

## Vulnerability of marine species to low oxygen

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Synopsis:

This review outlines the impacts of low oxygen on marine species. First, the causes of marine deoxygenation and low oxygen are illustrated. Then, the effects of low oxygen on some important taxa and marine ecosystems are discussed for a better understanding of marine species vulnerability to low oxygen.

## Abstract

In recent decades, the ocean is becoming less oxygenated due to the combined effect of global warming and the spread of coastal eutrophication, with extensive consequences to marine ecosystems. Past mass extinctions were at least in part due to anoxic conditions in the oceans. Thus, we should be concerned about ongoing and projected declining availability of well-oxygenated habitats in the oceans. Tolerance to low oxygen is greater in smaller than larger, and less mobile than mobile taxa. The most vulnerable taxa to low oxygen are large active fish, and the least are sessile mussels, hydrozoans, and jellyfishes. Expanding low oxygen waters leads to shifts in the composition, diversity, abundance, and distribution of marine species.

## Glossary

**Anoxia:** The absence and near absence of dissolved oxygen. Here, we consider dissolved oxygen  $< 0.5 \text{ mg l}^{-1}$  for the purpose of sustaining animal life.

**Bathypelagic:** The zone of the open ocean below the euphotic (well-lit) and mesopelagic (poorly lit) but above the abyssopelagic.

**Benthos:** The collection of organisms living on or within the seabed.

**Coastal waters:** The area of sea adjacent to global landmasses.

**Continental margin:** The submerged prolongation of continental landmass consisting of the seabed and subsoil of the continental shelf, slope and rise, but not the deep ocean floor.

**Critical oxygen concentration ( $P_{crit}$ ):** The level at which an organism can no longer maintain aerobic metabolism.

**Demersal:** A species living on or near the seabed. Commonly used for near-seabed living fish.

**Deoxygenation:** A decline in concentration of the dissolved oxygen.

**Epipelagic:** The collection of organisms living in well-lit (euphotic) surface waters of the open ocean; above the mesopelagic.

**Eutrophication:** The environmental problem of excessive nutrients, leading to plant growth (e.g., planktonic or benthic alga) oxygen fluctuations (hypoxia, anoxia, and supersaturation), and where dead and rotting plants create a public nuisance. Typically results from the release of nutrients from human activities.

**Hypoxia:** The situation where a volume of water has insufficient oxygen for most species to live. A level of  $2 \text{ mg l}^{-1} \text{ O}_2$  has been used as a threshold in some studies, but  $3 \text{ mg l}^{-1} \text{ O}_2$  appears more appropriate for marine species, and many organisms are negatively affected at higher oxygen concentrations.

**Lethal concentration:** The lowest concentration that produces death in an organism.

**Low oxygen areas:** Water bodies where oxygen concentrations are clearly below saturation. Here we consider waters with  $< 6 \text{ mg l}^{-1}$  as low in oxygen.

**Low oxygen threshold:** The level at which an organism can no longer maintain its normal life activities as it is stressed or limited by oxygen supply. Here we use three kinds of low oxygen thresholds: lethal, median lethal, and critical oxygen concentration.

**Median lethal concentration (LC50):** The concentration at which half (50%) of the exposed animals die.

**Mesopelagic:** Referring to the poorly lit open water habitat below the epipelagic (euphotic) and above the bathypelagic. Also called the twilight zone.

**Open ocean:** The area away from the coastal waters and above the seabed.

**Oxygen concentration units:** Dissolved oxygen concentration is related to water temperature, salinity, and barometric pressure. Different units are used. For ease of conversion, at  $20^\circ \text{ C}$  water temperature  $100\%$  air saturation =  $7.5 \text{ mg l}^{-1} = 5.7 \text{ ml l}^{-1} = 235.8 \text{ } \mu\text{mol l}^{-1} = 20.7 \text{ kPa}$ . This means that at  $20^\circ \text{ C}$ , seawater is in equilibrium with the atmosphere ( $100\%$  air saturation) and contains  $7.5 \text{ mg}$  dissolved oxygen per litre of water.

**Oxygen minimum zone:** Area of the ocean with seasonal or permanently low oxygen conditions.

**Oxygen saturation:** Water is considered  $100\%$  saturated when the partial pressure of oxygen in the water and the overlying air is equalised. The release of oxygen from photosynthesis can result in over  $100\%$  saturation.

