Reviews and synthesis on increasing hypoxia in eastern boundary upwelling systems: zooplankton under metabolic stress

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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 an expansion and intensification of the subsurface oxygen minimum zone (OMZ) is taking place further exacerbating hypoxic conditions for zooplankton inhabiting the upwelling zone. Hypoxia can affect zooplankton by limiting their aerobic respiration, and disrupting 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

It is widely recognized that the increase in atmospheric CO_2 and other greenhouse gasses is driving the warming of the Earth's surface and ocean (Oschlies et al., 2018) with 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 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 in about 2% (oxygen loss) since the middle of the 20th century (Strama et al., 2008; Schmidtko et al., 2017; Breitburg et al, 2018). 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). Hypoxia 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).

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, 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 the future of upwelling regarding its spatial and temporal variability (Bograd et al., 2023). Upon a potential increase of upwelling, alongshore 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 takes place and so compressing the upper highly oxygenated layer (Khön et al., 2022). The closely linked effects of potentially 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. 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^{-1}) 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 the position of the OMZ core and its upper boundary (Tutasi and Escribano, 2020; Riquelme-Bugueño et al., 2020).

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.

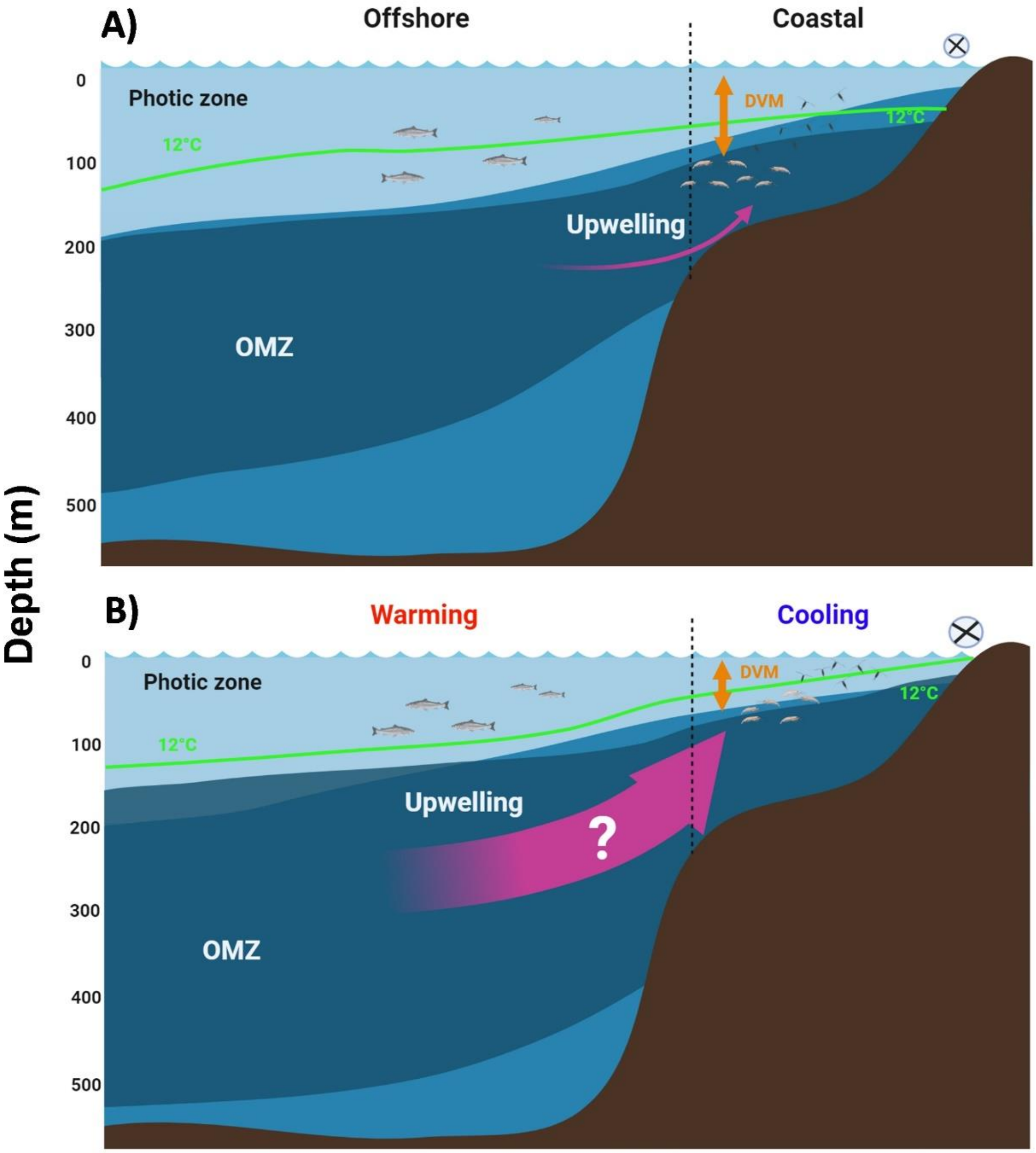

Figure 1. Projected effects of the expansion of the OMZ in eastern boundary upwelling systems (EBUS). A) Under present (initial) conditions, wind-driven upwelling rises the OMZ system and brings cold-water into shallow depths at the inshore as illustrated by the 12°C isotherm, and so fertilizes the photic zone and promotes plankton aggregation. B) Ocean warming effects manifest mainly at surface in the offshore region, while 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,

spreading 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.

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 therefore challenging for most of the biota (Ekau et al., 2010; Wishner et al. 2018; Breitburg et al., 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 and 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 driven 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 end 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 (P_{crit})

(Rogers et al., 2016). 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).

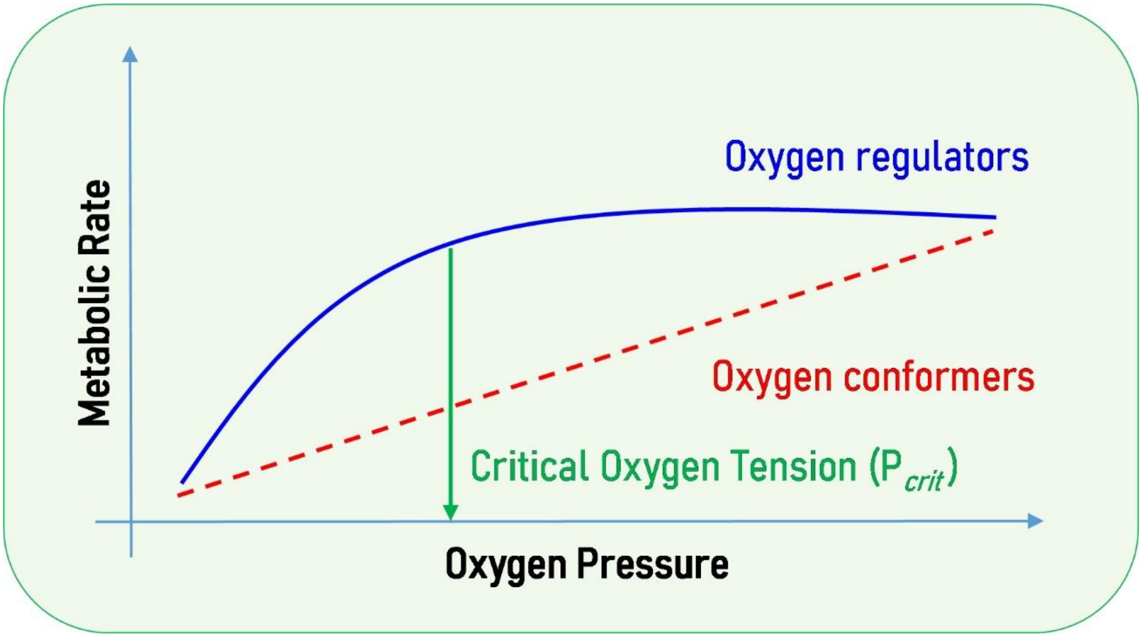

Figure 2: The metabolic rate as a function of oxygen pressure, illustrating two adaptive modes in marine zooplankton as a response to changing oxygen conditions (modified from Pörtner et al., 1993).

