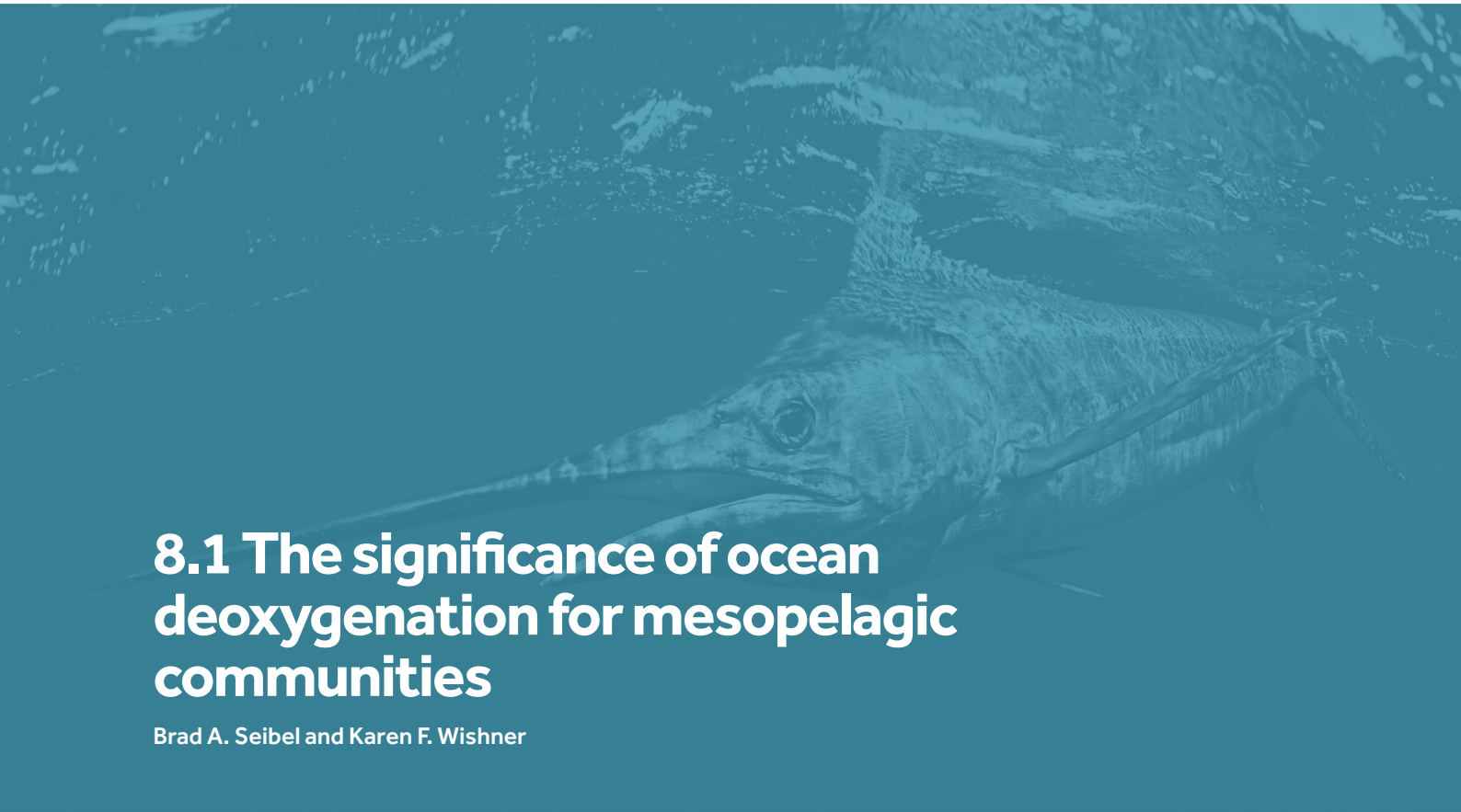




Ocean deoxygenation: Everyone's problem

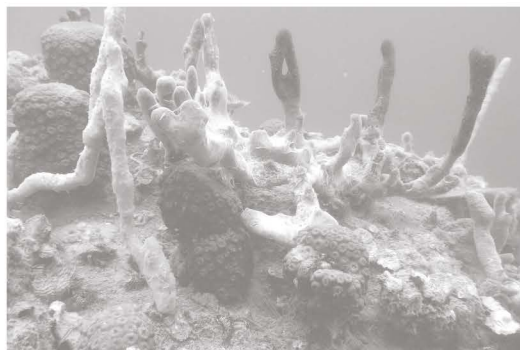
Causes, impacts, consequences and solutions

Edited by D. Laffoley and J.M. Baxter



8.1 The significance of ocean deoxygenation for mesopelagic communities

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IUCN GLOBAL MARINE AND POLAR PROGRAMME



8.1 The significance of ocean deoxygenation for mesopelagic communities

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Summary

- Mesopelagic community structure is directly dependent on the availability of oxygen for aerobic metabolism. Diversity, abundance, distribution and composition of mesopelagic species are all influenced by variations in oxygen at both large and small scales.
- Ocean deoxygenation will decrease the minimum oxygen content in the mesopelagic zone and cause oxyclines to shift vertically (i.e. expansion of the oxygen minimum zone (OMZ) core) in the water column.
- A species' ability to extract oxygen from sea water has evolved to meet specific oxygen demand. As a result, species do not have excess capacity, nor do they live in environments with excess oxygen relative to their evolved capacity; thus, they are susceptible to reductions in oxygen partial pressure and increasing temperature (which elevates metabolic demand).
- Changes in temperature and oxygen profiles within the water column may therefore decouple or enhance competition among different mesopelagic zooplankton species and the larger predators that forage on them at depth by changing zooplankton abundances, distributions, and the depth of layers, and altering species composition and diversity. The biogeochemical cycles (i.e. the biological pump and microbial assemblages) that rely on the mesopelagic zooplankton community will be substantially altered.

