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Reviews and synthesis: increasing hypoxia in eastern boundary upwelling systems: a major stressor for zooplankton

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Abstract. Eastern boundary upwelling systems (EBUS) are ecologically and economically important marine regions of the world ocean. In these systems, zooplankton play a pivotal role in transferring primary production up through the food web. Recent studies show that global warming is causing a gradual deoxygenation of the world ocean, while in EBUS a vertical expansion of the subsurface oxygen minimum zone (OMZ) along with increased wind-driven upwelling are taking place, further exacerbating hypoxic conditions for zooplankton inhabiting the upwelling zone. Hypoxia can affect zooplankton by disrupting their respiration, migration, reproduction, and development. These effects however depend on some specific adaptations of organisms that have evolved in habitats, permanently or episodically, subjected to low oxygen waters. Various metabolic, physiological, behavioural, and morphological adaptations have been described in zooplankton interacting with the OMZ. Nevertheless, these adaptive responses of zooplankton to withstand mild or severe hypoxia, and the eventual oxidative stress derived from highly fluctuating oxygen conditions, may develop in association with trade-offs related to other metabolic/energy-demanding processes. New demands imply a reduction in energy otherwise available for growth, feeding and reproduction with further ecological consequences for the populations. This paper reviews and explores the existence or lack of such adaptive responses and their role for zooplankton dynamics in EBUS with major consequences for the pelagic food web and biological productivity.

1 INTRODUCTION

Currently it is widely recognized that the increase in atmospheric CO2 and other greenhouse gasses is driving the warming of the Earth's surface and ocean (Oschlies et al., 2018). A warmer ocean drives several physical consequences, such as the increases in mean global sea surface temperature, increasing winds, more intense storms in some regions, and changes in ocean circulation (Schmidtko et al., 2017). The warming of the upper layers of the ocean also drives a greater stratification of the

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water column, reducing vertical mixing and thus affecting ocean ventilation. A warmer ocean also lowers oxygen solubility, and hence further challenging marine life. Under such a scenario, deoxygenation (a decline in oxygen) in the open ocean and coastal water has increased since the middle of the 20th century (Strama et al., 2008, Gregoire et al., 2021). Ocean warming also increases the metabolic rate of ectotherms, promoting a greater oxygen usage by marine communities, and further exacerbating the oxygen decline (Breitburg et al, 2018).

The decrease in oxygen concentration, evident in many areas of the ocean, becomes even more critical in regions with persistent and currently expanding oxygen minimum zones (OMZ) (Gregoire et al., 2021). These OMZ systems are defined by their extremely low oxygen concentrations (<20-45 µmol kg-1), covering large areas of the ocean, and associated with highly productive coastal and oceanic regions (Gilly et al., 2013). A vertical expansion of the OMZs has been evidenced and it is related to a shoaling of its upper boundary, and descent of the lower boundary, and thus increasing its total volume (Stramma et al., 2010). In some cases, the minimum oxygen concentrations in the OMZ cores have also been further reduced, intensifying the OMZ (Chan et al., 2008).

In 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), 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). The increase in upwelling favourable winds in EBUS brings colder water and more frequent occurrences of upwelling events (Breitburg et al., 2018). 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 takes place and so compressing the upper highly oxygenated layer. 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.

The ongoing combined processes, deoxygenation, increasing upwelling, and OMZ expansion will alter the oxygen conditions in upper layers (<50 m) in EBUS, where plankton becomes concentrated, with various ecological and biogeochemical consequences. Aerobic metazooplankton inhabiting the upwelling zone is thus expected to be exposed to variable levels of oxygenation from normoxia to mild or sever hypoxia, depending on their distribution and migrating behaviour. Their responses will also depend on the existence, absence, or development of new adaptations. In this paper, we review such adaptive responses of zooplankton and the ecological consequences driven by hypoxia, aiming at establishing the physiological/metabolic bases and directions when addressing issues related to the future of zooplankton dynamics in EBUS subjected to ongoing climate change.

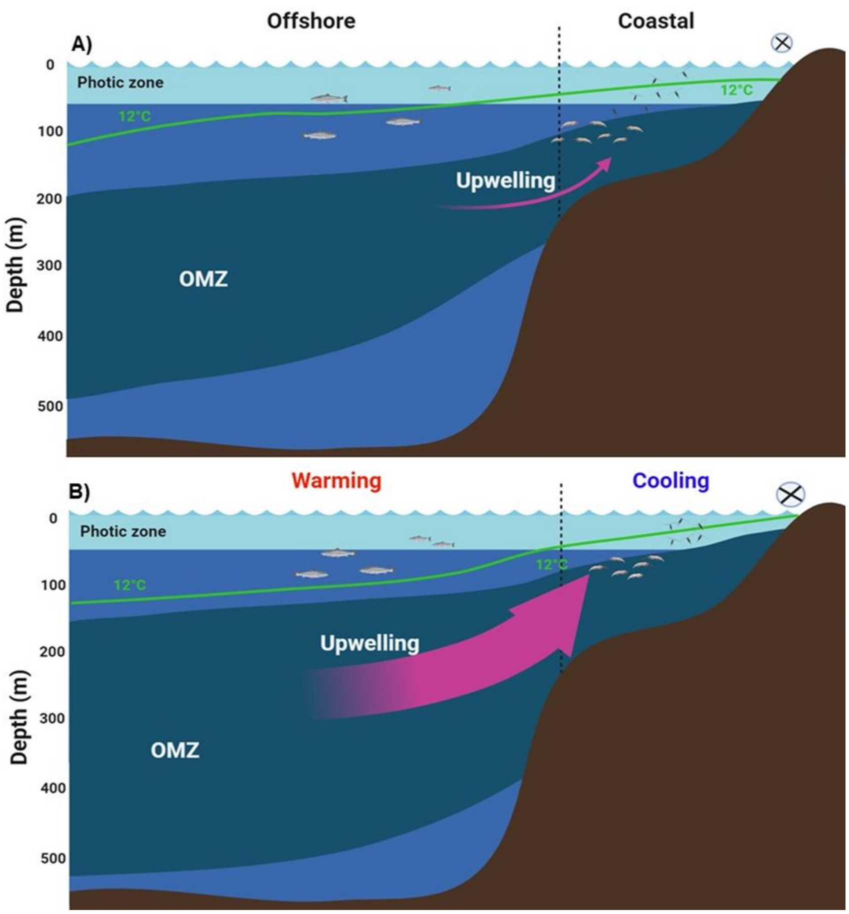

Figure 1. Projected effects of increasing upwelling in eastern boundary upwelling systems (EBUS). A) Under present (initial) conditions, wind-driven upwelling rises the OMZ system and brings cold-water into shallow depths at the inshore as illustrated by the 12°C isotherm, and so fertilizes the photic zone and promotes plankton aggregation. B) Ocean warming effects manifest mainly at surface in the offshore region, while increased upwelling may instead cool down the coastal zone (B), also vertically expanding and further shoaling the OMZ at the inshore area, causing more hypoxia and reducing the oxygenated habitat.