The adaptive responses to variable levels of oxygen illustrated in Fig. 2 may take place over short-term timescales (hours), as driven by the exposure to vertical gradients of oxygen in the water column associated with DVM in migrating species, or in the case of not migrating species due to vertical mixing in the water column forced by upwelling pulses, or by changes in wind conditions promoting mixing. Both migratory and non-migratory species can thus be exposed to variable oxygenation in the upwelling zone which is characterized by a marked oxygen-stratified water column. This condition is well illustrated by the oxygen distribution in the water column of central-southern Chile throughout an annual cycle (Fig. 3). Within the photic zone (about 50 m in the coastal zone), the annual cycle of oxygen conditions reveals the existence of normoxic, mild and severely hypoxic habitats, which vertically migratory and non-migratory zooplankton must face depending on their vertical distribution (Fig. 3). Also, shallower strata are more variable on dissolved oxygen during intense upwelling (above 30 m deep), while the deeper strata (30-50 m deep) is more variable in oxygen during a depressed upwelling in the winter.

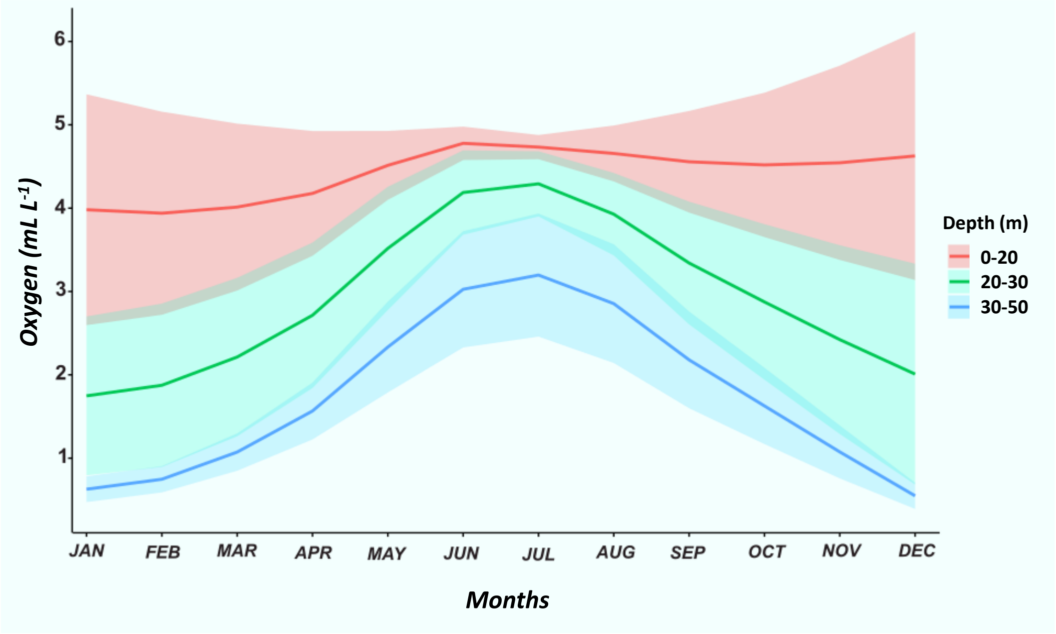

Fig. 3. The annual variability (monthly climatology) of dissolved oxygen in three strata in the upper 50 m layer at central-southern Chile (36°30 S). Oxygen data are from the time series study at Station 18 off central-southern Chile during the period 2002-2016 (Frederick et al., 2024). Shallower strata are more variable during intense upwelling in summer, while the deeper strata are more variable during depressed upwelling during the winter.

