Rebuttal report

Climatic Controls on Metabolic Constraints in the Ocean

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 # Reviewer1

This paper is quite interesting and logically organized. The motivating questions are made clear in the Introduction and the figures are appropriately used to tell the story. In general, the writing is quite clear outside of the Methods section, the last paragraph of the Discussion, and portions of the Conclusions paragraph. The authors will need to correct what seem to be multiple typos throughout the Methods section before this can be published, so I am recommending minor revisions. I also recommend that the authors consider adding a schematic to visually clarify relationships between key metrics of the paper. This would increase the accessibility of the paper significantly and serve as a valuable reference for the Discussion section, particularly when explaining some of the more complex impacts of oxygen and temperature changes on ectotherm habitability of high and low latitudes.

Response: We thank the reviewer for his/her insightful comments and suggestions. Indeed, the methods section had multiple typos in the equations, we apologies for this. We have addressed these typos as pointed out, and we will consider adding a schematic diagram to tie together and summarize the paper.

Line 27: Typo. Signals → signal

Response: Addressed as suggested

Line 44: It may be valuable to incorporate the concept of higher oxygen demand, independent of oxygen supply or circulation changes.

Response: We would like to address this comment; however, it is unclear what the reviewer is suggesting or pointing out with reference to line 44. There may be a mistake in the line reference.

Lines 109-110: Typo? $B\ \sigma$ is in the equation but you define $B\delta$

Response: We thank the reviewer for point this out, this was indeed a typo, it is now corrected.

Equation 1: The B term is missing, and this equation should be labeled equation 2. Even though the B term is ultimately dropped, it should be included for clarity, following Deutsch et al., 2020 equation 1.

Response: The B term was indeed excluded because it drops out, we have now included the full form of equations (Line 112 – 126).

Line 139: This text is not clear. Please stick to one concept at a time. For example: “Φ' is derived by dividing Φ by Φcrit , so when Φ falls below 1, the organism can no longer sustain its active metabolic demand and will need to make physiological trade-offs. Account for these active metabolic requirements, we use an adjusted definition of the hypoxic tolerance trait, A c = A o / Φcrit , where A c is termed the “ecological hypoxia tolerance”, consistent with Howard et al., 2020.”

Response: We thank the review for this suggestion, it was implemented as suggested, Line 143 – 150

Line 143 – 150 “Therefore, in this study, we define a quantity Φ' derived by dividing Φ by Φ_{crit}, so when Φ falls below 1, the organism can no longer sustain its active metabolic demand and will need to make physiological trade-offs. Account for these active metabolic requirements, we use an adjusted definition of the hypoxic tolerance trait, $A_c = A_o / \Phi_{crit}$, where A_c is termed the “ecological hypoxia tolerance”, consistent with Howard et al., 2020. Where $\Phi' > 1$ (i.e., $\Phi > \Phi_{crit}$) an organism can sustain an active metabolic rate; where $\Phi' < 1$ (i.e., $\Phi < \Phi_{crit}$), O_2 is insufficient and an active metabolic state is not viable. Henceforth, our analysis focuses on Φ'; in the subsequent $\Phi' = \Phi$ for the text and figures.”

Line 161: It’s not clear how this relationship yields cold tolerance, please elaborate, or reword for accuracy.

Response: This is illustrated in Fig. 1b, where the nearly parabolic curvature of pO_2 at Φcrit indicates an increase in oxygen demand at both low temperatures and high temperatures. Most of the manuscript focuses on the high-temperature oxygen demand based on metabolic demand. Nevertheless, at very low temperatures, gas transfer is limited by the decrease in molecular gas diffusion, and as a consequence, oxygen transfer into the organisms requires energy, leading to cold intolerance. We extend the text make the discreption clearer.
Line 169 – 173 “The reversing curvature of pO_2 at Φ_{crit} in Figure 1b at low temperature captures the decrease of the organism’s oxygen acquisition efficiency in cooler conditions yielding cold intolerance. At very low temperatures, gas transfer is limited by the decrease in molecular gas diffusion, as a consequence, oxygen transfer into the organisms requires energy, yielding cold intolerance, this is well illustrating by the blue line in Figure 1b.”