**Plankton:** The collection of organisms, often microscopic, that are suspended freely in the water column.

**Vulnerability:** The level or state of susceptibility to a threat.

## **The ocean is losing its breath**

The ocean receives oxygen in the upper waters from photosynthetic plants and bacteria, and also from the atmosphere. The ocean loses oxygen due to the respiration of organisms, chemical oxidation, and the release of oxygen to the atmosphere from the upper over-saturated layers following photosynthesis.

Evidence suggests that the ocean has lost about 2% of its oxygen since the middle of the last century due to global warming (Schmidtko et al., 2016). Climate change is projected to decrease global ocean oxygen by 3.5 ( $\pm 0.4$ ) % by the end of the century, when compared to the 1990s, in the high (no mitigation) fossil fuel emission scenario (Bopp et al., 2013). Since the 1960s, over 500 coastal water bodies have been identified as hypoxic, fewer than 10% of these systems were known to have hypoxia before 1950. Open-ocean oxygen- minimum zones (OMZs) have expanded by an area of approx. 4.5 million km<sup>2</sup> (based on water with  $< 2 \text{ mg l}^{-1}$  oxygen at 200 m of depth) (Breitburg et al., 2018).

The three leading causes of ocean deoxygenation are (1) eutrophication (see Glossary, Costello et al., 2020) in coastal areas (2) respiration in the OMZs and (3) global climate change, including warming and changes in ocean stratification (Fig. 1). Eutrophication occurs when an excess of nutrients from agricultural fertilisers, sewage and other wastewaters stimulates algal growth in coastal waters. The consumption of algae by animals, and decomposition of dead algae by bacteria, result in low oxygen levels in the water (Downing et al., 1999).

Global warming reduces ocean oxygen in three main ways: (1) warmer water holds less oxygen as oxygen solubility decreases as temperature increases, (2) warming increases biological respiration which consumes oxygen, and (3) warming intensifies the stratification of the water column, leading to a stronger thermocline. Stratification reduces ventilation and oxygen replenishment of the ocean below the thermocline (reviewed by Keeling et al., 2010).

Low dissolved oxygen concentrations occur naturally in the OMZs of the open ocean and deep basins of semi-enclosed seas, coastal upwelling zones, and systems like deep fjords with limited tidal exchange. The spatial extent, severity or duration of low oxygen events have increased in many of these areas, and low oxygen now occurs in water bodies that historically had high oxygen concentrations.

## **The vulnerability of marine species to low oxygen**

Oxygen is fundamental for the survival of most marine organisms. The vulnerability of marine species to low oxygen is nonlinear. Most species are not particularly sensitive to oxygen if concentrations are above their physiological tolerance limit. Yet once the oxygen drops below a certain concentration, organisms suffer from a variety of stresses that may ultimately lead to mortality.

The threshold of different marine species to low oxygen varies greatly between taxa, with fish and shrimp tending to be more sensitive, followed by, for example, octopus, polychaete worms, sea urchins and anemones (Fig. 2).

The vulnerability of marine species to low oxygen is closely related to their mobility, habitat, and body size (Fig. 3). “Fast moving” species (fishes and a few molluscs, such as octopus) are more sensitive, followed by ‘highly mobile’ (most plankton-like crustaceans) species, while species with “reduced mobility” (most benthos such as polychaetes, bivalves, sea urchins, echinoderms, anemones, jellyfishes) are the least sensitive. Organisms inhabiting the benthos generally experience higher exposure to low oxygen, and thus have evolved to be less sensitive than plankton, which are less exposed. Smaller metazoans are more tolerant to low oxygen waters, due to their larger surface area to volume ratio, which facilitates oxygen diffusion. Thus, it is not surprising that larger animals (macrofauna and megafauna) are more vulnerable to low oxygen versus smaller fauna (meiofauna), and that small taxa dominate within lower oxygen conditions (Gooday et al., 2009; Quiroga et al., 2005).

