

Reply to Rev. #1

This work is very detailed chemically, physically and biologically. It provides very accurate temporal measurements and data that characterize the Bouraké semi-enclosed lagoon of New Caledonia quite well. Consequently, although quite extensive, it is seem a good paper that address relevant scientific question for this journal. However, based on their results, I do not agree with the authors' assertion that this area is a natural analogue to the future affected by climate change.

Response: We really thank Rev. #1 for her/his appreciation of our study and for considering our manuscript suitable for publication in Biogeosciences. We also thank Rev. #1 for the constructive comments.

We agree that it is difficult or even impossible to find what can be correctly called “a natural analogue for future conditions”. Indeed, the definition of “natural analogues” has always been an issue, since the first time (Hall-Spencer et al., 2008, Nature) we proposed CO₂ vents for this role (comments by R. Rodolfo-Metalpa). A real “natural analogues” does not exist and honestly it is pure speculation as we do not know what the future will be, especially for a coastal reef where not only the most classic environmental drivers will fluctuate (one of the parameters that modern models do not take in account), but the environment will be affected by a combination of factor which has never been considered in our bench experiments. Among them, increasing turbidity, increasing organic and nutrient inputs, etc. We agree with you. Natural analogue is incorrect, and we will change it throughout the ms and in the title. However, it would be inexact to say that mangrove systems, particularly the mangrove system of Bouraké, cannot be used to study the future effect of CC on organisms *in situ*. Once we admit that conditions are even worse than expected in the future, once we show their variability, once we drastically smooth our predictions based on evidences from our natural lab, we firmly believe that the mangrove area we are using is much better than other largely accepted “natural analogues” because it offers a realistic combination of drivers that will (more or less) characterise future reefs.

Specific comments

The methods used here are well development and valid. The results support most of the conclusions (see comment below). The authors describe in great detail the measurements taken and the calculations performed, sufficiently for reproduction, and generate interesting results that are well represented by the corresponding figures and tables.

Response: We would like to thank Rev #1 to highlight the validity of our methods, the large amount of data collected and analyzed and the well representation of the results.

As the authors have pointed out, this work describes a "natural laboratory" of great scientific interest. However, the authors have described the mangrove of New Caledonia as a place with the characteristics "analogous to future climate change" and in my opinion this term is incorrect.

Response: We corrected it through the ms (see below).

Although the CO₂ seeps are considered to be analogous to future conditions, due to the extra input of CO₂-rich volcanic gases. This does not apply to the mangrove described in this paper. The results presented in this paper affirm that in addition to the chemical parameters typical of climate change (CC) studies, there are numerous external elements that are affecting the living things that live in the mangrove. When we talk about a natural laboratory to study the effect of climate change, we are talking about a place where we can study the future effect of CC on organisms in situ and in my opinion it is not possible to do this in mangrove areas.

Response: In our understanding, the Rev. #1 affirms that mangrove areas do not mimic future CC conditions while CO₂ seeps do. The phrase: “input of CO₂-rich volcanic gases” suggests us that the reason is the lack of CO₂ injection in the mangrove: i.e., the increase in CO₂ in the mangrove is chemical (likely due to a combination of mechanisms in the sediment; we did not discuss the mechanisms, just reported the data) and not directly due to a CO₂ input such as in the seeps. We agree, but the result is very similar even better than CO₂ seeps. For instance, at our site we showed that carbonate chemistry is variable according to the tide but largely predictable, and it does not radically and suddenly change as at seeps due to the effect of wind and current. In addition, the averaged total alkalinity measured, although significantly different between stations, only varied from 2256 to 2393 $\mu\text{mol Kg}^{-1}$ (see Table 2), so the chemical change does not affect it, which is important when mimicking future conditions.

That said, it is still a very interesting place as a natural laboratory. I agree that it is a special place to see the adaptation of corals and other living organisms to extreme environments. Therefore, I suggest that the authors change the comments related to being "analogous to future climate change", both in the title (see below), abstract (e.g. lines 17-19), introduction (e. g. lines 50-51), discussion (e.g. 562, 788) and conclusions (lines 804-805).

Response: We changed the term “natural analogue” with “natural laboratory” as:

Abstract.

L 19: “Although they do not perfectly mimic future conditions, these natural laboratories provide unique opportunities to explore how reef species could keep pace with climate change”.

