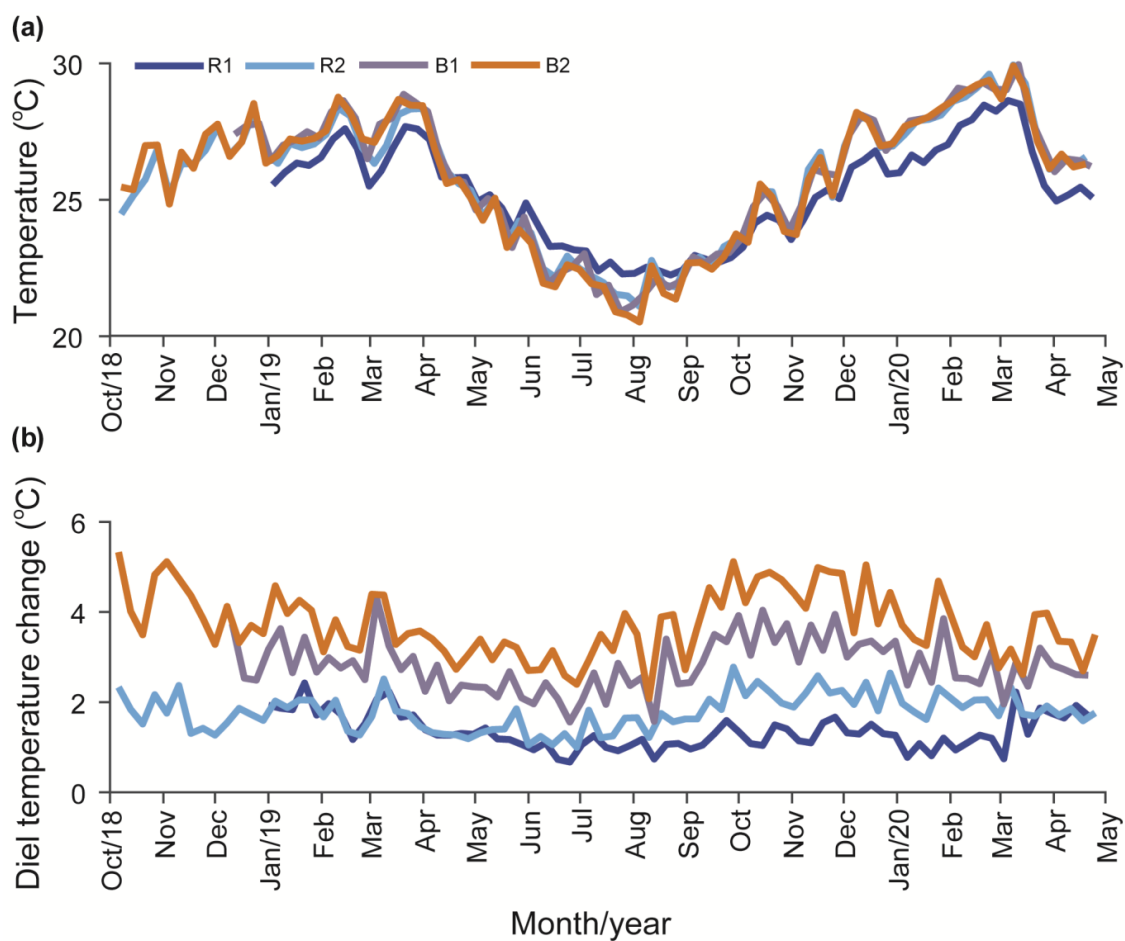
It is semidiurnal with a diurnal inequality ($M_2$= 0.44 m, $S_2$ = 0.16 m) and has a small diurnal component ($S_1$ = 0.15 m). It varies between 0.4 and 1.7 m, depending on the phase of the moon, with a mean of 1.1 m. The tidal range inside the Bouraké lagoon is lower and varies between 0.4 and 1.2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

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

275   compared to the other stations. On a weekly base, the averaged diel temperature variation was significantly different between

276   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

277   fluctuations of up to 3.4 °C at R1 and 6.5 °C at B2.

278

279

280   **Figure 3.** Long-term temperature monitoring from October 2018 to April 2020 at the reference (St R1 and R2) and Bouraké

281   reefs (St B1 and B2). Data are plotted using weakly averaged temperature **(a)** and weakly averaged diel changes **(b)**.

282
283
284
285
286
287
288
289
290
291
292

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

| 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 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 |
| $\Omega_{ara}$ | 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 |
| 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 |

346                                                                                          *(continue Table 1)*
347
348    DOC TOC            36      18.21                    **< 0.001**     (C) *p*<0.01 R2<Out<Inn<Mid;
349                                                                        Inn=Mid; Inn=Out
350    $Si(OH)_4$:DIN     66      43.77                    **< 0.001**     (C) *p*<0.01 R2< Inn>Mid;
351                                                                        Mid=Out; R1=R2
352    DIN:DIP            65      24.59                    **< 0.001**     (C) *p*<0.05 R1<R2>Inn;
353                                                                        R2=Out=Mid; Inn=Mid
354    $Si(OH)_4$:DIP     65      36.62                    **< 0.001**     (C) *p*<0.01
355                                                                        R1<R2<Inn=Mid=Out;
356

357         *Seawater pH.* During the entire study period, pH was measured during 22, 72, 31, and 72 semidiurnal tidal cycles at

358    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.

359    4b).

360

361

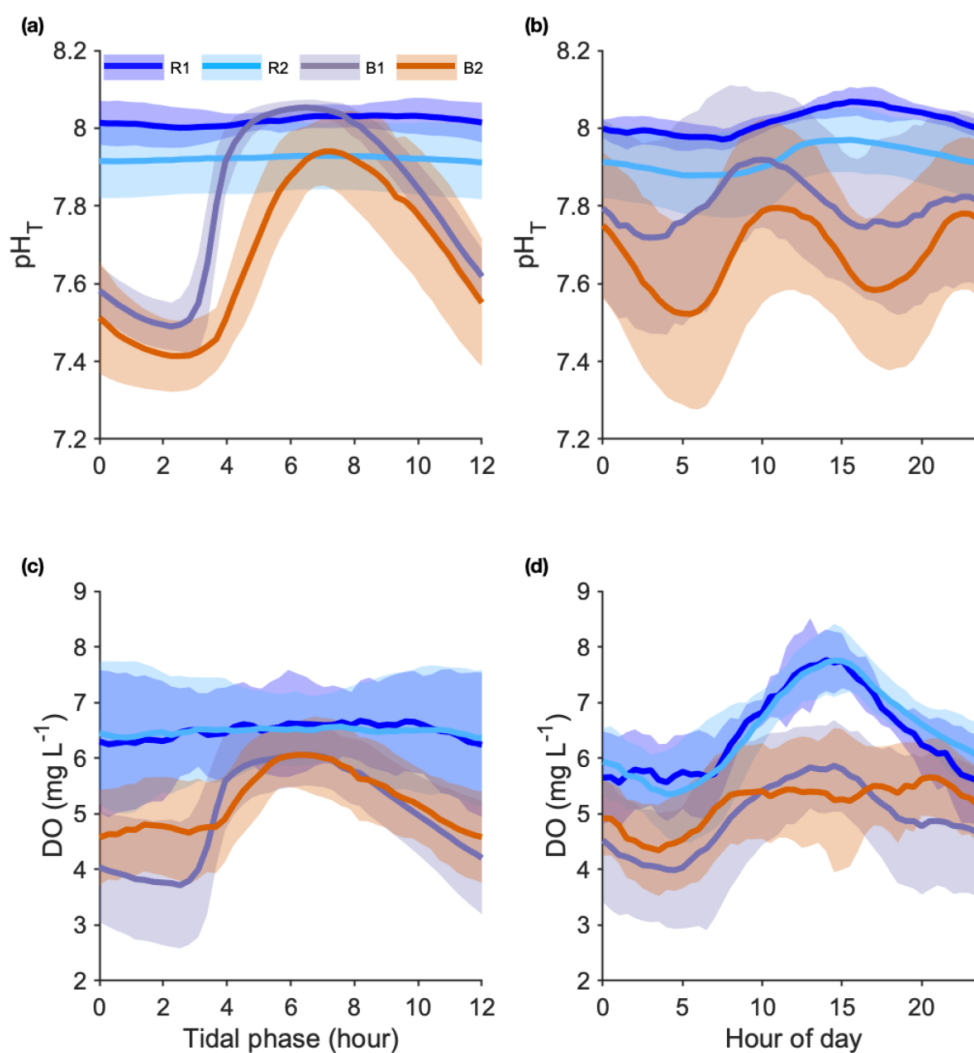



**Figure 4.** Seawater $pH_T$ **(a)**, **(b)** and dissolved oxygen (DO) **(c)**, **(d)** variations recorded at the reference (St R1 and R2) and

Bouraké reefs (St B1 and B2). Data were superimposed in single tidal phase **(a)**, **(c)**; and in a 24-hours cycle **(b)**, **(d)**. Data

are 22, 72, 31, and 72 semidiurnal tidal cycles for pH, and 36, 79, 34 and 42 semidiurnal tidal cycles for DO, for R1, R2, B1

and B2, respectively.

366

The pH differed significantly between stations. We recorded means of $8.01 \pm 0.04$ and $7.89 \pm 0.08$ $pH_T$ units at R1 and R2,

and $7.80 \pm 0.22$ and $7.67 \pm 0.23$ $pH_T$ units at B1 and B2, respectively. At both B1 and B2, pH was strongly correlated with

the tidal cycle (82 and 73% of the total variance were explained by the tidal harmonic analysis, respectively), while it

correlated only marginally with the 24-hours cycle. During each tidal phase, the pH changed on average by about 0.6 units

371   and reached a minimum of 7.23 and a maximum of 8.06 at B2 at low and high tide, respectively. The pH oscillations were

372   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).

373   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

374   mostly dependent on the 24-hours cycle ($S_1 = 0.058 \pm 0.004$ and $S_1 = 0.049 \pm 0.007$ $pH_T$ units for R1 and R2, respectively).

375   Simultaneous short-term pH measurements showed significant spatial differences (Fig. 5; Tables 1), between i) stations A

376   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).

377   There were also significant depth-related differences between shallow reefs and bottom water at stations R and S. In both

378   spatial and depth-related analyses, differences were approximately 0.05 to 0.1 $pH_T$ units, and we found the lowest values at

379   stations C and B2, and at the bottom of the channel (St R and S).

380

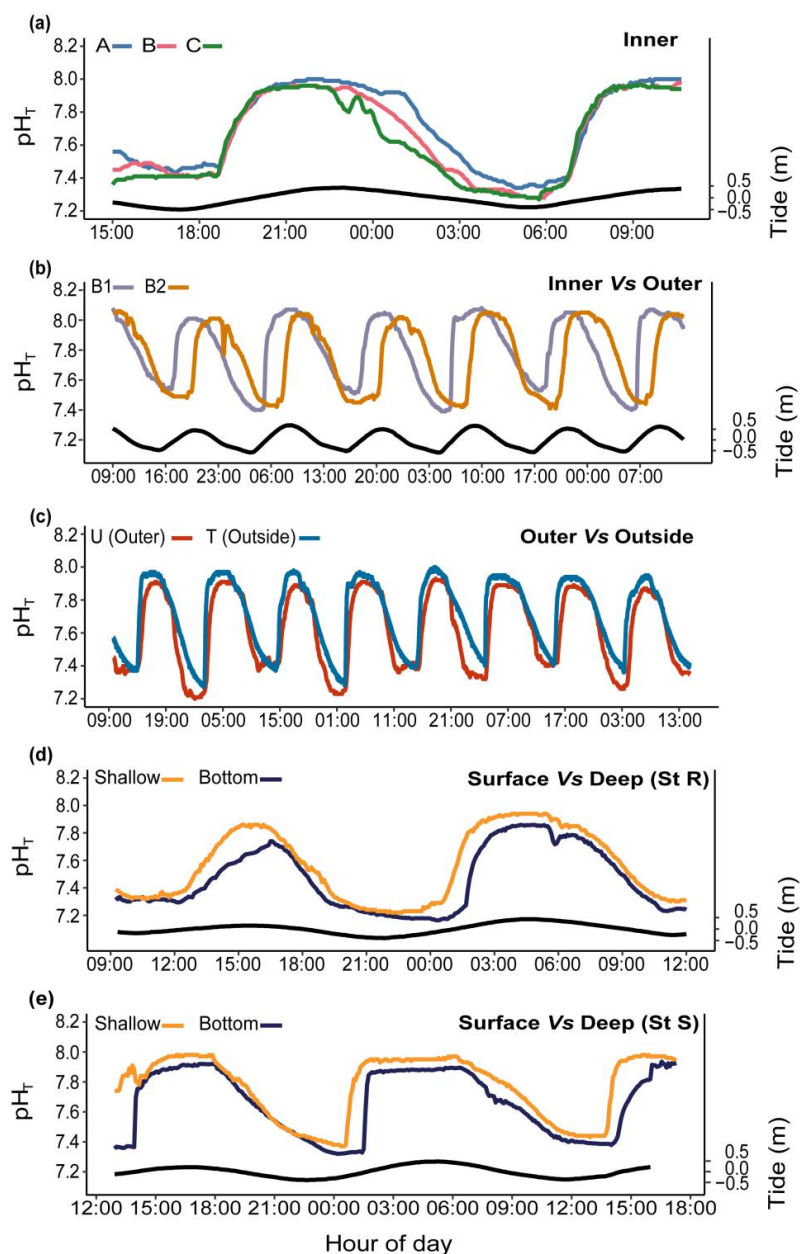



**Figure 5.** Spatial and depth-related short-term changes (24 h) in $pH_T$ at stations in the Bouraké lagoon (see Figure 1 for the
stations' location). Spatial variations were assessed: **(a)** within the inner reef (St A-C); **(b)** between the inner and the outer
reefs (St B1, B2); **(c)** between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

386

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

388   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

389   mean diel DO was higher at the reference reefs than in the Bouraké lagoon. Mean DO values were 4.89 ± 1.18 and 5.23 ±

390   0.89 mg $L^{-1}$ at B1 and B2, respectively, and 6.45 ± 0.95 and 6.48 ± 1.05 mg $L^{-1}$ at R1 and R2, respectively.

