eastern boundary upwelling systems: a major stressor for zooplankton' (Frederick et al)

General comments

This project aims to provide a synthesis of zooplankton responses to changes in hypoxia in Eastern Boundary Upwelling Systems (EBUS). To this end, the authors motivate their review by discussing changes in the biogeochemistry of the EBUS due to climate change, with a particular focus on upwelling and the vertical expansion of hypoxic layers and the Oxygen Minimum Zone (OMZ). The authors then introduce two different adaptive modes by which organisms change their metabolic activity to decreasing oxygen concentration and show possible adaptive responses, as well as the non-adaptive response. This is then followed by an extended section on the oxidative stress in zooplankton, where the authors explore the consequences of hypoxia and the production of reactive oxygen species for both migratory and non-migratory zooplankton.

This review is very timely as ocean deoxygenation is increasing globally. However, in my opinion, the review could go more into detail with respect to the mechanisms presented, and provide more details on the individual- and population-level consequences of an increase in the exposure of zooplankton to low oxygen levels.

R. We thank the reviewer for his(her) thoughtful comments and the very detailed revision. We agree on that the issues raised need to be addressed

Furthermore, the link between the adaptive responses and the oxidative stress was for me not entirely clear. In other words, It was unclear to me if the responses to oxidative stress change depending on the adaptive responses shown in Figure 3, and whether one response would be favored over another under increasing deoxygenation.

R. Thanks for this comment, inviting to further speculate on the oxidative stress consequences of the metabolic responses identified. We agree that the link between metabolic adaptation to variable oxygenation and the effect of oxidative stress (ROS) on this adaptive response is not so evident in our review and needs to be clarified. Indeed, the proposed mechanisms for metabolic adaptation to cope with changing oxygen may operate within a range of hypoxia above Pcrit, and below this the ROS can be triggered upon later re-oxygenation. However, this possibility was not clearly represented in the MS, and therefore in the section in which we describe ROS and POS we

are now recalling this Fig. 3 (now Fig. 4) and discuss on how these metabolic adaptations can relate to them. The actual paragraph is:

"An important biological response linked to variable oxygen levels, and rarely considered in the ocean, is oxidative stress. The phenomenon can occur because the variations in oxygen levels may range from normoxia to hypoxia at short spatial and temporal scales (hours) in some areas, such as in EBUS. Driven by such fluctuations, the oxidative stress appears related to a state of respiratory imbalance in terms of O_2 uptake, delivery, and usage, during which the animals cannot maintain a constant tissue oxygenation and, instead, undergo rapid changes between under-oxygenation and hyper-oxygenation (Tremblay et al., 2010). This can indeed occur under stressful conditions in individuals subject to oxygen levels below their Pcrit values (as shown in Fig. 4), and which thereafter undergo re-oxygenation. Therefore, as a product of aerobic respiration, the production of reactive oxygen species (ROS) can occur."

Finally, I felt that some of the physical and behavioral processes presented in the review are oversimplified or do not match other findings/definitions. Here I am referring to the oversimplification of increased wind-driven upwelling across the EBUS and the depth of diel vertical migration (DVM). I think the authors oversimplify the processes by which upwelling has changed across the EBUS, where for instance the review by Bograd et al. (2023) does a great job at detailing the differences in upwelling intensity across different EBUS. With respect to the DVM, the authors use a euphotic zone of 50 m rather than the usual 200 m, and the vertical extent of DVM shown seems extremely shallow, which does not match the description in the text.

R. We appreciate this comment and suggestions. We agree on that changes in upwelling in EBUS forced by global warming varies strongly spatially and so having influence on both vertical and horizontal distribution of the OMZ, possibly impacting DVM too. We considered 50 m as a prevailing photic zone in coastal waters more directly influenced by upwelling and presence of the OMZ, and where most zooplankton concentrate. Although the boundaries of the OMZ on oceanic waters must consider a deeper photic zone (likely between 100 and 200 m deep). We also agree that some zooplankton, such as euphaudiids can migrate deeper than w 200 m, entering the core of the OMZ. In this respect we have modified Fig. 1 to represent a cross-shelf variable depth of the photic zone and extend the discussion on how a spatially heterogeneous upwelling response to global warming can affect the OMZ distribution in different EBUS and over the meridional gradient. We have

also added vertical arrows to represent a variable DVM amplitude depending on the position of the upper boundary of the OMZ, although indicating in the text that some zooplankton (e.g. euphausiids) may override this potential barrier to perform DVM. Certainly, we are now citing the review of Bograd et al. (2023), as well as other important works, such as Xiu et al. (2018), Schneider et al. (2016). The most important modifications in Figures and text are detailed below.