2 ADAPTIVE RESPONSES OF ZOOPLANKTON TO HYPOXIA

Oxygen plays a key role in the structuring and functioning of marine ecosystems and so modulates the spatial-temporal distribution of many marine organisms. This is mainly because low oxygen levels challenge the maintenance of aerobic metabolism and can be harmful for most of the biota (Ekau et al., 2010; Wishner et al. 2018; Breitburg, 2018). The effects of depleted oxygen can affect organisms in many ways, including acute natatory and physiological impairment, diminished growth, and reproductive success, and altered behaviour of mobile forms when searching for more favourable oxygen regimes (Wishner et al., 2018).

At ecosystem level, the different tolerances to low oxygen across species will determine their survival, and so causing changes in community structure, the trophic webs, due to changes in predator-prey interactions because of changes in abundance, migration, and habitat compression (Tutasi and Escribano, 2020). While several species will be negatively affected (including commercially exploited species), others more hypoxia-tolerant may expand their range of distribution, exploit new niches (Stramma et al., 2010), and therefore have access to new resources.

The adaptation of animals to low oxygen is triggered by a strong selective pressure to maintain aerobic metabolism by optimizing and enhancing oxygen uptake from hypoxic water (Childress and Seibel, 1998), or alternatively by suppressing their metabolic rate to reduce the oxygen demands (Seibel, 2011). At the upper extreme of the oxygen cascade, oxygen uptake is satisfied by two adaptive modes: as an oxygen-conformer organism by reducing aerobic metabolic rate as environmental oxygen decreases, or as an oxygen-regulator by maintaining the aerobic metabolism down to an oxygen level known as critical oxygen tension (Pcrit) (Chisholm and Roff, 1990). The difference between these two adaptive modes can be illustrated by the changes in the metabolic rate as a function of oxygen pressure (Fig. 2).

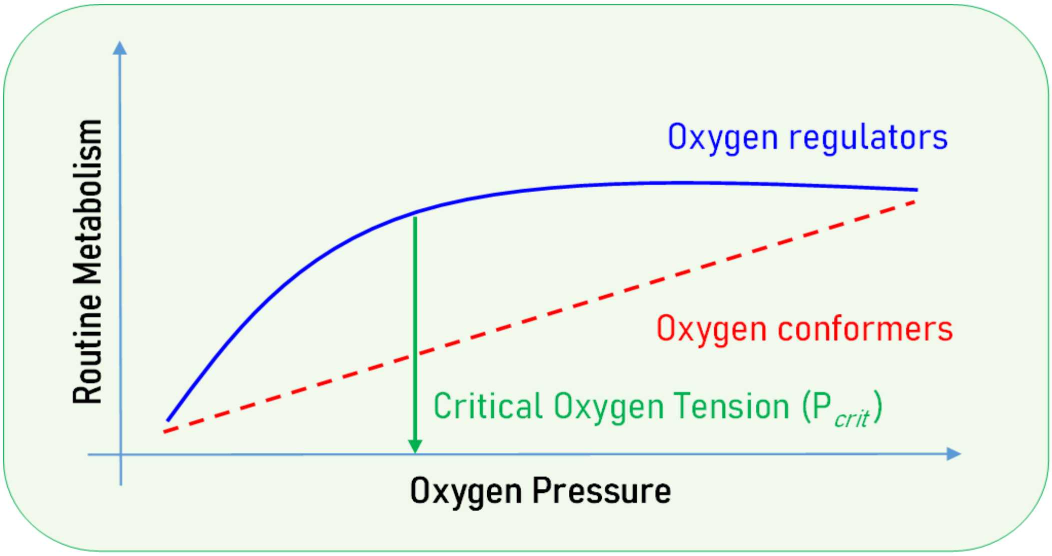

Figure 2. Two adaptive modes in marine zooplankton as a response to hypoxia (modified from Rogers et al., 2016).

The potential metabolic adaptation illustrated in Fig. 3, for instance by reducing Pcrit to cope with severe hypoxia, or a lack of adjusting capacity, may vary with the species (Frederick et al. 2024), and this may therefore favour some species while others are negatively impacted. Fig. 3 represents the potential metabolic responses to a variable oxygen condition from normoxia to hypoxia. A non-adaptive response (Fig. 3A) is reflected in changing metabolic rate (MR) as a function of oxygen levels and this also implies a variable Pcrit, whereas an adaptive response 1 (Fig. 3B) represents a constant MR at the cost of changing Pcrit, and adaptive response 2 (Fig. 3C) will maintain a constant Pcrit with a consequent change in MR.

It has recently been suggested that Pcrit is the point at which the physiological oxygen supply capacity reach its maximum, and as such is a species- and temperature-specific constant (Siebel et al., 2021). From past literature, in fact, Pcrit is constant within a given species (Rogers et al., 2016) and thus supporting the validity of the maximum oxygen supply capacity within species. Yet, the potential plasticity of Pcrit has not been explored on organisms inhabiting fluctuating oxygen regimes such as the ones living around OMZ zones. Furthermore, many of these pelagic organisms have several cohorts along the year, thus also allowing maternal effects on top of plasticity leading to shifts on either Pcrit or MR on some species of planktonic copepods along the year (Frederick et al., 2024). Such differential responses will ultimately alter the species composition with consequences for the food web structure. However, even for those oxygen-regulator species, severe hypoxia may cause oxygen levels lower than Pcrit with severe stress or deleterious effects on organisms.