L 36: “We describe the natural dynamics of the Bouraké ecosystem and its relevance as a natural laboratory to investigate the benthic organism’s adaptive responses to multiple extreme environmental conditions”.

Introduction.

L50: “These sites may be used as natural laboratories of future climatic conditions when at least one or more environmental parameters naturally mimic climate change-like conditions over a large area of the ecosystem”.

L 89: “The semi-enclosed lagoon of Bouraké (New Caledonia, SW Pacific Ocean) has been put forward to be as one of the most suitable natural laboratory to study the effects of future extreme environmental conditions (Camp et al., 2019)”.

Discussion.

L 562: “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 and extreme conditions”.

L804-805: “We used a multi-scale approach to characterize the physical and chemical environmental parameters of one of the most suitable natural laboratory for extreme environmental conditions, the semi-enclosed lagoon of Bouraké (New Caledonia), and accurately map its benthic community for the first time”.

Again, I want to emphasize the idea that these mangroves can be considered as tools for species conservation in the future that we will face due to climate change and human activity, and this can be commented on in the discussion perfectly well (which the authors have already done).

Response: We really thank Rev. #1. We intentionally avoided in the discussion all statements that could be considered too speculative.

Ergo, after reading the content of the article and knowing its results, I recommend to the authors a change of title: “The Bouraké semi- enclosed lagoon (New Caledonia). A natural laboratory to study the life-long adaptation of a coral reef ecosystem to extreme ambient conditions” or something like that.

Response: We changed the title with: “The Bouraké semi- enclosed lagoon (New Caledonia). A natural laboratory to study the life-long adaptation of a coral reef ecosystem to extreme environmental conditions”.

On the other hand, I have noticed some lack of bibliography in the discussion, as in the lines 562, 564, 610, 623, 653 comments that would be better if they were supported by the corresponding literature. I would also like to add my recommendation in line 657, I could replace the citation from Teixidó (paper on species diversity in the Mediterranean) by any other work related to corals or sponges in tropical seas, for examples, Enochs et al., 2015 nature climate change letters.

Response: We have added the requested bibliography at each suggested point. We also agree to add the citation (e.g., Enochs et al., 2015), which is more specific to tropical coral reef.

Technical corrections:

Although Figure 10 is added at the end with which the map was made and the source of the photographs, this information is missing in Figure 1. It is recommended to add the following information to Figure 1.

Response: We have added the required information.

Lines 236 and 237, in situ and in vitro should be in italic.

Response: Done.

Line 589 remove additional “(“.

Response: Done.

Reply to Rev. #2

Response: We really thank Rev. #2, and we were delighted to read her/his comments. We agree and changed accordingly, although we strongly believe that rapid physiological plasticity, and not an adaptation, could have a key role in corals to counteract the rapid climate change.

This research provides a detailed physical and biogeochemical characterization of a semi-enclosed coral reef lagoon in New Caledonia, remarkable for the presence of a diverse and healthy coral reef ecosystem. The authors carried out systematic sampling over a three years period, accomplishing the local characterization of diel and seasonal fluctuations. This work is definitively a valuable contribution to baseline knowledge of environmental conditions in natural laboratories, which can greatly contribute to shed light on the drivers of the biological responses of local organisms. Nevertheless, I have to draw the attention of the authors in two issues. The first one was already addressed by Referee1 (RC1) and I fully agree with RC1 that this site can't be claimed as a natural analogue to future climate change conditions. However, since RC1 already provided a detailed argumentation on this regard, my comment about this will be very general. The second issue I must comment on, is the claim that local adaptation of these coral species could hold new hope for the future of coral reefs in general. I explain my position in detail in the "Specific comments" section.

Response: We thank Rev. #2 for recognising our study as a valuable contribution toward a better understanding of organisms' response to extreme environmental conditions.

We fully agree that it was inappropriate to define our natural laboratory as a natural analogue for future conditions (natural analogues do not exist). We partially agree that local adaptation (if any) of the local corals could not hold new hope for the future (see below). While we agree and we thanks Rev. #2, it is important to note that our study aimed to describe the environmental fluctuations and give an extensive description of this unique natural laboratory. We certainly speculated on its potential use to address coral response to climate change, but this has only been evoked a few times throughout the ms.

2. SPECIFIC COMMENTS (individual scientific questions/issues)

- In general terms, the overall text could benefit from a better synthesis of ideas.