Furthermore, the response to oxygen variation illustrated in Fig. 2, may promote different metabolic adaptations, for instance by reducing P_{crit} to cope with severe hypoxia, or a lack of adjusting capacity. This adaptive response has been shown to vary among copepod species (Frederick et al., 2024), and can therefore favour some species while others are negatively impacted. Such differential species-specific responses are shown in Fig. 4 which describes the metabolic rate as a function of oxygen condition from normoxia to hypoxia. A non-adaptive response (Fig. 4A) is reflected in changing metabolic rate (MR) as a function of oxygen levels, and this also implies a change in P_{crit} (fix α), whereas an adaptive response 1 (Fig. 4B) represents a constant MR at the cost of changing P_{crit} (variable α), and adaptive response 2 (Fig. 4C) will maintain a constant P_{crit} with a consequent change in MR (also variable α). From these, only the adaptive response 1 (Fig. 4B) does not compromise aerobic scope, allowing better regulation of physiological processes along the year (Fig. 3). However, while far more stable, this adaptive response does not allow taking advantage of favourable periods (exploit spring bloom for example). The adaptive response 2 (Fig. 4C) instead, allow better exploiting favourable conditions on a changing ocean (likely spring and summer blooms) at expenses of lowering aerobic scope.

It has recently been suggested that P_{crit} is the point at which the oxygen supply capacity (α) reach its maximum physiological limit (uptake and delivery) and as such is a species- and temperature-specific value (Siebel et al., 2021). From past literature, in fact, P_{crit} has been found constant within a given species in fishes (Rogers et al., 2016) and thus supporting the validity of the maximum oxygen supply capacity within species. Yet, the potential plasticity of P_{crit} has rarely been explored on invertebrate inhabiting fluctuating oxygen regimes, such a copepods living around OMZ zones (Wishner et al., 2018; Frederick et al., 2024) Furthermore, many of these pelagic invertebrates have several cohorts along the year, thus also allowing maternal effects on top of plasticity leading to shifts on either P_{crit} 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 be lower than P_{crit} resulting on severe stress or deleterious effects on organisms.