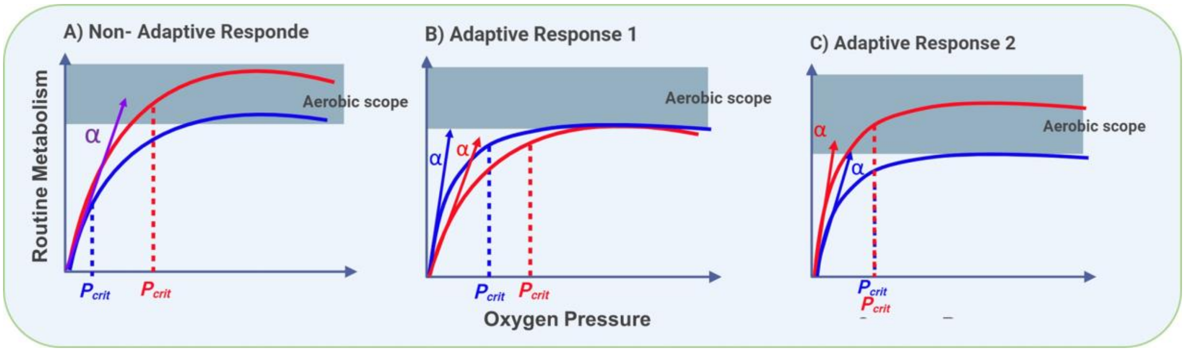

Figure 3. The expected metabolic rate (MR) as a function of environmental oxygen partial pressure (Pcrit). The MR is theorized for two seasonal conditions: Autumn-winter (blue line) and spring-summer (red line) in a coastal upwelling zone, where Pcrit will move following changes in MR and the slope (α) of the oxyconforming segment remains constant (A), an adaptive response 1 in which Pcrit increases upon a changing oxyconforming slope (α) to maintain a constant MR (B), and an adaptive response 2, where Pcrit is maintained constant by increasing α during the upwelling season (C) (modified from

Frederick et al, 2024). Here, the oxyconforming segment refers to the metabolic rate under oxygen levels below Pcrit, while the aerobic scope represents the range of MR between the basal metabolism and its maximum for a given species.

Other adaptive responses include a shift to anaerobic metabolism when entering extremely low oxygen concentrations, such as those found in the core of the OMZ. This adaptation has been reported in actively migrating species, such as the krill *Euphausia* spp. (Riquelme-Bugueño et al., 2020). However, several adaptive responses have already been described for zooplankton, inhabiting, or entering the OMZ. For instance, crustaceans inside the OMZ can experience rapid physiological adjustments, and this involves various adaptations: enhanced ventilatory capability, enlarged gill surfaces, shortened diffusion distances, and increasing respiratory proteins with high oxygen affinity (Childress & Seibel 1998). For example, in vertically migrating zooplankton entering the OMZ, Antezana (2002) observed the presence of enlarged gill surfaces, along with active respiration and swimming under depleted oxygen in *Euphausia mucronata* indicating oxygen usage in the OMZ. In another krill species, *Meganyctiphanes norvergica* (Spicer et al, 1999), the anaerobic metabolism has been assessed showing that lactate concentration increased significantly when the oxygen concentration decreased down to hypoxic levels, and so being able to resist prolonged periods to such conditions. In *M. norvergica*, the production of lactate is rather low and so explaining a limited diel vertical migration of this species compared to *E. mucronata* in which the increase in lactate dehydrogenase is quite high allowing long periods of exposure to hypoxia (Gonzales & Quiñones, 2002).

Finally, changes in behaviour and distribution may also obey specific hypoxia adaptive responses, as found in many dominant zooplankton that avoid the OMZ by restricting their vertical migration (Escribano et al. 2009, Tutasi and Escribano 2019, Kiko et al. 2019). Also, in the copepod, *Acartia tonsa*, it has been possible to observe behavioural adaptations when copepods previously exposed to oxygen gradients avoided hypoxic bottom waters, while copepods not exposed to hypoxia did not avoid lethal oxygen concentrations (Decker et al 2003).

3 OXIDATIVE STRESS IN ZOOPLANKTON

An important biological response linked to variable oxygen levels, and rarely considered in the open ocean, is oxidative stress. The phenomenon can occur because variations in oxygen levels in the ocean range from normoxia to hypoxia at short spatial and temporal scales in some areas. Driven by such fluctuations, the oxidative stress appears related to a state of respiratory imbalance in terms of O2 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). Therefore, as a product of aerobic respiration, the production of reactive oxygen species (ROS) can occur. ROS itself plays a crucial role as signalling molecule leaking out from the mitochondria, together with cytochrome c, AMP-activated protein kinase (AMPK), the release of mitochondrial DNA (mtDNA) and TCA (tricarboxylic acid) cycle metabolites (Martínes-Reyes & Chandel, 2022). Not surprisingly, all of them are highly dependent on the oxygen available for mitochondrial functioning, and thus their regulation is likely to be challenged under the unstable oxygen levels found in the vicinity of OMZ.

A higher production of ROS in the body may alter the DNA structure, result in modification of proteins and lipids, and trigger the activation of several stress-induced transcription factors (Birben et al., 2012). The available evidence suggests that oxidative stress can generate a significant physiological cost in life expectancy, reproduction, the immune response, in addition to the effect on metabolism and growth.

Molecular oxygen (O2) is the primer biological electron acceptor, crucial in regulating cell functions. However, it is also the precursor of reactive oxygen species (ROS) formation because of normal cellular metabolism. The 3 major ROS of physiological significance are superoxide anion (O2-.), hydroxyl radical (•OH), and hydrogen peroxide (H2O2) (Guérin et al., 2001). The generation of these reactive oxygen species (ROS) has been extensively studied (Welker et al., 2013, Moreira et al, 2016; Giraud-Billoud et al, 2019). When animals are re-oxygenated after hypoxic exposure, ROS formation occurs, and if not neutralized by the body's antioxidant defences, may cause oxidative damage and eventually cellular disorder and death. ROS production is species-dependent which can further vary as a function of the intensity of hypoxia and exposure time to an oxygen-deficient habitat. However, ROS are not only produced by re-oxygenation after hypoxic exposure, in fact the ROS production has also been reported to occur in hypoxic conditions for a variety of organisms, as reviewed by Hermes-Lima (2015).

The exposure to hypoxia may lead to ROS and eventually to production of antioxidant compounds as an adaptive response, a phenomenon described as preparation for oxidative stress (POS) (Hermes- Lima et al 1998, 2015; Moreira et al, 2016). Tremblay et al. (2010) showed that krill species adapted to hypoxia have a sufficiently high antioxidant protection whereas less adapted species suffered a strong oxidative stress measurable as lipid peroxidation. Thus, antioxidants play an important role in neutralizing the oxidative action of free radicals.

