Dear reviewer,

We would like to thank you again for your constructive comments. According to your comments, we will elaborate on existing studies and expand on the new aspects of our study, in particular with regard to zooplankton and ecosystem functioning. Your comments will help us set apart our manuscript more clearly from previous studies. A detailed point-by-point response to your detailed comments is listed below:

Abstract:

L7: “Intense upwelling coincides with deep mixed layers”: is this really unique? Are the layers deep?

R: We find that the pattern of intense upwelling coinciding with deep mixed layers in the seasonal cycle is unique to the HUS. As shown in fig. 2e of the manuscript, the Humboldt system is the only of the four major EBUS that reveals a positive temporal correlation between MLD and upwelling intensity. We will add a clarifying sentence to the manuscript.

L11: In contrast to previous studies, reduced phytoplankton growth due to enhanced upwelling of cold waters and lateral advection are second-order drivers of low surface chlorophyll concentrations”: not sure what previous studies were asserting.

R: We will rephrase this section and be more precise. We find that lateral advection plays a role for phytoplankton biomass (and hence in the ‘seasonal paradox’). This finding confirms previous studies by Messie and Chavez (2015), Lachkar and Gruber (2011) that address the importance of lateral advection for phytoplankton biomass build-up in Peru and other EBUS because of the inverse relationship of advection and water residence time. With respect to the role of temperature limitation due to cold surface waters in winter, Echevin et al. (2008) stated based on a sensitivity study that it was negligible in the Peruvian system and did not include the associated analyses (figure) on temperature...
limitation in their results. We here add our model results in terms of temperature limitation (temperature growth factor), as we do find an effect, even though it is of second order. We will reword and replace the above sentence with the following text (L11-13):

“The effect of advection on the build-up of phytoplankton biomass, though of second-order, is consistent with previous findings for the Peruvian system and other EBUS, with enhanced offshore export opposing the coastal build-up of biomass. In addition, we find that upwelling brings up relatively colder water and slightly slows down the build-up of phytoplankton biomass.”

L15: what about the role of nutrient enrichment? It could be reduced under climate change. See Echevin et al. (2020).

R: We agree that nutrients might be reduced under climate change due to increasing stratification and potentially weakening upwelling. As discussed in our manuscript (L156-158 and L341-343), our results suggest that the system in its present state is not nutrient-limited. Although surface DIN concentration shows a clear seasonal cycle, it is not the limiting factor of phytoplankton growth, even when concentrations are lowest in summer. Unless future nutrient concentrations drop substantially below ‘summer levels’, we expect that other limiting processes (dilution, light condition) would dominate the impact of reduced nutrients. Therefore, a dominant role of reduced nutrient supply in case of a weakening of upwelling seems less likely than other effects of increasing stratification. We will expand on the role of a potentially reduced nutrient supply in the climate change section.

Introduction:

L33-35: The seasonal paradox is also mentioned by EC08. At citing the latter, it would be fair to mention that they used a regional coupled physical-bgc model as in the present study. You should also mention Thomas et al. (2001) and Chavez et al (2005) who noted the seasonal paradox.

R: We agree that we did not present the EC08 study in the detail it deserves. We will give a more detailed description of Echevin et al. (2008) and also include Thomas et al. (2001) and Chavez (1995) in the introduction.

L38: Actually EC08 showed that the seasonal cycle of insolation did not play a major role in their model set-up, whereas Guillen and Calienes (1981) assumed it played a role.

R: We will rephrase and explain this part more clearly as follows (L38): “Guillen and Calienes (1981) suggest that lower surface radiation in winter might amplify light limitation and further limit the phytoplankton growth while insolation is found not to play a major role in Echevin et al. (2008).”

L39: I disagree here: this has been at least partly assessed in EC08. Rephrase and explain precisely which hypotheses have not been assessed in the latter and which new ones will be assessed in the present work. Overall, a more accurate review of the findings of EC08 to explain the out-of-phase seasonal cycle of chlorophyll is needed in the introduction.
R: As mentioned above, we will recap the study of EC08 in more detail and emphasise more clearly the difference between our study to EC08.