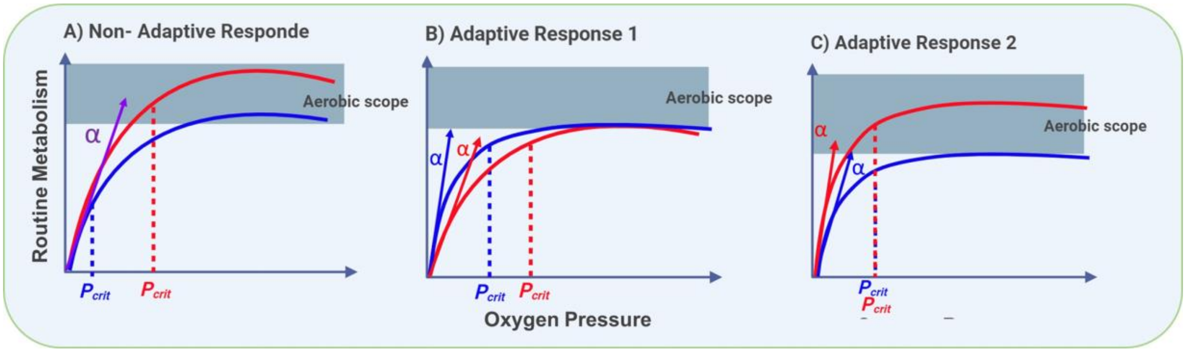

Figure 4. The expected metabolic rate (MR) as a function of environmental oxygen partial pressure (P_{crit}). The MR is theorized for two seasonal conditions: Autumn-winter (blue line) and spring-summer (red line) in a coastal upwelling zone, where P_{crit} will move following changes in MR and the slope (α) of the oxyconforming segment remains constant (A), an adaptive response 1 in which P_{crit} increases upon a changing oxyconforming slope (α) to maintain a constant MR (B), and an adaptive response 2, where P_{crit} 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 P_{crit}, 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 long term physiological adjustments involving enhanced ventilatory capability, enlarged gill surfaces, shortened diffusion distances, and increasing respiratory proteins with high oxygen affinity (Childress and 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 (Gonzáles and 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*, exposed to a seasonal hypoxia driven by estuarine conditions (not by presence of an OMZ) it has been observed behavioural adaptations, with copepods previously exposed to oxygen gradients avoiding hypoxic bottom waters, while copepods not exposed to hypoxia did not avoiding 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 marine environment, is oxidative stress. This 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/demand and, instead, undergo rapid changes between under-oxygenation and hyper-oxygenation (Tremblay et al., 2010). This can indeed occur under stressful conditions in individuals subjected to oxygen levels below their P_{crit} values (as shown in Fig. 4), and which thereafter undergo re-oxygenation. As a by-product of aerobic respiration, the production of reactive oxygen species (ROS) can occur. ROS production 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 and 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). 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 (Zheng et al., 2021).

Molecular oxygen (O_2) is the main 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 three major ROS of physiological significance are superoxide anion (O_{2-}), hydroxyl radical (^{-}OH), and hydrogen peroxide (H_2O_2) (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 production 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 production 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 role is critical in ROS detoxification processes in organisms subjected to oxidative stress. An imbalance between the level of ROS production 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 production and corresponding antioxidant responses in zooplankton, summarized in Table 1.

Table 1: Zooplankton species exposed to different stress leading to ROS production. DVM (daily vertical migration) can be “Y” (yes migration) or “N” (non-migration) and “NI” (no information). Arrows in column 5 indicate the increase or decrease in the biomarker signal in relation at the stressor agent. * Indicate that the samples were obtained from areas having 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 deshidrogenase; **POD**: Peroxidase; **GR**: Glutathione reductase

POS (preparing for oxidative stress, usually termed as preparation for oxidative stress), has been proposed as a mechanism to strengthen antioxidant defences (Hermes- Lima et al., 1998, 2015; Moreira et al., 2016). In the context of ROS associated with hypoxia, it is widely assumed that the antioxidant responses in a large variety of animals from marine, estuarine and freshwater systems (listed in Hermes-Lima et al., 2015) can indeed be preceded by changes at the molecular and biochemical levels after exposure to variable oxygen levels from anoxia to hyperoxia, and such combined responses is therefore known as the POS phenomenon (Welker et al., 2013).

Considering the metabolic responses outlined in Fig. 4. The adaptive response 1 (Fig. 4B) is likely less stressful from the oxidative stress perspective, as lacking large changes on aerobic metabolism (demands) should keep ROS production better regulated. The adaptive response 2 and the non-adaptive response (Fig. 4 A and C), instead, both demand a better regulation of antioxidant defences or POS, since changes on MR (changes in O_2 demand) and thus O_2 balance, will likely generate ROS at transitions between stable O_2 supply-demands states. Critical oxygen tensions (P_{crits}) measured in copepods species inhabiting the same area depicted in Fig. 3, in terms of oxygen variability, range from 2.77± 0.89 (*P.cf. indicus*) to 4.9 ± 0.59 kPa (*A. tonsa*), with *C. patagoniensis* in between with a P_{crit} value of 3.83 ± 1.89 kPa (Frederick et al., 2024). Considering these values and the oxygen variability found in their environment (Fig. 3), only *P.cf. indicus* could maintain an aerobic metabolism stable if staying in the shallower 20 m strata, while the other two species will inevitably transit from aerobic to anaerobic metabolism in some seasons along the year. These transitions are likely causing ROS, which likely also affects *P.cf. indicus* when performing DVM, and so crossing water layers differing in dissolved oxygen, as those shown in Fig. 3.

