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Reply on RC2

Alice E. Webb et al.

Author comment on "Quantifying functional consequences of habitat degradation on a Caribbean coral reef" by Alice E. Webb et al., Biogeosciences Discuss., https://doi.org/10.5194/bg-2021-64-AC2, 2021

Referee #2 (Comments to the Author):

Webb et al., measured the community metabolism of small areas of a degraded Caribbean coral reef through in-situ incubations of benthic communities. Five incubation tents were deployed over coral, algae, and sand dominated benthos, representative of different states of coral reef degradation. Biogeochemical parameters were measured over 4-hour incubations at night and day. An inverse modelling approach was applied to the collected data. The key results were interpreted in the context of ecological function. Calcification and productivity were low and night-time respiration outweighs daytime productivity. The manuscript presents a unique and interesting approach to quantifying differences in biogeochemical processes on degraded coral reefs, however, there are some limitations to the study which should be addressed, and the inferences/conclusions that the authors make may need to be re-framed accordingly. The experimental design had low replication, and the measurements were made at one single location over just a few days / nights. The tents were leaking during the incubations, which would also have impacted the measurements. The logistics of such in-situ incubations are very challenging, and it was a good idea deploy the tents in duplicates / triplicates, but there is some variability within substrate replicates (in terms of composition and biogeochemical activity) to suggest that they could be evaluated individually. I think that the authors could provide some more information about the inverse modelling approach they use, and the advantages of using such an approach.

We thank the reviewer for this relevant remark. The modelling approach used in this study to estimate biogeochemical processes was first and foremost to relate the measured change in concentrations of variables (A_T, DIC, etc.) to the responsible metabolic processes. The reviewer is correct in pointing out that the limited number of replicates may be insufficient to permit the use of a PERMNOVA to analyse our data. Although we group the incubations in five

different categories based on the dominant group, we do acknowledge that these communities do harbour differences in terms of composition and therefore refrain from performing analysis using the community composition as a categorical factor.

In line with the reviewer's key concerns:

- **we removed the claim of functional homogenisation**
- **altered the title to put a bit of emphasise on the methodology aspect of the paper, it now reads:**

'*Quantifying functional consequences of habitat degradation on a Caribbean coral reef*'

- **We removed the PERMANOVA analysis (see below) and replaed it by PCA was conducted on a centred multivariate data set consisting of the four main biogeochemical processes (i.e., NCC, NCP, nitrification and denitrification).**
- **We rephrased some parts of the introduction and discussion and included a more cautious interpretation of the results.**
- **Although for visual ease, we do group the incubations in 5 different categories (with various colours), we refrained from performing analysis using composition as a categorical factor, rather treating each incubation as an individual.**
- **The water exchange rate was accounted for in his study by quantifying it using saline water and by measuring ambient variables (outside tent) in order to account for the water characteristics leaking in.**

Specific points to highlight:

Introduction: Overall, the introduction is nicely written. An explanation and/or justification of the inverse modelling approach could be described either at the end of the introduction or within the methods.

We have added some text within the methods to better explain the inverse modelling approach l. 179.

The use of inverse modelling is advantageous as it enables us to derive unknown parameters (here rates of biogeochemical processes) simultaneously from all measured data. The mathematical "state" of the incubation's dynamic system can be described based on the mass balance between A_T, DIC, O_2, NH_4 and NO_3 which is influenced by various biogeochemical processes. The rate of these processes are the unknown parameters that need to be quantified by fitting against an incomplete data set (only three-time points for A_T, DIC, NH_4 and NO_3).

We also added rewrote the last paragraph of the introduction l.92 to clarify our methods.

To account for the convoluted influence that various processes have on measured variables at the same time, the change in their concentrations is related to the responsible metabolic processes by solving a model consisting of ordinary differential equations describing the contribution of each process to the measured chemical fluxes. With this approach, model parameters (i.e., rates of biogeochemical processes) are derived from concurrent changes in all measured variables. The aim being to provide accurate estimates of biogeochemical processes that underlie functions of the newly configured shallow Caribbean reefs.