391   At stations B1 and B2, DO was strongly correlated with the tidal cycle (82 and 72 % of the total DO variance were explained

392   by the tidal harmonic analysis, respectively). DO oscillations were mainly semidiurnal ($M_2$ = 1.17 ± 0.08 mg $L^{-1}$, and $M_2$ =

393   0.83 ± 0.09 mg $L^{-1}$ for B1 and B2, respectively) with a substantial diurnal component ($S_1$ = 1.12 ± 0.04 mg $L^{-1}$, and $S_1$ = 0.681

394   ± 0.04 mg $L^{-1}$ for B1 and B2, respectively). During a semidiurnal tidal cycle, DO was lower at low tide (3.7 mg $L^{-1}$ and 4.6

395   mg $L^{-1}$ at B1 and B2, respectively). During a 24-hours cycle, DO was lower in the early morning (4.0 and 4.3 mg $L^{-1}$ at B1

396   and B2, respectively) and higher in the middle of the day (5.8 and 5.5 mg $L^{-1}$ at B1 and B2, respectively). In a single day, we

397   recorded DO fluctuations of up to 6.37 mg $L^{-1}$ at R1 and 4.91 mg $L^{-1}$ at B2. The minimum DO value, 1.89 mg $L^{-1}$, was

398   measured during low tide, and the maximum DO value, 7.24 mg $L^{-1}$, was measured at B1during high tide (data not shown).

399   At stations R1 and R2, DO was mainly diurnal ($S_1$=1.34 ± 0.06 mg $L^{-1}$ and $S_1$ = 1.53 ± 0.09 mg $L^{-1}$ for R1 and R2, respectively)

400   with lower values during the night (5.5 mg $L^{-1}$ at both stations), and higher values in the middle of the day (7.8 mg $L^{-1}$, both

401   stations). Simultaneous short-term DO measurements (Fig. 6; Table 1) did not show significant differences over a 24-hours

402   cycle at the inner (St A-G; except for some specific deviations, e.g., St A), the middle (St H-N) or the outer reef (St O-Q).

403   Dissolved oxygen did not change on a vertical gradient at stations R and I, but the bottom DO was significantly lower at

404   station N.

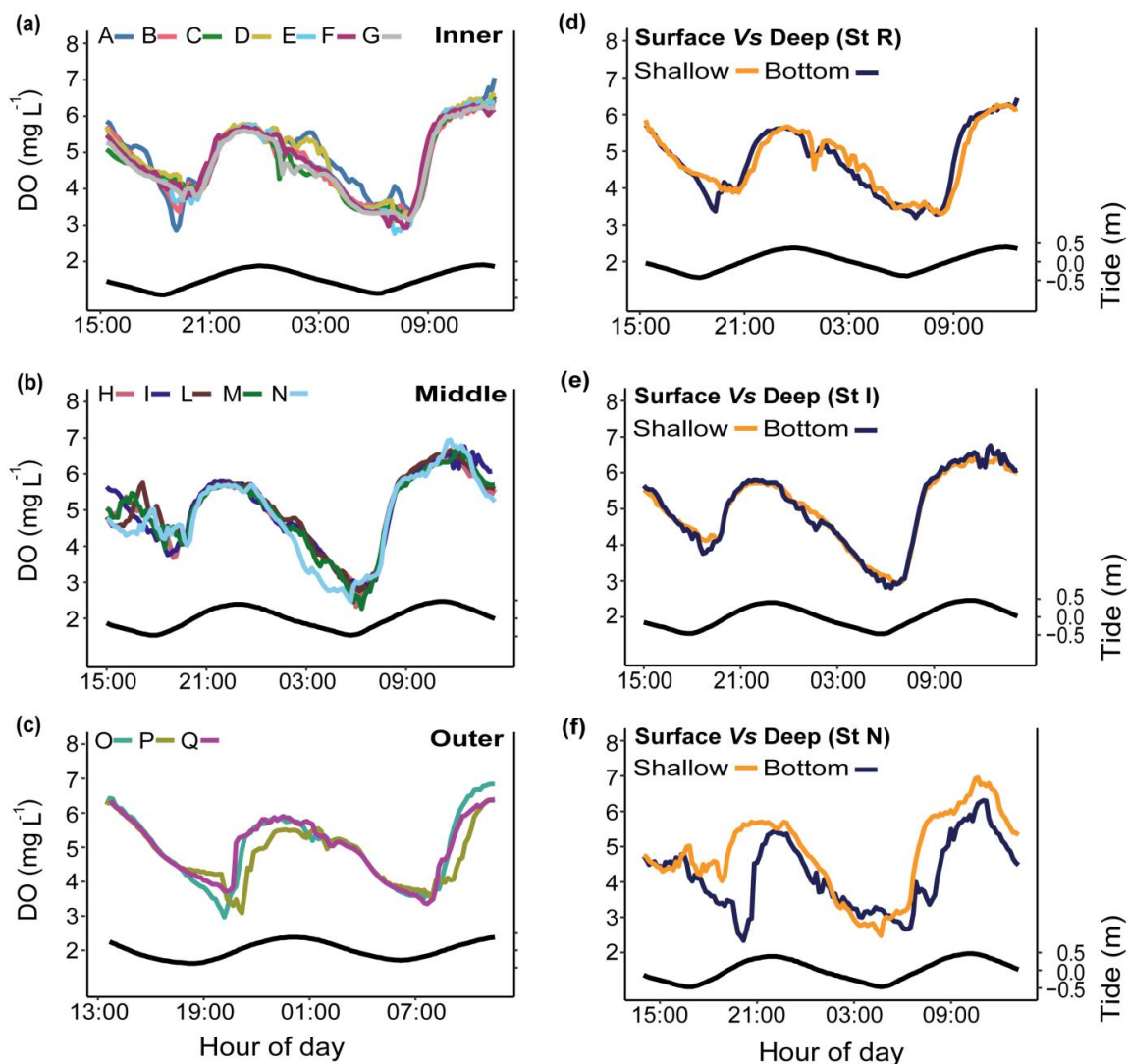
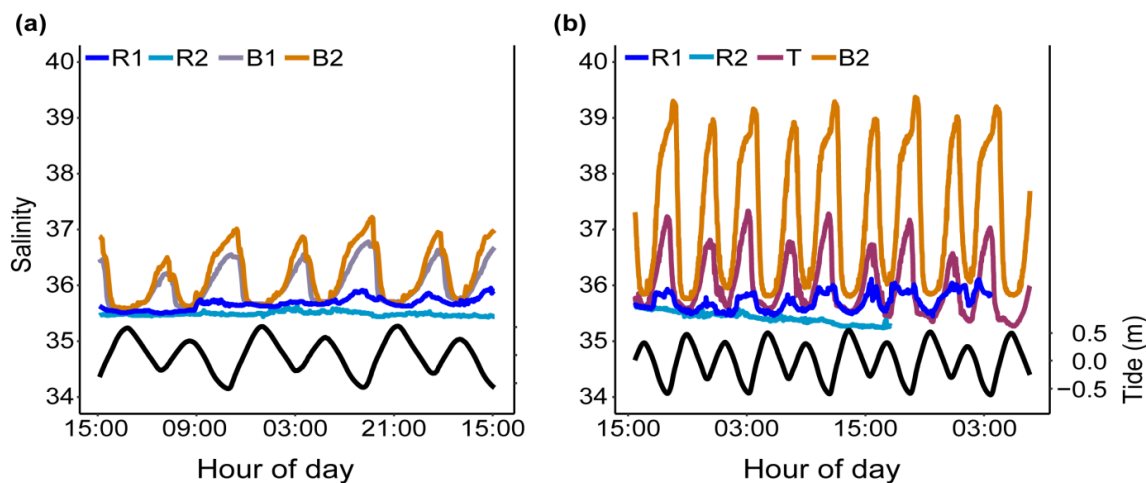



**Figure 6.** Spatial and depth-related short-term measurements (24 h) in dissolved oxygen (DO) at stations in the Bouraké lagoon (see Figure 1 for the location of the stations). Spatial variations were assessed on **(a)** the inner reef (St A-G), **(b)** the middle reef (St H-N), and **(c)** the outer reef (St O-Q). Depth-related variations between shallow reefs and bottom water within the Bouraké lagoon were assessed **(d)** at the inner reef (St R), and **(e, f)** at the middle reef (St I and N). Tide (black line) refers to St B2.

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

416

417     **Figure 7.** Short-term salinity monitoring during **(a)** the winter of 2019 (from 15/07/2019 to 18/07/2019) at the reference (St

418     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

419     R1 and R2) and Bouraké reefs (St T and B2). Tide (black line) refers to St B2.

420     Its variations in the Bouraké lagoon was strongly correlated with the tidal cycle, and the highest mean values were measured

421     during both winter and summer. Salinity was lower at reference reefs. The mean salinity during the winter of 2019 was 35.49

422     $\pm$ 0.04 at R1, 35.67 $\pm$ 0.10 at R2, 36.00 $\pm$ 0.35 at B1, and 36.17 $\pm$ 0.47 at B2 with significant differences between stations

423     (Tables 1). Salinity in the Bouraké lagoon peaked at 37.22 at B2 during low tide, while it was 35.65 at R1. During the summer

424     of 2020, the mean salinity increased significantly in the Bouraké lagoon with 37.22 $\pm$ 0.53 at B2, reaching up to 39.37, while

425     it remained lower at R1 with 35.42 $\pm$ 0.10 and at R2 with 35.71 $\pm$ 0.16. In the summer of 2020 we also measured short-term

426     variations in salinity at station T, which is outside the Bouraké system. Although its distance from the entrance of the lagoon,

427     the water mass discharged during falling tide increased seawater salinity also at this station where we measured a maximum

428     value of 37.33 during low tide.

429     **3.2 Diel cycles of carbonate chemistry and chemical parameters**

430     We monitored diel cycles in June 2017 and July 2019 at two reference reefs and three reefs within the semi-enclosed lagoon

431     of Bouraké (i.e., the outer, the middle and the inner reefs). The seawater carbonate chemistry differed significantly between

432     the reference and the Bouraké lagoon reefs (Fig. 8a-c; Supplementary Fig. S1; Tables 1, 2).