Altogether, how this oxidative balance and POS operates in zooplankton inhabiting areas subjected to a shallow OMZ is an open question. The timing for developing antioxidant defences also becomes an important issue in both migratory and non-migratory 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 and Haus, 2019, Tutasi and Escribano, 2019). The highly variable DVM behaviour may thus play a key role for the adaptive response to hypoxia in the context of ROS production 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 production and certainly antioxidant response. A potential adaptive response to this periodical exposure to low-high oxygen is the possibility of enacting POS during the hypoxic phase of DVM. The interplay between ROS production and POS linked to DVM behaviour is illustrated in Fig. 5. In Euphausiids, which perform extensive DVM, they are exposed to normoxia oxygen levels >200 µM in the photic zone, and subsequent hypoxia ($O_2 < 3$ 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/increase in oxygenation per hour while swimming up or down. Such stressful oxygen conditions over a short-time scale can indeed trigger ROS production (Tremblay et al., 2010), and potentially POS during the nighttime phase (Fig. 5).

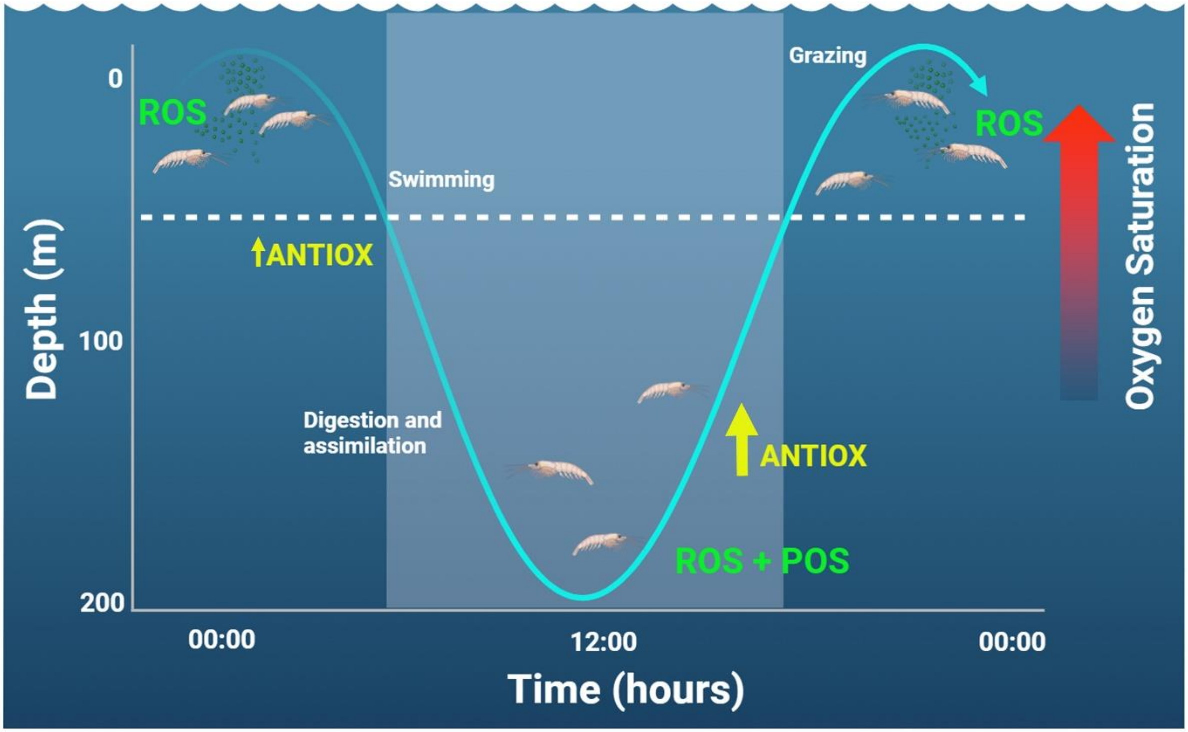

Fig. 5: Changes in the daily vertical migration and short-term response to oxidative stress in zooplankton. Lighter area shows the daytime. The vertical amplitude of migration represents that of euphausiids (Riquelme-Bugueño et al., 2020). At nighttime an increase in the production of reactive oxidant species (ROS) is expected while ROS and the preparation for an antioxidant response (POS) can take place during the daytime while animals stay below the photic zone (here represented by the dashed line at about 50 m).