The expansion of low oxygen waters due to ocean warming leads to shifts in the composition, diversity, abundance, and distribution of marine species (Fig. 4). Sensitive species will move from low oxygen layers into better-oxygenated layers, losing previously suitable habitats and compressing the remaining suitable areas. Low oxygen also strongly reduces biodiversity, as tolerant species become dominant in the absence of sensitive ones. Species that cannot move away from low oxygen areas may experience mass mortalities when tolerances are exceeded. At the end of the Permian Period, 250 million years ago, rapid warming and accompanying oxygen loss contributed to the largest mass extinction in Earth’s history due to the widespread loss of aerobic habitat (Penn et al., 2018). In the following sections, the effects of low oxygen conditions on some important taxa and marine ecosystems will be illustrated for a better understanding of the topic.

### **Effects on marine fishes**

Research on the effects of low oxygen conditions to fish species date back to the last century. Low oxygen directly affects fish physiology. Thus, fish must either escape from low oxygen or suffer the consequences of reduced oxygen. The physiological responses of fishes to low oxygen have been well investigated under laboratory experiments. Low oxygen has been found to reduce fish movement, predation, consumption, growth, reproduction, recruitment and increases mortality and vulnerability to other stressors (Pollock et al., 2007). Severe low-oxygen events could directly cause mass mortalities of sensitive species.

As large and highly mobile marine vertebrates, fish are sensitive to low oxygen and often behaviourally avoid low oxygen waters. Field observations have found that many fishes actively avoid low oxygen waters. For example, the inland

silverside (*Menidia beryllina*), whiting (*Merlangius merlangus*), dab (*Limanda limanda*), and flounder (*Platichthys flesus*) escape to well-oxygenated waters when dissolved oxygen falls (Table 1). Thus, low oxygen can drive changes in the distribution of fishes in the water column by restricting individuals to generally better-oxygenated areas.

Some fishes can benefit from low oxygen if their prey is also compelled to move into habitats that are easily exploited by predators. For example, an increase in striped bass (*Morone saxatilis*) has been observed in Chesapeake Bay, due to their prey moving into oxygenated mixed layers when bottom hypoxia occurs (Costantini et al., 2008). As such, whether the effects of low oxygen on fish populations are positive or negative can be context and species-specific.

### **Effects on coastal benthos and plankton**

The benthos at seasonally intermittent hypoxic regions is dominated by taxa like crustaceans, bivalves and gastropods, and the most dominant group is small, surface-feeding polychaetes. When exposed to intermittent hypoxia over extended periods of time, the benthic community becomes less diverse, often shifting community composition from mature, deep burrowing species to smaller species associated with the upper several centimetres of the sediment.

Field observations have found that benthic species exhibit stress behaviours when seasonal, severe eutrophication-induced bottom hypoxia occurs. It has also been observed that mobile benthos that are more vulnerable to low oxygen can escape from oxygen-deficient conditions to better-oxygenated waters. Overall, as dissolved oxygen continues to decrease, sessile benthic organisms such as coral, sponges, and worms that are unable to move or are severely limited in their mobility will experience stress, and eventually die when tolerances are exceeded (Table 1). Benthic species richness, abundance, and biomass has been found to decline sharply when oxygen is below 0.5 mg l<sup>-1</sup> (Rabalais et al., 2001b).

The effects of eutrophication-induced low oxygen on coastal and estuarine plankton include reduced growth and adult size; lower abundance; shallower vertical migration range and reduced vertical distributions, plus shifting community composition with smaller species and an increase of gelatinous zooplankton (Roman 2019). Bottom hypoxia in coastal and estuarine waters may favour smaller copepod species that have a higher surface to volume ratio. For example, increased eutrophication and hypoxic bottom waters resulted in an increase in the percentage of smaller copepod species (*Paracalanus* spp.) in the Pearl River Estuary (Shi et al., 2019). Also, low oxygen may favour gelatinous species over fish and crustaceans. For example, two kinds of gelatinous plankton, the ctenophore *Mnemiopsis leidyi* and scyphomedusan *Chrysaora quinquecirrha*, are found to be more tolerant of hypoxia than fish (Breitburg et al., 1994; Purcell et al., 2001). Field observations have found increased gelatinous zooplankton in

the Gulf of Mexico along with the expansion of water low in oxygen (Graham, 2001).