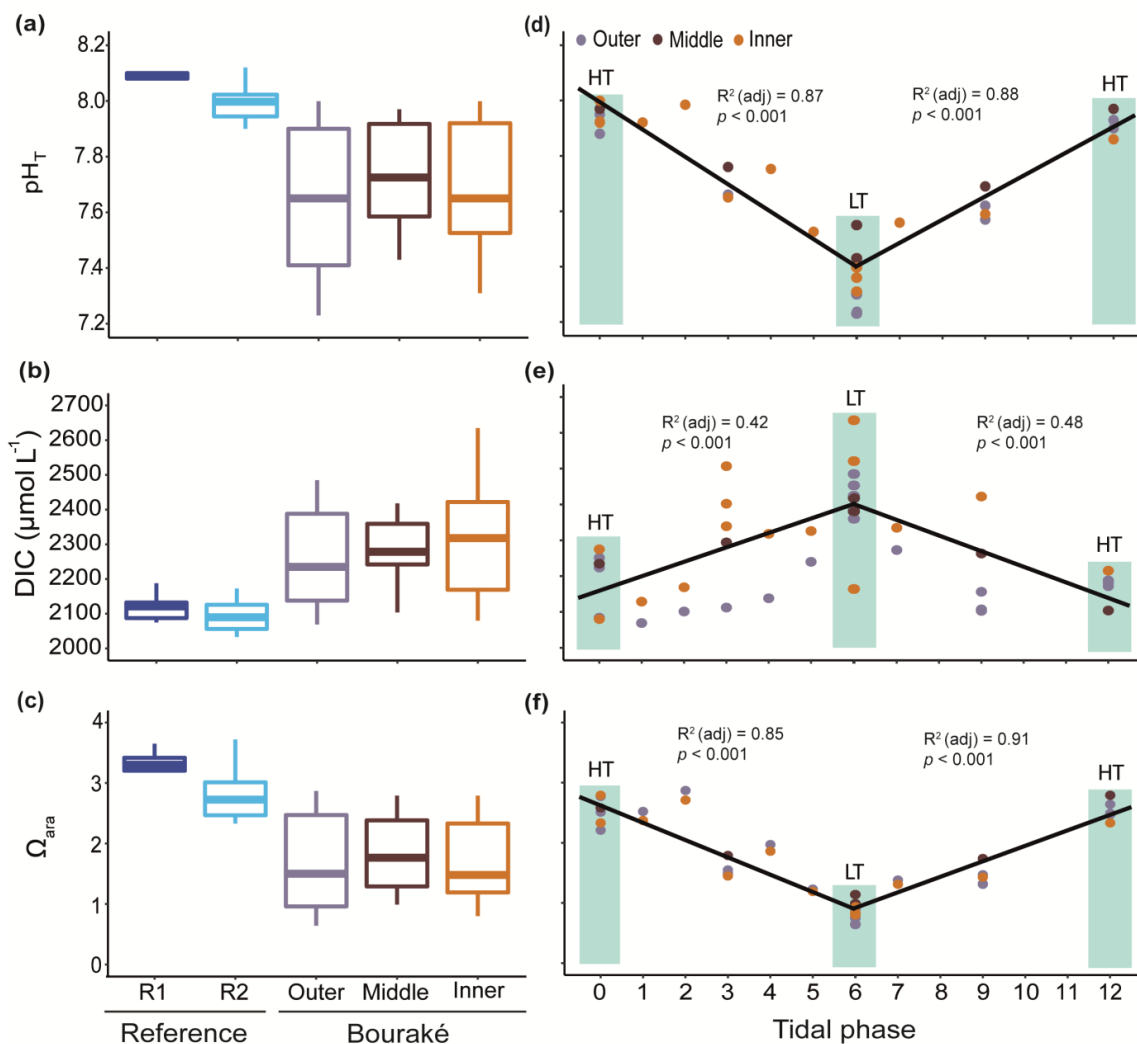



**Figure 8.** Seawater carbonate chemistry measured (pH$_T$) and calculated (DIC and $\Omega_{ara}$) during diel cycles in 2017 and 2019 (pooled data, see also Supplementary Figure S1) at R1, R2 and the Bouraké reefs (outer, middle and inner) **(a-c)**. Boxes (n = 6-14) represent the interquartile range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

**Table 2**. Summary of the seawater physical and chemical data (mean ± SD) measured in July 2017 and June 2019 and calculated using the CO$_2$SYS 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 | 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 | 7.20 ± 0.64 | 6.91 ± 1.01 | 6.11 ± 0.68 | nd | 5.98 ± 0.67 |
| $A_T$ | 2294.1 ± 0.3 | 2261.2 ± 0.04 | 2357.8 ± 0.1 | 2256.3 ± 0.06 | 2393.7 ± 0.08 |
| Si(OH)$_4$ | 0.71 ± 0.42 | 2.86 ± 1.41 | 8.22 ± 3.14 | 8.88 ± 2.72 | 11.93 ± 4.27 |
| No$_x$ | 0.21 ± 0.05 | 0.51 ± 0.16 | 0.65 ± 0.20 | 0.54 ± 0.09 | 0.54 ± 0.12 |
| PO$_4^{3-}$ | 0.63 ± 0.08 | 0.19 ± 0.05 | 0.26 ± 0.13 | 0.19 ± 0.01 | 0.42 ± 0.23 |
| NH$_4^+$ | 0.08 ± 0.06 | 0.23 ± 0.09 | 0.27 ± 0.12 | 0.34 ± 0.12 | 0.23 ± 0.14 |
| DOC | nd | 81.15 ± 5.49 | 96.89 ± 10.78 | 95.70 ± 8.38 | 112.82 ± 14.41 |
| DIC | 2117.7 ± 39.4 | 2092.4 ± 42.9 | 2251.1 ± 132.2 | 2282.5 ± 112.0 | 2315.1 ± 168.1 |
| POC | 9.28 ± 1.47 | 11.15 ± 1.97 | 24.07 ± 5.31 | 29.37 ± 7.03 | 38.11 ± 10.43 |
| PON | 1.24 ± 0.46 | 1.21 ± 0.22 | 1.64 ± 0.22 | 1.98 ± 0.35 | 2.43 ± 0.52 |
| | | | | | |
| *Calculated* | | | | | |
| $p$CO$_2$ | 353.42 ± 7.24 | 467.76 ± 112.03 | 1402.92 ± 896.42 | 1047.06 ± 599.07 | 1318.95 ± 819.79 |
| CO$_3^{2-}$ | 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 | nd | 93.22 ± 6.18 | 121.63 ± 14.07 | 125.07 ± 13.32 | 144.72 ± 17.5 |
| DIN | 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 $\Omega_{ara}$, and consequently, lower DIC and $p$CO$_2$ 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 $p$CO$_2$ > 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 L$^{-1}$ during low tide on the inner reef with an average of 109.02 ± 45.59.

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

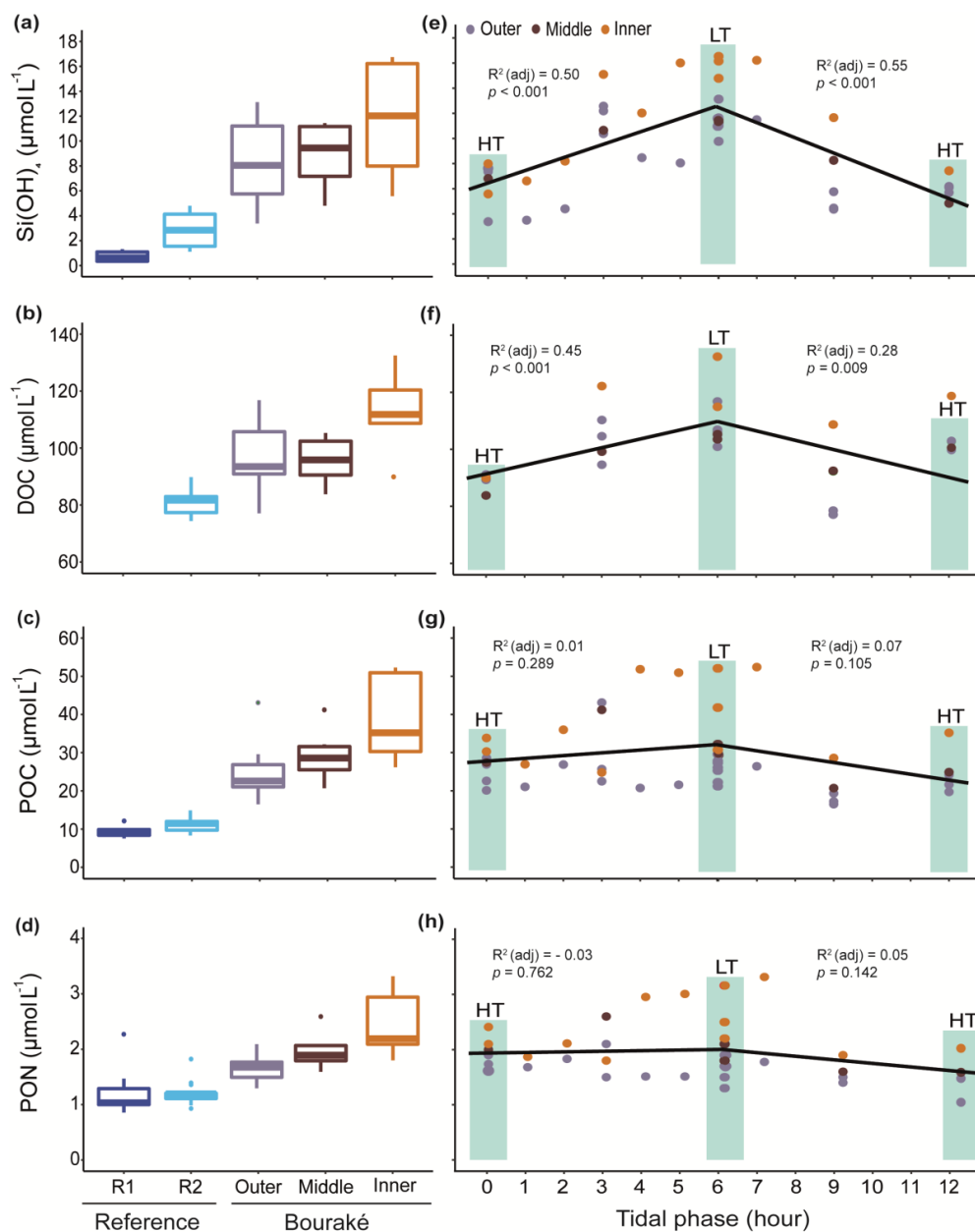



**Figure 9.** Orthosilicic acid, organic carbon and nitrogen parameters measured during diel cycles in 2017 and 2019 (pooled data, see also Supplementary Figure S2) at R1, R2 and the Bouraké reefs (outer, middle and inner) **(a-d)**. Boxes (n = 6-14) represent the interquartile range (25th and 75th percentile); the horizontal line is the median, and the whiskers represent the data range (i.e., minimum and maximum). Changes are illustrated across a 12-h tidal phase in Bouraké **(e-h)**. Linear regression lines are plotted for each falling (HT to LT) and rising tide (LT to HT). Shaded boxes have only a graphical significance and only suggest the tide changes during measurements.

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

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

494     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

495     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 ±

496     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

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

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

499     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

500     Bouraké lagoon compared to reference reefs.

501     **3.3 Benthic community distribution and species identification**

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

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

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

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

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

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

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

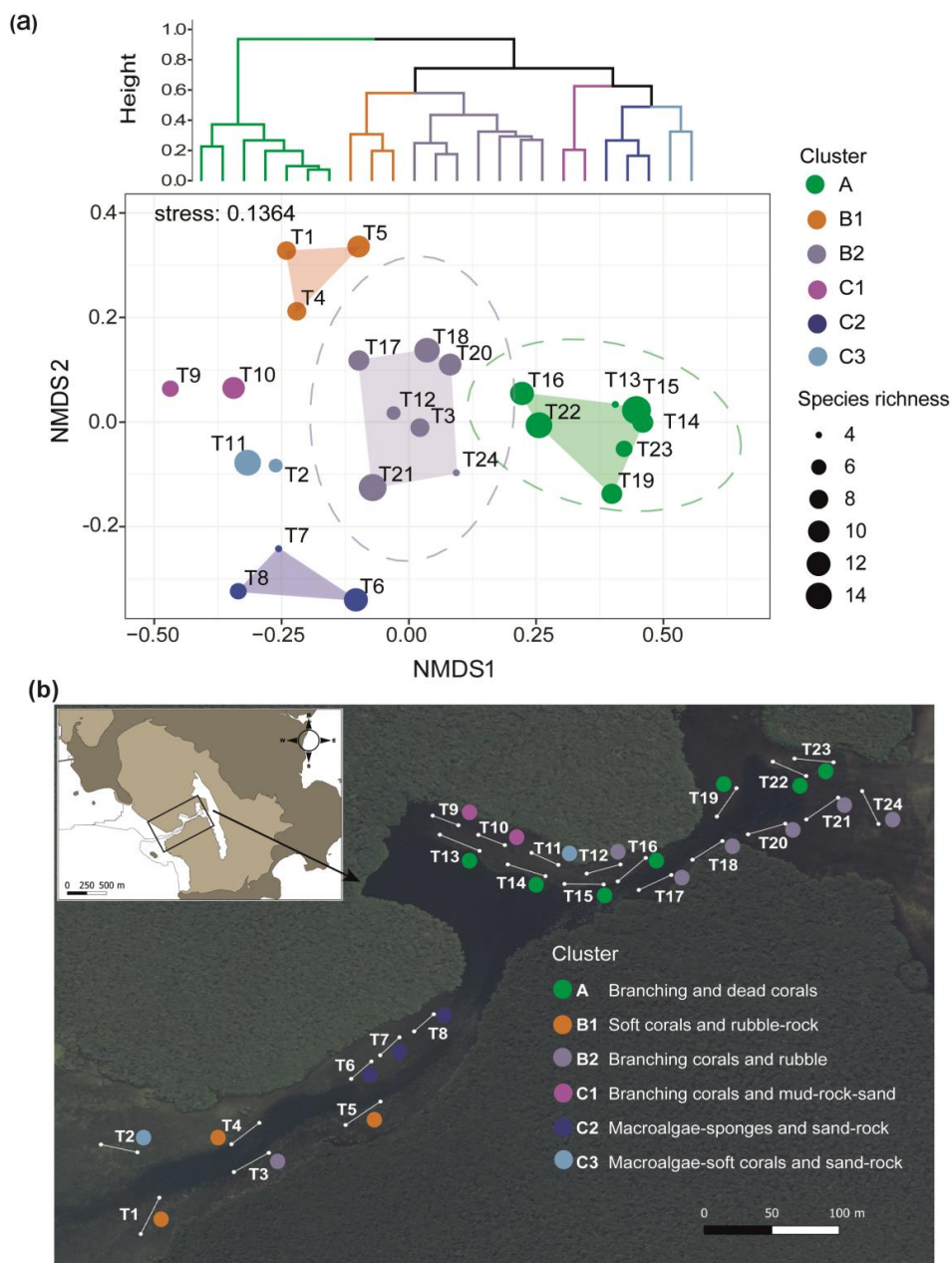



**Figure 10.** Benthic community and bottom substrate characterization in the Bouraké lagoon. Hierarchical Ward's method cluster dendrogram (top) and non-metric multidimensional scaling (nMDS) of abiotic and biotic percent cover and species richness per transect (T1-T24) **(a)**. Colored circles represent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

516 For both, branching corals were the dominant biotic descriptor with 81% and 31% cover, respectively) (Supplementary Fig.