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 production effects. Diel cycles triggering antioxidant responses to ROS production 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 production and subsequent POS. Several energy demanding possesses occur during DVM, such as grazing at oxygenated conditions, then swimming down (increased activity) to digest the ingested food (specific dynamic action; SDA) at hypoxic conditions. The contribution of all these to ROS production is still unknown, whose production will likely mirror the gradients between available oxygen at the environment and the metabolic demands.

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 with a rather narrow vertical distribution or small DVM) (<50 m) (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 O_2) into near-surface water (Schneider et al., 2016). Upon strong upwelling such hypoxic conditions may even reach surface waters (Escribano et al., 2009). Also, as mentioned above, occasional extreme events driven by intrusion of mesoscale eddies into the coastal zone may also cause episodes of severe hypoxia in shallow water and so affecting non-migratory copepods.

Over the annual cycle 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 triggering ROS production during the 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 within the upper 50 m layer, promoting ROS production and POS are illustrated in Fig. 6 for a present and projected conditions. Fig. 6 illustrates a condition of depressed upwelling (autumn-winter with prevailing downwelling) with the upper limit of the OMZ below the photic zone where non-migratory zooplankton is dispersed and normoxic conditions prevail. This oxic condition promotes the existence of ROS production, whereas a condition of strong upwelling (spring-summer) with shoaling of the OMZ intruding the photic zone can cause that the non-migratory zooplankton become exposed to hypoxia and therefore POS+ROS may occur as a response to a changing hypoxia-normoxia condition. The expansion of the OMZ may exacerbate this condition in the future of EBUS, also vertically compressing the oxygenated habitat (Fig. 6).