Response: We revised the whole ms, and we thank both Rev. #1 and #2's comments. We have better organised our ideas about the relevance of this site to study the response of corals to environmental change.

- Along all the manuscript, it's advice to use "extreme environmental conditions" instead of "climate change-like conditions".

Response: We changed it, also accordingly to Rev. #1.

- I fully agree that coral reefs growing on extreme environments are remarkable and perfect natural laboratories to study local adaptation. However, I disagree with the idea of using these ecosystems to predict the general response of coral reefs under future projected changes, as the rate of change is totally different (different time scales).

The fact that some coral species currently thrive in extreme environments (such as volcanic CO vents, semi-enclosed lagoons and mangrove estuaries) resulted from an extensive period of

exposition to these particular conditions, therefore adaptation. This is not the case under future projections, where the exposition time will be considerably shorter and it is very likely that coral species growing on “more stable” environments (other than volcanic CO vents, semi-enclosed lagoons and mangrove estuaries) won’t be able to adapt to this rate of change. And even if they do, probably it would be due to acclimation but not necessarily adaptation.

Response: Respectfully, we believe that adaptation in corals might be much faster than previously thought. Coral adaptation is a timely and debated field of research and we recognise that pieces of evidence are scant. However, microbiome’s role in the coral host adaptation (e.g., Woolstra and Ziegler 2020, *BioEssays*) have been already largely demonstrated. Several studies showed that plasticity in some physiological traits might be heritable and help corals cope with the rapid environmental change (e.g., Donelson et al. 2017, *Global Change Biology*; Torda et al. 2017, *Nature Climate Change*; Putnam 2021, *Journal of Experimental Biology*).

We agree that corals in Bouraké have been exposed for a long period (i.e., certainly > 80 y) to similar conditions and such long exposure might allow them eventually to adapt (which would be great). However, it is not so simply since Bouraké is an open system and larvae can come from outside, where the conditions are at ambient level. It is always tricky to affirm if they have adapted through a multi-generation selection or acclimated just within a generation. We will never be able to correctly test the effect of climate change until we find a natural magic lab that started *ca.* 100 y ago gradually, but fast as projected, to change in at least the main environmental parameters. With such magic lab, and with the certainty that larvae from surrounding normal conditions do not set into this site, we would be able to affirm that corals can adapt (or acclimate, and this would be even better than an adaptation) to climate change.

All this said and taking into account a recent publication regarding persistence of coral reefs under future ocean acidification and warming conditions (Cornwall et al. 2021, PNAS), I disagree with the authors (lines 16-17) when they state that the sole presence of “diverse and high cover reefs that already thrive under extreme conditions” contradict the projections of coral reefs disappearing under the CO2 business-as-usual scenario.

Response: We used this sentence once, in the abstract. We wrote: “*..seems to contradict these projections*” and respectfully is not wrong when looking to the extreme conditions where they live. However, we smoothed this sentence in “*However, recent discoveries of diverse and high cover reefs that already thrive under extreme conditions seem to suggest that some corals might be able to thrive well under hot, high pCO₂ and deoxygenated seawater*”. With regard to the recent awesome study by Cornwall, Comeau et al. (2021), their models on existing data from lab and field-based experiments to real reef showed that future climatic projections would cause the decline of coral reef, mostly due to the reduced coral cover due to bleaching event and subsequent mortality. What this study does not consider (because the lack of robust evidence) is the ability to rapidly adapt to climate change. This study assumes that “*The fast rate of environmental change relative to the time required for adaptation suggests it will be difficult for corals to maintain their current role, especially those with longer generation times*”. Respectfully, this does not take into account recent findings on the potential ability of corals to adapt rapidly. We understood, thanks to the Reviewers’ comments that we were wrong saying that our results can be used as a model to study future response to climate change, and we changed the ms accordingly.

Even if you bear to consider these special sites as future analogues to future conditions, you must keep in mind that these coral species with high diversity and coral cover are thriving

because they were able to adapt to these local environmental conditions over a long time scale. Therefore, they won't be a good worldwide model to "explore how reefs could keep pace with climate change" (lines 19-20). The way as I see it, you are dealing with two different issues: in one hand you have the physical location per se (site), which could be a great natural scenario to explore how coral species would respond to future-like conditions, by transplanting coral species from other "stable" locations. And on the other hand, you can study the adaptation of the local coral species currently living on these natural laboratories. But you can't extrapolate the response of all coral reefs to future conditions by using these local "super corals" broad as models.