L41: "the unique mechanism": not clear what this unique mechanism is.

R: The unique mechanism refers to the first question ("what is the uniqueness of PUS compared to other EBUS that leads to the seasonal paradox?"). And here it represents "the deep MLD coinciding with strong upwelling intensity". We will modify the sentence to (L42-43):

"(2) What are the mechanisms that limit phytoplankton from growing in a situation of ample supply of nutrients due to strong upwelling; and (3) How will these mechanisms further affect ecosystem functioning."

Data and methods:

L50: why do you cite ROMS here? Explain that CROCO is the next generation ROMS-AGRIF model.

R: Thanks for pointing out that we missed to mention the link of ROMS and CROCO. The citation here is according to what is suggested on the CROCO website (see https://www.croco-ocean.org/how-to-cite/). We will later add ‘CROCO is the next generation of the ROMS AGRIF model’ in the manuscript.

L54: do you use bulk forcing

R: No, we did not use bulk forcing but a forcing file (croco-frc) created with the croco-tools (a collection of Matlab scripts that are provided on the CROCO website for pre- and postprocessing purposes, see https://www.croco-ocean.org/download/croco-project/) that contains the variables wind stress (zonal and meridional components), surface net heat flux, surface freshwater flux (E-P), solar shortwave radiation, SST, SSS etc.

L61: I think the authors should explain why these variables are important for the simulation of chlorophyll. Fig. 1 of José et al shows that the PCC is too strong in the model at 12S, not too weak!

R: Yes, the Peru coastal current (PCC) is too strong in the model at 12S and south of 12S in José et al. fig. 1. But north of about 12S (that is in most of our focus region), the PCC is underestimated by the model compared to observations. Overall, José et al. conclude in their model evaluation section that the model underestimates the Equator–Peru coastal current and the Peru–Chile undercurrent.

L66: I do not think it can be said that N is a species. I think the authors could have done a better job at proofreading the english in the submitted paper.

R: The expression "N species" refers to different forms of nitrogen in the water and is
commonly used by chemists. Take, for example, the title of Michalski et al. (2006): 'Determination of Nitrogen Species (Nitrate, Nitrite and Ammonia Ions) in Environmental Samples by Ion Chromatography'. To simplify the reference to nitrate, nitrite and ammonium we will stick to summarise them as N species.

L72: *Table A1 is useful. Please indicate values in the table instead of "see ref."*

R: The parameters for which values are given as 'see refs' are regarding zooplankton diet preference. The references we cite are biological papers based on observations. The parameter values in the model are general estimates that orient themselves on the observations of stomach contents of individual taxa given in the references. As model parameters need to integrate over different taxa and their traits and feeding strategies, their values do not directly correspond to observed values. Therefore, we do not list specific diet preference values for the observations to avoid misleading the readers.

L73: *Good to know that the model has been adjusted to fit zooplankton biomass, which to my knowledge, has not been done before: which figure and section is it?*

R: Indeed, we had not included the zooplankton evaluation in the manuscript as it was not fundamental to the main points of the manuscript. We will include this part of the model calibration in the appendix while including additional results regarding ecosystem functioning (see the response to the comment below).

Figure C1: *I think showing N at 100 m is more relevant than at 1000m, as it would be in the depth range of upwelled waters. Besides, N at 1000m is not at quasi-equilibrium after 25 years, it is still drifting quite a lot.*

R: Thank you for the advice. We will replace the N at 1000 m with N at 100 m (fig. R1.1). N at 100 m is equilibrated well before the analyses period of the last five years.

L82: "analyze with...": another typo. There are too many of them, the language really needs to be corrected, I am sure the authors can do a better job at it or get some help from a native speaker.

R: We apologise for the typos. We will pay thorough attention to improve the language in the revised manuscript.

L90: *add an equation for J and the limitation terms L(x).*

R: Thank you for pointing this out. We will update equ. 2 in the manuscript to equ. R1.1. Primary production (PP) is related to phytoplankton biomass (C), phytoplankton maximal growth rate ($J_{max}$, constant) and growth factors due to light, temperature and nitrogen conditions ($L_{(PAR)}$, $L_{(T)}$, $L_{(N)}$).
I do not understand equation (3). What is \( L_{\text{mld}} \) and how is it related to \( J \)? Does it play a role in the model equations? Please clarify.

