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Interactive comment on "High bacterial organic carbon uptake in the Eastern Tropical South Pacific oxygen minimum zone" *by* Marie Maßmig et al.

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Anonymous Referee #2 (AR2): This is a useful study investigating the complicated microbial dynamics within oxygen minimum zones with many different biogeochemical and physical measurements made. The authors focus on calculating bacterial production predominantly associated with carbon cycling, but then also use other studies to consider the input of nitrogen cycling and anoxic processes. The manuscript is very well written, generally clear and detailed. I have a few suggestions to revise the text and figures to make some of the points clearer and to hopefully clarify some uncertainties. One point that was not mentionned was that the bacteria were collected from

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suboxic concentrations but rates measured in oxic conditions I assume? How might the fact the microbes are being oxidised affect your results? It is difficult to work in OMZs and many of the studies cited would have done a similar thing but i think this should be discussed.

Author Comment (AC): We thank the reviewer for this comment. Regarding the extracellular enzyme rates, we are aware of having conducted a challenging method. This is because we had a trade-off between feasible measurements of extracellular enzyme rates at different substrate concentrations to calculate Vmax and reducing the contamination of oxygen. In the revised version, we will include in the discussion that results have to be interpreted with care: "The extracellular enzymes rates of our study have to be interpreted carefully since incubation was not fully anoxic and the remaining oxygen might have biased the results. Still, we assume that most extracellular enzymes were present at the time of sampling and thus oxygen contamination during the incubations did not strongly influence the rate measurements."

Samples of bacterial production were incubated in closed vials and bubbled with a N2/CO2 mixture (section 2.5)., avoiding oxygen contamination during the incubation time. Therefore, we assume that bacterial production was not affected by oxygenation.

AR2: Also the authors seemed to switch between top/bottom hypoxic and upper/lower oxycline, which i took to mean the same thing. If not this should be clarified.

AC: The term low_hypoxic is defined in the method section 2.7 (>5 to <20 μmol O2 kg-1). Therefore, it is correct that "bottom_low_hypoxic" is identical to the lower oxycline, since at the lower oxycline oxygen concentrations only increased up to 15 μmol. The term "upper_low_hypoxic" differs from the term "upper oxycline" since the upper oxycline includes waters with oxygen concentrations between 5 to 60 μmol L-1. Within the revised version of the manuscript we will replace the statistical test that were until now only done for the "upper_low_hypoxic" waters by statistical tests with samples from the entire oxycline, to be consistent.

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AR2: Line 16 - Change to 'from the upper AND lower oxyclines', using 'or' makes it seem negative and I had to read it a few times to understand you were saying production was high.

AC: In the revised version, we will change the sentence to: "Nevertheless, high cell-specific bacterial production was observed in samples from oxyclines and extracellular enzyme rates were especially high at the lower oxycline, corroborating earlier findings of highly active and distinct micro-aerobic bacterial communities. "

AR2: Line 73 - I noticed the transects had data from both cruises. They are quite close together temporally, but even so some discussion on how the data is aggregated and if temporal affects are accounted for is needed. Did you look at the data separately per cruise too? Which data/transects are used in the figures? What is the seasonality like in the region?

AC: We thank the reviewer for his/her advice and agree with the proposal to include more information about the different cruises. Therefore, we will i) describe the seasonality within the sampling region in the introduction of the revised manuscript, ii) describe the study area in more detail for each cruise and iii) show the oxygen content, chlorophyll a concentrations and temperatures for each station in the revised supplement (see also first comment of the first reviewer). However, we prefer not to distinguish between cruises for statistical tests of bacterial production and extracellular enzyme rates since we focus on possible differences between oxygen regimes. Moreover, bacterial production was only sampled during April and combining extracellular enzyme rates of both cruises increases sampling size. Still in the revised manuscript we will include the represented cruises in the subtitle of the figures.

i) "In austral winter, upwelling and subsequently nutrient supply to surface waters strengthens (Bakun and Nelson 1991, Echevin et al 2008). However, Chl a concentration is highest in austral summer, with the seasonal amplitude being stronger for surface Chl a concentrations than for depth averaged Chl a concentrations (Echevin et al