Response: We agree that this unique site (as all unique areas found so far) is not an analogue to future conditions. We also agree that corals at such natural laboratories are not an excellent worldwide model to explore how reefs could keep pace with climate change. It currently seems to be a normal practice in the literature to extrapolate the response of coral reefs worldwide from a single site, mechanisms, species or general findings (examples could be numerous). We made our best to avoid such speculation in the revised ms. Many thanks to the Reviewers. About the experiments suggested, both are underway.

Based on their results, the authors can definitively draw a future projection for the Bouraké coral reefs. But they must be cautious and restrain themselves from extrapolating these conclusions to coral reefs in general (L818-819).

Response: The sentence of conclusions said: *"It was beyond the scope of this already multidisciplinary study to assess the contribution of environmental variability and nutrient imbalance to the organism's stress tolerance under extreme conditions. However, both coexist in the Bouraké lagoon, and we believe there is evidence of their contribution to the survival of organisms to future-like environmental conditions. Our study provides evidence that this is possible in nature, giving a glimmer of hope for the future of coral reefs."* This sentence is correct and does not speculate over the future of coral reefs worldwide. At the same time, we agree to change future-like env. conditions with extreme env. Conditions. We prefer to maintain this sentence as it is, since we showed that survival is possible under extreme conditions, and this definitely gives a glimmer (not the certitude) of hope for the future of coral reefs. This study, as we mentioned, was not designed to investigate the mechanisms that allow organisms to survive in Bouraké, but what if we will demonstrate that they are not adapted and that their resistance is only physiological? Or that their microbiome itself allows them to survive? We see it as hope.

Additionally, precaution must be taken when drawing conclusions for these potential refuges (lines 98-99). It's true that these coral species can cope with a great environmental variability and thrive under extreme conditions. However, this not necessarily means that they will survive under future changes, as it's also possible that they are already living close to their environmental threshold and future conditions might push them beyond it (see Sánchez-Noguera et al. 2018, Biogeosciences). For example, this site already presents low-pH conditions as expected under climate change projections, but it's very likely that the pH values will continue decreasing in the future due to buffer capacity (TA) of its waters. Therefore, despite these corals thrive under current low-pH conditions, probably they will experience lower pH values (or "harsh conditions" as the authors state in L799-801) as CO2 uptake continues.

Response: The Reviewer is right. We removed this pure speculation from the ms. Many thanks.

Material and methods

Glass electrodes (as the one from the Metrohm pHmeter and the SeaFET) are not very accurate and it's valuable that the authors carried out a calibration with TRIS buffer. Nevertheless, on top of the TRIS calibration, it's strongly advised that the authors validate their surface pH measurements with pH values calculated from TA and DIC samples.

Response: We are a bit confused. We are quite sure that the SeaFET does not use glass electrodes but a new generation of electrode (ISFET, Martz et al. 2010, *Limnology and Oceanography Methods*). This kind of electrode reads stable and accurate pH even during long-term deployments (i.e., the effect of biofouling) and without an additional calibration (Bresnahan et al. 2014, *Methods in Oceanography*). Among the three SeaFET we used (L140) “Two SeaFETs were calibrated by the manufacturer, while the third was corrected before deployment by measuring its deviation from the two others in the same seawater.” Likely, it would always be a best practice to check values also using another method such as the spectrophotometer technique, but if we consider the large variation in pH measured at the site, even if our measurements have a 0.05 pH error, results do not change. Concerning the seawater pH measurements, we did during the diel cycles in 2017 and 2019, and the use of a glass electrode coupled with a Metrohm pHMeter. We thought that having the Rolls Royce of the Metrohm electrodes (>1,000 euro the probe) and Tris calibration was enough as a guarantee of high accuracy. Our data did not differ from the range already measured in Camp et al. (2017, *Scientific reports*) for the same stations.