Ocean hypoxia effect	Potential consequences
Decreasing oxygen partial pressure (PO_2) in any habitat will reduce aerobic metabolic performance of all species living there (but PO_2 will not decrease in surface waters that are in equilibrium with the atmosphere).	<ul style="list-style-type: none"> • Reduced capacity for prey capture and predator evasion. • Depending on extent of deoxygenation and interacting effects of rising temperature, may lead to species-specific reductions in survival, growth and reproduction.
Shallower upper oxycline and hypoxic layers may result in species-specific suppression of vertical movements and compression of aerobic vertical habitat towards the surface.	<ul style="list-style-type: none"> • May alter the ecological relationships between species living in different depth strata. • May reduce abundance of species as they are forced into shallower, well-lit waters with higher predation pressure. • May reduce diversity in OMZ core and alter species composition of the ecosystem. • May alter biogeochemical cycles and efficiency of biological carbon pump.
Expansion of OMZ will force the lower oxycline community into deeper waters.	<ul style="list-style-type: none"> • May alter life histories (diapause and reproduction) of seasonal inhabitants. • Will alter predator-prey interactions with deeper bathypelagic species. • May alter biogeochemical cycles and efficiency of biological pump.

8.1.1 Introduction

Oceanic oxygen minimum zones (OMZs) refer to sections of the water column at intermediate depths where oxygen concentrations are depleted relative to over- and under-lying waters. OMZs form in subsurface waters, usually between 100 and 1000 m depth, due to a mismatch between heterotrophic oxygen consumption (by microbes and animals) and oxygen input by photosynthetic production, atmospheric diffusion and deep-water ventilation (Figure 8.1.1). OMZs are most pronounced in upwelling regions along the eastern edges of oceans because of high productivity in surface waters and enhanced heterotrophic activity at depth, especially in the Eastern Tropical Pacific (ETP) where deep waters have been out of contact with the atmosphere and oxygen consumption has been occurring for hundreds or thousands of years (Figure 8.1.2). The horizontal and vertical extent of the OMZ, as well as the intensity of the hypoxia (low oxygen) found there, varies considerably between ocean basins and, to a lesser extent, over many spatial and temporal scales within ocean basins (Figure 8.1.2). Dissolved oxygen has declined and hypoxic zones have expanded and shoaled (ocean deoxygenation) throughout much of the ocean as a result of reduced solubility of oxygen in warming waters and enhanced stratification (reduced mixing) that impacts surface

productivity and deep-water oxygen content and utilization (Bograd et al., 2008; Brietburg et al., 2018; Deutsch et al., 2011; Keeling et al., 2010; Paulmier & Ruiz-Pino, 2009; Stramma et al., 2008; Whitney et al., 2007). The variation in oxygen and temperature throughout the mesopelagic zones of the ocean has important implications for organismal performance as well as community structure and composition (Maas et al., 2014; Robinson et al., 2010; Smith & Madhupratap, 2005; Saltzman & Wishner, 1997; Wishner et al., 2013, 2018).

8.1.2 Oxygen concentration, partial pressure and tolerance thresholds

the term 'hypoxia' is most appropriately used to denote an oxygen (O_2) concentration less than some arbitrary value perceived as normal. Within the oceanographic community, hypoxia is typically defined by O_2 concentration, usually without knowledge of the effect of that particular O_2 level on organism or ecosystem function. For example, Kamykowski and Zentara (1990) define hypoxia as a concentration less than 0.2 ml L^{-1} ($\sim 9 \mu\text{M}$) while Diaz and Rosenberg (1995) define it as less than 2.0 ml L^{-1} ($90 \mu\text{M}$). Among all marine animals, a median lethal concentration of $60 \mu\text{M}$ was identified by Vacquer-Sunyer and Duarte (2008). However, this reported threshold concentration exerts a partial