517 S3). Among branching corals, the two most abundant genera were *Acropora* and *Montipora* (data not shown). For the abiotic

518 features of the substrate, dead corals and rubbles characterized transects in clusters A and B2, respectively. Species richness

519 (Fig. 10a) was high in all transects of the Bouraké lagoon, except T13 and T24, both found at the middle and inner reefs'

520 limits. The abiotic substrate of cluster C1 was characterized by 66% mud, 12% rocks and 10% sand (see Supplementary Table

521 S4 for detailed cover data per transect). Only a few branching corals (<10%) were found, but species richness was relatively

522 high (6 at T9 and 10 at T10). Cluster C2 was distinct, which is not surprising due to its location in a relatively shallow

523 convergence zone that divides the lagoon into two parts. There, the substrate is made of coarse sand (13%) and rocks (12%)

524 and is mainly colonized by macroalgae and sponges (31% and 32%, respectively). Species richness in the area was

525 heterogeneous and ranged from 4 to 12. *Dictyota* spp. and *Halimeda discoidea* were the main macroalgal species, while

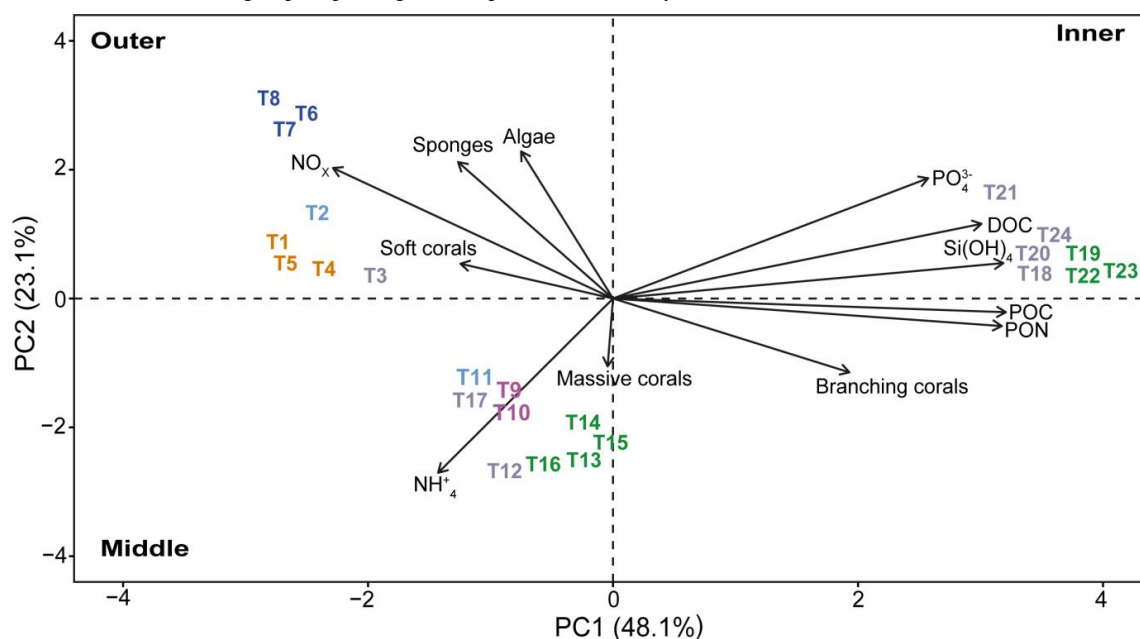
526 *Rhabdastrella globostellata* was the dominant sponge species in the area. Cluster B1, located on the outer reef, is characterized

527 by an abundance of soft corals (48%) and rubbles (21%), and high biological richness (Fig. 10a). Cluster C3 is characterized

528 by coarse sand (49%), rocks (17%) and a few benthic organisms such as macroalgae (10%) and soft corals (8%).

529 Principal component analysis (PCA) reduced multicollinearity problem and the first two Principal Components

530 accounted for a cumulative 71.2% of the dataset variance. In particular. The PCA plot (Fig. 11) allowed us to assign the

531 transects to three distinct groups depending on their position in the study area.

532

533 **Figure 11.** Principal component analysis (PCA) between benthic community (macroalgae, sponges, corals, branching corals

534 and massive corals) data and environmental parameters (PON, POC, DOC, $Si(OH)_4$, $PO_4^{3-}$, NOx, and $NH_4^+$) measured for

535 each transect (n = 24). The length of the vectors indicates the contribution of each parameter. The first dimension explains

536 48.1 % of the variance, and the second dimension explains 23.1% of the variance. Red dots indicate the transects. Colors refer

537 to the cluster subdivision (Fig. 10).

538    The distinction among transects groups in the biplot is clear and they are grouped based on their location in the outer, middle

539    or inner lagoon reefs. The outer reef sites are characterized by the presence of sponges, macroalgae and soft corals, which

540    appear to correlate with NOx. Conversely, branching corals are the shared and characteristic feature of the middle and inner

541    reef sites. These two reef groups, however, differ in their major correlation to $NH_4^+$ for middle reef sites and POC, DOC,

542    $Si(OH)_4$, and $PO_4^{3-}$ for the inner sites.

543        *Species identification.* A total of 66 coral species were identified from the Bouraké lagoon (Supplementary Table

544    S5). Most of the species belong to the family Acroporidae (17 *Acropora* species, 2 *Anacropora* and 4 *Montipora*) and

545    Merulinidae (15 species). A total of 58 species were identified from the reference reef R2, 29 of which were also found in the

546    Bouraké lagoon. Overall, the hard coral fauna within the lagoon was characterized by species commonly found around the

547    Grande Terre, with some of them typically found in turbid coastal environments such as *Pseudosiderastrea tayamai* and

548    *Heliofungia actiniformis.* They were not encountered at the reference site. Remarkably, two New Caledonia endemic coral

549    species, namely *Cantharellus noumeae* and *Polycyathus fulvus*, both described from coastal habitats characterized by

550    terrigenous sediment input (Noumea lagoon and Prony Bay, respectively), were common in the innermost reef of the Bouraké

551    lagoon. The Bouraké lagoon also had 28 species of macroalgae (14 Phaeophyceae, 9 Chlorophyta and 5 Rhodophyta),

552    including the crustose coralline algae *Lithothamnium* sp., *Lithophyllum* sp., and *Hydrolithon reinboldii*, and 11 sponge species

553    belonging to eight families of the class Demospongiae (Supplementary Tables S5 and S6), which were found mainly in the

554    coral matrix and sediment.

555

## 4 Discussion

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

### 4.1 Physical and chemical characteristics of the Bouraké lagoon

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

We found several marked differences in the environmental conditions between the Bouraké lagoon and the reference reefs. First, the seawater temperature is higher in summer in the Bouraké lagoon (Fig. 3), but it is also colder during winter, occasionally more than 25 °C. If we compare temperature recorded at the reference St R2, which showed the most typical temperature range for shallow water temperatures in the south of New Caledonia (i.e., 22 - 28 °C, (Varillon et al., 2021), we notice that in Bouraké temperatures were 40% of the time above 28°C during the summer of 2020, while winter temperatures were on average 46.5 % of the time lower than 22 °C. While warming is considered the main threat for coral reefs, low temperatures (< 20 °C) can cause coral bleaching by inducing responses similar to high temperatures, including a reduction in the *Symbiodiniaceae* cell density and chlorophyll *a* content (e.g., Saxby et al., 2003; Hoegh-Guldberg and Fine, 2004; Hoegh-Guldberg et al., 2005; Kemp et al., 2011; (Bellworthy and Fine, 2021). The negative effect of cold temperatures is even more substantial during neap tides when colonies on the reef crest are exposed to air for hours at low temperatures during cold winters. For example, Porter et al. (1982) and Davis (1982) reported > 90 % coral mortality in shallow (< 2 m) reefs of the Dry Tortugas following the winter of 1976 - 1977 when temperatures reached 14 °C. This is consistent with our

593    observations (data not shown) during the cold winter of 2019 when we found that the upper 12 - 20 cm of several massive

594    and branching corals had died.

595    Second, in the Bouraké lagoon, benthic assemblages are continuously exposed to suboptimal fluctuations in the main

596    environmental parameters, and some of these environmental fluctuations are entirely predictable. For instance, marine

597    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

598    single day. Dissolved oxygen fluctuations were similar between stations but in a significantly different range: 3.7 to 6.8 mg

599    $L^{-1}$ at B2 and 5.4 to 7.8 mg $L^{-1}$ at the reference stations. Besides, our tidal modelling revealed that, at the reference reefs, pH,

600    DO (Fig. 4), and temperatures (data not shown) slightly increased in the afternoon and decreased during the night. This agrees

601    with what should be expected from reef metabolic activities and daily cycles but, in the Bouraké lagoon, these parameters,

602    including salinity (Fig. 7), are entirely driven by tides. Here, seawater pH and DO varied between extremely low values at

603    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

604    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.

605    2).

606    The unique environmental conditions measured in the Bouraké lagoon are mainly due to the topographical and

607    geomorphological characteristics of this unique site, the resulting water circulation and the direction of the tide. At each rising

608    tide, new water enters through the channel, flows into the semi-enclosed lagoon towards the large mangrove area behind it,

609    and mixes with the acidic, warm and deoxygenated water that was already in the system and the mangrove area. There, we

610    hypothesize that the water chemistry changes due to the metabolic reactions in the sediments, coral reefs and mangrove roots.

611    Conversely, on a falling tide, the seawater becomes gradually more acidic, hot and oxygen-depleted because the water that

612    resided in the mangrove area gradually drains out of the system. This takes about 6 hours, during which the vast reservoir of

613    shallow mangrove water continues to be chemically altered, becoming increasingly acidic, oxygen-depleted and hot. As a

614    result, we measured a significant spatial differences in pH between the outer reef (the entry of the lagoon) and the inner reef

615    (near the mangrove forest), as well as a considerable delay in the synchronization of the tidal shift (Fig. 5b). Interestingly,

616    because the volume of seawater discharged in 6 hours is so large, it affects also the area outside the system where we measured

617    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

618    the area (and the organisms) affected by the suboptimal parameters is larger than previously thought. It is likely that the

619    species living in this area have developed specific mechanisms to withstand the very fluctuating environmental conditions,

620    and as such, they warrant further attention.

621    It could be argued that because the fluctuations are linked to tidal phases, organisms living in the Bouraké lagoon may benefit

622    from periods of normal conditions at high tide during which they can recover from the stress they have experienced at low

623    tide. While this could be partially the case for species living on the outer reef, close to the main lagoon, the environmental

624    conditions inside the Bouraké lagoon rarely reach normal values (Fig. 8a-c), and also persist longer since the low tide is

625    delayed by 1.5 h compared to the reference reef (Fig. 2).