### **Effects on continental margin communities**

Oxygen-limited waters along continental shelf margins drives the distribution of hypoxia-tolerant species. For example, Levin et al. (2009) found the burrowing amphinomid polychaete (*Linopherus* sp.) exhibited high density and near complete dominance at low oxygen level (Table 1). Surprisingly, some demersal fish may tolerate even lower dissolved oxygen than some benthic invertebrates. The cusk eel (*Cherublemma emmelas*) and catshark (*Cephalurus cephalus*) can occur in near anoxic conditions (0.15 mg l<sup>-1</sup>, 0.06 mg l<sup>-1</sup> respectively) environments in the Gulf of California (Gallo et al., 2019). Some field studies reported that more than 77 demersal fish species have been found within OMZs (Gallo & Levin, 2016). How the fish stay within these low oxygen conditions is poorly known, and it is possible they go anaerobic to forage in such hypoxic areas and then return to more oxygenated waters to recover.

The mesopelagic organisms found within OMZs are unique and well-known for their adaptations to oxygen-limited conditions, including small body sizes (Gallo et al., 2019). Species can have morphological, physiological and/or behavioural adaptations to survive in low oxygen concentrations, such as increased gill surface, special respiratory proteins with high oxygen affinities, and/or decreased activity levels. Hypoxia-tolerant taxa living within OMZs include crustaceans (copepod *Rhincalanus nasutus*, euphausiid *Euphausia exima*) and fish (gonostomatid *Cyclothone signata*, myctophid *Triphoturus mexicanus*, phosichthyid *Vinciguerria lucetia*) (Brinton, 1962; Castro et al., 1993; Ekau et al., 2010; Seibel et al., 2016). Because of these adaptations, the diversity and biomass of tolerant mesopelagic communities will not significantly decrease until oxygen content approaches anoxic conditions. However, expanding OMZs and low oxygen waters will lead to habitat expansion for such hypoxia tolerant species and habitat compression for hypoxia-sensitive species, both in benthic and mesopelagic communities.

There are few time-series studies that assess the effects of reduced oxygen on the mesopelagic communities of continental margins. However, one study has reported a broad suite of mesopelagic fishes have decreased by approximately 77% in correlation with a 22% decline in midwater oxygen concentrations in the California Current (Proud et al., 2017). In contrast, the Humboldt squid (*Dosidicus gigas*) has adapted to preying on mesopelagic fishes in the hypoxia boundary layer, thus expanding its geographic range and apparent abundance (Stewart et al., 2014).

## Effects on corals

Low oxygen is an important but largely overlooked stressor on coral reefs. Some species can survive low oxygen and hypoxia conditions: the branching coral *Acropora yongei* has a lethal oxygen concentration of 4 mg l<sup>-1</sup> (Haas et al., 2014), the cold-water coral *Desmophyllum pertusum* (formerly called *Lophelia pertusa*), which can form reef in the deep-sea, thrives under relatively low O<sub>2</sub> (< 1.3 mg l<sup>-1</sup>) in the southeast Atlantic (Hebbeln et al., 2020). Altieri et al. (2017) reported that the hemispherical shallow water tropical Atlantic corals *Stephanocoenia intersepta* can survive for a week when exposed to 0.5 mg l<sup>-1</sup> oxygen. In contrast, the foliaceous coral *Agaricia lamarcki* experienced significant mortality under similar conditions (Altieri et al., 2017). Field studies suggest differential susceptibility to low oxygen between morphological coral groups, as branching and solitary species are likely more sensitive to low oxygen and suffer high mortality during severe hypoxic events, while massive, sub-massive, and encrusting species are likely less affected (reviewed by Hughes et al., 2020).

## Conclusion

Exposure of marine species to low oxygen can alter behaviour, reduce growth, and cause mortality. The expansion of low oxygen waters due to climate change driven ocean warming may reduce available oxygenated habitats for most marine organisms. This will potential shift the spatial distribution of organisms by favouring low oxygen tolerant species and excluding sensitive ones.

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Table 1. Examples of behavioural responses of marine species to low oxygen.