Figure 1b. It may help to clarify in the figure caption that below the pO2 lines shown, the organism would experience an oxygen deficit relative to its active metabolism requirements, effectively signifying the species-specific hypoxic conditions, based on physiological traits, for this range of temperatures. Figure 2: Center the global map on the Pacific to make the transect location easier to see.

Response: We thank the reviewer for this suggestion, we added the suggested description in Figure 1b

Figure 3: Add prime to Φ color bars.

Response: We have now add general comment in methods to clarify that Φ text refers to Φ’ throughout the text according to Howard et al., 2020’s definition.
Line 148 – 150: “Where $\Phi' > 1$ (i.e., $\Phi > \Phi_{crit}$) an organism can sustain an active metabolic rate; where $\Phi' < 1$ (i.e., $\Phi < \Phi_{crit}$), O_2 is insufficient and an active metabolic state is not viable. Henceforth, our analysis focuses on Φ'; in the subsequent $\Phi' = \Phi$ for the text and figures.”

Line 347: Can you validate this hypothesis by looking at interannual variations in model density versus temperature or oxygen?

Response: We thank the reviewer for this comment, we have referenced Long et al., 2016 where this hypothesis is discussed.

Figure 8 Caption: Note that the same decades for differencing apply to the top row of plots in addition to the bottom row.

Response: We added a title to figure 8

Line 480: Is this a typo? Aren't high temperature regions mostly suited for organisms with high-temperature tolerance or reduced temperature sensitivity (Figure 2)?

Response: This is not a typo; this phenomenon is better explained by Figure 1.b. Due to high temperatures in the tropics, habitability requires either high oxygen tolerance or high temperature sensitivity (high E_o). High E_o organisms have particularly strong temperature sensitivity at high temperatures.

Line 494: Should this say epipelagic and mesopelagic? This entire paragraph stands out as being particularly unclear relative to all other text (outside of the methods).

Response: Indeed, this was a typo and we apologies for this sloppy paragraph. We have updated this paragraph

Line 529 – 544: "In the epipelagic and mesopelagic regions (200 m and 500 m), the forced temperature trend and natural variability are broadly smaller than the surface ocean, while pO_2 changes show the opposite. Thus, at depth pO_2 play a more intricate role in perturbating marine ectotherm habitats in the context of anthropogenic warming with respect to the surface ocean, where temperature plays a dominant role. Contrasting the regression between pO_2 and temperature in the natural climate, and forced trends provides an instructive framework to analysing ectotherms' long-term changes. Regions showing different correlations between temperature and pO_2 in the forced trends in comparison to the natural climate suggest a loss metabolic resilience; loss of habitat, and these regions tend to have a relatively early ToE. For instance, in the epipelagic and mesopelagic North Pacific, temperature-pO_2 regressions switched from a positive correlation in the unperturbed climate to a strong negative correlation in the forced trend (Figure 7). The North Pacific pelagic – epipelagic regions is projected to lose nearly half of the present climate ecotype viability by end of the 21st century, the projected habitat loss start emerging by the late 2030s under the RCP85 climate scenario, On the other hand, in the Arctic Ocean and some parts of the Southern Ocean, same sign pO_2-temperature correlations in the forced trends result in the preservation of the marine habitat and even slight enhancements."

Line 498: Sentence starting with "At depth" could be reworded for clarity.

Response: This entire paragraph is reformulated.

Line 500: By "distinct" do you mean correlations of opposite sign?
Response: Distinct is replaced by "differences" which clarify the meaning of the sentence.

Line 509: It's not clear what is meant by "concomitant pO2 -temperature correlations in the forced trends". I assume this means trends of the same sign, but it would be ideal if this were clearly stated

Response: We thank the reviewer for this suggestion, concomitant is replaced by same-sign

Line 521: Suggest changing to: "We find that forced perturbations to pO2 and temperature will strongly exceed those associated with the natural system…"

Response: We thank the reviewer for this suggestion, implemented as suggested.