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

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

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

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

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

631    probably change the seawater physical and chemical properties. We measured significant spatial differences in pH within
632    each reef area (inner, middle and outer reefs; Fig. 5a, b), as well as throughout the water column (i.e., between the surface
633    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
634    pumping mechanism by the water mass of more acidic pore water from the sediments. The pH also differed spatially within
635    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
636    the edges of the mangrove or a more intense metabolic activity by the local benthic community. Dissolved oxygen
637    concentrations between the surface and the bottom were only significantly different on the middle reef (Fig. 6f), and only at
638    St. N which is mainly characterized by mud as the current there is lower than anywhere else in the Bouraké lagoon. Here, the
639    sediment's biological activity possibly traps the oxygen making it less available to the water column.
640    We can assume that, throughout the Bouraké lagoon, organisms are exposed to extreme and fluctuating suboptimal physical
641    parameters, such as pH, and DO which are more pronounced on the bottom and last longer, and with more extreme values,
642    on the inner reefs. It is also true for the seawater chemistry with higher concentrations in the Bouraké lagoon than on the
643    reference reefs (see Table 2). For instance, we found that orthosilicic acid, phosphate, dissolved and particulate organic
644    carbon, and particulate organic nitrogen were 1.4 to 4.2-fold more concentrated on the inner reef than at station R2. Within
645    the Bouraké lagoon in general, chemicals increased from the outer to the inner reef and with the exception of $[NO_x]$, $[NH_4]^+$,
646    $[PO_4]^{3-}$, they never return to "normal" values despite the Bouraké system receives new seawater during the rising tide. The
647    high concentrations in orthosilicic acid and organic compounds, both dissolved and particulate are due to the combined effect
648    of more acidic and organic rich water coming out of the mangrove forest during a falling tide (Fig. 9) and the particular
649    morphology of the system which limits the full seawater renew, especially at the inner reefs.

650    **4.2 Effects of physical and chemical conditions on species distribution**
651    Extreme environmental conditions, such as those measured in the Bouraké lagoon, are known to strongly affect the
652    metabolism, growth and even survival of several marine organisms, particularly those that are commonly considered
653    stenotopic like scleractinian corals. For instance, $in$ $situ$ studies at volcanic $CO_2$ seeps have shown that chronic exposure to
654    ocean acidification (near-future $pCO_2$ levels) can cause a reduction in coral diversity, lower recruitment and abundances of
655    structurally complex hermatypic corals. Moreover, shifts in competitive interactions between taxa and a decrease in cover and
656    richness of soft corals and sponges were also observed (e.g., Fabricius et al., 2011; Sunday et al., 2017; Agostini et al., 2018;
657    Teixidó et al., 2018). However, the Bouraké lagoon features high coral, sponge, macroalgae and CCA cover and species
658    richness, adding at the check-list proposed by Camp et al., (2017) an additional 46 coral species (totaling 66 species and 33
659    genera), 23 species of macroalgae and 11 species of sponges (Supplementary Table S5). Such a high number of species has
660    never been reported for mangrove systems characterized by marginal conditions, at least with regard to the three major benthic
661    groups taxa investigated here (e.g., Yates et al., 2014; Camp et al., 2019). In general, given the extensive literature
662    demonstrating the negative effects of suboptimal abiotic conditions on corals, our findings are unexpected and suggest that
663    corals in the Bouraké lagoon may have developed unique survival and adaptive mechanisms. Some studies have reported
664    similar findings, but none has ever reported such a high coral species diversity (e.g.,Yates et al., 2014; Schoepf et al., 2015;
665    Shamberger et al., 2018; Camp et al., 2019). For instance, in Palau (Micronesia), the highest coral cover (> 60%) and species
666    diversity (21 scleractinian genera) were found at the lowest pH study site of the Nikko Bay station (Barkley et al., 2015).
667    Studies in the Virgin Islands' mangrove system have reported over 30 coral species growing in marginal conditions (Yates et

al., 2014; Rogers, 2017). Similarly, in a recent study of two Australian mangrove lagoons, both characterized by relatively
extreme environmental conditions (low pH, low oxygen and high temperature), Camp et al., (2019) identified 12 and 29
scleractinian coral species in the Woody Isles and at Howick Island, respectively. Among the 66 species we identified, a total
of 29 of the most abundant coral species in New Caledonia are shared between the reference reef and the Bouraké lagoon,
indicating that species living at our study site are not very different than on a typical bay-sheltered fringing reef. There is not
an apparent selection in the coral form, since massive (e.g., *Porites* spp.), corymbose (e.g., *Pocillopora digitata*), phaceloid
(*Galaxea fascicularis*) and branching (*Acropora* spp.) species are equally abundant, as well as in their thermal and pH
tolerance. Further experiments are underway at both the molecular and phenotypic level to better understand the mechanisms
of resilience used by the corals from Bouraké.

Remarkably, the two coral species currently considered New Caledonia endemics thrive in the innermost benthic assemblages
of the Bouraké lagoon, making it not only a unique natural laboratory but also a potential conservation priority site in light of
its overall uniqueness characterized in this study. In the Bouraké lagoon, benthos species richness was very high throughout
the system and the distribution of branching and massive corals was spatially heterogeneous (Fig. 10b; Supplementary Fig.
S3). Coral cover decreased near the mangrove, where the accumulation of fine sediments and exposure to air during low tide
do not allow corals' survival, but the percent cover reached up to 90 % on the reef margin (Supplementary Fig. S3). Branching
corals were particularly abundant on the inner and middle reefs. They became sparse on the outer reef, even absent at the
system's entrance where soft and massive corals dominated. Macroalgae and sponges, including CCA (data not shown), were
quite cryptic throughout the Bouraké lagoon, but found almost everywhere both in the coral matrix and buried in the sediment.
They are particularly abundant only in a shallow area that divides the lagoon into two parts (transects T6-T8). There, a Venturi
effect generates a strong current and the substrate is made of coarse sand and rocks. Both the high flow and the bottom
characteristics likely promote macroalgae and sponge occurrences (averaged 30 % and 32 % cover, respectively). There, the
sponge *Rhabdastrella globostellata* is particularly abundant (up to 40 % cover) and form massive banks embedding adjacent
coral colonies. In general, macroalgae and sponges diversity is not particularly rich with respectively only 28 and 11 species
have been detected, likely due to the sampling method. However, sponge diversity, in the Indo-pacific mangrove systems, is
in general not extremely high especially if compared to the Caribbean (Nagelkerken et al., 2008). Few studies are available
from Indo-Pacific mangrove sponges and the highest diversity was reported in a study in the mangrove of Banka Island (North
Sulawesi, Indonesia), where 19 species of sponges were found (Calcinai et al., 2017). Our findings on mangrove sponges in
such a unique mangrove area in New Caledonia improve the limited knowledge on the sponge species diversity in Pacific
mangrove systems.

Water flow may play a critical role in the response of organisms to acidification (Hurd, 2015; Comeau et al., 2019), warming
(Schoepf et al., 2018) and deoxygenation (Hughes et al., 2020). It has been reported to affect the diffusion boundary layer
(i.e., a thin layer of stagnant water located around aquatic organisms) of corals, CCA and other calcareous macroalgae, altering
their ability to calcify at low pH and to excrete metabolic wastes (reviewed in Nelson and Altieri, 2019). Knowing that flow
speed could play a key role which deserves further investigations and measurements at the study site, we found two hypotheses
to explain the high diversity of the Bouraké species and their resilience to suboptimal parameters: i) the species may benefit
from the constant fluctuations of the physico-chemical parameters, ii) the species may benefit from heterotrophic inputs of
the mangrove (in term of nutrients and organic matter).

705    With regards to environmental fluctuations, we measured averaged daily variations in temperature, DO, and pH of about 3.79

706    °C, 3.80 mg L$^{-1}$, and 0.63 pH$_T$ units, respectively. Temperature changed of up to 6.55 °C on a single day. Frequent exposure

707    to stressful temperatures can induce acclimatization or adaptation in corals if the period of exposure is short enough to avoid

708    mortality (Oliver and Palumbi, 2011; Palumbi et al., 2014; Schoepf et al., 2015; Rivest et al., 2017; Safaie et al., 2018). For

709    example, in the Kimberly region (Australia), corals exposed to temperatures up to 37 °C with daily variations of up to 7 °C

710    appear less prone to bleaching and grow and calcify at rates comparable to those in more thermally stable environments

711    (Dandan et al., 2015; Schoepf et al., 2015; 2020), although they are not immune to extreme heat stress event (Le Nohaïc et

712    al., 2017). Another example is the corals in the back reef and shallow pools around the island of Ofu (American Samoa),

713    which despite occasional daily fluctuations of up to 6 °C, and an average daily temperature of 29 °C in summer (Piniak and

714    Brown, 2009; Oliver and Palumbi, 2011) sustain reasonable levels of coral cover (25 - 26 %) and high diversity (Craig et al.,

715    2001). Some studies tend to indicate that corals depended on the *a priori* 'frontloading' of genes involved in heat resistance in

716    the coral host and/or the host's ability to adjust its physiology during short-term (weeks) environmental changes (Barshis et

717    al., 2013; Palumbi et al., 2014). However, physiological adjustments have an energetic cost that corals cannot sustain in the

718    long term, affecting other metabolic functions such as calcification. It could explain in part the lower calcification rates

719    observed in some coral species, as seems to be the case for corals in the Bouraké lagoon (e.g., Camp et al., 2017). There is

720    also evidence that exposure to short-term oscillations in low pH, alone or in combination with high temperature, can mitigate

721    the impact of extreme environmental stressors on corals (Warner et al., 1996; Oliver and Palumbi, 2011; Dufault et al., 2012;

722    Schoepf et al., 2015; Safaie et al., 2018). With regard to the large seawater pH (up to 0.6 pH$_T$ units) variability, species in the

723    Bouraké lagoon appear to be thriving. In general, species exposed to $p$CO$_2$ fluctuations above 500 µatm in their natural

724    environment display enhanced plasticity to future ocean acidification scenarios (Vargas et al., 2017; Carstensen and Duarte,

725    2019). For example, fluctuations in pH could increase CCA tolerance to ocean acidification by providing respite periods at

726    low pH (Rivest et al., 2017) during which organisms can calcify at a standard rate, compensating for decreased calcification

727    during periods of lower pH (Comeau et al., 2013; Cornwall et al., 2018). Diurnal variability in pH, typical of more variable

728    pH habitats, may confer tolerance to resident calcifying species via the selection of individuals better adapted to survive in

729    these environments (Rivest et al., 2017; Kapsenberg and Cyronak, 2019), although transgenerational acclimatization is

730    required (Cornwall et al., 2020). In addition to changes in temperature and pH, which are the two most commonly tested

731    environmental parameters, oxygen must also be considered. Although the impact of reduced oxygen levels and its natural

732    fluctuations on coral reefs have yet to be established, it appears that low DO (2-4 mg L$^{-1}$) increases the sensitivity of branching

733    corals, resulting in a decline in coral health, bleaching, and tissue loss (Haas et al., 2014; Hughes et al., 2020; Alderdice et al.,

734    2021). However, our study shows that although the Bouraké system can reach conditions close to hypoxia (< 3 mg L$^{-1}$; Fig.

735    4), species seem to have promoted compensation mechanisms that allow them to survive in these conditions. The natural

736    laboratory of Bouraké, where DO fluctuates with the tide, in combination with other environmental stressors, offers a perfect

737    setting to test the practically unknown effects of deoxygenation and hypoxia thresholds in reef-building corals exposed to acid

738    and hot conditions (Nelson and Altieri, 2019; Hughes et al., 2020).

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

740    extreme conditions, a series of other physical and chemical parameters in the Bouraké lagoon may work in combination to

741    offset or enhance these effects. Mangrove habitats are highly productive ecosystems and are sites of intense carbon processing,

742    with a high potential impact on the global carbon budget (e.g., Borges et al., 2003; Dittmar et al., 2006; Bouillon et al., 2014).

743 In the Bouraké lagoon, benthic communities might have access to a range of heterotrophic inputs, nutrients, carbon and

744 nitrogen sources. These sources can be metabolized by the species to increase their energy budget and cope with the

745 suboptimal parameters, but they can also become toxic, if too concentrated, or depleted, leading to functional limitations. We

746 measured particularly high concentrations of organic and inorganic carbon and nitrogen, but also of some nutrients, notably

747 silicates and phosphorus, and we confirmed the potential contribution of the mangrove in those inputs, especially during the

748 falling tide (Fig. 8 and 9; Supplementary Fig. S1 and S2; Table 2). We found that dissolved organic carbon contributes

749 significantly to the TOC pool (POC+DOC), with an increasing concentration between the reference sites and the Bouraké

750 lagoon, reaching maximum values on the inner reef. High organic matter content can increase DOC availability to corals,

751 providing the with sustainable energy to withstand extreme environmental conditions (Levas et al., 2015). Some studies

752 showed that the high organic matter of turbid reefs can support elevated coral heterotrophy that can facilitate energy

753 maintenance during periods of stress (Anthony and Fabricius, 2000).