Specific comments

L.15: As mentioned above, I think the authors should address the uncertainty in upwelling trends depending on the data set, region, and proxy variable used, since this seems to be the one of the key process in the paper by which organisms can be exposed to low oxygen concentration. For instance, regional observations have shown a weakening or no significant trend in upwelling intensity for the Canary Upwelling System (Bode et al. 2019). Or Pardo et al. (2011) that found a small weakening trend in the Humboldt System and no trend in the California Current System using trends in sea surface temperature.

R. We thank for the suggestions and references. We are modifying the text saying that this issue may vary depending on projections for different EBUS and there is still debate and uncertainty on the future of upwelling. There are several works suggesting increasing upwelling in EBUS, though it seems that increasing upwelling may mostly occur at mid-latitudes (Wang et al. 2015, Xiu et al., 2018), including the Benguela EBUS (Santos et al. 2012), the Chilean EBUS (Schneider et al. 2016), although there is also no evidence of increasing upwelling in other EBUS (Pardo et al. 2011, Bode et al., 2019). We are now including these references to discuss the issue related to the uncertain future upwelling in EBUS. We have also modified Fig. 1 to illustrate that increasing upwelling is a possibility, but still uncertain. This is New Fig. 1 and its caption:

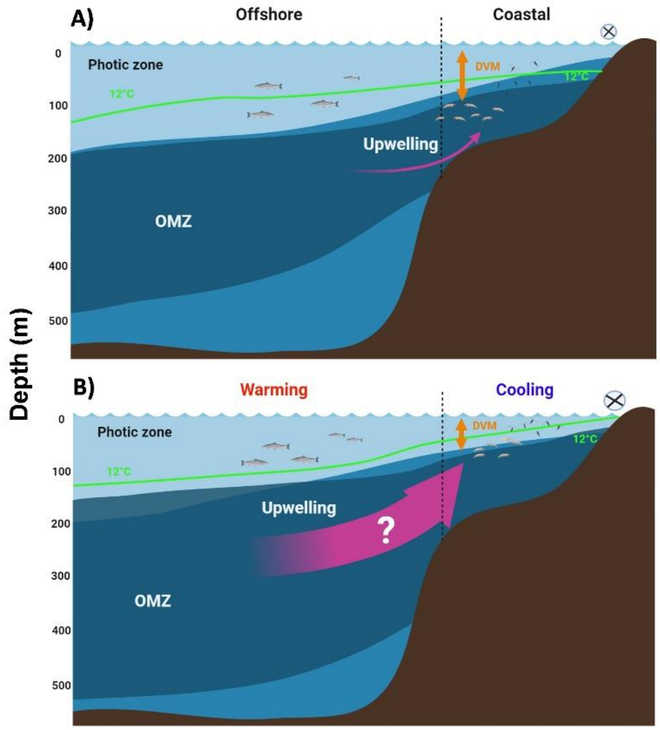


Figure 1. Projected effects of expansion of the OMZ in eastern boundary upwelling systems (EBUS). Upper panel) Under present (initial) conditions, wind-driven upwelling rises the OMZ system and brings cold-water into shallow depths at the inshore as illustrated by the 12°C isotherm, and so fertilizes the photic zone and promotes plankton aggregation. Lower panel) Ocean warming effects manifest mainly at surface in the offshore region, while a vertically expanded OMZ along with an eventual (although uncertain) increase in upwelling may cool down the coastal zone and further shoaling the OMZ at the inshore area, causing more hypoxia and vertically reducing the oxygenated habitat. Vertical compression of the oxygenated habitat may restrict the vertical distribution and diel vertical migration (DVM) of zooplankton.