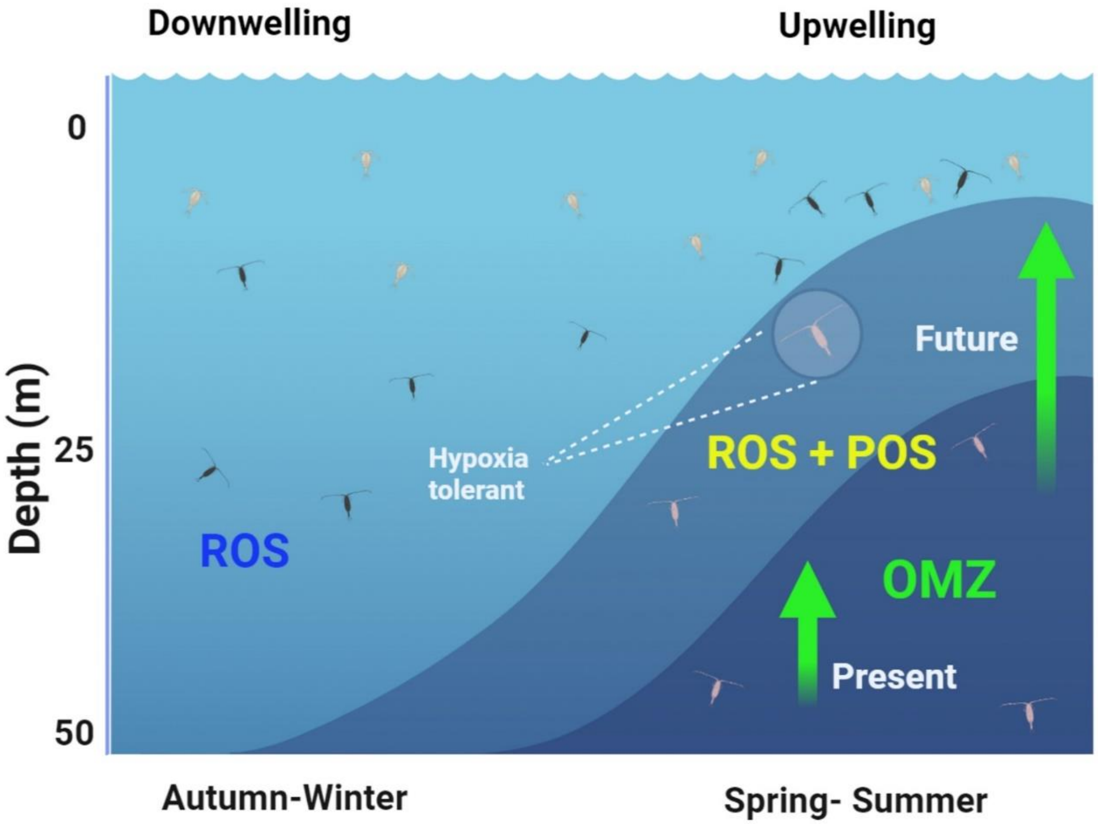

Fig. 6. The seasonal cycle of oxygen conditions of the photic zone (50 m) in EBUS at temperate regions. Downwelling conditions prevail in the autumn-winter without presence of the OMZ within the photic zone and so promoting oxidative stress (ROS). Contrasting conditions of spring-summer (active upwelling) characterized by presence of the OMZ promoting both ROS and the adaptive response (POS). Future condition may exacerbate the expansion of the OMZ also compressing the oxygenated habitat for zooplankton.

Both migratory and non-migratory zooplankton may have possibly evolved adaptive responses to deal with ROS production, 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 is 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 in EBUS, so it is imperative to consider the effects of a changes in temperature, pH and dissolved oxygen (DO). An increase of enzymatic activity indicates the activation of an antioxidant defence mechanism to deal with environment changes. The same effect was reported by von Weissenberg et al.

(2021) in *Acartia spp*. exposed to heatwaves, in experiments carried out at temperatures ranging between 9°C and 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 some numerically dominant 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-migratory populations, which comprise most upwelling inhabitant species.

3.1 NATURAL ANTIOXIDANT AGENTS FOR ZOOPLANKTON

In coastal upwelling environments, zooplankton must face extremely variable conditions, likely stressful for most organisms. In this very same environment, however, the presence of an exogenous source of antioxidants provided for example by diatoms might help mitigate the effect of oxidative stress due to such environmental pressure. Some 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 against UV. Some diatoms such as *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. For instance, Foo et al. (2017) quantified the total content of some antioxidants and their bioactive capacity in six diatom species and found that *Chaetoceros calcitrans* (16.92 ± 0.87 mg TE. g^{-1} DW) and *Isochrysis galbana* (21.55 ± 1.58 mg TE. g^{-1} DW) showed the highest antioxidant activity, followed by *Odontella sinens* and *Skeletonema costatum* which exhibited moderate bioactivity (<13 mg TE. g^{-1} DW), while *Phaeodactylum tricornutum* and *Saccharina japonica* displayed the lowest antioxidant activity (<5 mg TE. g^{-1} DW) among the examined algae species. Most of these diatoms dominate the upwelling zone, specially *Chaetoceros, Odontella* and *Skeletonema*, during the upwelling season (spring-summer) (Anabalón et al., 2007), and they are an important item of the zooplankton diet (Vargas et al., 2006).

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, (on average) and a changing dynamic of the ocean (change in occurrence and extreme events). 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. The highly dynamic water column in EBUS, in factors such as light, oxygen, carbon dioxide, temperature, food, together with the several processes zooplankton perform along these, such as feeding, DVM, and digestion among others, makes extremely hard to identify strata more challenging than others, and even harder considering temporal variation. 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.

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