The mechanisms of cellular protection against ROS include several antioxidant enzymes such as Superoxide dismutase (SOD), Catalase (CAT), Peroxidase, Glutathion S-transferase (GST), and Glutathione Peroxidase (GPx), and non-enzymatic such as Ascorbic acid (Vitamin C), Glutathione (GSH, Tocopherol and Carotenoids, where their participation becomes relevant in ROS detoxification processes in organisms subjected to oxidative stress. An imbalance between the level of ROS and antioxidant protection, it can result in oxidative damage to tissues and a state of oxidative stress (Birben et al., 2012).

Linked to the presence of these radicals, a defence mechanism is the synthesis of antioxidant molecules capable of neutralizing the oxidative action of these free radicals. Several studies have described the presence of ROS and corresponding antioxidant responses in zooplankton, summarized in Table 1.

Table 1: Zooplankton species exposed to different stress leading to reactive oxygen species (ROS). DVM (diel vertical migration) behavior can be performed and indicated by "Y" or not "N" (non-migration) and "NI" (no DVM information). Arrows in column 5 indicate the increase or decrease in the biomarker signal in relation at the stressor agent. * Indicates that the samples were obtained from areas under presence of an Oxygen Minimum Zone.

Group	**Species**	**DVM**	**Stressor**	**Biomarker**	**Reference**
Copepoda	*Acartia tonsa*	Y	Temp. (Heatwave)	↑GST	von Weissenberg et al, 2021
	Acartia sp.	Y	Temp/pH/DO	↑GST	Glippa et al, 2018
	Calanus pacificus	Y*	Temp/pH	↑GST	Engström-Öst et al, 2019
	Limnocalanus macrurus	Y	Contaminants	↑SOD/↓LPX	Vuori et al 2015
	Eurytemora affinis	Y	Temp/Sal	↑GST	Cailleaud et al, 2007
Euphausiacea	*Nictiphanes simplex*	Y*	Temp/Sal	↑SOD/CAT/GST	Tremblay et al, 2010
	Nematocelis difficilis	N*	Temp/Sal	↑SOD/CAT/GST	Tremblay et al, 2010
	Euphausia eximia	Y*	Temp/Sal	↑SOD/CAT/GST/↓LPX	Tremblay et al, 2010
Mysidae	*Neomysis awatschensis*	Y	DO	↓SOD/↑↓CAT-LDH	Wang et al, 2021
Pteropoda	*Limacina helicina*	Y*	Temp/pH	↑GR/CAT/↓LPX	Engström-Öst et al, 2019
Decapoda	*Scylla serrata*	N	Seasonal effect	↑SOD/CAT/GPX	Kong et al, 2008
Cephalopoda	*Sepiella maindroni*	NI	DO	↑↓SOD-CAT-POD-LDH	Wang et al, 2008

SOD: Superoxide dismutase; **CAT**: Catalase; **GST**: Glutathione S-transferase; **LPX**: Lipid peroxidation;

GPX: Glutathione peroxidase; **LDH**: Lactato deshidrogenasa; **POD**: Peroxidasa

POS has been proposed as a mechanism to strengthen antioxidant defences (Hermes- Lima et al 1998, 2015; Moreira et al, 2016). However, how this mechanism operates in zooplankton inhabiting areas subjected to a shallow OMZ is an open question. The timing for developing antioxidant responses also becomes an important issue in both migrants and non-migrant zooplankton, because of the short-time (few hours) within which animals are exposed to hypoxia-normoxia conditions during migration or due to the irregular pulses of upwelling causing the ascent or descent of the OMZ. In the same context, and as mentioned above, most zooplankton avoid hypoxic waters by restricting their vertical distribution to the narrow and shallow normoxic layer in coastal waters, or by limiting the diel vertical migration (DVM) avoiding entering the OMZ or at least the extremely low oxygen layer found at the OMZ core (Kiko & Haus, 2019, Tutasi & Escribano, 2019). The highly variable DVM behaviour may thus play a key role for the adaptive response to hypoxia in the context of ROS and POS processes.

Zooplankton performing extensive DVM can indeed enter the core of the OMZ, as described in several euphausiid species (Escribano et al. 2009; Riquelme-Bugueño et al. 2020). The incursions in extremely low oxygen waters and rapid re-oxygenation when ascending to near surface at nighttime may trigger ROS and certainly antioxidant response. A potential adaptive response to this periodical exposure to low-high oxygen is the possibility of doing POS during the hypoxic phase of

DVM. The interplay between ROS and POS linked to DVM behaviour is illustrated in Fig. 4. In Euphausiids, which perform extensive DVM, the process of normoxic at oxygen levels >200 µM in the photic zone, and subsequent hypoxia ($O2 < 3$ µM), when diving down to 200 m at the sunrise, can take less than 3 hours (Riquelme-Bugueño et al., 2020), i,e. being exposed to >30% reduction/increasing in oxygenation per hour while swimming up or down. Such stressful oxygen conditions over a short-time scale can indeed trigger ROS (Tremblay et al. 2010), and potentially POS during the nighttime phase (Fig. 4). 190

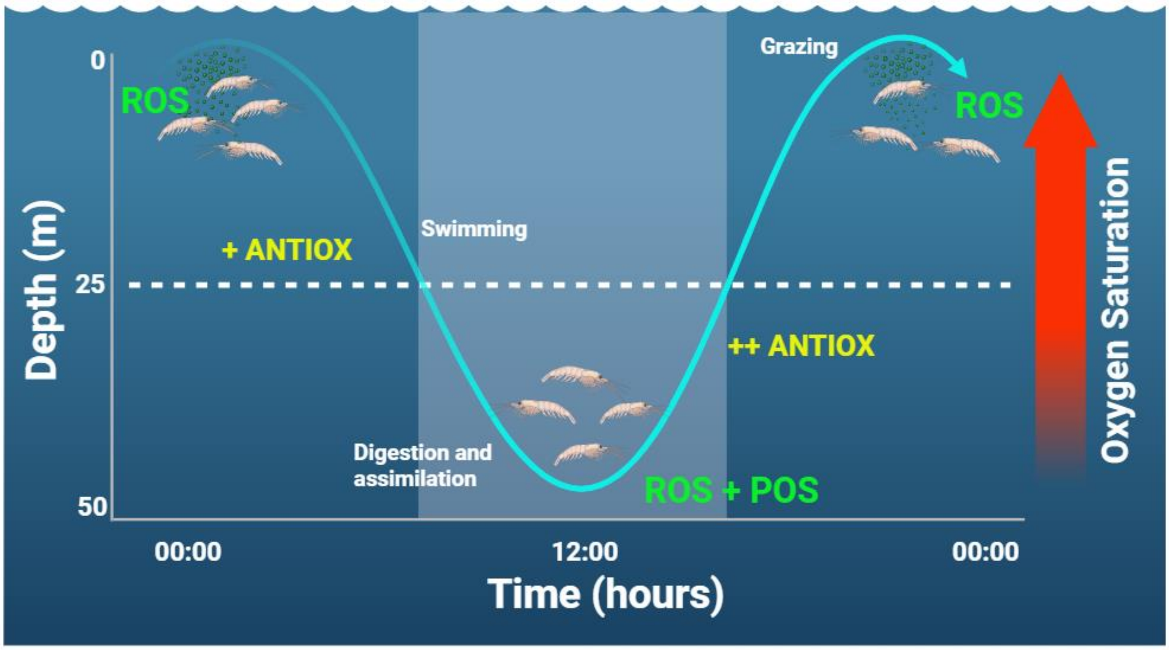

Fig. 4: Changes in the daily vertical migration and short-term response to oxidative stress in zooplankton. Illuminated area shows the daytime.