\( L_{\text{mld}} \) represents the average growth factor phytoplankton experiences within the MLD. The average phytoplankton growth rate within the MLD, \( J_{\text{mld}} \) can then be calculated as equ. R1.2, where \( J_{\text{max}} \) is the constant maximum growth rate (see previous response). We will include the explanation in the revised text.

Cmld is the concentration or the concentration change? If it is the concentration change, what is \( \Delta C_{\text{mld}} \)? I am lost here.

\( C_{\text{mld}} \) refers to the average phytoplankton biomass concentration in the mixed layer. \( \Delta C_{\text{mld}} \) refers to the change of the concentration over time. We will explain the equation more clearly in the revised manuscript.

What is the chain rule?

We refer here to the mathematical expression "chain rule", the formula to compute the derivative of a composite function (equ. R1.3). We will clarify this in the revised manuscript.

This is an interesting figure: could you indicate the number of data per 1x1 grid point? How does it compare to the Boyer Montegut climatology (can be downloaded here: http://www.ifremer.fr/cerweb/deboyer/mld/home.php). It would be nice to add an error bar indicating the model’s MLD internal variability.

Thank you for pointing us to the additional data set. Please see fig. R1.2 for the number of Argo float profiles and a comparison of the seasonality of MLD of the different data sets: the de Boyer Montegut climatology (de Boyer Montegut et al., 2004) exhibits the shallowest MLD. The internal variability of the model MLD encompasses both the Argo estimate and the de Boyer Montegut climatology.

I am surprised the model chlorophyll is low: is this really the best fit after parameter tuning? Could you add an “error” bar to represent the model internal variability of Chl? Also, I think that Pennington’s plot was not exactly the same coastal area as shown in Fig.1a.

One reason for the simulated Chl being relatively low is that we used the Chl:N ratio from the model's croco-tool (the Matlab toolbox as mentioned above) to convert from nitrogen to chlorophyll (Chl:N=0.795). If we use the Chl:N ratio of Gutknecht et al. (2013) (Chl:N=1.59), the simulated Chl would double its value. The Chl:C and C:N ratios are both very variable in nature and it is not possible to resolve this variability with a fixed-stoichiometry model as used here. Therefore, we tuned the model chlorophyll so that the observed chlorophyll values fall between the simulated chlorophyll values using the different Chl:N ratios. We will add the error bars in fig. R1.3. And thank you for clarifying that in Pennington et al. (2006) primary the data is taken for a 250 km band off the coast. We will mention this in the manuscript.
Results

L137: “suggested” is a bit weak here. See my previous comment about the introduction.
R: We will emphasise the findings by EC08 more strongly in the revised manuscript.

L138: “the weaker increase…”: you need a reference here.
R: The reference is the Peruvian system. We will clarify this in the manuscript.

L141: Are the ARGO MLD estimates reliable off Peru? This should be addressed somewhere and ARGO data should be described in the Data and Methods section.
R: We will address the Argo data in the Data and Methods section. As also shown in fig. R1.2, there are on average 120 profiles available summed up over the focus region every month, which allows to robustly estimate the seasonality of the MLD.

We use the Argo MLD calculated based on the temperature threshold, to be consistent with the MLD calculated by the model. As pointed out by Holte et al. (2017), the MLD calculated from hybrid algorithms (an algorithm modeling the general shape of each profile by fitting lines to the seasonal thermocline and the mixed layer, Holte and Talley (2009)) are generally shallower than those derived from the temperature threshold. The de Boyer Montegut data exhibits shallower MLD than Argo but still falls within the median 50% range of the Argo spatial variability for most of the months.

L142: I think there are other hypothesis supporting the high chlorophyll values in the Canary system. This section comparing the different systems is too long and does not focus enough on the main topic of the paper.
R: We will shorten and streamline this section and focus more on the main topic of the paper.