Also, the modified paragraph is now:

"In some areas, mainly at mid-latitudes, of the four major eastern boundary current systems (EBUS) (Chavez and Messié, 2009), the effect of climate change has been associated with an intensification of the physical forcings driving coastal upwelling (Bakun et al., 2010; Xiu et al. 2018, Bograd et al., 2023), leading to several changes on the physical-chemical properties of the water column, including a gradual cooling in the last few decades (Santos et al., 2012; Schneider et al., 2016). However, other studies have found no evidence of increasing upwelling or trends in upwelling intensity, as based on time series observations for several decades in same EBUS (e.g. Pardo et al., 2011; Bode et al., 2019). Trends of upwelling intensity in EBUS is therefore still matter of controversy, and the predictive models reveal much uncertainty on future upwelling regarding its spatial and temporal variability (Bograd et al. 2023). Upon potential increase of

upwelling, favourable winds in EBUS bring colder water and more frequent occurrences of upwelling events (Breitburg et al., 2018), although some modelling work also suggests an extension of the upwelling period and spatial homogenization of upwelling over the alongshore axis (Wang et al., 2015). Stronger upwelling is ultimately thought to be a response to the strengthening of large-scale pressure gradients linked to global-scale climate change (Garcia-Reyes and Largier, 2009). With the intensification of the coastal upwelling, a shoaling of the oxygen minimum zones (OMZ) in coastal waters may take place and so compressing the upper highly oxygenated layer (Khön et al., 2022). The closely linked effects of increasing upwelling, cooling of the water column and shoaling of the OMZ in EBUS driven by global warming are illustrated in Fig. 1..”

L.29-31: This sentence contains a strange redundancy stating that a warmer ocean drives increases in mean global sea surface temperature. In addition, I would argue that the warming drives the physico-chemical changes rather than just a warmer ocean. Please revise the sentence.

R. Agree. We have modified this paragraph to avoid redundancy. Now it should read “climate change drives several physical processes.....”

L.34: Here, I suggest the authors be more quantitative and say by how much the oxygen concentration has changed since the middle of the 20th century. With such a measure, the authors can compare the long-term changes with seasonal and spatial changes in oxygen concentration.

R. we have added an estimated reduction in oxygenation in about 2% of the global ocean with corresponding cites.

L.40-43: Given that short-term changes in oxygen are of interest for this review, I suggest to also include the role of extreme events, which can lead to transient habitat reductions of variable duration in EBUS such as the California Current System and the Humboldt System (Köhn et al., 2022).

R. We are now referring to such extreme events as potential perturbations related to OMZ distribution and hypoxia and their potential effects of zooplankton, citing the work of Köhn et al. (2022). The added paragraph is:

“ In some cases, the minimum oxygen concentrations in the OMZ cores have also been further reduced, intensifying the OMZ (Chan et al., 2008). Increasing hypoxia driven by these trends in loss of oxygen can be further exacerbated by extreme events caused by the action of mesoscale eddies producing intense episodes of hypoxia in the upwelling zone (Khön et al., 2022).”

L.47-48: As spatial heterogeneity in oxygen conditions is one of the key factors determining the exposure of zooplankton to low oxygen, I urge the authors to explore how the spatial changes in upwelling due to the poleward displacement of coastal upwelling winds (Rykaczewski et al. 2015) has or will likely change the overall oxygen conditions in the poleward vs the equatorward boundaries of EBUS.

R. Although there is much uncertainty and debate on the future of upwelling in EBUS (Bograd et al. 2023), some modelling suggests a potential extension of the upwelling period and alongshore spatial homogenization of upwelling. Considering these possibilities the level of oxygenation for zooplankton may not change vertically, but perhaps also horizontally alongshore and cross-shelf as well due to the OMZ expansion (Grégorie et al., 2021). This implies spatial variation in the oxygenated habitat with ecological consequences for zooplankton. In this respect, we are now describing these modelling results and their consequences in the Introduction and Discussion of the Review. The paragraph being modified now reads like:

"Upon potential increase of upwelling, favourable winds in EBUS bring colder water and more frequent occurrences of upwelling events (Breitburg et al., 2018), although some modelling work also suggests an extension of the upwelling period and spatial homogenization of upwelling over the alongshore axis (Wang et al., 2015)."

L.54-55: Here the authors should provide some examples of the various ecological and biogeochemical consequences, preferably with a quantitative metric, as this would add more meaning to their statement and improve their review for future readers.