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2008). This is because in winter, phytoplankton growth is, next to iron, mainly limited by light due to deeper mixing , whereas in summer macronutrients are limiting phytoplankton growth (Echevin et al 2008). Further, irregular variability in the El Niño–Southern Oscillation raises (during La Niña) or deepens (El Niño) the upper oxycline. Subsequently, anaerobic respiratory processes become stimulated or restricted, respectively and biogeochemical cycling of organic and inorganic matter changes (Llanillo et al. 2013). During the year of sampling (2017), neither a strong La Niña nor an El Niño was detected (https://ggweather.com/enso/oni.htm). However, in January, February and March 2017 there was a strong coastal El Niño with enhanced warming (+1.5°C) of sea surface temperatures in the eastern Pacific (Gerreaud 2018)."

"During our two cruises to the Peruvian upwelling system (Fig. 1), seasonal variability caused higher maximum Chl a concentrations and warmer temperatures in April compared to June 2017. Chl a concentration reached up to 11 and 4 μg l-1 within the upper 25 m in April and June, respectively. Still, average Chl a concentrations within the upper 10 m (M136: 3.1$\pm$2.6 μg l-1; M138: 2.8 $\pm$ 1.3 μg l-1) were not significantly different between the two cruises (nM136=75, n M138= 40, W=1416, p= 0.6). At depths >50 m, Chl a concentration was generally below detection limit (Fig. 2a, supplementary Figure 1). Within the upper 10 m the water was warmer in April (21.3 $\pm$1.6°C) compared to June (17.6 $\pm$ 0.6°C) (nM136=75, n M138= 40, W=2886, p<0.01) (Fig. 2b, supplementary Figure 1). Oxygen >100 μmol kg-1 was observed in the surface mixed layer, decreased steeply with depth and reached suboxic concentrations (<5μmol L-1) at > 60 $\pm$ 24 m (Fig. 3a and 4a, supplementary Figure 1). Shallowest depth with suboxic oxygen concentrations were 14 m in April (station Q) and 29 m in June (station D), probably influenced by the distance from shore (Q<D). Oxygen increased again to up to 15 μmol kg-1 at >500 m (Fig. 3a and 4a, supplementary Figure 1). TDN concentrations increased with depth from 18$\pm$8 μmol l-1 and 22$\pm$7 μmol l-1 within the upper 20 m in April and June, respectively, and reached a maximum of 54 μmol l-1 at 850 m (Fig. 2c). DOC decreased with depth from 94 $\pm$37 μmol l-1 and 69 $\pm$12 μmol l-1 in the upper 20 m in April and June, respectively, to lowest values of 37 μmol l-1 at 850 m.

The steepest gradient in DOC concentration was observed in the upper 20-60 m (Fig. 2d) during both cruises. “

AR2: Line 139 - citation for first use of BOD and write in full first time used in main text

AC: In the revised version, we will improve this sentence: “The bacterial oxygen demand (BOD) is the amount of oxygen needed to fully oxygenize organic carbon that has been taken up and not transformed into biomass by bacterial production (BP)”

AR2: Line 145 - what temperature dependance? Is a conversion used? Cite

AC: In the revised version, we will include the formula for temperature dependence of the cited study: “. . .ii) the bacterial growth efficiency (BGE) follows the established temperature dependence (BGE=0.374[$\pm$0.04] -0.0104[$\pm$0.002]T), resulting in a BGE between 0.1 and 0.3 in the depth range of 10-60 m and an in situ temperature of 14 to 19°C (Rivkin and Legendre, 2001) . . .”

AR2: Line 198 - Perhaps place oxygen concentration in Fig. 2 with the other ‘standard’ oceanographic measurements, as it is a key plot for this paper. I would also add on horizontal layers onto the transect images, i.e. by using black lines to show oxycline/ omz/hypoxic/oxic layers.

AC: We appreciate the suggestion of the reviewer. However, we placed the oxygen concentration on purpose as first panel of Figure 2, since all statistical analysis are referred to this parameter and therefore it should appear together with the biological rates. This also enables an overview about the respective oxygen concentrations at sampling depth that we will further indicate by black lines in the revised version of the manuscript.

AR2: Also, what was lowest oxygen concentration, was it 5 umol/L so only suboxic or even lower to maybe anoxic as set by your definitions in the introduction? The study refers to ‘suboxic’ throughout which makes me think outside of the OMZ, but actually this is the OMZ. Being clear about this early on in the results would help.