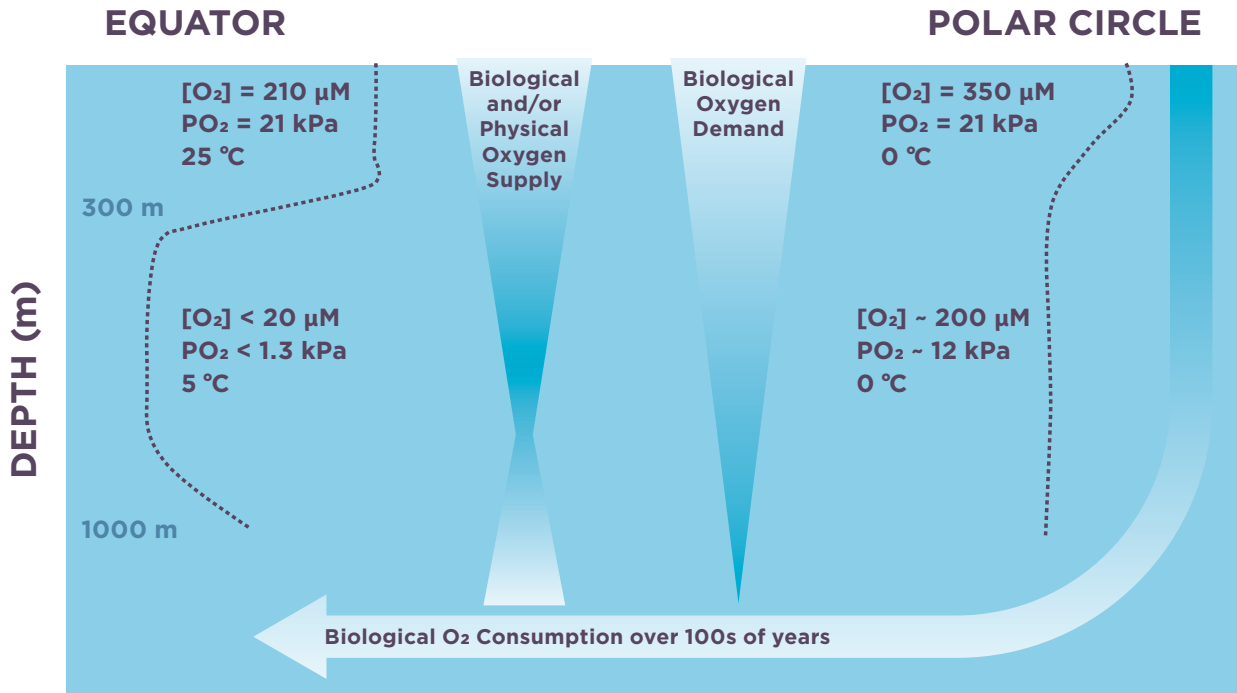


Figure 8.1.1 Schematic showing the processes involved in oxygen minimum zone formation and the resulting oxygen profiles with depth. Biological oxygen supply results from photosynthetic production in shallow waters along with physical diffusion from the atmosphere. The biomass of microbes and animals declines with depth resulting in reduced oxygen consumption (respiration associated with decomposition and metabolism). Deep bottom water formed in polar regions supplies additional oxygen to depths below the oxygen minimum. However, organismal oxygen consumption over 100s of years results in oxygen depletion of deep water by the time it reaches the Eastern Pacific. Approximate oxygen concentrations ($[O_2]$), partial pressure (PO_2) and temperatures across a 1000 m depth range are shown in tropical and polar regions.

pressure ranging from ~4 kPa at 0 °C to more than 7 kPa at 30 °C because oxygen concentration is driven by oxygen solubility, which declines with increasing temperature. The concentration of oxygen in air-saturated sea water varies across the range of ocean temperatures from less ~180 μM in the tropics to over 350 μM at the poles. Thus, defining hypoxia by O_2 concentration is problematic because a concentration

that is lethal at one temperature may not be at another and is species-specific. Moreover, it is the partial pressure (PO_2), not the O_2 concentration, that drives O_2 across gill membranes into organismal tissues and determines the effect of hypoxia on organism function. Sea water in equilibrium with the atmosphere has an oxygen partial pressure of 21 kPa (21% of atmospheric pressure) regardless of temperature. For a parcel of water that

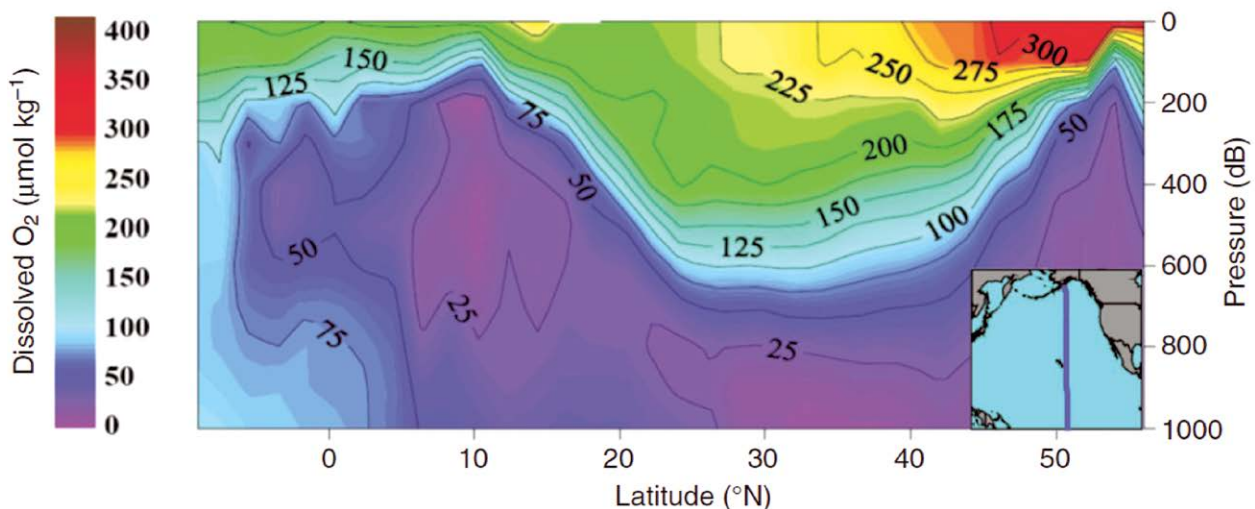


Figure 8.1.2 Oxygen concentration (μM) as a function of depth along a transect from north to south in the Eastern Pacific. A map of the transect line is inset (Seibel, 2011).

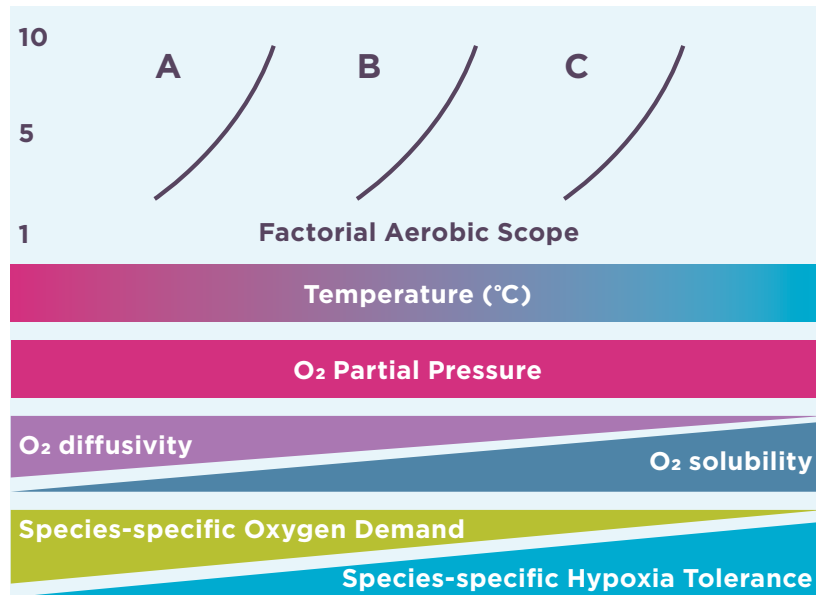


Figure 8.1.3 Temperature influences oxygen availability for organismal metabolism via the counter-acting effects of diffusivity, solubility, metabolic demand and physiological capacity for oxygen extraction and transport (hypoxia tolerance). Oxygen partial pressure in air-saturated water is constant across a temperature range. The result is that oxygen availability is slightly higher in warm water despite reduced solubility, but that physiological hypoxia tolerance compensates for increased demand. Factorial Aerobic Scope (FAS) is the species-specific ratio of maximum to resting oxygen demand and is quantitatively equivalent to the ratio of environmental PO_2 (The Metabolic Index; Deutsch et al., 2015). The FAS in most species (shown for hypothetical species A, B and C) ranges from ~6 to 2 and typically declines with increasing temperature toward a value that characterizes a species' evolved upper temperature limit.