Low oxygen threshold (mg l <sup>-1</sup> )	Species	Response	Reference
4.7	Inland silverside ( <i>Menidia beryllina</i> )	Escape from low oxygen waters to better oxygenated waters	Weltzien et al., 1999
4	Branching coral <i>Acropora yongei</i>	Survive in low oxygen	Haas et al., 2014
3	Whiting ( <i>Merlangius merlangus</i> )	Escape from low oxygen waters to better oxygenated waters	Pollock et al., 2007
2	Blue crab ( <i>Callinectes sapidus</i> Rathbun)	Escape from low oxygen waters to better oxygenated waters	Pihl et al., 1991
1.8	Dab ( <i>Limanda limanda</i> ) and flounder ( <i>Platichthys flesus</i> )	Escape from low oxygen waters to better oxygenated waters	Pollock et al., 2007
1.3	Cold-water coral <i>Desmophyllum pertusum</i>	Thrive under relatively low oxygen	Hebbeln et al., 2020
1	Gastropods ( <i>Oliva sayana</i> , <i>Terebra</i> sp., <i>Solenosteira cancellaria</i> , <i>Distorsio clathrata</i> )	Move through the surface sediments with their siphons extended directly upward	Rabalais et al., 2001a
0.5	Foliaceous coral <i>Agaricia lamarcki</i>	Mass mortality in low oxygen condition	Altieri et al., 2017
0.5	Tropical Atlantic corals <i>Stephanocoenia intersepta</i>	Survive for a week when exposed to low oxygen	Altieri et al., 2017
0.2	Portunid crabs ( <i>Callinectes similis</i> , <i>C. sapidus</i> , <i>Achelous gibbesii</i> ) rock shrimp ( <i>Sicyonia brevirostris</i> , <i>S. dorsalis</i> )	Aggregate at the surface water when bottom waters were severely hypoxic	Rabalais et al., 2001a
0.16	Amphinomid polychaete ( <i>Linopherus</i> sp.)	Exhibited high density and near complete dominance at low oxygen	Levin et al., 2009
0-0.2	Bacterial mats ( <i>Beggiatoa</i> sp.)	Patches of white bacterial mats cover the sediment surface	Rabalais et al., 2001a

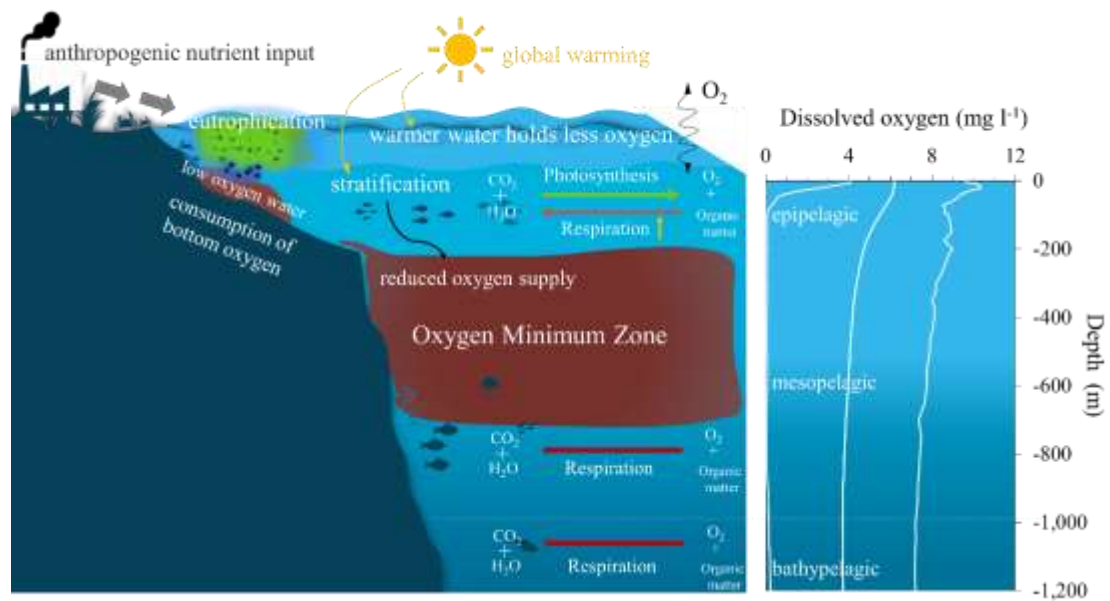


Fig. 1. Causes of ocean deoxygenation and depth profile of dissolved oxygen in the ocean. From left to right in the depth profiles are the minimum, average, and maximum dissolved oxygen redrawn after Costello & Breyer (2017).