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AC: We thank the reviewer for this advice. Indeed, we only distinguished between suboxic and hypoxic conditions. We are confident that the OMZ core includes zones with oxygen concentrations below our detection limit, as it is described in section 3.1. This is also indicated by increased nitrate concentrations ($\sim$6μmol L-1) in the OMZ core, suggesting anaerobic reduction of nitrate (data not included in the manuscript). In the revised version we will include a sentence in section 3.1 to clarify which oxygen concentrations were relevant for our statistical analysis: "Oxygen decreased steeply with depth and fell below detection of Winkler titration. For further analysis and within the text in situ oxygen concentrations below 5 μmol O2 L-1 are referred to as "suboxic"."

AR2: Line 199 - Does this mean OMZ is 100-500 m depth, be explicit

AC: Within the revised version, we will be more explicit and reformulate this paragraph (see also comment concerning line 73) : "Oxygen >100 μmol kg-1 was observed in the surface mixed layer, decreased steeply with depth and reached suboxic concentrations (<5μmol L-1) at > 60 $\pm$ 24 m (Fig. 3a and 4a, supplementary Figure 1). Shallowest depth with suboxic oxygen concentrations were 14 m in April (station Q) and 29 m in June (station D), probably influenced by the distance from shore (Q<D). Oxygen increased again to up to 15 μmol kg-1 at >500 m (Fig. 3a and 4a, supplementary Figure 1)." Consequently, the suboxic waters was between 60 and 500 m. AR2: Line 206 - 'except for most coastal stations' - what happened at these stations? AC: In the revised version we will include an additional sentence (thereby bacterial production will differ from the submitted manuscript, since bacterial production will be corrected for differences between incubation and in situ temperature; see comments of first reviewer): "Bacterial production varied strongly throughout the study region and ranged from 0.2 to 2404 μmol C m-3 d-1 (Fig. 3b), decreased in general from surface to depth and showed significantly higher rates in the oxygenated surface compared to the OMZ (Fig. 3b). At the most coastal station (G) bacterial production remained high near the bottom depth of 75 m (280 μmol C m-2d-1 at 72 m) (Fig. 3b)"

AR2: Line 235 - full statistical results in parentheses is great to see and the correct way

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to present results, however with so many tests and parts of the text in parentheses it stops the flow when reading. Can you shorten the statistical results in some way? Or add a table to the supplementary material?

AC: We agree, that the flow of reading is disturbed and will include the statistical results in the supplement.

AR2: Line 242 - normalisation completely changes the pattern of production with depth and oxygen, reverses it compared to un-normalised data. It would be good to show this and discuss further, perhaps using scatter plots too.

AC: We very much appreciate this comment of the reviewer. Producing the scatter plot helped us to see that the trends between cell-specific and total production are not completely invers. Still, cell-specific production is correlating more strongly with oxygen than total production. Thus, as described in the manuscript, cell abundance seems to counteract the lower cell-specific bacterial production at suboxic oxygen concentrations compared to the oxyclines. A further statistical test revealed that at the coastal stations (G and T) cell-specific production is more similar between suboxic waters and the oxycline. This suggests that the supply of organic matter stimulates bacterial production under suboxia. We will include this thought within the discussion of the revised manuscript: “Baltar et al. (2009) showed increasing cell-specific enzymatic rates and decreasing cell-specific bacterial production, with increasing depth in the subtropical Atlantic. Baltar et al. (2009) explained this pattern with decreasing organic matter lability. In our study, differences in cell-specific bacterial production between suboxic waters and the oxycline did not persist at the most coastal stations (G and T). This indicates the stimulation of bacterial activity, including anaerobic respiratory processes, by the input of labile organic matter from the shore. Therefore, our study suggests that a possible impairment of cell-specific bacterial production under suboxia is reduced by supply of organic matter. However, this hypothesis is restricted to a very limited number of samples and should be tested in further studies”

The scatter plot with cell-specific and total bacterial production rates in relation to oxygen will be included in the supplement of the revised manuscript and referred to within the results: “A detailed view at bacterial production in dependence of in-situ oxygen concentrations, reveals a stronger increase of cell-specific bacterial production, especially at < 10 μmol O2 L-1 at different stations (new supplementary Figure).”