R. We are now adding several examples on some ecological consequences of hypoxia. The paragraph is:

"The ongoing combined processes, deoxygenation, increasing upwelling, OMZ expansion and potential latitudinal expansion of upwelling will alter the oxygen conditions in upper layers (<50 m) in EBUS, where plankton becomes concentrated, with various ecological and biogeochemical consequences. In this respect, Ekau et al. (2010) demonstrated that hypoxic conditions can alter the zooplankton community composition in the Benguela EBUS. This occurs because of variable tolerance to hypoxia in some distinctive groups, being euphausiids for example better adapted to low oxygen (<0.1 mL/L) compared to

copepods. Escribano et al. (2009) also described a strong vertical zonation of zooplankton depending on variable tolerance to hypoxia in the northern upwelling zone of Chile. Variable tolerance to hypoxia is also reflected in some species-dependent physiological rates of copepods, as found in the calanoids *A. tonsa* and *C. chilensis* whose egg production rate and hatching success were strongly positively correlated to oxygen concentration under laboratory conditions (Ruz et al., 2015). In the same context, not only vertical distribution, but also the vertical amplitude of the diel vertical migration can also be strongly modulated by hypoxic conditions forced by position of the OMZ core and its upper boundary (Tutasi and Escribano, 2020; Riquelme-Bugueño et al., 2020). "

L.56: The authors introduce the terms normoxia and mild or severe hypoxia. I understand that these levels are species-specific, however, it would help to have a range or a mean of a selected number of species. I would also imagine that using the levels for copepods would suffice given their abundance and importance.

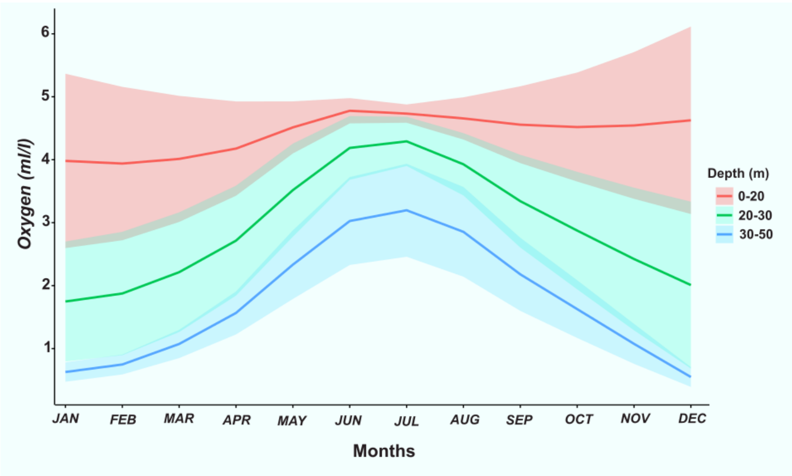
R. Agree. We are adding a paragraph to define these terms. This is:

"Aerobic metazooplankton inhabiting the upwelling zone is thus expected to be exposed to variable levels of oxygenation from normoxia to mild or severe hypoxia, depending on their distribution and migrating behaviour, but also depending on variable levels of tolerance to hypoxia. In copepods, which represent the major contributors to zooplankton biomass in EBUS, oxygen levels 1-2 mL L^{-1} may represent mild hypoxia, while concentrations <1 mL L^{-1} should be considered as severe hypoxia for most species (Wishner et al., 2018; Frederick et al., 2024)."

L.79-85: The authors explain very clearly two adaptive modes and illustrate the differences between them. To increase the impact of the review, they should also mention characteristic timescales at which such changes can occur in zooplankton and provide examples of possible organisms that follow each adaptive mode if possible.

R. Agree. We are now providing the timescales over which these adaptive responses can take place for vertically migrant and non-migrant zooplankton. To better illustrate this, we are also adding a new Figure (new Fig.3) in which we illustrate the oxygen gradient in the upwelling zone from a database of oxygen of a time series at the upwelling zone off central-southern Chile. The new paragraph and Figure are:

"The adaptive responses to variable levels of oxygen illustrated in Fig. 2 may take place over short-term timescales (hours), as driven by exposure to a vertical gradient of oxygen in the water column when performing DVM in migrating species, or in the case of non-migrating species due to vertical mixing in the water column as forced by upwelling pulses or changes in wind conditions promoting mixing. Both migrating and non-migrating species can thus be exposed to variability in oxygenation in the upwelling zone which is characterized by a marked oxygen-stratified water column (Fig. 3). Clearly within the photic zone (about 50 m in the coastal zone) the annual cycle of oxygen conditions reveals the existence of normoxia, mild and severe hypoxia habitats with which vertical migrant and non-migrant zooplankton must cope with depending on their vertical distribution in this layer (Fig. 3)."