is isolated from the atmosphere, the concentration of oxygen in that parcel will exert a lower pressure at cooler temperatures. Moreover, oxygen diffusivity increases with temperature, which more than offsets temperature-induced reductions in solubility (Figure 8.1.3). Thus oxygen availability at a given concentration is improved in warm waters (Verberk et al., 2011). Regardless, organismal oxygen demand increases with temperature while the capacity for physiological gas exchange has evolved to meet demand within their primary habitat (Figure 8.1.3). Thus, any definition of hypoxia related to the survival or performance of organisms is necessarily species-specific and will depend on the particular physiological requirements of the species and on the environment to which the species is adapted.

The median lethal oxygen concentration reported by Vacquer-Sunyer and Duarte (2008) ($60 \mu M$); did not include animals evolved to persist in OMZs. An oxygen content above that threshold is found only in the mixed layer above pronounced OMZs suggesting that half of all marine species would not survive for long at depths below ~50 m in the ETP or below ~300 m in the California Current. However, virtually all zooplankton living in these regions can actually tolerate $60 \mu M$ oxygen ($PO_2 \sim 5$ kPa at $5^\circ C$) and many can tolerate a PO_2 less than 1 kPa ($15 \mu M$ at $5^\circ C$; Childress & Seibel, 1998; Seibel, 2011). More recent studies show some species have critical PO_2 thresholds as low as 0.2 kPa (Wishner et al., 2018).

Such extreme hypoxia tolerance permits movement and habitation across the entire water column in the California Current and expanded movements in the upper few hundred metres in the ETP. Even so, most species are precluded from the core of the most pronounced OMZs. The lack of ability to extract sufficient oxygen from such an oxygen-depleted environment explains the reduction in biomass, abundance and diversity in the core of the ETP OMZ and also why most remaining biomass undergoes diel vertical migration, returning to more oxygenated waters at night in these regions (Maas et al., 2014; Wishner et al., 2013).

8.1.3 Mesopelagic community structure and composition

Mesopelagic communities are structured by trade-offs in food availability, predator avoidance (associated with light level), and species-specific responses to hydrographic features including tolerance to the strong gradients in temperature and oxygen with depth. In regions with intense OMZs, the epipelagic habitat is distinctly separated from deeper water by the strong thermocline and oxycline at the base of the mixed layer (coinciding with the upper boundary of the OMZ; Figure 8.1.4). While this constrains vertical distributions of many taxa, some zooplankton and nekton, such as krill and pelagic crabs (Figure 8.1.5) show strong diel and ontogenetic vertical migration hundreds of metres

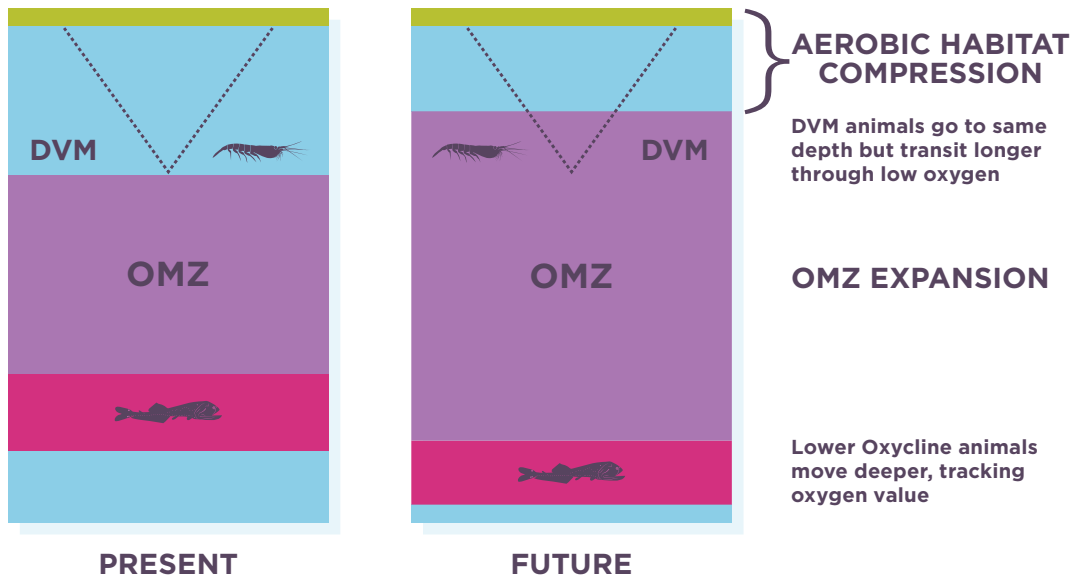


Figure 8.1.4 Schematic showing simplified community structure in oxygen minimum zones and possible consequences of OMZ expansion due to climate change. Diel vertical migrators, such as euphausiids (e.g. krill), migrate to similar depths regardless of oxygen. This is driven primarily by light and the resulting risk of predation during daytime migration. In pronounced OMZs, many vertically migrating animals suppress metabolism during the daytime. The deep lower oxycline community does not migrate but alters depth to persist at a particular oxygen partial pressure.

into hypoxic water (e.g. Ambriz-Arreola et al., 2016; Maas et al., 2014; Seibel, 2016; Wishner et al., 1998, 2013, 2018). The lower boundary of the OMZ, where oxygen increases with depth, has more gradual physical gradients, although there are associations of organism layers with particular oxygen concentrations (Wishner et al., 2013, 2018). Epipelagic and mesopelagic communities also interact as part of the biological pump via the vertical flux and processing of sinking particles (Steinberg & Landry, 2017), a phenomenon that may be influenced in OMZs by effects of low oxygen on distributions and metabolic processes of microbes, zooplankton, and nekton. Additionally, both the upper and lower OMZ oxyclines, as well as the low oxygen core of the OMZ, provide specialized habitats for microbes that may provide novel food resources for mesopelagic zooplankton (Gowing & Wishner, 1992, 1998).