As suggested, we re-calculated pH with the Seacarb R package using TA, DIC, temperature, and a mean salinity of 35 since we did not measure it in parallel with the other parameters. Surprisingly, our results were consistently different from one we measured using the Metrohm probe and definitely far from reality. While at the control, where we should expect a typical ambient seawater pH, only few data were close to pH 8, and most of them around 7.7-7.8, at Bouraké pH was a couple of times 8.3 (too high) and down to 6.8 (too low). These differences could be due to several factors. Firstly, accurately measuring DIC and TA is not so easy, from the sample collection, through the sample preservation, and to its measurement. While we are pretty sure about the TA measurement since we used accurate standards, the DIC samples had to be sent overseas in France to be measured. In addition, we did not measure salinity, which might affect the recalculation of pH. This can affect the calculation. Secondly, another unexplored source of incertitude could be the chemical of the seawater in Bouraké, with high organic content, which could change the seawater carbonate chemistry, but this should not affect the control. We are terribly sorry we could not be able to validate our measurements using a different calculation as suggested. However, SeaFET loggers are accurate instruments worldwide validated. These data perfectly validated the pH measurements we made using an accurate glass electrode, calibrated using Dickson tris buffers. All these data are in agreement with data already presented for the same stations by Camp et al. (2017).

Discussion

- *L577-580: the last two sentences fit better in section 4.2, as section 4.1 focuses on physical and chemical characteristics of the lagoon but not the species responses.*

Response: We agree, and we moved the whole sentence in section 4.2 as suggested also improving the discussion about the effect of high and variable salinity on corals.

- *Line 583: suggest replacing “occasionally more than 25°C” by the range of temperature measured during winter.*

Response: It was a typing error as this sentence should underline that temperature during winter in Bouraké is lower than at a normal reef. 25 °C, as indicated, was not correct. We changed with: “First, the seawater temperature is higher in summer in the Bouraké lagoon (Fig. 3), but it is also colder during winter, resulting in a temperature range of 17.5-33.8 °C”.

- *L597: temperature fluctuations are mentioned when discussing all environmental parameters (L596-L598). However, temperature was previously discussed from L582 to L594. In this second point the authors should focus the discussion on environmental parameters other than temperature and move up the sentence from L596-L598 to the first point of this subsection.*

Response: We agree and we moved accordingly. We intended first to discuss the absolute temperatures (cold and warm) and then present the actual fluctuations, first in temperature, to link with the previous paragraph, and then in DO and pH.

- *Sentences from L607-L615 could benefit from a simplified explanation highlighting the main findings. The way as it’s currently presented it seems that all the seawater (inflowing and outflowing) is acidic, warm and oxygen depleted.*

Response: Clearly, we fail to correctly explain how the system works. We changed with:

“At each rising tide, new water from the lagoon enters through the channel, flows into the semi-enclosed lagoon towards the large mangrove area behind it. This water, which had ambient values of pH, temperature and dissolved oxygen, mixes with the acidic, warm and deoxygenated water that was already in the system and the mangrove area, therefore already changing with respect to its original condition. At the mangrove area, we hypothesize that the water chemistry further changes due to the metabolic reactions in the sediments, coral reefs and mangrove roots (e.g., Alongi et al. 2004, *Marine geology*; Bouillon et al. 2007, *Biogeosciences*; Gleeson et al. 2013, *Marine Chemistry*; Call et al. 2015, *Geochimica et Cosmochimica Acta*). Conversely, on a falling tide, the seawater becomes gradually more acidic, hot and oxygen-depleted because the water that resided in the mangrove area gradually drains out of the system. This takes about 6 hours, during which the vast reservoir of shallow mangrove water continues to be chemically altered, becoming increasingly acidic, oxygen-depleted and hot. As a result, we measured a significant spatial differences in pH between the outer reef (the entry of the lagoon) and the inner reef (near the mangrove forest), as well as a considerable delay in the synchronization of the tidal shift (Fig. 5b).”

- *L642: clarify higher concentrations of what? (chemical species in general....?).*

Response: We changed with: “It is also true for some of the seawater chemical parameters we measured, which show higher concentrations in the Bouraké lagoon than on the reference reefs (see Table 2). For instance....”

3. TECHNICAL CORRECTIONS (*typing errors, etc.*)

- *Lines 281, 302, : replace “weakly” by “weekly”*
Response: Done
- *L589: delete extra “(“ before Bellworthy*
Response: Done
- *Fig. 1: use a brighter color (red?) or enlarge the square marking the location in the embedded globe.*
Response: Done
- *Fig. 3: in caption*
Response: Done
- *Fig.5 d,e: include “inner/outer” label inside the panel (instead or in addition to St S/St R)*
Response: Done
- *Fig. 7: include “winter/summer” in plot*
Response: Done