New Fig. 3. The annual cycle (monthly climatology) of oxygen concentration in three strata in the upper 50 m layer at central-southern Chile (36°30 S). Oxygen data are from the time series study at Station 18 off central-southern Chile during the period 2002-2016 (Frederick et al., 2024).

Furthermore, given the evidence from Cobbs and Alexander (2018) on the existence of other response types to progressive hypoxia among marine animals; including zooplankton; the authors could expand their review to include more response types.

R. We thank for this comment. Our proposed model based on two types of metabolic responses to variable oxygenation is the traditional view, based on studies on a variety of organisms. The analysis provided by Cobbs and Alexander (2018) mostly describes potential empirical results, although as they state these results do not necessary can reflect a functional or adaptive response. In any case, we agree that is an important issue to consider,

because we have seen that the evolution of respiration as a function of oxygen is indeed very variable and not easy to interpret or to fit to single mathematical functions. For examples, in situations with animals under stress regulation or no regulation can occur or having different phases during the response. We are now discussing this issue in the text and including this reference.

L.99-103: The authors explain very briefly how maternal effects can play a role in shaping the plasticity of stress responses in organisms, putting a focus on the effects of life-history on individual-level responses and possible consequences for the population. However, the authors then remain relatively vague in explaining how this mechanism works and do not explain possible feedbacks and consequences on the population.

R. We agree with reviewer in the need for extending and clarifying this issue. Since copepods are rather short-lived animals (<months), we hypothesize that even though maternal effects can be passed on to seasonal cohorts, allowing the offspring inherit adaptive characters to cope with variables conditions, this offspring can also react to new upcoming conditions by activating some genes coding for proteins developed for physiological or biogeochemical functions for improved fitness. We have no data or evidence for this, although many works have evidenced the environmental effects on gene expression (epigenetics). We are now extending this paragraph to propose such mechanism as a hypothesis that needs consideration in future studies.

L.125-129: The authors name some changes in behavior and distribution as a result of exposure to hypoxia. While I agree with the examples in the text, it would help to give other examples of strategies observed in the field (e.g. Hauss et al., 2016).

R. We are now adding more examples on responses to low-oxygen conditions, such as those provided by Hauss et al. (2016) who reported various responses to a shallow OMZ associated to a subsurface eddy in the northeast tropical Atlantic, depending on the different groups of zooplankton. We have also found aggregations of zooplankton just at the base of the oxycline to avoid predation, but also avoiding extremely low-oxygen water (Donoso and Escribano, 2014). We are also adding the migration response of some copepods to the lower boundary of the OMZ, such as that reported by Wishner et al. (2008).

L.132-133: Here again, it would be important to have a sense of the spatio-temporal scales to fully grasp how the exposure to low oxygen conditions changes along the life-history of individual organisms.

R. Agree. We are now describing that processes of interaction between copepods and oxygen gradients controlled by distribution of the OMZ may occurs across short-term time scales (hours) due to vertical migration and some physical processes controlled by vertical mixing and upwelling pulses, also over microscale and mesoscale spatial scales due to oxygen gradients occurring within the photic zone and across physical structures, such as mesoscale eddies and fronts.

L.143-145: Here, it would be important to get some comparison of the effect of oxidative stress on the different physiological costs, or rather how was the significance measured?

R. We are now expanding the issues related to consequences of ROS on physiological and metabolic changes. For example, in addition to changes in behavior (such as avoiding hypoxia), stressful conditions may result in reduced activity (slow swimming, reduced vertical migration), as reported in Euphausiids (Tremblay et al., 2010) and reduced enzimatic activity in copepods Glippa et al. (2018).

L.153-154: The authors explain how ROS production occurs both during hypoxic conditions and after re-oxygenation. Thus my question was what are the implications of this, or can you say something about the difference in ROS production under the different conditions and by how much it changes?

R. Here, the issue is that ROS will always occur under oxygenated conditions and therefore animals are producing antioxidant responses. However, an individual exposed to hypoxia with lower tolerance to low oxygen is subject to a stressful condition which will trigger ROS when reoxygenating, although as we also said ROS can been occur during the exposure to hypoxia. However, the most important point here is being subject to an extremely variable oxygen condition, and so inducing POS and ROS with metabolic costs. We are now modifying some of the text to clarify this statement.

L.179: Can you say something about the consequences of a limited DVM and compare it to other strategies observed in the field (see Hauss et al., 2016)?

R. Reduced DVM may have implications for populations and with some biogeochemical consequences. For example, increasing mortality from predation, promoting other biological interactions from more aggregation, and limiting the vertical fluxes of C and N mediated by active transport (Steinberg and Landry, 2017).