Within strong OMZs, the steep oxygen gradients (oxyclines) at the upper and lower OMZ boundaries create microhabitats of differing oxygen concentration (and temperature regime related to their depth) that are characterized by layers of high zooplankton biomass and abundance, with distinct species zonation (Maas et al., 2014; Wishner et al., 1995, 1998, 2013). For some zooplankton species, including the copepod *Lucicutia hulsemannae* and the shrimp *Gennades* spp. (Figure 8.1.5), oxyclines at the upper and lower OMZ boundaries are loci of distributional peaks in the water column. These characteristics contrast notably

with the OMZ core, where oxygen is extremely low but relatively stable, and where resident zooplankton biomass, abundance and diversity are much reduced (Koppelman et al., 2005; Longhurst, 1967; Smith & Madhupratap, 2005; Wishner et al., 1998, 2008). Responses of the mesopelagic zooplankton community to the OMZ vary geographically. For example, the zooplankton community in the very hypoxic ETP is dominated by population peaks at the upper and lower oxyclines and by diel vertical migrators that inhabit the OMZ core for hours each day. In the California Current, slightly higher oxygen levels and colder temperatures also play a role in structuring the community, however, a diverse midwater assemblage lives permanently in the OMZ core (Gilly et al., 2013).

Under continuing ocean deoxygenation, mesopelagic communities, including those at oxycline boundaries, and the processes they support, may be displaced vertically and horizontally. Boundary-related effects could include altering the depth of zooplankton biomass layers and species distributions and impacting diel vertical migration patterns and life history strategies. In a recent study (Wishner et al., 2013), comparison of two ETP locations differing in the depths of their upper and lower oxyclines served as a natural experiment demonstrating the sort of shifts in faunal distributions that may occur in the future with deoxygenation and OMZ expansion. A large zooplankton biomass peak at the lower OMZ boundary appeared to be strongly locked