AR2: Line 243 - Units of ‘amol per cell per day’ are incredibly low as one may expect from a ’per cell’ measurement, but is this comparable with results from other studies?

AC: We agree with the reviewer that these rates seem low. Baltar et al. (2009) presents cell-specific production rates in the subtropical Atlantic (Figure 1 c) that varied between $\sim$ 0.006-0.03 fmol C cell d-1 (corresponding to 6-30 amol C cell d-1) between 96 and 503 m depth. Our original measurements range between 2-286 amol C cell d-1 between surface waters and $\sim$650 m depth. After temperature correction, cell-specific production rates ranged between 1 and 1120 amol C cell d-1. Consequently, our data include the measurement range of the former study in the Atlantic.

AR2: Line 284 - Is this finding because experiments were run in oxic conditions, as were some of the studies you cited too. But should consider the affects of exposing microbes from OMZ to oxygen.

AC: In the revised version, we will include in the discussion that results have to be interpreted with care (see also answer to the first comment of this reviewer): ” The extracellular enzymes rates of our study have to be interpreted carefully since incubation was not fully anoxic and the remaining oxygen might have biased the results. Still, we assume that most extracellular enzymes were present at the time of sampling and thus oxygen contamination during the incubations did not strongly influence the rate measurements.”

AR2: Line 375 - where did the data of amount of reduced nitrogen come from, was it Kalvelage? I found this section, whilst interesting, a little hard to follow which numbers were from this study and which from others. For instance, why use BGE from Del

Giorgio 1998 when you calculated it in this study?

AC: We thank the reviewer for this comment that includes one comment of the first reviewer. First, we will explain the choice of a BGE of 20% in the revised manuscript: "The amount of carbon oxidized by denitrification based on the studies of Dalsgaard et al. (2012) and Kalvelage et al. (2013) can be converted into bacterial production applying a BGE. The average temperature dependent BGE was 20%. A BGE of 20% agrees well with other studies (Del Giorgio and Cole, 1998). Assuming a BGE of 20%, the denitrification rates in Dalsgaard et al. (2012) and Kalvelage et al. (2013) suggest a bacterial production of $\leq$5 μmol C m-3 d-1, equivalent to only about 14% of total heterotrophic bacterial production in suboxic waters determined in our study."

Second, we will clearly indicate the source of data: "We compared bacterial production, i.e. rates of carbon incorporation, with denitrification rates previously reported for the South Pacific. Therefore, we converted one mol of reduced nitrogen that were measured by Dalsgaard et al. (2012) and Kalvelage et al. (2013) to 1.25 mol of oxidized carbon after the reaction equation given by Lam and Kuypers (2011). This calculation indicates that on average $\leq$19 μmol C m-3 d-1 are oxidized by denitrifying bacteria in the Eastern Tropical Pacific (Dalsgaard et al., 2012; Kalvelage et al., 2013). . ..."

Third, we will expand the calculation and include a BGE of 6%. For this we will not focus on the denitrification rates mentioned in the paragraph above, but on the sum of anaerobic carbon oxidation rates including denitrification, DNRA and simple nitrate reduction, as it is also discussed within the manuscript for a BGE of 20% (line 380). Absolut values will change within the revised version because of temperature correction: "The same calculation can be repeated assuming a BGE of 6%, which is the average BGE within this study based on DOC loss and bacterial production. Assuming a BGE of 6%, the estimated 109 μmol C m-3 d-1 that are respired by anaerobic carbon oxidation (Kalvelage et al., 2013) would represent 94% of the carbon uptake. Consequently, 7 μmol C m-3 d-1, i.e. 6% of the carbon uptake, are incorporated into the bacterial biomass. A bacterial biomass production of 7 μmol C m-3 d-1 is even lower than the

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bacterial production of 27 μmol C m-3 d-1, based on a BGE of 20% and cannot explain the average bacterial production measured in suboxic waters during our study (37 μmol C m-3 d-1). Therefore, this estimation suggests higher rates of heterotrophic anaerobic respiratory processes than previously measured. Since denitrification rates were not measured directly, the comparability of published denitrification rates and our measurements of bacterial production are limited. However, our data suggest that the carbon oxidation potential off Peru is more evenly distributed than expected . . . .."