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

755 Indeed, $NO_x$ concentrations were higher on the outer reef, dominated by sponges, macroalgae and soft corals, while $NH_4^+$ was

756 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

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

758 sponges and macroalgae, while ammonium is the preferred source used by coral symbionts (Raven et al., 1992). While it is

759 not obvious to demonstrate experimentally the nutrient negative or positive effect on corals' physiology (Atkinson et al., 1995;

760 Szmant, 2002; Bongiorni et al., 2003). Van De Waal et al., (2009) have shown that the performance of organisms does not

761 only depend on concentrations, but also on the ratios between different nutrients, and between organic and inorganic

762 matter/components and the possible imbalance due to environmental changes. We found that the Bouraké lagoon is mostly

763 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

764 conditions observed in other New Caledonian mangroves (Jacquet et al., 2006). On the other hand, it has been experimentally

765 demonstrated that nutrient limitation lowers the temperature effect at which coral bleaching occurs (Wiedenmann et al., 2013;

766 Ezzat et al., 2016a; 2019), which is in contrast to the Bouraké coral's resilience to the warming of summer 2016 (10-20 %

767 bleaching only) compared to other reefs in New Caledonia (up to 90 % bleaching) (Benzoni et al., 2017). Corals symbionts

768 recycle their host's metabolic wastes and take up dissolved inorganic nitrogen (DIN) and phosphorus (DIP) from seawater

769 (Grover et al., 2003; Pernice et al., 2012; Rosset et al., 2015), both of which are used to produce vital organic molecules.

770 Nutrient starvation can occur when the availability of one type of essential nutrient decreases, resulting in an imbalanced N:P

771 ratio of inorganic nutrients in seawater (Wiedenmann et al., 2013; D'Angelo and Wiedenmann, 2014). Based on our

772 measurements, the N:P ratio in the Bouraké lagoon was 2.8:1 and 4.6:1 on the middle and the reference reefs, respectively,

773 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).

774 Although these data should be considered with caution, they suggest that the Bouraké lagoon seawater is not limited in

775 phosphorus, a key nutrient in coral resilience to bleaching (Rosset et al., 2017; Ezzat et al., 2016a).

776 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

777 was six times more abundant on the inner reef than elsewhere in the system (Fig. 9; Table 2). Silicates are an important source

778 of nutrition and skeletal construction for primary producers such as sponges. Orthosilicic acid is a biologically available form

779 of silicon that is poorly soluble at a very low pH. In the Bouraké lagoon, pH fluctuates with the tide, and it can be expected

780 that orthosilicic acid would rise during falling tide. This elevated concentration of orthosilicic acid could be involved in the

781    growth and persistence of the Bouraké large banks of *Rhabdastrella globostellata*, as previously reported for other sponges

782    in the shallow hydrothermal vents in the Pacific Ocean (Maldonado et al., 1999; Cárdenas and Rapp, 2013; Bertolino et al.,

783    2017).

784    We are still missing information about light, turbidity, current, bacteria biomass and phytoplankton sources as well as other

785    biological communities (e.g., fish) to fully understand this complex and dynamic system and the functioning of its coral

786    community. However, we recognize the Bouraké lagoon's uniqueness as a natural laboratory for studying the adaptive

787    responses of corals and other reef species to the combination of multiple suboptimal environmental parameters, which are

788    similar to or perhaps worse than those projected for the future. Our investigations indicate that the geomorphology of this

789    unique site has not changed for the last 80 to 100 years probably longer. With this in mind, we assume that the situation is

790    similar for environmental conditions and that the corals of the Bouraké lagoon have experienced the current extreme

791    conditions for several generations. Most importantly, the species found in the Bouraké lagoon are not unique to the mangrove

792    habitat; they are common throughout New Caledonia as well as in the SW Pacific region, suggesting that they have used

793    specific strategies to cope with the suboptimal environmental conditions.

794    We are also unsure how the different parameters will fluctuate at bay-sheltered reefs over time and under future climate

795    change conditions and if the variability measured in the Bouraké lagoon is representative of the natural fluctuations expected

796    for coastal habitats in the future. Indeed, earth system model simulations, which are mostly based on open-ocean system

797    models, project that the seasonal amplitude for pH and $p\mathrm{CO_2}$ in the future climate will increase by 81 % (Landschützer and

798    Orr, 2018) and ocean acidity extremes will be more frequent (Burger et al., 2020), which could mean that future diel pH

799    variability will increase even more at sites with the most significant variability today. If this is the case, coral reef in Bouraké

800    will face in the next decades incredible harsh environmental conditions since physical and biogeochemical parameters

801    measured in this study already exceed future climatic simulations.

802

803    **5 Conclusion**

804    We used a multi-scale approach to characterize the physical and chemical environmental parameters of one of the most

805    suitable natural analogue for future environmental conditions, the semi-enclosed lagoon of Bouraké (New Caledonia), and

806    accurately map its benthic community for the first time. We studied several physico-chemical parameters such as pH,

807    dissolved oxygen, temperature, and salinity, but also nutrients and organic matter and we found that: i) they fluctuate between

808    low and high tides, ranging from suboptimal-extreme to near normal values; ii) although predictable according to the tide,

809    they differed spatially, and iii) suboptimal values persisted longer and were more acute on the inner reef. Our data clearly

810    show that fluctuations are: i) predictable, at least for some (pH, DO, temperature and salinity) of the physical parameters for

811    which we have enough data; ii) mainly driven by the tide; and iii) that seawater nutrient imbalance and organic inputs increase

812    during the falling tide and originate from the mangrove forest and associated sediments. Although several studies suggest that

813    ocean acidification, warming and, to some extent, deoxygenation will lead to a reduction in biodiversity, increase in bleaching

814    and reef dissolution, in the Bouraké lagoon, we found a rich and healthy reef with high coral cover and species richness, but

815    also sponges and macroalgae (including CCA). It was beyond the scope of this already multidisciplinary study to assess the

816    contribution of environmental variability and nutrient imbalance to the organism' stress tolerance under extreme conditions.

817    However, both coexist in the Bouraké lagoon, and we believe there is evidence of their contribution to the survival of

818    organisms to future-like environmental conditions. Our study provides evidence that this is possible in nature, giving a

819    glimmer of hope for the future of coral reefs. Further experiments are needed to reveal the mechanisms involved in the

820    organisms' resilience to such conditions and the potential role of this unique site as a refuge for organisms threatened by

821    climate change. However, we also provides the compelling basis for using this site as a natural laboratory and to better study

822    the multitude of complex stressors acting together on life-long adapted coral reefs.

823

*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.

*Acknowledgements.* This study was supported by the" Fonds Pacifiques" and data were collected during the "Supernatural 1 & 2" missions (alis). We wish to express our thanks to captains of the IRD vessels and the diving technical staff for their fieldwork assistance. Thanks to the IRD, LAMA and LOMIC laboratories for the analysis and use their instruments and facilities. Thanks to the University of New Caledonia for the PhD fellowship project REEF-ENGINE. Thanks also to the "Province sud" for samples collection permits.

## 6 References

Agostini, S., Harvey, B. P., Wada, S., Kon, K., Milazzo, M., Inaba, K. and Hall-Spencer, J. M.: Ocean acidification drives community shifts towards simplified non-calcified habitats in a subtropical−temperate transition zone, Scientific Reports, doi:10.1038/s41598-018-29251-7, 2018.

Alderdice, R., Suggett, D. J., Cárdenas, A., Hughes, D. J., Kühl, M., Pernice, M. and Voolstra, C. R.: Divergent expression of hypoxia response systems under deoxygenation in reef-forming corals aligns with bleaching susceptibility, Global Change Biology, doi:10.1111/gcb.15436, 2021.

Anthony, K. R. N. and Fabricius, K. E.: Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity, Journal of Experimental Marine Biology and Ecology, doi:10.1016/S0022-0981(00)00237-9, 2000.

Atkinson, M. J., Carlson, B. and Crow, G. L.: Coral growth in high-nutrient, low-pH seawater: a case study of corals cultured at the Waikiki Aquarium, Honolulu, Hawaii, Coral Reefs, doi:10.1007/BF00334344, 1995.

Barkley, H. C., Cohen, A. L., Golbuu, Y., Starczak, V. R., DeCarlo, T. M. and Shamberger, K. E. F.: Changes in coral reef communities across a natural gradient in seawater pH, Science Advances, doi:10.1126/sciadv.1500328, 2015.

Barkley, H. C., Cohen, A. L., McCorkle, D. C. and Golbuu, Y.: Mechanisms and thresholds for pH tolerance in Palau corals, Journal of Experimental Marine Biology and Ecology, doi:10.1016/j.jembe.2017.01.003, 2017.

Barshis, D. J., Ladner, J. T., Oliver, T. A., Seneca, F. O., Traylor-Knowles, N. and Palumbi, S. R.: Genomic basis for coral resilience to climate change, Proceedings of the National Academy of Sciences of the United States of America, doi:10.1073/pnas.1210224110, 2013.

Bellworthy, J. and Fine, M.: Warming resistant corals from the Gulf of Aqaba live close to their cold-water bleaching threshold, , (1843), doi:10.7717/peerj.11100, 2021.

Benzoni, F., Houlbrèque, F., André, L. V. and Payri, C.: Plan d'action rapide et adaptatif en cas de blanchissement corallien : Le cas de la Nouvelle-Calédonie, épisode 2016, synthèse, Sciences de la Mer. Biologie Marine. Rapports Scientifiques et Techniques ; 6, (December), 90, 2017.

Bertolino, M., Oprandi, A., Santini, C., Castellano, M., Pansini, M., Boyer, M. and Bavestrello, G.: Hydrothermal waters enriched in silica promote the development of a sponge community in North Sulawesi (Indonesia), European Zoological

860    Journal, doi:10.1080/11250003.2016.1278475, 2017.

861    Bongiorni, L., Shafir, S., Angel, D. and Rinkevich, B.: Survival, growth and gonad development of two hermatypic corals

862    subjected to in situ fish-farm nutrient enrichment, Marine Ecology Progress Series, doi:10.3354/meps253137, 2003.

863    Borges, A. V., Djenidi, S., Lacroix, G., Théate, J., Delille, B. and Frankignoulle, M.: Atmospheric CO2 flux from mangrove

864    surrounding waters, Geophysical Research Letters, doi:10.1029/2003GL017143, 2003.

865    Bouillon, S., Yambélé, A., Gillikin, D. P., Teodoru, C., Darchambeau, F., Lambert, T. and Borges, A. V.: Contrasting

866    biogeochemical characteristics of the Oubangui River and tributaries (Congo River basin), Scientific Reports,

867    doi:10.1038/srep05402, 2014.

868    Boyd, P. W., Cornwall, C. E., Davison, A., Doney, S. C., Fourquez, M., Hurd, C. L., Lima, I. D. and McMinn, A.: Biological

869    responses to environmental heterogeneity under future ocean conditions, Global change biology, doi:10.1111/gcb.13287,

870    2016.

871    Burger, F. A., John, J. G. and Frölicher, T. L.: Increase in ocean acidity variability and extremes under increasing atmospheric

872    CO2, Biogeosciences, doi:10.5194/bg-17-4633-2020, 2020.

873    Calcinai, B., Bastari, A., Makapedua, D. M. and Cerrano, C.: Mangrove sponges from Bangka Island (North Sulawesi,

874    Indonesia) with the description of a new species, Journal of the Marine Biological Association of the United Kingdom,

875    doi:10.1017/S0025315416000710, 2017.

876    Camp, E. F., Nitschke, M. R., Rodolfo-Metalpa, R., Houlbreque, F., Gardner, S. G., Smith, D. J., Zampighi, M. and Suggett,

877    D. J.: Reef-building corals thrive within hot-acidified and deoxygenated waters, Scientific Reports, doi:10.1038/s41598-017-

878    02383-y, 2017.

879    Camp, E. F., Schoepf, V., Mumby, P. J., Hardtke, L. A., Rodolfo-Metalpa, R., Smith, D. J. and Suggett, D. J.: The future of

880    coral reefs subject to rapid climate change: Lessons from natural extreme environments, Frontiers in Marine Science,

881    doi:10.3389/fmars.2018.00004, 2018.

882    Camp, E. F., Edmondson, J., Doheny, A., Rumney, J., Grima, A. J., Huete, A. and Suggett, D. J.: Mangrove lagoons of the

883    Great Barrier Reef support coral populations persisting under extreme environmental conditions, Marine Ecology Progress

884    Series, doi:10.3354/meps13073, 2019.

885    Cárdenas, P. and Rapp, H. T.: Disrupted spiculogenesis in deep-water Geodiidae (Porifera, Demospongiae) growing in shallow

886    waters, Invertebrate Biology, doi:10.1111/ivb.12027, 2013.

887    Carstensen, J. and Duarte, C. M.: Drivers of pH Variability in Coastal Ecosystems, Environmental Science and Technology,

888    doi:10.1021/acs.est.8b03655, 2019.

889    Castillo, K. D., Ries, J. B., Weiss, J. M. and Lima, F. P.: Decline of forereef corals in response to recent warming linked to

890    history of thermal exposure, Nature Climate Change, doi:10.1038/nclimate1577, 2012.