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The DVM behaviour, considered as an adaptive response evolved to avoid visual predators during daylight conditions (Giraud-Billoud et al, 2019), may at the same time require the evolution of POS and hence allow a mechanism to mitigate ROS effects. Diel cycles triggering antioxidant responses to ROS have been shown to occur in planktonic organisms exposed to light-dark conditions, such as *Daphnia pulex* (Cai et al., 2020), suggesting the existence of circadian rhythms of ROS and subsequent POS. 200 However, not all zooplankton perform DVM, and indeed many species, mostly composed by copepods, which significantly contribute to the bulk of zooplankton biomass remain restricted to the upper 50 m layer (Escribano et al., 2009). These species however can still be exposed to hypoxia upon highly fluctuating upwelling intensity allowing the incursion of the upper limit of the OMZ (<3 kpa of O2) into near-surface water (Schneider et al., 2016). Upon strong upwelling such hypoxic conditions may even reach surface waters (Escribano et al., 2009).

In EBUS, depending on latitude, the active upwelling period can be strongly seasonal in temperate areas or having a weak seasonal signal being semi-permanent year-round in subtropical regions. For example, in the coast of Chile at mid-latitudes (30°-40° S) the Spring-Summer southern winds drives a very active upwelling period and consequently a shallow OMZ, whereas the Autumn-Winter exhibits a condition of depressed upwelling also known as downwelling period. This seasonal variation can temporarily expose non-migrating zooplankton populations to hypoxia during high frequency change (hours to days) in the upwelling season, and potentially demanding POS during the downwelling (spin-down) or transitional period before spin-up phase of upwelling. The combined effects of seasonal upwelling conditions, vertical distribution of the OMZ, and lack of DVM behaviour, promoting ROS and POS are illustrated in Fig. 5. Fig. 5A illustrates a condition of depressed upwelling (spin-down of upwelling or downwelling) with the upper limit of the OMZ below the photic zone where non-migrant zooplankton aggregates and normoxic conditions prevails. This conditions may trigger re-oxygenation and thus presence of ROS. Fig. 5B shows a condition of strong upwelling with shoaling of the OMZ which can intrude the photic zone, such that some of the non-migrant zooplankton becomes exposed to hypoxia and therefore POS may potentially occur as a response to a changing hypoxia-normoxia condition. Fig. 5C represents an exacerbated condition of hypoxia upon a much stronger and recurrent upwelling in a future condition.

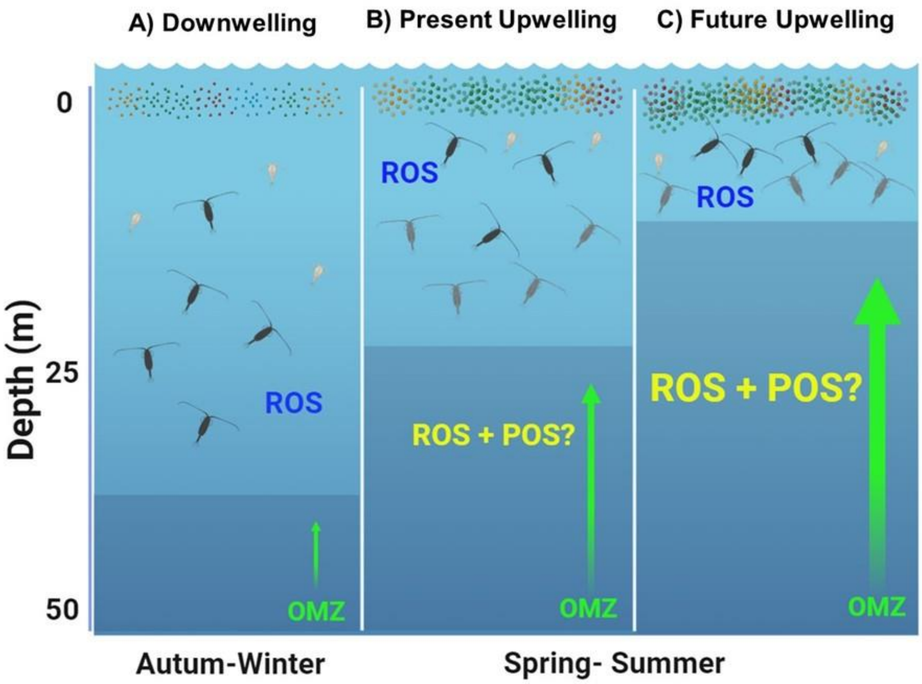

Fig. 5 Oxidative stress (ROS) and the potential adaptive response (POS) of zooplankton subjected to seasonal upwelling-hypoxia conditions.

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Both migrant and non-migrant zooplankton may have possibly evolved adaptive responses to ROS, although available information on this issue is scarce. Most studies on antioxidant response in marine organisms have been focused in coastal, intertidal, or benthic species.

It seems more difficult to carry out these studies in organisms inhabiting the water column, such as zooplankton, given the high variability in the physical-chemical parameters to which they are exposed. For example, planktonic copepods are very abundant, and they make up about 80% of the zooplankton biomass, so it is imperative to consider the effects of a changing environment and the response of these organisms to oxidative stress. Glippa et al. (2018) studied the copepod *Acartia* spp., which showed an increase in the enzymatic activity of GST over a two-weeks period when exposed to changes in temperature, pH and DO. An increase of enzymatic activity indicates the activation of an antioxidant defence mechanism front to environment changes. The same effect was reported by von Weissenberg et al. (2021) in *Acartia* spp. exposed to heatwaves, in experiments carried out in temperature range to 9-16°C. The authors observed a positive relationship between the increases in glutathione in response to increased environmental temperature and showed the deleterious effect over reproductive success during warming.