AR2: Line 388 - Do you mean distributed evenly vertically or horizontally, or both?

AC: We were able to measure heterotrophic bacterial production at every depth and station. Therefore, we here suggest a more evenly horizontal and vertical distribution of heterotrophic anaerobic production, than indicated by heterotrophic anaerobic respiration measurements. We will add the words "horizontally " and "vertically", within the revised version.

AR2: Line 399 - I agree with final sentence of paper but not mentioned anywhere how can improve understanding or quantification processes, so on its own this final sentence is a bit weak for such a thorough study.

AC: We thank the reviewer and will add a suggestion for future studies in the conclusion of the revised manuscript:

"Our study suggests that suboxia does not reduce enzymatic degradation of organic matter and bacterial production in the Eastern Tropical South Pacific off Peru and therefore supports alternative explanations for the enhanced carbon export in OMZs compared to oxygenated waters. Differences between cell-specific and total rates of bacterial activity allude to different controls of cell abundance in suboxic systems and highlight the OMZ as a specific ecological niche. The combination of bacterial and physical rate measurements suggests that low BGEs in the upper oxycline contribute to sustaining the OMZ. Meanwhile, new findings during our study call for additional studies: i) DOC loss differed strongly between our investigation and the study of Logi-

nova et al (2019). Therefore, combined physical and biological rate measurements in the Peruvian upwelling system should be repeated during austral summer, to learn more about the interplay of DOC loss and bacterial production rates during different seasons. ii) Integrated measurements of denitrification, microaerobic respiration and bacterial production are needed to estimate the fractions of incorporated and respired carbon under suboxia. The BGE received in that way could support or disprove the low BGE estimate, which was calculated from DOC loss and bacterial production in our study. Consequently, our study highlights the need for a better mechanistic understanding and quantification of processes responsible for oxygen and dissolved organic matter loss in OMZs that is inevitable to predict future patterns of deoxygenation in a warming climate."

AR2: Figures: Fig. 2 and Fig.3 - show horizontal oxygen regions as suggested above. Also, reduce extrapolation with ODV, large gap _ 100 km where no station/data between coastal and offshelf. Which interpolation did you use in ODV? The stations are running from the coast which is more east than offshore according to figure 1, so perhaps flip horizontally to reflect the east to west/coast to offshore nature of the spatial distribution. Having longitude instead of distance from coast (or both preferably) may be more useful, and make clear the inset is top 100 m.

AC: In the revised version, we will indicate the oxygen concentration at the sampling depths in Figure 2 and 3. Until now we used "Diva setting" with automatic scale adjustment, but in the revised version we will reduce the extrapolation to visualize the gap between stations. Further we will flip the y axis as well as indicate the longitude. Furthermore we will indicate the depth in the insets.

AR2: Fig 4 - labels of oxygen regimes different to text where instead oxyclines often referred to, is that the same as top and bottom hypoxic? Continuity throughout would be helpful.

AC: In the revised version, we will replace the words "top hypoxic" and "bottom hypoxic"

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by “upper-“ and “lower oxycline” in figure 4.

AR2: Fig. 5. Add a title for each panel so do not need to refer to legend as much.

AC: In the revised version, we will add subheadings to each panel of Figure 5.

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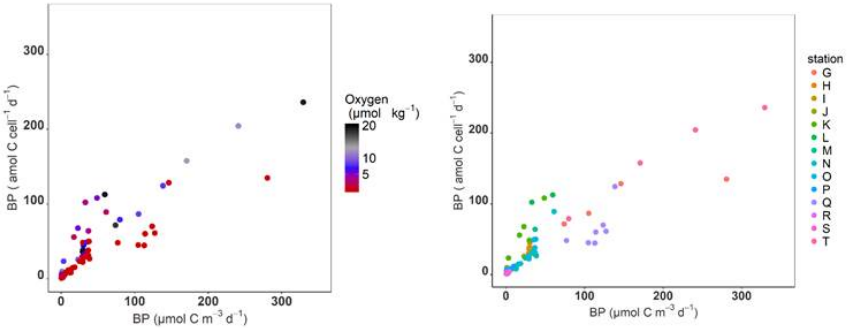

Fig. 1. New supplementary Figure: Total vs cell-specific bacterial production with oxygen concentrations (left) and stations (right) indicated by color-coding

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