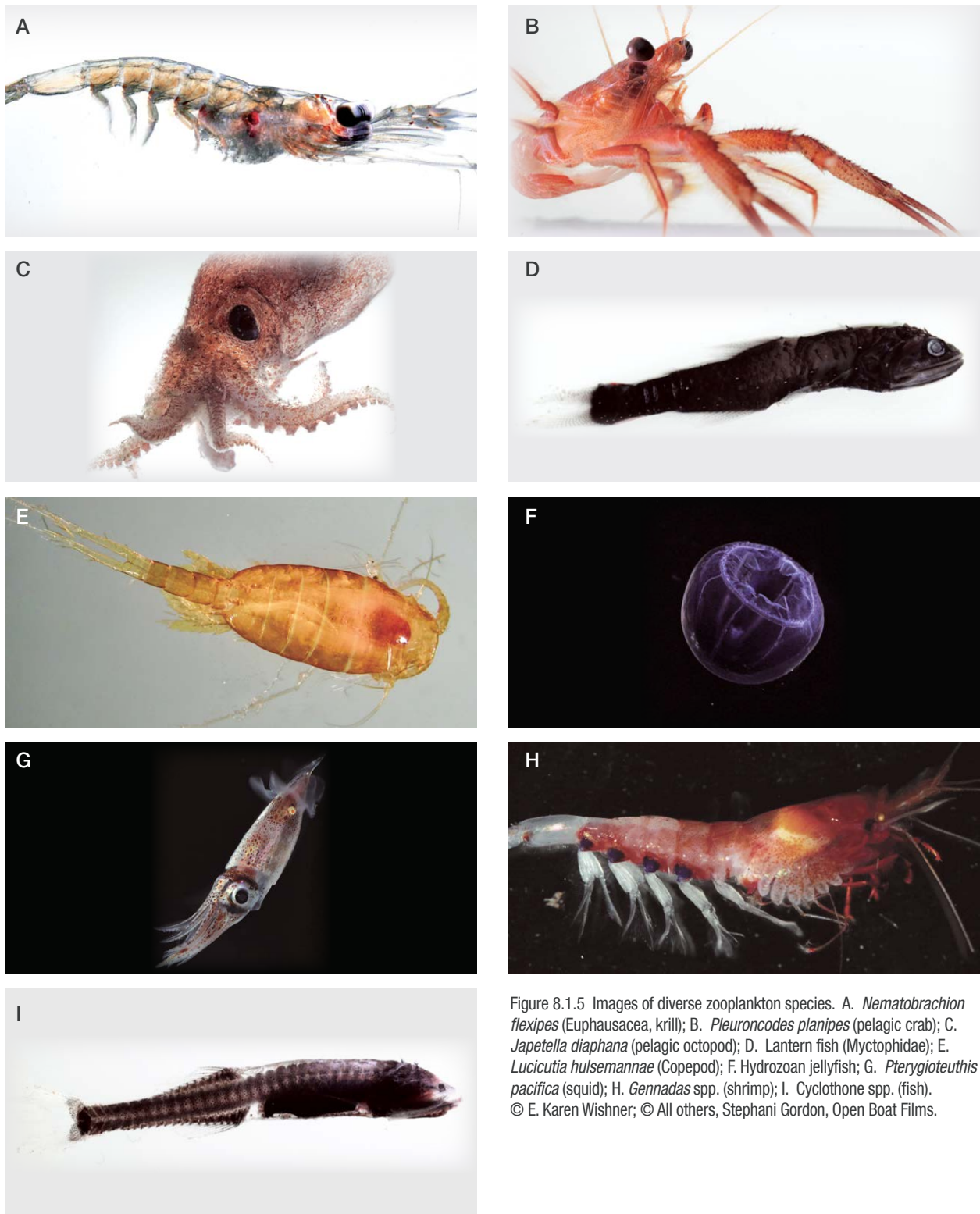


Figure 8.1.5 Images of diverse zooplankton species. A. *Nematobrachion flexipes* (Euphausacea, krill); B. *Pleuroncodes planipes* (pelagic crab); C. *Japetella diaphana* (pelagic octopod); D. Lantern fish (Myctophidae); E. *Lucicutia hulsemannae* (Copepod); F. Hydrozoan jellyfish; G. *Pterygioteuthis pacifica* (squid); H. *Gennadas* spp. (shrimp); I. *Cyclothone* spp. (fish). © E. Karen Wishner; © All others, Stephani Gordon, Open Boat Films.

into position by oxygen concentration. It changed in depth by over 200 m between the two locations, with a depth-associated change in temperature. However, the oxygen concentration at the two depths where this layer was located was virtually identical at both stations ($\sim 2\text{--}8 \mu\text{M}$). In contrast, for animals within the upper

oxycline, the depth (and temperature at that depth) of the daytime diel migration peak was similar at the two stations (200 – 300 m, $11.0\text{--}1.9\text{ }^\circ\text{C}$), even though oxygen concentration at that depth varied between the two regions. Thus, on a daily basis, animals (total biomass) at these two stations migrated to a nearly

constant depth that appeared to be set by light even though the animals at one station had to transit through a broader hypoxic habitat. On a more global scale, however, the depth of diel migration of sound scatterers does appear to be influenced by oxygen concentration (Bianchi et al., 2013; Netburn & Koslow, 2015). In the California Current, even a small future decline in oxygen could result in a shift of this ecosystem and midwater community towards a more highly oxygen-structured system similar to the more sparsely populated Eastern Tropical Pacific OMZ.

Long-term deoxygenation trends (Brietburg et al., 2018) reportedly play a role in declines in abundance of mesopelagic fishes (Koslow et al., 2011), shifts in zooplankton diel migration depths (Bianchi et al., 2013), potential threats to fisheries (Townhill et al., 2016), and alterations in diving depths of top predators (Mislán et al., 2017; Prince & Goodyear, 2006; Stramma et al., 2011). These community changes likely reflect complex interactions of multiple variables including deoxygenation, over-fishing, long- and short-term climate cycles and change, and cascading ecological shifts. Known with much more certainty is that interactions between temperature and oxygen availability on aerobic metabolism will have strong direct effects on oceanic species distributions and performance (Deutsch et al., 2015; Pierson et al., 2017; Seibel, 2016).

8.1.4 Deoxygenation and organismal physiology

The ability of organisms to cope with long-term hypoxia depends on their metabolic rate, which is dependent on temperature and physiological state (activity level, feeding history, reproductive state, etc.), and the ability to extract oxygen from the sea water and transport it to the tissues. Permanent zooplankton residents of oxygen minimum zones tend to have oxygen-binding proteins (haemoglobin or haemocyanin) with a high affinity for oxygen, high ventilatory and circulatory capacity, and enlarged gas-exchange surfaces (i.e. gills) with thin membranes that reduce diffusion distances (Childress & Seibel, 1998; Seibel, 2011). These integrated physiological characteristics set a critical oxygen partial pressure (P_{crit} ; Figure 8.1.6), below which aerobic metabolism can no longer be maintained. The P_{crit} correlates strongly with historical long-term hypoxia exposure (Figure 8.1.7) but may respond to short-term changes via acclimation and, in species with short generation times, adaptation. P_{crit} is species-specific,

and no strong phylogenetic, temperature or size-related trends in hypoxia tolerance appear to exist across marine animals more broadly (see Table S4 in Wishner et al. (2018) for a compilation of all measured P_{crit} values to date for marine crustaceans).

Species without complex oxygen transport systems, such as gelatinous zooplankton, are often reported as oxyconformers, meaning that the rate of oxygen consumption declines with environmental oxygen. However, oxyconformation must merely describe the metabolic response of organisms to O_2 levels below their P_{crit} . This is because there must always be a species-specific upper limit to resting metabolism above which additional O_2 will have no influence. The appearance of oxyconformation may result from 1) a very high P_{crit} (low hypoxia tolerance) most often found in species with limited metabolic scope (low capacity for activity), 2) experimental methods that fail to distinguish a true baseline level of metabolism, or 3) a complex response to declining oxygen that includes multiple processes with distinct oxygen limits. The latter case implies that a baseline level of metabolism that supports all maintenance processes must exist with a higher organismal P_{crit} and that oxygen-dependent metabolic rates are not sustainable in the long-term. Nevertheless, several studies on gelatinous zooplankton demonstrate a clear ability to regulate a constant rate of oxygen consumption as PO_2 falls (Rutherford & Thuesen, 2005; Thuesen et al., 2005). In gelatinous species, which typically have low metabolic rates and short diffusion distances, the P_{crit} may result from simple diffusion limitation as opposed to a limitation in heart or ventilation rate or oxygen carrying capacity as may be seen in fishes, crustaceans and cephalopods.