Regarding dominant zooplankton in EBUS, a relevant issue to consider is the short life cycle of copepods (<2 months) and euphausiids (<1 year). Under a seasonal upwelling regime, the exposure to hypoxia-normoxic may occur to different cohorts, and therefore the adaptive response (e.g. POS) might be seasonally adjusted. Although, if the OMZ continues its vertical expansion, there may not be sufficient time for developing adaptive responses with deleterious consequences for non-migrant populations, which comprise most upwelling inhabitant species.

3.1 NATURAL ANTIOXIDANT AGENTS FOR ZOOPLANKTON

Studies show that planktonic diatoms have a high antioxidant potential (Goiris et al, 2012). Diatoms are rich in carotenoids, such as fucoxanthin and astaxanthin that play a crucial role in protecting UV. Some diatoms as a *Skeletonema marinoi* and *Odontella aurita* can synthesize and accumulate ascorbic acid (Vitamin C) and phenolic compounds which also have antioxidant properties (Smerilli et al, 2019; Hemalatha et al, 2015).

The concentrations of antioxidants in diatoms are species-specific (Foo et al. 2017), where they quantified the total content of some antioxidants and their bioactive capacity in six diatom species, where *Chaetoceros calcitrans* and *Isochrysis galbana* showed the highest antioxidant activity, followed by *Odontella sinens* and *Skeletonema costatum* which exhibited moderate bioactivity. Meanwhile *Phaeodactylum tricornutum* and *Saccharina japonica* displayed the lowest antioxidant activity among the examined algae species.

In coastal upwelling environments, zooplankton must face a wide variability of the environmental parameters to which they are subject. For this reason, the presence of an exogenous source of antioxidants provided by diatoms would help mitigate the effect of oxidative stress due to environmental pressure.

4 CONCLUSION

Ocean deoxygenation and the loss of oxygen in EBUS is an ongoing phenomenon, and planktonic organisms must inevitably cope with this gradually increased hypoxia, and a changing dynamic of the ocean. The ecological consequences are far from understood and, will largely depend on the ability of zooplankton to strengthen their capacity to tolerate mild or severe hypoxia, exploit plasticity and maternal effects to their maximum, or to develop new adaptations. In any case these responses may likely come at some cost and likely with trade-offs on other metabolic/energy-demanding processes. The outcome from the new demands implies a reduction in energy otherwise available for growth, feeding and reproduction with further consequences in the population dynamics. Hypoxia conditions can also lead to changes in behaviour (upon stress) and spatial distribution, and so altering for example prey-predator interactions. Ultimately, the pelagic food-web and community structure will likely be affected with biogeochemical consequences in the context of the C and N recycling and ecosystem productivity. The assessment of plankton community structure through time series observations in the upwelling zone constitutes the most suitable proxy to examine the community responses to ongoing deoxygenation, and so long-term time series are extremely valuable for accurate predictions. The use of molecular methods to examine how individuals can modify their gene expression to cope with hypoxia, and eventually activate antioxidant responses, are also necessary approaches when aiming to the understanding and prediction of the ecological consequences upon expected severe conditions of an oxygen-deprived water column.

COMPETING INTEREST

The contact author has declared that none of the authors has any competing interests.

References

Antezana, T.: Adaptive behaviour of *Euphausia mucronata* in relation to the oxygen minimum layer of the Humboldt Current, Oceanography of the Eastern Pacific, II, 29-40, 2002.

Bakun, A., Field, D. B., Redondo-Rodriguez, A., and Weeks, S. J.: Greenhouse gas, upwelling-favourable winds, and the future of coastal ocean upwelling ecosystems. Glob. Change Biol, 16, 1213–1228, https://doi.org/10.1111/j.1365-2486.2009.02094.x, 2010.

Birben, E., Sahiner, U.M., Sackesen, C., Erzurum, S., and Kalayci, O.: Oxidative stress and antioxidant defence, World Allergy Organization Journal 5: 9-19, doi: 10.1097/WOX.0b013e3182439613, 2012.

Breitburg, D., Levin, L. A., Oschlies, A., Gregoire, M., Chavez, F.P., Conley, D.J., Garcon, V., Gilbert, D., Gutierrez, D., and Isensee, K.: Declining oxygen in the global ocean and coastal waters, Science 359, eaam7240, DOI: 10.1126/science.aam 7240, 2018.

Cai, M., Liu, Z., Yu, P., Jiao, Y., Chen, Q., Jiang, Q., and Zhao, Y.: Circadian rhythm regulation of the oxidation–antioxidant balance in *Daphnia pulex*, Comparative Biochemistry and Physiology, Part B 240, 110387, https://doi.org/10.1016/j.cbpb.2019.110387, 2020.

Cailleaud, K., Maillet, G., Budzinski, H., Souissi, S., and Forget-Leray, J.:Effects of salinity and temperature on the expression of enzymatic biomarkers in *Eurytemora affinis* (Calanoida, Copepoda), Comparative Biochemistry and Physiology, Part A 147, 841–849, DOI: 10.1016/j.cbpa.2006.09.012, 2007.

Chan, F., Barth, J.A., Lubchenco, J., Kirincich, A., Weeks, H., Peterson, W.T., and Menge, B.A.:Emergence of anoxia in the California Current large marine ecosystem, Science 319- 920, DOI: 10.1126/science.1149016, 2008.

Chavez, F.P., and Messié, M.: A comparison of eastern boundary upwelling ecosystems, Prog. Oceanogr, 83, 80-96, https://doi.org/10.1016/j.pocean.2009.07.032, 2009.

Childress, J., and Seibel, B.: Life at stable low oxygen levels: Adaptations of animals to oceanic oxygen minimum layers, J. Exp.Biol., 201, 1223–1232, DOI: 10.1242/jeb.201.8.1223, 1998.

Decker, M. B., Breitburg, D.L., and Marcus, N. H.: Geographical differences in behavioural responses to hypoxia: local adaptation to anthropogenic stressor?, Ecol. Appl.13, 1104–9, https://www.jstor.org/stable/4134746, 2003.

Ekau, W., Auel, H., Portner, H. O., and Gilbert, D.: Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish), Biogeosci. 7, 1669–1699, https://doi.org/10.5194/bg-7-1669-2010, 2010.