Reviewer 2

The paper examines the effects of warming and deoxygenation on marine ecosystems by analyzing the temperature sensitivity and oxygen requirements of metabolic rates. Utilizing CESM-LE, the research explores the natural variability and anthropogenic impacts on the support for aerobic metabolisms in marine ecosystems over various timescales. The study emphasizes that future climatic changes will intensify the challenges faced by marine organisms, driving them toward their physiological thresholds and heightening the vulnerability of marine ecosystems to extreme events.

The manuscript is well-written, and the line of thought is clear. I believe this paper is of interest to the general audience of Biogeosciences. I only have very minor technical and clarification questions.

Response: We thank the reviewer for his/her well considered comments and suggestions.

L112: This equation should be labeled as Eq. 1

Response: This entire session is reformulated to show all equations explicitly as suggested.

L113 – 127: The definitions of E_O, E_D, and E_S, are not clear in this section. I suggest bringing the Eq. in L123 earlier.

Repones: This entire session is reformulated to show equations explicitly as suggested.

Line 105 – 131: " Deutsch et al. (2015) formalized these concepts into a quantity termed the "Metabolic Index (Φ)", which is defined as the ratio of oxygen supply to an organism's resting metabolic demand. Oxygen supply is parameterized according to a biomass-dependent scaling of pO_2, capturing variation in the efficiency with which organisms acquire and utilize O_2. This can be expressed as $S = \hat{\alpha}_s \, B^{\sigma} pO_2$, where $\hat{\alpha}_s$ represent gas transfer between an organism and its environment and B^{δ} is the scaling of supply with biomass, B (Piiper et al., 1971). Gas supply is represented as an Arrhenius function;

$$\hat{\alpha}_s = \alpha_s exp\{\frac{-E_s}{K_B}\left[\frac{1}{T} - \frac{1}{T_{ref}}\right]\} \quad (1)$$

Resting metabolic demand is also expressed using the Arrhenius equation as

$$D = \alpha_D B^{\delta} exp\{\frac{-E_d}{K_B}\left[\frac{1}{T} - \frac{1}{T_{ref}}\right]\}, \quad (2)$$

where α_D is a species-specific basal metabolic rate, E_d (eV) is the temperature dependence of oxygen supply, T is temperature, T_{ref} is the reference temperature (15°C), and k_B is the Boltzmann constant (Gillooly et al., 2001). Gas transfer is kinematically slow at low temperatures, and hence organism viability can be limited by the energy to acquire oxygen at low temperatures, thus E_o varies with temperature. Here we account for this by adding the temperature dependence (dE_o/dT) to E_o in equations above ($E_o + \frac{dE_o}{dT}(T - T_{ref})$), using the mean value of $dE_o/dT = 0.022$ eV consistent with Deutsch et al. (2020). The Metabolic Index can thus be written as the ratio of *S/D*:

$$\Phi = \frac{\alpha_S}{\alpha_D}\frac{B^{\sigma}}{B^{\delta}}\, pO_2 exp\{\frac{-E_S}{K_B}\left[\frac{1}{T} - \frac{1}{T_{ref}}\right] + \frac{E_d}{K_B}\left[\frac{1}{T} - \frac{1}{T_{ref}}\right]\},$$

$$= A_o B^{\sigma-\delta} pO_2 exp\{\frac{E_d - E_s}{K_B}\left[\frac{1}{T} - \frac{1}{T_{ref}}\right]\},$$

$$= A_o pO_2 exp\{\frac{E_o}{K_B}\left[\frac{1}{T} - \frac{1}{T_{ref}}\right]\}, \qquad (3)$$

where $A_o = \alpha_S/\alpha_D$ *(1/atm)* is the hypoxic tolerance, $E_o = E_d - E_s$ (E_s is the temperature dependence of oxygen supply) (Deutsch et al., 2015; Penn et al., 2018). The exponent, $\varepsilon = \sigma - \delta$, is the allometric scaling of the supply to demand ratio with biomass, is typically near zero. Therefore, in the analysis that follows, we presume unit biomass and thus neglect potential impacts of variations in biomass."

L241: Could you comment on the negative bias in pO_2 in CESM-LE at 200 and 500 meters? This bias is mainly due to limitations in biogeochemistry or physical circulation. How does this bias project to future scenarios?

Response: This is a documented CESM bias. We will provide a description of the sources of the bias.