L38: ‘similarity’ does not describe species homogenisation well. Maybe rephrase.

We rephased this sentence l.41 to:

Communities within ecosystems and across spatial scales have become more biologically homogeneous.

L39: ‘This is worrisome...’; change this to something less emotive. E.g., This threatens ….

We removed this phrasing; the sentence now reads l.41:

Communities within ecosystems and across spatial scales have become more biologically homogeneous (Burman et al. 2012; Cramer et al. 2021) which may lead to a decrease in functional diversity therefore limiting services provided by biological communities (Matsuzaki et al. 2013; White et al. 2018).

L55 ‘compromised’ should be compromise; change ‘was’ to ‘were’.

We changed these accordingly.

L59 ‘mirroring’ might not be the correct word, as the decrease in corals is the opposite of increases in the other functional groups.

Now l.64, we changed this wording to:

have increased alongside to the decrease in stony corals

Methods: The benthic incubation tent has a great design; there are some really strong features, such as the long sampling tube which samples from the middle of the incubated area rather than a typical sampling port. The photo in figure 1 shows that a metal chain was used as a weight to hold the chamber in place, which should be mentioned in the text, and perhaps some discussion of this as a source of the reported leakage.

We thank the reviewer for his positive comment. We have added a sentence explaining we used metal chains l.112. The leakage was indeed taken into account when calculating the fluxes. The equations relating changes in concentration of the measured variables to the responsible process incorporate the leak rate as well as the ambient measurement that were always taken at the same time as interior measurements.

There are some details in this section which could be clarified to assist the reader in fully understanding how the study was carried out and to improve replicability of the experiment. In particular, the sampling regime should be further detailed: at what time of day were the tents deployed? Over how many days? Were the days and nights within the same 24-hours?

We have added text to clarify these points l.124:

The incubations were carried out one at a time, over the study period and lasted four hours each. Prior to each incubation, the tent was place with flaps open over the substrate and lefts for a minimum of 3 hours before the incubation was started. When day incubations were terminated, the tent was left in place with flaps open until the night incubation was carried out on the same substrate. All daytime incubations were started at 10:00 and all night-time incubations were started at 18:30.

Incubations were carried between February 12th and March 22th 2018. This

information can be found l.102.

Section 2. 3: How were the compositions measured? Were they 2D only, and could a 3D area be approximated from the data you collected? Normalising the rates to substrate-specific surface area and volume might give a more accurate representation of the processes being quantified.

We measured surface areas in situ and subsequent processing with ImageJ. Relating processes to particular components within each community was not possible. The aim of this work is to look at community biogeochemical processes as a whole.

In section 2.6 it was not immediately clear if the testing of the chamber was conducted at the same time as the incubations and, if so, for how many of them? How was the impact of high salinity controlled for? A rapid change in salinity might affect coral photosynthesis for example.

We injected high saline water at the start of every single incubation to determine the water exchange rate in every tent. Although we saturated the water with salt prior to injection, this did not increase the overall salinity of the incubation by more than 1 unit each time (most of the time less than that). At this site, salinity change over the day is higher than what occurred in these tents. We therefore do not expect a significant impact on community metabolism from this increase.

We clarified when high saline water was injected in the tents l. 168.

After sampling water at T0 for AT, CT and nutrients in each incubation, 450ml of salt-saturated water was injected into the tent.

Results: In terms of structure, the order of findings could be adapted so that the key finding is first or have a summary which outlines the most important results before going through each finding in detail.

We have added the below subsections to improve clarity.

3.1 Ambient conditions

3.2 Water exchange quantification

3.3 Model output

3.4 Estimated biogeochemical processes

3.5 Incubation comparison

Verification of the chamber method could be its own sub-section. The rate of water exchange is high and this should be addressed in more detail. If salinity returns to the ambient level after 1-2hrs, this indicates that changes to other measured parameters are only reliable within the same time frame (i.e., the water within the tent is renewing over the course of the incubation).