L145-146: I do not agree with the conclusion here: as SST is also strongly correlated with insolation, you can not conclude that the seasonal cycle of temperature drives the phytoplankton growth. For your information, EC08 showed that the temperature effect was negligible in their model set-up (see the end of section 3.3).
R: We agree that a correlation does not imply causality, that is the relationship of SST and Chl does not necessarily mean that a higher SST is causing Chl to increase because SST and Chl could commonly be forced by another variable, namely insolation. We will phrase our sentence more carefully, and include the following arguments that support that the seasonality of light limitation due to insolation is not the driving factor of the correlation of SST and Chl:

(i) EC08 showed based on a sensitivity study that in their model the light limitation due to the seasonality of insolation was weak (see their section 3.5).
(ii) In fig. R1.4, the surface light and temperature growth factors show different seasonal patterns. In addition, the temperature growth factor reveals a greater seasonal variation than the surface light growth factor which would more directly reflect insolation.

Figure 2: the regions where data is averaged in a coastal band in the four systems should be indicated in the supplementary.

R: Thank you for pointing this out. We will add fig. R1.5 in the appendix to indicate the EBUS regions that were used to produce Fig. 2 in the manuscript.

L150: The reason for this is well known: the along-shore wind forcing is enhanced during winter, increasing upwelling and vertical mixing, and the lower winter insolation decreases surface stratification and increases the MLD.

R: We agree that the reasons for stronger upwelling and deep MLD in winter are well known. We here describe the relationships that we find in figure 2e, and emphasise that the Peruvian EBUS is the only EBUS that shows such a positive correlation between MLD and upwelling.

L181: "DV contributes...": in which figure is this shown?

R: The contribution of ΔV is calculated based on equ. 5, and the effect of dilution is evident from figure 3b-c. This will be stated more clearly in the revised text.

L206: "advection is picking up": I can not see that, advection seems negligible with respect to mixing (Fig.4d).

R: Yes, we agree that the absolute value of advection is small with respect to mixing. However, less phytoplankton biomass is mixed out of the mixed layer (the change of mixing promotes an increase of phytoplankton biomass, fig. 4f). In contrast, the divergence of advection is increasing (opposing an increase of phytoplankton biomass, fig. 4f), even if it is small in absolute terms. Considering that the fluxes and their changes over the decline phase are 1 - 2 orders of magnitude bigger than the change of phytoplankton biomass, even the changes of fluxes that appear small compared to PP or mixing can contribute to a change of the biomass, and we prefer to show the changes of all the fluxes in fig. 4f.

We noticed that fig. 4 contained a lot of information and was not discussed in sufficient detail in the manuscript to be easily digestible as also indicated by the other reviewer. This is why we will split up fig. 4 into two figures (fig. R2.3-2.4) and add additional detail.

L208-209: "the decreasing rate...": I do not understand this sentence

R: The entrainment of phytoplankton biomass is decreasing from summer to winter as the MLD deepens. The entrainment is related to the magnitude of the MLD increase, and to the phytoplankton concentration of the water that is entrained from below. The reason for
the decreasing rate of entrainment between \(t_1\) and \(t_2\) is the decreasing phytoplankton concentration below the base of the mixed layer. This will be stated in more detail in the revised manuscript.

L202-2011: *This paragraph is very difficult to follow and lacks precise references to the figures in the core of the text.*

R: Thank you for pointing this out. As mentioned in our response above, we will split up fig. 4 into two figures (fig. R2.3-2.4) and restructure the paragraph to make it easier to follow.

L222: *How do you obtain this 60% decrease based on Eq.3?*

R: We used the start of the decline phase as the reference, and checked how the three growth factors changed until the end of the decline phase. Then we used the mathematical product rule to calculate how each growth factor was contributing to the total change of the growth factor. This will be described in more detail in the revised text.

L229: The weak role of temperature is in agreement with EC08.

R: We will explicitly state this general agreement in the text, but will point out also that while in EC08 the role of temperature was concluded to be negligible, in our model it is, while minor, not negligible. That is, the sensitivity of phytoplankton (and the ecosystem) to temperature and potential temperature changes will be model dependent and might be worthwhile to be investigated further.