891    Cauwet, G.: HTCO method for dissolved organic carbon analysis in seawater: influence of catalyst on blank estimation, Marine

892    Chemistry, doi:10.1016/0304-4203(94)90013-2, 1994.

893    Codiga: Unified Tidal Analysis and Prediction Using the UTide Matlab Functions, , (September), 59,

894    doi:10.13140/RG.2.1.3761.2008, 2011.

895    Comeau, S., Edmunds, P. J., Spindel, N. B. and Carpenter, R. C.: The responses of eight coral reef calcifiers to increasing partial

896    pressure of CO2 do not exhibit a tipping point, Limnology and Oceanography, doi:10.4319/lo.2013.58.1.0388, 2013.

897    Comeau, S., Cornwall, C. E., Pupier, C. A., DeCarlo, T. M., Alessi, C., Trehern, R. and McCulloch, M. T.: Flow-driven micro-

898    scale pH variability affects the physiology of corals and coralline algae under ocean acidification, Scientific Reports,
899    doi:10.1038/s41598-019-49044-w, 2019.

900    Cornwall, C. E., Comeau, S., DeCarlo, T. M., Moore, B., D'Alexis, Q. and McCulloch, M. T.: Resistance of corals and coralline
901    algae to ocean acidification: Physiological control of calcification under natural pH variability, Proceedings of the Royal
902    Society B: Biological Sciences, doi:10.1098/rspb.2018.1168, 2018.

903    Cornwall, C. E., Comeau, S., DeCarlo, T. M., Larcombe, E., Moore, B., Giltrow, K., Puerzer, F., D'Alexis, Q. and McCulloch,
904    M. T.: A coralline alga gains tolerance to ocean acidification over multiple generations of exposure, Nature Climate Change,
905    doi:10.1038/s41558-019-0681-8, 2020.

906    Craig, P., Birkeland, C. and Belliveau, S.: High temperatures tolerated by a diverse assemblage of shallow-water corals in
907    American Samoa, Coral Reefs, doi:10.1007/s003380100159, 2001.

908    Crook, E. D., Cohen, A. L., Rebolledo-Vieyra, M., Hernandez, L. and Paytan, A.: Reduced calcification and lack of
909    acclimatization by coral colonies growing in areas of persistent natural acidification, Proceedings of the National Academy
910    of Sciences of the United States of America, doi:10.1073/pnas.1301589110, 2013.

911    Crossland, C., Hatcher, B., Atkinson, M. and Smith, S.: Dissolved nutrients of a high-latitude coral reef, Houtman Abrolhos
912    Islands, Western Australia, Marine Ecology Progress Series, doi:10.3354/meps014159, 1984.

913    D'Angelo, C. and Wiedenmann, J.: Impacts of nutrient enrichment on coral reefs: New perspectives and implications for coastal
914    management and reef survival, Current Opinion in Environmental Sustainability, doi:10.1016/j.cosust.2013.11.029, 2014.

915    Dandan, S. S., Falter, J. L., Lowe, R. J. and McCulloch, M. T.: Resilience of coral calcification to extreme temperature variations
916    in the Kimberley region, northwest Australia, Coral Reefs, doi:10.1007/s00338-015-1335-6, 2015.

917    Davis, G. E.: A century of natural change in coral distribution at the Dry Tortugas: a comparison of reef maps from 1881 and
918    1976., Bulletin of Marine Science, doi:10.1016/0198-0254(82)90301-6, 1982.

919    DeCarlo, T. M., Harrison, H. B., Gajdzik, L., Alaguarda, D., Rodolfo-Metalpa, R., D'Olivo, J., Liu, G., Patalwala, D. and
920    McCulloch, M. T.: Acclimatization of massive reef-building corals to consecutive heatwaves, Proceedings of the Royal
921    Society B: Biological Sciences, doi:10.1098/rspb.2019.0235, 2019.

922    Dittmar, T., Hertkorn, N., Kattner, G. and Lara, R. J.: Mangroves, a major source of dissolved organic carbon to the oceans,
923    Global Biogeochemical Cycles, doi:10.1029/2005GB002570, 2006.

924    Dufault, A. M., Cumbo, V. R., Fan, T. Y. and Edmunds, P. J.: Effects of diurnally oscillating pCO2 on the calcification and
925    survival of coral recruits, Proceedings of the Royal Society B: Biological Sciences, doi:10.1098/rspb.2011.2545, 2012.

926    Ezzat, L., Maguer, J. F., Grover, R. and Ferrier-Pagès, C.: Limited phosphorus availability is the Achilles heel of tropical reef
927    corals in a warming ocean, Scientific Reports, doi:10.1038/srep31768, 2016a.

928    Ezzat, L., Towle, E., Irisson, J. O., Langdon, C. and Ferrier-Pagès, C.: The relationship between heterotrophic feeding and
929    inorganic nutrient availability in the scleractinian coral T. reniformis under a short-term temperature increase, Limnology and
930    Oceanography, doi:10.1002/lno.10200, 2016b.

931    Ezzat, L., Maguer, J. F., Grover, R., Rottier, C., Tremblay, P. and Ferrier-Pagès, C.: Nutrient starvation impairs the trophic
932    plasticity of reef-building corals under ocean warming, Functional Ecology, doi:10.1111/1365-2435.13285, 2019.

933    Fabricius, K. E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., Muehllehner, N., Glas, M. S.
934    and Lough, J. M.: Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations, Nature Climate
935    Change, doi:10.1038/nclimate1122, 2011.

936  Fabricius, K. E., De'ath, G., Noonan, S. and Uthicke, S.: Ecological effects of ocean acidification and habitat complexity on
937      reef-associated macroinvertebrate communities, Proceedings of the Royal Society B: Biological Sciences,
938      doi:10.1098/rspb.2013.2479, 2013.

939  Furnas, M., Mitchell, A. W. and Skuza, M.: Nitrogen and phosporus budgets for the Central Great Barrier Reef., 1995.

940  Gattuso, J. P., Magnan, A., Billé, R., Cheung, W. W. L., Howes, E. L., Joos, F., Allemand, D., Bopp, L., Cooley, S. R., Eakin,
941      C. M., Hoegh-Guldberg, O., Kelly, R. P., Pörtner, H. O., Rogers, A. D., Baxter, J. M., Laffoley, D., Osborn, D., Rankovic,
942      A., Rochette, J., Sumaila, U. R., Treyer, S. and Turley, C.: Contrasting futures for ocean and society from different
943      anthropogenic CO2 emissions scenarios, Science, doi:10.1126/science.aac4722, 2015.

944  Golbuu, Y., Gouezo, M., Kurihara, H., Rehm, L. and Wolanski, E.: Long-term isolation and local adaptation in Palau's Nikko
945      Bay help corals thrive in acidic waters, Coral Reefs, doi:10.1007/s00338-016-1457-5, 2016.

946  Grover, R., Maguer, J. F., Allemand, D. and Ferrier-Pagès, C.: Nitrate uptake in the scleractinian coral Stylophora pistillata,
947      Limnology and Oceanography, doi:10.4319/lo.2003.48.6.2266, 2003.

948  Haas, A. F., Smith, J. E., Thompson, M. and Deheyn, D. D.: Effects of reduced dissolved oxygen concentrations on physiology
949      and fluorescence of hermatypic corals and benthic algae, PeerJ, doi:10.7717/peerj.235, 2014.

950  Hall-Spencer, J. M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S. M., Rowley, S. J., Tedesco, D. and
951      Buia, M. C.: Volcanic carbon dioxide vents show ecosystem effects of ocean acidification, Nature, doi:10.1038/nature07051,
952      2008.

953  Hill, J. and Wilkinson, C.: Methods for ecological monitoring of coral reefs - A Resource for Managers, Australian Institute of
954      Marine Science, 2004.

955  Hoegh-Guldberg, O. and Fine, M.: Low temperatures cause coral bleaching, Coral Reefs, doi:10.1007/s00338-004-0401-2,
956      2004.

957  Hoegh-Guldberg, O., Fine, M., Skirving, W., Johnstone, R., Dove, S. and Strong, A.: Coral bleaching following wintry weather,
958      Limnology and Oceanography, doi:10.4319/lo.2005.50.1.0265, 2005.

959  Holmes, R. M., Aminot, A., Kérouel, R., Hooker, B. A. and Peterson, B. J.: A simple and precise method for measuring
960      ammonium in marine and freshwater ecosystems, Canadian Journal of Fisheries and Aquatic Sciences, doi:10.1139/f99-128,
961      1999.

962  Hughes, D. J., Alderdice, R., Cooney, C., Kühl, M., Pernice, M., Voolstra, C. R. and Suggett, D. J.: Coral reef survival under
963      accelerating ocean deoxygenation, Nature Climate Change, doi:10.1038/s41558-020-0737-9, 2020.

964  Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., Baird, A. H., Baum, J. K., Berumen,
965      M. L., Bridge, T. C., Claar, D. C., Eakin, C. M., Gilmour, J. P., Graham, N. A. J., Harrison, H., Hobbs, J. P. A., Hoey, A. S.,
966      Hoogenboom, M., Lowe, R. J., McCulloch, M. T., Pandolfi, J. M., Pratchett, M., Schoepf, V., Torda, G. and Wilson, S. K.:
967      Spatial and temporal patterns of mass bleaching of corals in the Anthropocene, Science, doi:10.1126/science.aan8048, 2018.

968  Hurd, C. L.: Slow-flow habitats as refugia for coastal calcifiers from ocean acidification, Journal of Phycology,
969      doi:10.1111/jpy.12307, 2015.

970  Iglesias-Prieto, R., Galindo-Martínez, C. T., Enríquez, S. and Carricart-Ganivet, J. P.: Attributing reductions in coral
971      calcification to the saturation state of aragonite, comments on the effects of persistent natural acidification, Proceedings of
972      the National Academy of Sciences of the United States of America, doi:10.1073/pnas.1318521111, 2014.

973  IPCC: Climate Change 2014 Synthesis Report - IPCC., 2014.

974 Jacquet, S., Delesalle, B., Torréton, J. P. and Blanchot, J.: Response of phytoplankton communities to increased anthropogenic

975 influences (southwestern lagoon, New Caledonia), Marine Ecology Progress Series, doi:10.3354/meps320065, 2006.

976 Justić, D., Rabalais, N. N., Turner, R. E. and Dortch, Q.: Changes in nutrient structure of river-dominated coastal waters:

977 Stoichiometric nutrient balance and its consequences, Estuarine, Coastal and Shelf Science, doi:10.1016/S0272-

978 7714(05)80014-9, 1995.

979 Kapsenberg, L. and Cyronak, T.: Ocean acidification refugia in variable environments, Global Change Biology,

980 doi:10.1111/gcb.14730, 2019.

981 Kemp, D. W., Oakley, C. A., Thornhill, D. J., Newcomb, L. A., Schmidt, G. W. and Fitt, W. K.: Catastrophic mortality on

982 inshore coral reefs of the Florida Keys due to severe low-temperature stress, Global Change Biology, doi:10.1111/j.1365-

983 2486.2011.02487.x, 2011.

984 Kerrison, P., Hall-Spencer, J. M., Suggett, D. J., Hepburn, L. J. and Steinke, M.: Assessment of pH variability at a coastal CO2

985 vent for ocean acidification studies, Estuarine, Coastal and Shelf Science, doi:10.1016/j.ecss.2011.05.025, 2011.

986 Kroeker, K. J., Micheli, F., Gambi, M. C. and Martz, T. R.: Divergent ecosystem responses within a benthic marine community

987 to ocean acidification, Proceedings of the National Academy of Sciences, doi:10.1073/pnas.1107789108, 2011.

988 Kurihara, H., Suhara, Y., Mimura, I. and Golbuu, Y.: Potential Acclimatization and Adaptive Responses of Adult and Trans-

989 Generation Coral Larvae From a Naturally Acidified Habitat, Frontiers in Marine Science, doi:10.3389/fmars.2020.581160,

990 2020.

991 Leopold, A., Marchand, C., Deborde, J. and Allenbach, M.: Water Biogeochemistry of a Mangrove-Dominated Estuary Under

992 a Semi-Arid Climate (New Caledonia), Estuaries and Coasts, doi:10.1007/s12237-016-0179-9, 2017.

993 Levas, S., Grottoli, A. G., Warner, M. E., Cai, W. J., Bauer, J., Schoepf, V., Baumann, J. H., Matsui, Y., Gearing, C., Melman,

994 T. F., Hoadley, K. D., Pettay, D. T., Hu, X., Li, Q., Xu, H. and Wang, Y.: Organic carbon fluxes mediated by corals at elevated

995 pCO2 and temperature, Marine Ecology Progress Series, doi:10.3354/meps11072, 2015.