L.203-204: The authors explain how hypoxic conditions may reach the surface due to strong upwelling. Here, it would be important to compare the exposure of such surface conditions to what migratory zooplankton experience during DVM. Maybe you could provide some characteristic intensities or durations of exposure?

R. Upwelling pulses prevail over a time scale of a few days, and therefore these events can have more drastic consequences than exposure to oxygen gradients during hours by DVM. Hypoxia driven by such upwelling events may affect the entire near-surface community, while exposure to sharp oxygen gradients can affect just to vertically migratory populations. Hypoxia events have been reported causing massive mortalities in some pelagic organisms inhabiting the upper mixed layer. We are now expanding the discussion on the time and spatial scales over which zooplankton may become exposed to hypoxia.

Technical corrections

L.37: What do you mean by “becomes even more critical”? Do you mean deoxygenation is enhanced or that it is more critical for marine life?

R. We meant for marine life, so we have modified to sentence to better state this.

L.54: It should be become rather than becomes. In addition, what is meant by “plankton become more concentrated”? Do you mean they are more abundant? There is also a similar phrasing in the caption of Figure 1.

R. Ok. Corrected. We mean more abundant. Corrected now

L.74: It should be “At the ecosystem level…”. This sentence is also rather convoluted. Can you rephrase it for clarity as it has many clauses.

R. Corrected

L.84: The reference Chisholm and Roff, 1990 is not in the bibliography.

R. This reference was removed from the text

L.85: Please introduce the abbreviations used on the first mention. Here you can introduce the abbreviation for metabolic rate (MR).

R. Agree. Done

L.89-91: Please split up this sentence to increase readability.

R. Agree. Done

Figure 2: The term routine metabolism was not introduced in the main text. In addition, the axis descriptors do not match the text descriptors, making the interpretation of the figure more difficult. The caption should include more information of what is shown in the figure. Finally, unless I missed something, I was not able to find a similar figure in Rogers et al., 2016 from which figure 2 was adapted.

R. We are now defining routine metabolism and better describing this Figure 2. The figure was indeed based on Figure 1 of Rogers et al. 2016. We are now specifying that is based on, but not modified from

L.97: The authors introduce the term “maximum oxygen supply capacity” without definition. As this is a review, I feel that important terms like this should be defined.

R. Agree this term is now defined.

L.137: Here, a lot of abbreviations are used without introducing them first.

R. We have revised all acronyms and symbols to introduce them.

Table 1: Some abbreviations are not introduced (e.g., GR in Pteropoda). Also, what is the difference between having different biomarkers linked by a slash and a dash? In the caption, to the best of my knowledge it should be “Lactato deshidrogenase” and “Peroxidase”.

R. We have revised all acronyms and symbols to introduce them.

L.173-174: Can you say in which organisms POS has been proposed as a mechanism to strengthen antioxidant defences?

R. We are now citing examples provided in Hermes-Lima et al. (2015).

L.175: To the best of my knowledge, it should be migratory and non-migratory.

R. Agree. We have corrected to text.

L.185: The abbreviation POS seems strange because “doing POS” would mean “doing preparation for oxidative stress” rather than preparing for oxidative stress.

R. Agree correction done.

L.186: Should read “The interplay between ROS production and POS…”. Please revise throughout the manuscript when using abbreviations (e.g. L 190).