The evolutionary adjustments in oxygen extraction and transport in individual species have compensated for variations in oxygen demand and availability in their specific habitats such that all species are living similarly near their ultimate limits (P_{crit} , where environmental oxygen supply equals resting demand; Figure 8.1.3). Thus, any decrease in oxygen partial pressure or increase in temperature will reduce the scope for metabolic activity toward critical levels for all species (i.e. Metabolic Index) (Deutsch et al., 2015; Wishner et al., 2018). Because PO_2 is near 21 kPa in surface waters in equilibrium with the atmosphere regardless of temperature, ocean deoxygenation will not impair organismal performance in shallow oceanic waters (but will in coastal regions where PO_2 declines due to eutrophication or upwelling; Chan

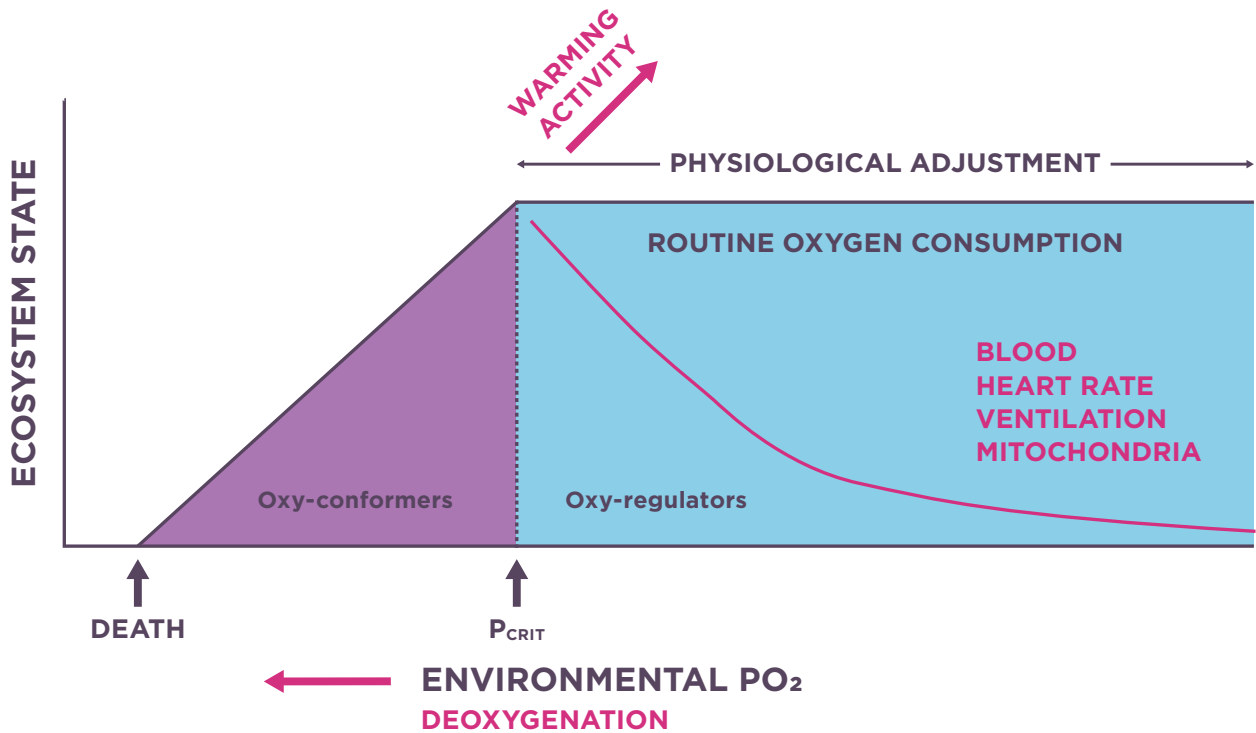


Figure 8.1.6 Schematic of the metabolic response of organisms to declining oxygen partial pressure. Most organisms maintain a constant resting rate of oxygen consumption until a critical PO (P_{crit}) is reached, below which supply fails to meet demand. The red curve represents the physiological adjustments that permit regulation of the metabolic rate at PO above P_{crit} . Ocean warming or increased activity will result in an elevated oxygen consumption rate and higher P_{crit} (reduced hypoxia tolerance). Ocean deoxygenation will reduce PO toward the critical level for any species.

et al., 2008; Rabalais et al., 2002). Thus, organismal oxygen limitation in surface waters may result only from temperature-driven increases in oxygen demand and consequent reductions in the scope for aerobically-fuelled activities such as growth, reproduction and locomotion (Deutsch et al., 2015; Pörtner et al., 2017). However, the transport of waters with reduced $[O_2]$ to deeper layers and alterations in oxygen utilization there will lead to expansion of oxygen minimum zones and reductions in the PO_2 , pushing organisms beyond their evolved tolerance. Thus, all zooplankton are susceptible to warming and deoxygenation.

Species living in cold, well-oxygenated regions, such as the mesopelagic zone of the Southern Ocean, have low metabolic oxygen demand, while oxygen concentration is high in cold water. This has led to a belief that polar waters contain “excess oxygen” and that species living there will not be strongly impacted by deoxygenation (Chapelle & Peck, 1999). However, polar animals have evolved relatively limited oxygen uptake systems and have correspondingly high P_{crits} (i.e. low hypoxia tolerance, Torres et al., 1994). For example, the Antarctic krill, *Euphausia superba*, has a P_{crit} of ~5 kPa at 0 °C, substantially higher than related species living

in pronounced OMZs in the Eastern Tropical Pacific. The krill, *Nematobrachion flexipes*, for example, has a metabolic rate at 10 °C that is similar to that of *E. superba* at 0 °C. However, its P_{crit} is ~10x lower (0.68 kPa; Wishner et al., 2018; Figure 8.1.5). *Euphausia superba* routinely experience oxygen values of ~10 kPa at depths below 200 m. This provides a potential aerobic scope for activity (i.e. Metabolic Index) of only 2, a value known to delineate metabolically suitable habitat for many species (Deutsch et al., 2015). The ocean deoxygenation and warming that have already occurred in the Southern Ocean are substantial and are likely to continue (Schmidtko et al., 2017). Any further decline in PO_2 or increase in temperature will restrict the habitable depth range of polar zooplankton with likely consequences for their growth, reproduction and survival. Thus, excess oxygen does not exist anywhere.