996 Maldonado, M., Carmona, M. C., Uriz, M. J. and Cruzado, A.: Decline in Mesozoic reef-building sponges explained by silicon

997 limitation, Nature, doi:10.1038/44560, 1999.

998 Manzello, D. P., Kleypas, J. A., Budd, D. A., Eakin, C. M., Glynn, P. W. and Langdon, C.: Poorly cemented coral reefs of the

999 eastern tropical Pacific: Possible insights into reef development in a high-CO2 world, Proceedings of the National Academy

1000 of Sciences of the United States of America, doi:10.1073/pnas.0712167105, 2008.

1001 Mayfield, A. B. and Gates, R. D.: Osmoregulation in anthozoan-dinoflagellate symbiosis, Comparative Biochemistry and

1002 Physiology - A Molecular and Integrative Physiology, doi:10.1016/j.cbpa.2006.12.042, 2007.

1003 Milazzo, M., Rodolfo-Metalpa, R., Chan, V. B. S., Fine, M., Alessi, C., Thiyagarajan, V., Hall-Spencer, J. M. and Chemello,

1004 R.: Ocean acidification impairs vermetid reef recruitment, Scientific Reports, doi:10.1038/srep04189, 2014.

1005 Nagelkerken, I., Blaber, S. J. M., Bouillon, S., Green, P., Haywood, M., Kirton, L. G., Meynecke, J. O., Pawlik, J., Penrose, H.

1006 M., Sasekumar, A. and Somerfield, P. J.: The habitat function of mangroves for terrestrial and marine fauna: A review, Aquatic

1007 Botany, doi:10.1016/j.aquabot.2007.12.007, 2008.

1008 Nelson, H. R. and Altieri, A. H.: Oxygen: the universal currency on coral reefs, Coral Reefs, doi:10.1007/s00338-019-01765-

1009 0, 2019.

1010 Le Nohaïc, M., Ross, C. L., Cornwall, C. E., Comeau, S., Lowe, R., McCulloch, M. T. and Schoepf, V.: Marine heatwave

1011 causes unprecedented regional mass bleaching of thermally resistant corals in northwestern Australia, Scientific Reports,

1012    doi:10.1038/s41598-017-14794-y, 2017.

1013    Oliver, T. A. and Palumbi, S. R.: Do fluctuating temperature environments elevate coral thermal tolerance?, Coral Reefs,
1014    doi:10.1007/s00338-011-0721-y, 2011.

1015    Palumbi, S. R., Barshis, D. J., Traylor-Knowles, N. and Bay, R. A.: Mechanisms of reef coral resistance to future climate
1016    change, Science, doi:10.1126/science.1251336, 2014.

1017    Paytan, A., Crook, E. D., Cohen, A. L., Martz, T. R., Takashita, Y., Rebolledo-Vieyra, M. and Hernandez, L.: Reply to Iglesias-
1018    Prieto et al.: Combined field and laboratory approaches for the study of coral calcification, Proceedings of the National
1019    Academy of Sciences of the United States of America, doi:10.1073/pnas.1319572111, 2014.

1020    Pernice, M., Meibom, A., Van Den Heuvel, A., Kopp, C., Domart-Coulon, I., Hoegh-Guldberg, O. and Dove, S.: A single-cell
1021    view of ammonium assimilation in coral-dinoflagellate symbiosis, ISME Journal, doi:10.1038/ismej.2011.196, 2012.

1022    Pichler, T., Biscéré, T., Kinch, J., Zampighi, M., Houlbrèque, F. and Rodolfo-Metalpa, R.: Suitability of the shallow water
1023    hydrothermal system at Ambitle Island (Papua New Guinea) to study the effect of high pCO2 on coral reefs, Marine Pollution
1024    Bulletin, doi:10.1016/j.marpolbul.2018.11.003, 2019.

1025    Pierrot, D., Lewis, E. and Wallace, D. W. R.: MS Excel program developed for CO2 system calculations, in ORNL/CDIAC-
1026    105a. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge,
1027    Tennessee., 2006.

1028    Piniak, G. A. and Brown, E. K.: Temporal variability in chlorophyll fluorescence of back-reef corals in Ofu, American Samoa,
1029    Biological Bulletin, doi:10.1086/BBLv216n1p55, 2009.

1030    Porter, J. W., Battey, J. F. and Smith, G. J.: Perturbation and change in coral reef communities, Proceedings of the National
1031    Academy of Sciences, doi:10.1073/pnas.79.5.1678, 1982.

1032    Raven, J. A., Wollenweber, B. and Handley, L. L.: A comparison of ammonium and nitrate as nitrogen sources for
1033    photolithotrophs, New Phytologist, doi:10.1111/j.1469-8137.1992.tb01088.x, 1992.

1034    Rivest, E. B., Comeau, S. and Cornwall, C. E.: The Role of Natural Variability in Shaping the Response of Coral Reef
1035    Organisms to Climate Change, Current Climate Change Reports, doi:10.1007/s40641-017-0082-x, 2017.

1036    Rogers, C. S.: A unique coral community in the mangroves of Hurricane Hole, St. John, US Virgin Islands, Diversity,
1037    doi:10.3390/d9030029, 2017.

1038    Rosset, S., D'Angelo, C. and Wiedenmann, J.: Ultrastructural biomarkers in symbiotic algae reflect the availability of dissolved
1039    inorganic    nutrients    and    particulate    food    to    the    reef    coral    holobiont,    Frontiers    in    Marine    Science,
1040    doi:10.3389/fmars.2015.000103, 2015.

1041    Rosset, S., Wiedenmann, J., Reed, A. J. and D'Angelo, C.: Phosphate deficiency promotes coral bleaching and is reflected by
1042    the ultrastructure of symbiotic dinoflagellates, Marine Pollution Bulletin, doi:10.1016/j.marpolbul.2017.02.044, 2017.

1043    Safaie, A., Silbiger, N. J., McClanahan, T. R., Pawlak, G., Barshis, D. J., Hench, J. L., Rogers, J. S., Williams, G. J. and Davis,
1044    K. A.: High frequency temperature variability reduces the risk of coral bleaching, Nature Communications,
1045    doi:10.1038/s41467-018-04074-2, 2018.

1046    Saxby, T., Dennison, W. C. and Hoegh-Guldberg, O.: Photosynthetic responses of the coral Montipora digitata to cold
1047    temperature stress, Marine Ecology Progress Series, doi:10.3354/meps248085, 2003.

1048    Schoepf, V., Stat, M., Falter, J. L. and McCulloch, M. T.: Limits to the thermal tolerance of corals adapted to a highly
1049    fluctuating, naturally extreme temperature environment, Scientific Reports, doi:10.1038/srep17639, 2015.

1050   Schoepf, V., Cornwall, C. E., Pfeifer, S. M., Carrion, S. A., Alessi, C., Comeau, S. and McCulloch, M. T.: Impacts of coral
1051      bleaching on pH and oxygen gradients across the coral concentration boundary layer: a microsensor study, Coral Reefs,
1052      doi:10.1007/s00338-018-1726-6, 2018.

1053   Schoepf, V., Jung, M. U., McCulloch, M. T., White, N. E., Stat, M. and Thomas, L.: Thermally Variable, Macrotidal Reef
1054      Habitats Promote Rapid Recovery From Mass Coral Bleaching, Frontiers in Marine Science, doi:10.3389/fmars.2020.00245,
1055      2020.

1056   Shamberger, K. E. F., Lentz, S. J. and Cohen, A. L.: Low and variable ecosystem calcification in a coral reef lagoon under
1057      natural acidification, Limnology and Oceanography, doi:10.1002/lno.10662, 2018.

1058   Soares, M. de O.: Marginal reef paradox: A possible refuge from environmental changes?, Ocean and Coastal Management,
1059      doi:10.1016/j.ocecoaman.2019.105063, 2020.

1060   Sugimura, Y. and Suzuki, Y.: A high-temperature catalytic oxidation method for the determination of non-volatile dissolved
1061      organic carbon in seawater by direct injection of a liquid sample, Marine Chemistry, doi:10.1016/0304-4203(88)90043-6,
1062      1988.

1063   Sunday, J. M., Fabricius, K. E., Kroeker, K. J., Anderson, K. M., Brown, N. E., Barry, J. P., Connell, S. D., Dupont, S., Gaylord,
1064      B., Hall-Spencer, J. M., Klinger, T., Milazzo, M., Munday, P. L., Russell, B. D., Sanford, E., Thiyagarajan, V., Vaughan, M.
1065      L. H., Widdicombe, S. and Harley, C. D. G.: Ocean acidification can mediate biodiversity shifts by changing biogenic habitat,
1066      Nature Climate Change, doi:10.1038/nclimate3161, 2017.

1067   Szmant, A. M.: Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline?, Estuaries,
1068      doi:10.1007/BF02804903, 2002.

1069   Teixidó, N., Gambi, M. C., Parravacini, V., Kroeker, K., Micheli, F., Villéger, S. and Ballesteros, E.: Functional biodiversity
1070      loss along natural CO2 gradients, Nature Communications, 9(1), 5149, doi:10.1038/s41467-018-07592-1, 2018.

1071   Vargas, C. A., Lagos, N. A., Lardies, M. A., Duarte, C., Manríquez, P. H., Aguilera, V. M., Broitman, B., Widdicombe, S. and
1072      Dupont, S.: Species-specific responses to ocean acidification should account for local adaptation and adaptive plasticity,
1073      Nature Ecology and Evolution, doi:10.1038/s41559-017-0084, 2017.

1074   Varillon D., Fiat S., Magron F., Allenbach M., Hoibian T., de Ramon N'Yeurt A., Ganachaud A., Aucan J., Pelletier B., H. R.:
1075      ReefTEMPS : The Pacific Island coastal ocean observation network, , doi:https://doi.org/10.17882/55128, 2021.

1076   Veron, J. E. N. and Wallace, C. C.: Scleractinia of Eastern Australia – Part V. Family Acroporidae, Australian Institute of
1077      Marine Science, Monograph, Series 6: 1–485, 1984.

1078   Veron, J. E. N.: Corals of the world, Institute of Marine Science. Townsville, 11, Corals of the World, 2000.

1079   Vizzini, S., Di Leonardo, R., Costa, V., Tramati, C. D., Luzzu, F. and Mazzola, A.: Trace element bias in the use of CO2 vents
1080      as analogues for low pH environments: Implications for contamination levels in acidified oceans, Estuarine, Coastal and Shelf
1081      Science, doi:10.1016/j.ecss.2013.09.015, 2013.

1082   Van De Waal, D. B., Verspagen, J. M. H., Lürling, M., Van Donk, E., Visser, P. M. and Huisman, J.: The ecological
1083      stoichiometry of toxins produced by harmful cyanobacteria: An experimental test of the carbon-nutrient balance hypothesis,
1084      Ecology Letters, doi:10.1111/j.1461-0248.2009.01383.x, 2009.

1085   Wall, C. B., Ricci, C. A., Wen, A. D., Ledbetter, B. E., Delania, E., Mydlarz, L. D., Gates, R. D. and Putnam, H. M.: Shifting
1086      Baselines: Physiological legacies contribute to the response of reef coral to frequent heat waves, bioRxiv, 1–47,
1087      doi:https://doi.org/10.1101/2020.04.23.056457, 2020.

1088 Wallace, C. C.: Staghorn corals of the world: a revision of the coral genus Acropora (Scleractinia; Astrocoeniina; Acroporidae)
1089    worldwide, with emphasis on morphology, phylogeny and biogeography, Choice Reviews Online, CSIRO, Collingwood,
1090    1999.
1091 Ward, J. H.: Hierarchical Grouping to Optimize an Objective Function, Journal of the American Statistical Association,
1092    doi:10.1080/01621459.1963.10500845, 1963.
1093 Warner, M. E., Fitt, W. K. and Schmidt, G. W.: The effects of elevated temperature on the photosynthetic efficiency of
1094    zooxanthellae in hospite from four different species of reef coral: A novel approach, Plant, Cell and Environment,
1095    doi:10.1111/j.1365-3040.1996.tb00251.x, 1996.
1096 Wiedenmann, J., D'Angelo, C., Smith, E. G., Hunt, A. N., Legiret, F. E., Postle, A. D. and Achterberg, E. P.: Nutrient
1097    enrichment can increase the susceptibility of reef corals to bleaching, Nature Climate Change, doi:10.1038/nclimate1661,
1098    2013.
1099 Wittmann, A. C. and Pörtner, H. O.: Sensitivities of extant animal taxa to ocean acidification, Nature Climate Change,
1100    doi:10.1038/nclimate1982, 2013.
1101 Yates, K. K., Rogers, C. S., Herlan, J. J., Brooks, G. R., Smiley, N. A. and Larson, R. A.: Diverse coral communities in
1102    mangrove habitats suggest a novel refuge from climate change, Biogeosciences, doi:10.5194/bg-11-4321-2014, 2014.
1103