Yes this is correct, this is why most measured variable and modelled behaviour level out after 2 hours. Rates are measured from the initial slope of rate of change.

We checked for correlation between processes and the amount of leaking using

the Kendall rank correlation test. No significant correlation was found. Text was added in the methods l. 240:

To evaluate if water exchange rate had an impact on estimated processes, the non-parametric Kendall rank correlation test was performed. All inferred biogeochemical process rates (mineralisation, primary production, NCP, NCC, nitrification and denitrification) were tested against incubation water exchange rates.

and the results l.302:

The Kendall rank correlation test did not reveal significant correlation between water exchange rates and rates of mineralisation (p=0.79, tau=0.04), primary production (p=0.47, tau=0.12), NCP (p=0.75, tau=0.05), NCC (p=0.17, tau=0.21). Nitrification (p=0.81, tau=0.04), and denitrification (p=0.27, tau=0.18). The Kendall correlation coefficient tau is closer to zero than 1 in all cases, implying there is no significant association between the two tested variables.

It would be interesting to see TA: DIC plots and relationships between photosynthesis and calcification. If PAR data is available, you might also plot the rates against light as this could explain some of the variability. For example, if the weather conditions changed and light was reduced during some of the incubations this might explain the non-linear change in DO seen in some of the individual plots in figure S1.

The non-linear change in DO is indeed linked to light. However, as the model is unable to predict irregular oxygen evolution caused by light variability during the day-time, we do not plot that data.

We added a NCC:NCP plot to assess the position of each community within the different quadrants of the NCC vs. NCP diagram (Figure 7).

For the modelling approach presented in Fig 5 and Fig S1, the models were fit to each incubation rather than each substrate type (as they were for Fig.6). Was there a reason for this? Would it be more appropriate to describe the incubated substrates as individual substrate types rather than grouping them into categories (as per Table S1)?

Although we group them in categories, they are indeed different communities, therefore we do not fit the model through 3 incubations at a time for day data and 2 incubations at a time for night data. In line with reviewer 1 and 2's comments we have removed the PERMANOVA.

Instead, we performed a PCA (now figure 7) based on the four main biogeochemical processes estimated for each incubation. We added text to the methods l. 243:

Principal component analysis (PCA) was used to identify grouping among the 23 tent incubations (day n = 13, night: n = 10) in relation to their biogeochemical signature (i.e., NCC, NCP, nitrification and denitrification). PCA was conducted on a centred multivariate data set consisting of the four main biogeochemical processes (i.e., NCC, NCP, nitrification and denitrification).

And in the results l. 309:

The PCA based on the four main biogeochemical processes revealed two main different groups between night incubations and day incubations (Figure 7A). Sand incubations were the exception as night and day incubations grouped relatively close to each other. The first two principal component axes (PC1 and PC2) explained 88.68% of the total variability

within the data. PC1 described a gradient in NCP and NCC from high (negative PCA scores) to low (positive PCA scores) and an opposite pattern for nitrification and denitrification. PC2 further explains the variability in NCC and nitrification, and to a lesser extent NCP and denitrification. One of the communities dominated by bioeroding sponges (rep.1) is separate from other communities both during the day and during the night due to high rates of nitrification and denitrification compared to other communities.

Table S1 presents useful information about the species composition of each chamber and could be used to describe reef patch as a distinct substrate type. This could be used to align individual compositions with variations in rates as the different species compositions might explain some of the variation between replicates.

We added this table for transparency about the composition of our incubations, however the aim of this research was to investigate communities as a whole. There is unfortunately no way we can relate fluxes to specific components inside the tent.

Figure S1: The data presented in these plots should be included in the manuscript. You might consider combining the plots showing the distinct replicates / substrate types with different colours or symbols. The data could be converted to rates before plotting unless there was a reason not to do this (which might also be good to explain). Figure S1 demonstrates that the DO slopes are variable for corals, with irregularities in oxygen evolution. If PAR data is available, the DO could be plotted with PAR to identify if there were changes in light to cause this (or were they all deployed on the same day?).