In regions with pronounced OMZs, species that undergo diel vertical migration are capable of short-term survival at sub-critical oxygen levels via metabolic suppression. Some additional energy is acquired through anaerobic metabolic pathways. However, anaerobic metabolism typically accounts for a small fraction of the total energy demand and does not fully compensate for the energy

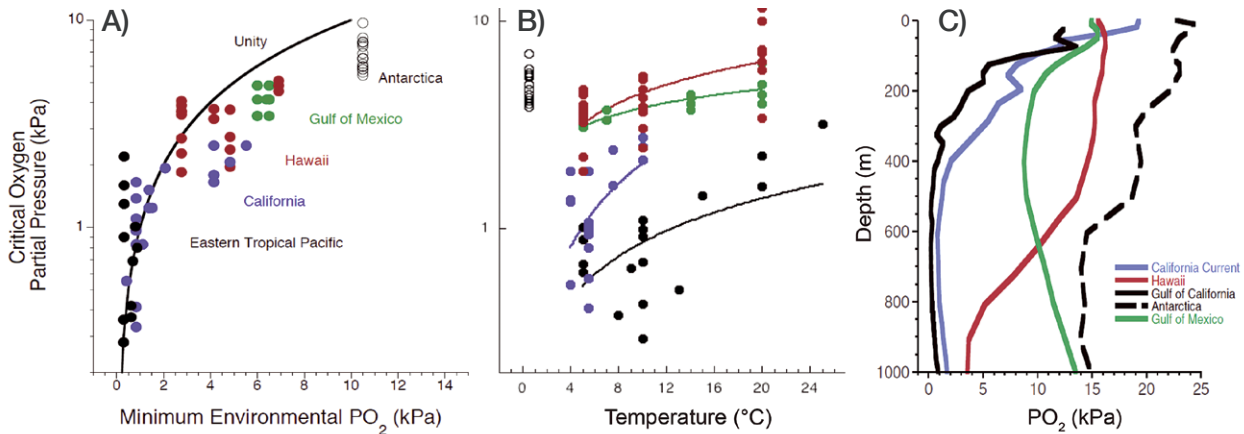


Figure 8.1.7 Critical oxygen partial pressures (P_{crit}) for diverse zooplankton species, including fishes, crustaceans and cephalopods, living in different oceanic regions. Each point is a unique species. A) P_{crit} plotted as a function of the minimum oxygen partial pressure experienced by each species indicates that all species are living similarly near their oxygen limits (unity line). Some vertical migrators experience oxygen levels below their P_{crit} (left of the unity line) during the daytime and must migrate to surface waters at night. B) P_{crit} of each species as a function of temperature demonstrating that species in relatively hypoxic regions (Eastern Tropical Pacific and California Current) have evolved greater physiological capacity for oxygen uptake and transport compared to species in relatively well-oxygenated regions (Antarctica, Hawaii and Gulf of Mexico). C) Oxygen depth profiles from each region investigated (Gulf of California profile represents the Eastern Tropical Pacific species).

deficit due to oxygen limitation. Metabolic suppression is achieved by limiting energetically expensive processes such as ion transport, transcription and translation. Reductions in total metabolism of 40-80% have been demonstrated in mesopelagic squids, pteropods, krill, crabs, copepods and amphipods (Childress, 1977; Elder & Seibel, 2015; Kiko et al., 2015, 2016; Maas et al., 2012; Seibel, 2011, 2016; Seibel et al., 2014, 2016, 2018; Figure 8.1.5). Such reductions in oxygen consumption are accompanied by reduced carbon dioxide and ammonia excretion, with consequences for biogeochemical cycles. Below critical oxygen levels, some energy is still acquired from aerobic metabolism. Thus, continued deoxygenation may restrict the distributions and abundances of key vertically migrating species and their predators.

As the ocean warms and oxygen declines, the metabolically viable habitat of the upper ocean will shoal (aerobic habitat compression). Oxygen limitation is, of course, not the only potential limitation on habitat depth. Light, temperature, pH and food availability may impose independent limits and selective pressures. Figure 8.1.3 illustrates that all species live within a similar range of metabolically available habitat. A PO_2 near 1 kPa appears to be a lower limit for meso-zooplankton diversity and abundance (Childress & Seibel, 1998). The OMZ core of the California Current is near this limit. Further deoxygenation may cause an ecosystem shift there from a diverse mesopelagic community to one largely devoid of permanent mesopelagic inhabitants and dominated by vertical migrators that return to

oxygenated waters night. That said, some species are known to permanently occupy the lower oxycline despite lower oxygen values there. For example, persistent (non-migrating) layers of several copepod species occur at about 2 – 8 μM (~0.2 to 0.8 kPa at 5 $^{\circ}C$) at the lower oxycline of the ETP and Arabian Sea OMZs where they are actively feeding and reproducing (Wishner et al., 1998, 2000, 2013). Some copepod species have life history stages that undergo diapause (a type of hibernation) and form layers, presumably lasting months, at these same low oxygen depths in OMZs around the world; these species are not feeding at depth and are probably inactive (Hidalgo et al., 2005; Wishner, 2013). Recent measurements for Eastern Tropical Pacific lower oxycline species reveal the greatest hypoxia tolerance reported for any species ($P_{crit} \sim 0.3$ kPa; Wishner et al., 2018). Interestingly, they display a reverse temperature effect where hypoxia tolerance is improved at higher temperatures despite higher oxygen demand. This trait is adaptive in the lower oxycline where temperature and oxygen are inversely correlated (Wishner et al., 2018).

Future research must address, with greater precision, the vertical and horizontal distribution and physiology of organisms, the mesoscale variability of oxygen and temperature, and the rate and magnitude of future changes in these parameters. These goals can be accomplished utilizing a greater diversity of techniques and new technologies including acoustics, camera systems, towed measurement systems and more precise net sampling. Hypoxia tolerance is species- and temperature-specific and can only be determined

through measured response of live animals to a range of oxygen partial pressures. There are as yet no proxies for simple estimation of hypoxia tolerance. However, a variety of metrics have been used, including P_{crit} , loss of equilibrium, anaerobic metabolite accumulation (e.g. lactate), and lethal concentrations (LC_{50}) at specified temperatures that provide useful measures of hypoxia tolerance. Modelling efforts, such as the Metabolic Index (Deutsch et al., 2015), may incorporate these metrics to assess metabolically available habitat across latitudinal and depth gradients.

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