Engström-Öst. J., Glippa, O., Feely, R. A., Kanerva, M., Keister, J. E., Alin, S. R.,Carter, B. R., McLaskey, A. K., Vuori, K. A., and Bednaršek, N.:Eco-physiological responses of copepods and pteropods to ocean warming and acidification, Scientific Report, 9, 4748, https://doi.org/10.1038/s41598-019-41213-1, 2019.

Escribano, R., Hidalgo, P., and Krautz, C.: Zooplankton associated with the oxygen minimum zone system in the northern upwelling region of Chile during March 2000, Deep-Sea Res. II., 56, 1083-1094, https://doi.org/10.1016/j.dsr2.2008.09.009, 2009.

Foo, S.Ch., Yusoff, F. Md., Ismail, M., Basri, M., Yau, S.K., Khong, N.M.H., Chan, K.W., and Ebrahimi, M.: Antioxidant capacities of fucoxanthin-producing algae as influenced by their carotenoid and phenolic contents, Journal of Biotechnology, 241, 175-183, https://doi.org/10.1016/j.jbiotec.2016.11.026, 2017.

Frederick, L., Urbina-Foneron, M., and Escribano, R.: Adjusting metabolic rates and critical oxygen tension in planktonic copepods under increasing hypoxia in highly productive coastal upwelling zones, Limnology and Oceanography, 9999, 1–14, doi: 10.1002/lno.12556, 2024.

Garcia-Reyes, M., and Largier, J.L.: Seasonality of coastal upwelling off central and northern California: New insights, including temporal and spatial variability, Journal of Geophysical Research, 117, C03028, https://doi.org/10.1029/2011JC007629, 2009.

Gilly, W.G., Beman, M., Litvin, S.Y., and Robison, B.H.: Oceanographic and biological effects of shoaling of the oxygen minimum zone, Annual Review Marine Science 5:393–420, DOI: 10.1146/annurev-marine-120710-100849, 2018.

Giraud-Billouda, M., Rivera-Ingrahamb, G., Moreira, D., Burmesterd,T., Castro-Vazqueza, A., Carvajalino-Fernándeze, J., Dafref, A., Cuijuan Niug, Tremblay N., Paital, B., Rosa, R., Storey, J., Vega,I., Zhangg, W., Yepiz-Plascencial, G., Zenteno-Savinm, T., Storey, K., and Hermes-Lima, M.: Twenty years of the 'Preparation for Oxidative Stress' (POS) theory: Ecophysiological advantages and molecular strategies, Comparative Biochemical and Physiology: Molecular and Integrative Physiology Part A, 234, 36-49, DOI: 10.1016/j.cbpa.2019.04.004, 2019.

Glippa, O., Engström-Öst, J., Kanerva, M., Rein, A., and Vuori, K.: Oxidative stress and antioxidant defense responses in *Acartia* copepods in relation to environmental factors, PLoS One, 13(4), e0195981, https://doi.org/10.1371/journal.pone.0195981, 2018.

Goiris, K., Muylaert, K., Fraeye, I., Foubert, I., De Brabanter, J., and De Cooman, L.: Antioxidant potential of microalgae in relation to their phenolic and carotenoid content, J. Appl. Phycol., 24, 1477–1486, https://doi.org/10.1007/s10811-012-9804-6, 2012.

Gonzalez, R., and Quiñones, R.:Ldh activity in *Euphausia mucronata* and *Calanus chilensis*: implications for vertical migration behavior, Journal of Plankton Research. 24(12), 1349-1356, https://doi.org/10.1093/plankt/24.12.1349, 2002.

Grégoire, M., Garçon, V., Garcia, H., Breitburg, D., Isensee, K., Oschlies, A., Telszewski, M., Barth, A., Bittig, H. C., Carstensen, J., Carval, T., Chai, F., Chavez, F., Conley, D., Coppola, L., Crowe, S., Currie, K., Dai, M., Deflandre, B., Dewitte, B., Diaz, R., Garcia-Robledo, E., Gilbert, D., Giorgetti, A., Glud, R., Gutierrez, D., Hosoda, S., Ishii, M., Jacinto, G., Langdon, Ch., Lauvset, S. K., Levin, L. A., Limburg, K. E., Mehrtens, H., Montes, I., Naqvi, W., Paulmier, A., Pfeil, B., Pitcher, G., Pouliquen, S., Rabalais, N., Rabouille, C., Recape,V., Roman, M., Rose, K., Rudnick, D., Rummer, J., Schmechtig, C., Schmidtko, S., Seibel, B., Slomp, C., Sumalia, U.R., Tanhua, T, Thierry, V., Uchida, H., Wanninkhof, R., Yasuhara, M.: A Global Ocean Oxygen Database and Atlas for Assessing and Predicting Deoxygenation and Ocean Health in the Open and Coastal Ocean, Frontiers in Marine Science. 8, 724913, https://doi.org/10.3389/fmars. 2021.72491, 2021.

Hemalatha, A., Parthiban, C., Saranya, C., Girija. K., and Anatharaman, P.: Evaluation of antioxidant activities and total phenolic contents of different solvent extracts of selected marine diatoms, Indian Journal of Geo-Marine Sciences, 44(10),1630-1636, https://doi.org/10.1186/s40538-017-0110-z, 2015.

Hermes-Lima, M., Storey, J.M., and Storey, K.B.: Antioxidant defences and metabolic depression. The hypothesis of preparation for oxidative stress in land snails, Comp. Biochem. Physiol. B., 120, 437-448, https://doi.org/10.1016/S0305-0491(98)10053-6, 1998.

Hermes-Lima, M., Moreira, D.C., Rivera-Ingraham, G.A., Giraud-Billoud, M., Genaro-Mattos, T.C., and Campos, E.G.: Preparation for oxidative stress under hypoxia and metabolic depression: Revisiting the proposal two decades later, Free Radic Biol Med., 89, 1122-43, DOI: 10.1016/j.freeradbiomed.2015.07.156, 2015.

Kiko, R., and Hauss, H.: On the Estimation of Zooplankton-Mediated Active Fluxes in Oxygen Minimum Zone Regions, Frontiers in Marine Science, 6, 741, https://doi.org/10.3389/fmars.2019.00741, 2019.

https://doi.org/10.5194/egusphere-2024-836
Preprint. Discussion started: 6 May 2024

Kong, X., Wang, G., and Li, Sh.: Seasonal variation of ATPasa activity and antioxidant defences in gills of the mud crab Scylla serra (Crustacea, Decapoda), Marine Biology, 154, 269–276, DOI 10.1007/s00227-008-0920-4, 2008.