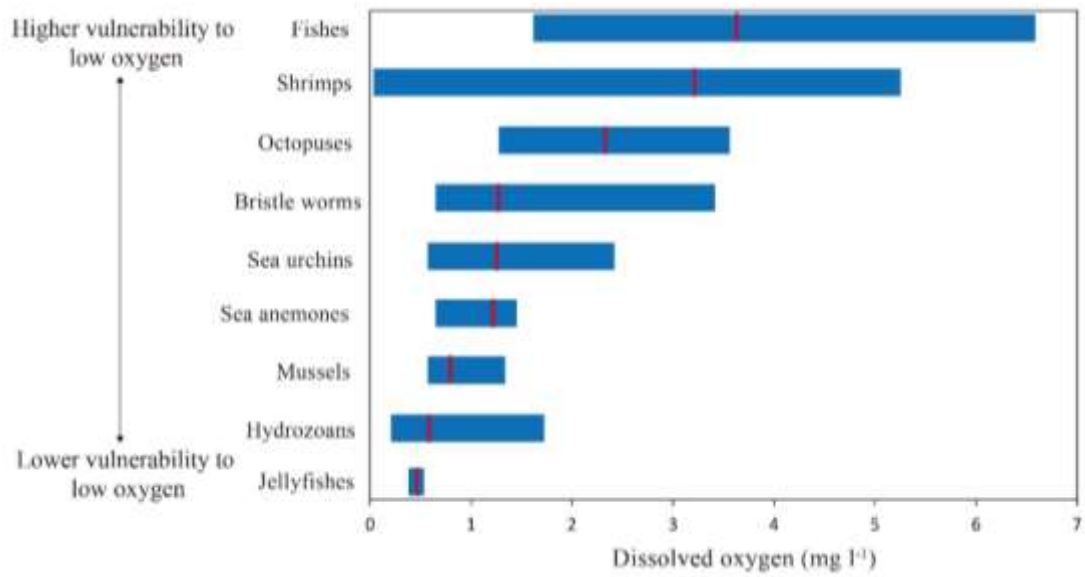


Fig. 2. Median (red line) and range (blue bar) of low oxygen thresholds (including sub-lethal and critical oxygen concentrations) among different kinds of marine species. Data from Pollock et al. (2007) (fish only) and Vaquer-Sunyer & Duarte (2008).

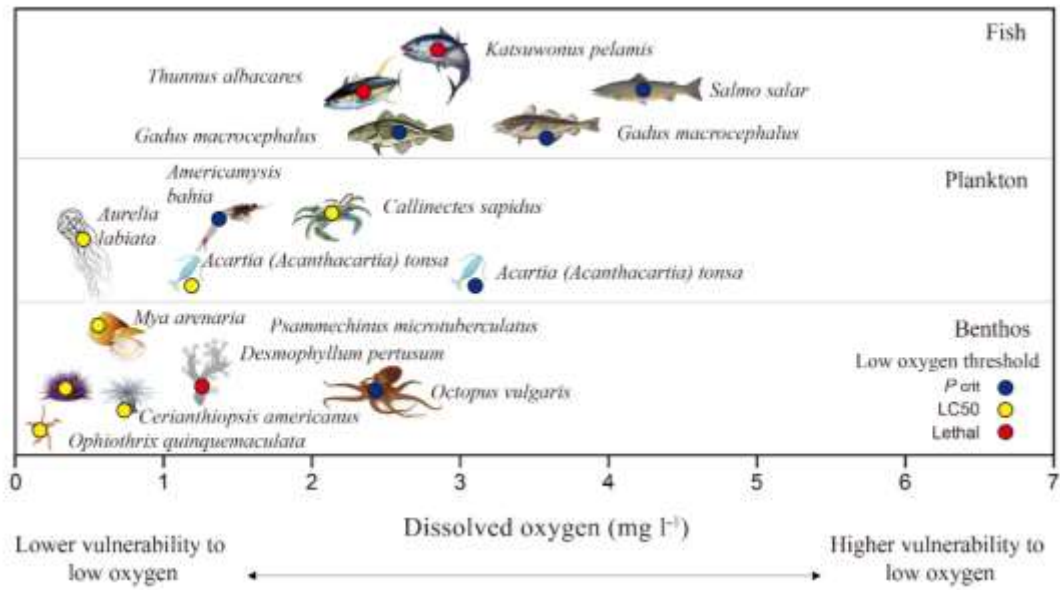


Fig. 3. Schematic indicating low oxygen thresholds of representative marine fish, plankton, and benthos. Data from Elliott et al. (2013), Goodman & Campbell (2007), Lehodey et al. (2011), Miller et al. (2002), Pihl et al. (1991), Plante et al. (1998), Remen et al. (2013), Riedel et al. (2012), Schurmann & Steffensen (1992), and Vaquer-Sunyer & Duarte (2008).