Line 261 – 264: "This CESM pO_2 bias is common among coarse-resolutions ocean models and it is attributed to a sluggish circulation and hence weak ventilation (Long et al., 2016). These differences ultimately matter most near the hypoxic zones and at the boundaries of habitable zones like the Oxygen Minimum Zones (OMZs)."

L269: OMZ = Oxygen Maximum Zone? This has not been defined in the paper.

Response: Thanks for point this out, corrected

L278: How do you calculate the natural variability? 1σ uncertainty of the period 1920 to 1965?

Repones: Yes, natural variability is calculated as 1σ uncertainty of the period 1920 to 1965, now stated explicitly.

L309: Curious if you compared temperature and pO_2 trend between CESM-LE and observation. I am wondering if the CESM-LE shows reasonable trend. Any trend bias in CESM-LE here could project bias in future scenarios.

Response: We did not compare CESM-LE and observations in this study.

L367: Texts on the left of the bottom row should indicate a trend (difference between 2020–2099 and 1920–1965)

Response. No, these plots show a pO_2-temperature regression at 50 m, 200 m and 500 m, the top row is the natural climate (1920 – 1965) and bottom row, the forced trend (2020 – 2099).

CESM-LE seems to suggest deoxygenation has started only since ~2000. Observation data, however, support an earlier onset of ocean deoxygenation. Could you comment on this?

Response: Thanks for pointing this out, this reflect CESM's underestimation of deoxygenation with warming which also came in the above comment.

Reviewer ##3

In this manuscript, the authors use a synthesis of empirical data and ESM large ensemble to assess the influence of both oxygen and temperature in determining habitat suitability for a series of ecotypes in the surface and subsurface ocean, and they study how these factors, and their interaction, change distribution of these ecotypes under climate change. The study is compelling, well thought out, and very well written. It was truly an enjoyable read.

The only pointed criticism I have is that it is missing some context on the empirical data used. Although the dataset is referenced in the manuscript, some added text on how it was synthesized and broad description of types of species included, their ecological role, and how the values used were obtained would be helpful. Rough data distribution and possible geographical biases could also be mentioned.

Other than that, any comments I have are very minor (some cosmetic) and I would recommend this manuscript for publication with minor revisions. Specific comments are mentioned below.

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Response: We thank the reviewer for his/her well considered comments and suggestions.
We added more details on the physiological datasets we used.
Line 153 – 159: "We make use of a dataset describing physiological parameters for a collection of 61 marine ecotypes spanning a range of ecological hypoxic tolerances (A_c) and temperature sensitivities (E_o) (Penn et al., 2018; Deutsch et al., 2020, Figure 1a). The 61 species span benthic and pelagic habitats across four phyla in all ocean basins (Arthropoda, Chordata, Mollusca, and Cnidaria). The dataset include 28 malacostracans, 21 fishes, three bivalves and cephalopods, two copepods, and one each for gastropods, ascidians, scleractinian corals, and sharks with body mass spans of eight orders of magnitude (Penn et al., 2018)."

L109: check the exponent on B

Reponses: This was indeed a typo and it is corrected.

L147: add more information about the dataset used

Response: We added more details on the physiological datasets we used.
Line 153 – 159: "We make use of a dataset describing physiological parameters for a collection of 61 marine ecotypes spanning a range of ecological hypoxic tolerances (A_c) and temperature sensitivities (E_o) (Penn et al., 2018; Deutsch et al., 2020, Figure 1a). The 61 species span benthic and pelagic

habitats across four phyla in all ocean basins (Arthropoda, Chordata, Mollusca, and Cnidaria). The dataset include 28 malacostracans, 21 fishes, three bivalves and cephalopods, two copepods, and one each for gastropods, ascidians, scleractinian corals, and sharks with body mass spans of eight orders of magnitude (Penn et al., 2018)."

Figure 1: the blue star is really hard to see, consider using a different color

Figure 5: Perhaps add a label with the variables to the left to make interpretation easier?

Response: A variable description added on the left of figure 5

L376: Figure 8?

Response: This was as indeed a typo, corrected

Figure 8: could add title with the depth on panels a-c

Response. Thanks for the suggestion, title added.

L479: remove "in the surface ocean"

Response: Removed.