Martínez-Reyes, I., and Chandel, N.S.: Mitochondrial TCA cycle metabolites control physiology and disease, 11, 102, https://doi.org/10.1038/s41467-019-13668-3, 2022.

Moreira, D., Venancio, L., Sabino, M., and Hermes-Lima, M.: How widespread is preparation for oxidative stress in the animal kingdom, Comparative Biochemical and Physiology: Molecular Integrative and Physiology, 200, 64-78, https://doi.org/10.1016/j.cbpa.2016.01.023, 2016.

Oschlies, A., Brandt,P., Stramma, L., and Schmidtko, S.: Drivers and mechanisms of ocean deoxygenation, Nature Geoscience, 11, 467-473, https://doi.org/10.1038/s41561-018-0152-2, 2018.

Riquelme Bugueño, R., Pérez Santos, I., Alegría, N., Vargas, C. A., Urbina, M. A., and Escribano, R.: Diel vertical migration into anoxic and high pCO2 waters: acoustic and net based krill observations in the Humboldt Current Ramiro, Nature, Sci. Rep., 10, 17181, https://doi.org/10.1038/s41598-020-73702-z , 2020.

Rogers, N. J., Urbina,M. A., Reardon, E. E., McKenzie, D. J. and Wilson, R. W.: A new analysis of hypoxia tolerance in fishes using a database of critical oxygen level (Pcrit), Conserv. Physiol., 4 (1), cow012, DOI: 10.1093/conphys/cow012, 2016.

Santosa, F., Gomez-Gesteira, M., de Castro, M., and Alvarez, I.: Differences in coastal and oceanic SST trends due the strengthening of coastal upwelling along the Benguela Current System, Cont. Shelf Res. 34, 79–86, https://doi.org/10.1016/j.csr.2011.12.004, 2012.

Schmidtko, S., Stramma, L., and Visbeck, M.: Decline in global oceanic oxygen content during the past five decades, Nature, 542, 335–339, https://doi.org/10.1016/j.csr.2011.12.004, 2017.

Schneider, W., Donoso, D., Garcés-Vargas, J., and Escribano, R.: Water-column cooling and sea surface salinity increase in the upwelling region off central-south Chile driven by a poleward displacement of the South Pacific, Prog. Oceanogr., 141, 38-58, https://doi.org/10.1016/j.pocean.2016.11.004, 2016.

Seibel, B. A.: Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones, J. Exp. Biol., 214, 326-336, DOI: 10.1242/jeb.049171, 2011.

Smerilli, A., Balzano, S., Maselli, M., Blasio, M., Orefice, I., Galasso, Ch., Sansone, C., and Brunet, Ch.: Antioxidant and photoprotection networking in the coastal diatom *Skeletonema marinoi*, Antioxidant, 8, 154, DOI: 10.3390/antiox8060154, 2019.

Spicer, J.I., Thomasson, M.A., and Strömberg, J.: Possessing a poor anaerobic capacity does not prevent the diel vertical migration of Nordic krill *Meganyctiphanes norvegica* into hypoxic waters, Marine Ecology Progress Series, 185, 181-187, https://www.jstor.org/stable/24853208, 1999.

Stramma, L., Johnson, G.C., Sprintall, J., and Mohrholz. V.: Expanding oxygen minimum zones in the tropical oceans, Science, 320, 655–658, DOI: 10.1126/science.1153847, 2008.

Stramma, L., Schmidtko, S., Levin, L., and Johnson, G.: Ocean oxygen minima expansions and their biological impacts, Deep-Sea Res., 57, 587-595, https://doi.org/10.1016/j.dsr.2010.01.005, 2010.

Tremblay, N., Gómez-Gutiérrez, J., Zenteno-Savín, T., Robinson, C.J., and Sánchez-Velascoa, L.: Role of oxidative stress in seasonal and daily vertical migration of three krill species in the Gulf of California, Limnol. Oceanogr. 55, 2570–2584, https://doi.org/10.4319/lo.2010.55.6.2570, 2010.

Tutasi, P., and Escribano, R.: Zooplankton diel vertical migration and downward C flux into the oxygen minimum zone in the highly productive upwelling region off northern Chile, Biogeosci., 17, 455–47, https://doi.org/10.4319/lo.2010.55.6.2570, 2020.

Vuori, K.A., Lehtonen, K.K., Kanerva, M., Peltonen, H., Nikinmaa, M., Berezina, N.A., and Boikova, E.: Oxidative stress biomarkers in the copepod *Limnocalanus macrurus* from the northern Baltic Sea: effects of hydrographic factors and chemical contamination, Marine Ecology Progress Series, 538, 131–144, doi:10.3354/meps11471, 2015.

Wang, C.L., Wu, D. H., Dong, T. Y., and Jiang, X. M.: Oxygen consumption rate and effects of hypoxia stress on enzyme activities of *Sepiella maindron*, Chin J Appl Ecol. 19, 2420–2427, 2008.

Wang, Q., Li, X, Yan, T., Song, J., Yu, R., and Zhou, M.: Detrimental impact of hypoxia on the mortality, growth, reproduction, and enzyme activities of planktonic mysid *Neomysis awatschensis*, Aquat Ecol. 55, 849–859, https://doi.org/10.1007/s10452-021-09864-3, 2021.

von Weissenberg. E., Jansson, A., Vuori, K.A., and Engström-Öst, J.: Copepod reproductive effort and oxidative status as responses to warming in the marine environment, Ecol and Evol, 12, e8 594, https://doi.org/10.1002/ece3.8594, 2021.

Welker, A.F., Moreira, D.C., Campos, E.G., and Hermes-Lima, M.: Role of redox metabolism for adaptation of aquatic animals to drastic changes in oxygen availability, Comparative Biochemistry and Physiology: Molecular and Integrative Physiology 165, 384–404, https://doi.org/10.1016/j.cbpa.2013.04.003, 2013.

Wishner, K.F., Seibel, B.A., Roman, C., Deutsch, C., Outram, D., Shaw, C.T., Birk, M.A., Mislan, K.S., Adams, T. J., Moore, D., and S. Riley.:Ocean deoxygenation and zooplankton: Very small oxygen differences matter, Sci. Adv. 4(12), eaau5180 doi:10.1126/sciadv.aau5180, DOI: 10.1126/sciadv.aau5180, 2018.

Xiu, P., Chai, F., Curchitser, E. N., Frederic, S., and Castruccio, S.: Future changes in coastal upwelling ecosystems with global warming: The case of the California Current System, Sci. Rep. 8, 2866., https://doi.org/10.1038/s41598-018-21247-7, 2018.