**Discussion**

L258-261: *I suggest a closer examination of EC08 findings and expand the comparison with their modelling work, which is very similar to what is presented here. In particular, they relaxed iron limitation in their model and found an Chl increase of 20-80% (depending on the latitude) during winter and spring, which corroborates the impact of iron limitation on the seasonal cycle found by Messié and Chavez (2015).*

R: Thank you for your suggestion. We will include a discussion of the results of the Fe-sensitivity study by EC08.

L272: *the sentence seems incomplete.*

R: We will correct this sentence as follows (L272-274):

"As we argued in the previous paragraphs based on the differences of the seasonalities of MLD and upwelling in the Peruvian system, the upwelling of nutrient-rich waters happens when growth conditions are the worst, in particular, light availability is lowest due to deep mixed layers."
L274: “and in deep …“: rephrase
R: We will rephrase the sentence as follows (L274):
"Also, the upwelled waters are comparatively cool."

L275: “charge”
R: We will add the quotes.

L276: I am not convinced by this hypothesis: the residence time of the upwelled water in the mixed layer near the coast is probably quite short as upwelled waters are rapidly transported offshore by Ekman currents. Thus I do not believe in such preconditioning. Unless you can prove it using the model.
R: Thank you for your feedback with respect to our hypothesis that the co-occurrence of deep mixed layers and upwelling may precondition the summer maximum of phytoplankton biomass. While we think that the hypothesis could be worthwhile to further explore, we agree that it is very speculative. We will remove the section.

L295: “higher” with respect to what? Clarify.
R: Higher with respect to other times/months of the year. We will rephrase the sentence as follows (L295):
"The high surface nitrate concentrations in conditions of deep mixed layers in the Benguela system could be interpreted this way."

L314: Is this a result of the study? It has not been described. I think elaborating on the seasonal cycle of export and zooplankton could have been interesting.
R: Yes, the source of export is part of an analysis of export production not shown so far in the manuscript that we are happy to include (fig. R1.6). Compared with the integrated phytoplankton biomass, integrated small zooplankton biomass appears rather steady. On the contrary, integrated large zooplankton biomass shows a relatively stronger seasonal variance with higher biomass when mixed layers are shallow compared to when they are deep. In our model, large zooplankton is the only source of large detritus, which in turn is the major contributor to the export of particulate organic material (fig. R1.6b). Therefore, the seasonal cycle of export follows closely the seasonal cycle of large zooplankton, with maximal export in austral summer and minimal export in austral winter. As large zooplankton exhibits a stronger seasonal variance than phytoplankton, also export efficiency is correlated with MLD. We will include a more detailed discussion of these results and their implications in the revised manuscript.
This discussion is very speculative and vague. I do not find it very useful.

R: We agree that without a more detailed discussion of our results with respect to the seasonality of ecosystem functioning, the discussion appeared speculative. We will streamline this part of the discussion after including the results regarding zooplankton and export as described above.

Echevin et al. (2020) also investigated the mixed layer evolution under climate change (Figure 7), not only changes in upwelling. I encourage the authors to read the papers they cite more carefully.

R: We apologise as we did not want to imply that Echevin et al. (2020) did not investigate the mixed layer evolution under climate change. We will rephrase this part to make it more clear.

Surface chl only slightly increases in the different simulations (2%-17%, Fig. 12a).

R: Thank you for pointing it out. We will indicate the amplitude of the increase in the paper.

The propagation of the seasonal variability up the food web is not documented in the results sections and only mentioned in the discussion: it is not worth mentioning in the conclusion.

R: We will add a more detailed presentation of this aspect to the results section.

what are the remaining open questions about the interactions behind the mixed layer and upwelling dynamics? Be more specific.

R: We will be more specific in the revised version, including that we feel more research is required on how physics will affect ecology, e.g., how the mixed layer and upwelling jointly affect the food web processes and thus food web structure.

References


Please also note the supplement to this comment: https://bg.copernicus.org/preprints/bg-2021-113/bg-2021-113-AC3-supplement.pdf