R. Corrected

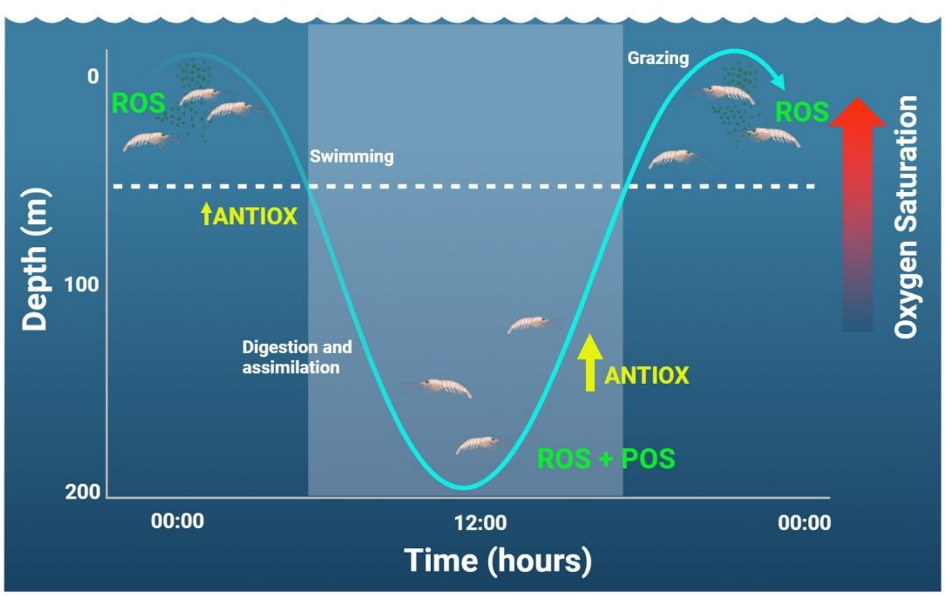
L.189: Should read “reduction/increase”

R. Corrected

Figure 4: The depth axis does not match the reference “Riquelme-Bugueño et al. (2020)” or the main text. The abbreviations used in the figure are not explained. It might be better to show the direction of change with arrows rather than with multiple “+” signs, as this would resemble the symbols used in Table 1. Also, what is the meaning of the dotted line.

R. Corrected now

New Figure 4

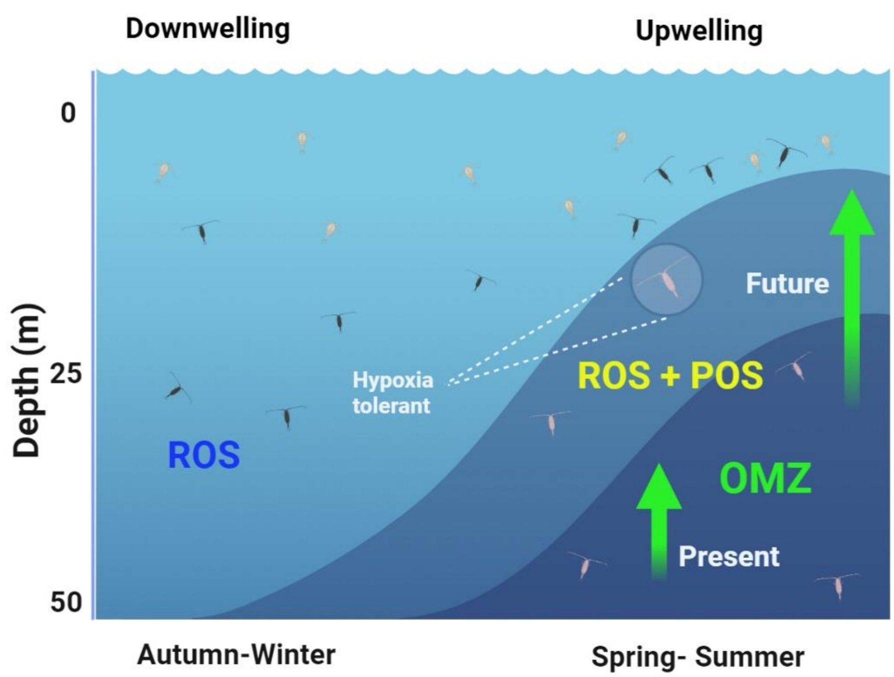


L.209: What is meant by "during high frequency change"?

R. We meant during high frequency pulses of upwelling. Corrected now

Figure 5: As the main text refers to seasonal changes, I was expecting to see a timeseries (resembling Figure 4). Also, the abbreviations are not properly explained in the caption.

R. Fig. 5 (now Fig 6) has been modified. This is new Figure:



L.227: Rather than saying it seems more difficult, you can simply say that it is more difficult.

R. Agree. Corrected

L.232: DO has not been introduced.

R. Corrected

L.232: Remove “front”.

R. Done

L.234: Rephrase to “experiments carried out at temperatures ranging between 9°C and 16°C.”

R. Thanks. Done

Section 3.1: I was initially confused as this section begins with explaining the high antioxidant potential of diatoms in a zooplankton paper. It wasn’t until the last paragraph in this section that I realized how this fits in the story line. Thus I would suggest changing the sequence in which the information is presented to increase readability.

R. Thanks for the suggestions, we have modified the text following your recommendation.

Thanks for the references, they are all very important for the review.

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Reply