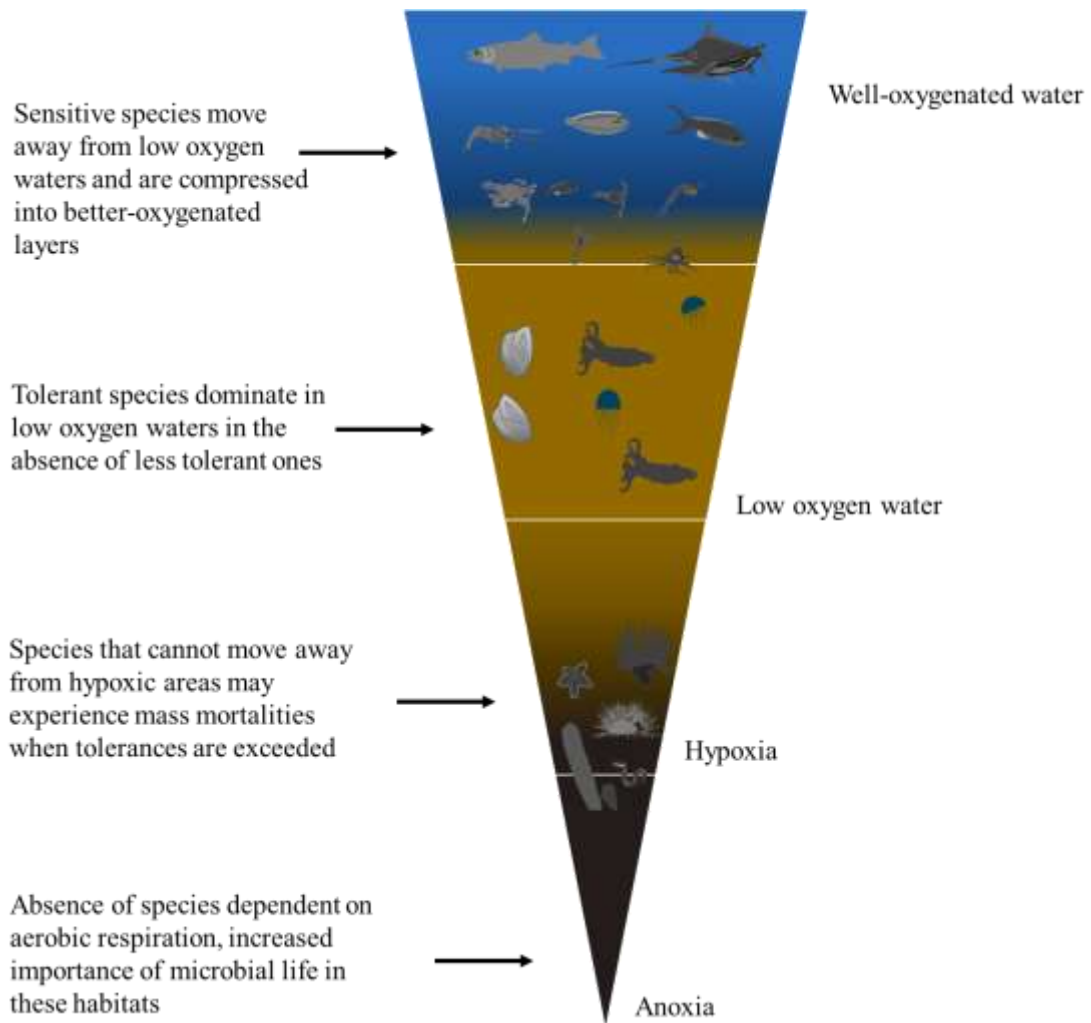


Fig.4. Diagram showing expansion of low oxygen water, and resulting compressed habitat, reduced biodiversity, and altered composition and distribution of marine organisms.