Figure 5 now illustrates all incubation model output.

This comment is probably based on our unclear description of the approach we used. We have therefore rephrased part of the methods (see above). We assume rates to be constant over time and therefore cannot plot them in a similar fashion to figure 5. The estimated rates are plotted out in Figure 6.

Light was indeed the cause for irregular DO evolution. The model enables predicting irregular evolution caused by light variability during the day-time. For this reason, the overall fit is usually better on night data.

Figure 4: were the tents deployed under the same conditions, or are these from distinct days?

Incubations were carried between February 12th and March 22th 2018. This information can be found l.102.

Figure 5: Plots should be combined so that all data can be presented. Visual notes: The parameter boxes should be tables to make it easier to read. All the axis tick labels should be horizonal.

Figure 5 was replotted to depict model output for all incubations. The old Figure 5 is now in Supplements (Fig. S1) with proposed alterations.

Figure 6: for each of the bars sample size should be displayed. Since n is low (either 2 or 3), the results could be displayed differently to show each data point, e.g., jitter plot, or scatterplot by assigning a numeric value to each category (e.g., coral dominated would be 5, sand would be 0). Also it looks like there would be some differences between night respiration for example, however 'no significant differences were found' in L243. Could this be due to the way the stats were run rather than a true representation?

We thank the reviewer for this relevant comment and changed the plot to a scatter plot depicting raw data and means.

In line with above comments, we removed the PERMANOVA analysis and we do not perform analysis using composition as a categorical factor, rather treating each incubation as an individual.

Discussion: The discussion is interesting and very well-written; however, it will likely need revisions according to the suggested edits in the results section. It would be good to include some discussion of relationships between the measured parameters (i.e., TA:DIC). Additionally, more in-depth discussion could be included to address the limitations of the study: (1) low replication and modelling with so few data points, and (2) the leakage of the chambers. The interpretation of findings should account for these uncertainties.

We thank the reviewer for the overall positive feedback, and we agree that addressing the limitations of our work is an essential part of the discussion. We have added the paragraph below l. to point out methodology considerations:

Nonetheless, due the limited number of incubations that were carried out for this study, we interpret results with caution. Additionally, incubations were only deployed on the reef flat of one degraded reef, future application of this or similar incubation methods should consider multiple sites. Lastly, methods would be further improved by continuous monitoring of the exchange rate, rather than assuming it to be constant throughout the incubation.

In the conclusions, information is presented about the local distribution of some coral species. This information should be described elsewhere and be incorporated into the discussion at an earlier point.

L218**:** if salinity returns to normal after 1-2 hours, this would indicate that the first hour or two of dDO or dTA is also lost?

We take the T0 samples before adding high saline water and correct TA if salinity has not return to ambient by T2. As mentioned previously the increase of salinity is very modest and well withing what these communities are used to.

L220: 'relatively good fit', this should be detailed further. The authors refer to Figure S1 as evidence of this, however, the model fit cannot be evaluated from figure S1 only.

This is an error; we should have also added a reference to Table S1 which presents standard errors and p values for the estimated parameters. This has been corrected.

L21: potential reasons for 'irregular oxygen evolution during the daytime'?

This is due to light variability. We have added the underlined text below for clarity l.275:

"*… irregular oxygen evolution caused by light variability during the day-time"*

L254: 'no significant gain in primary habitat' is confusing because the measurements were over a matter of hours not months, so we would not expect any change to the habitat through accretion.

This is true, here we want to make clear what these processes translate to in terms of function. But as our incubations lasted only 4 hours we should be more

cautious in the way we write this. We have rephased this sentence l. to:

Very low or negative NCC rates were recorded on all substrates, suggesting reduced net accretion potential.

L275: ‘an’ = and

Change has been made accordingly.