IUCN

Ocean deoxygenation: Everyone's problem

Causes, impacts, consequences and solutions

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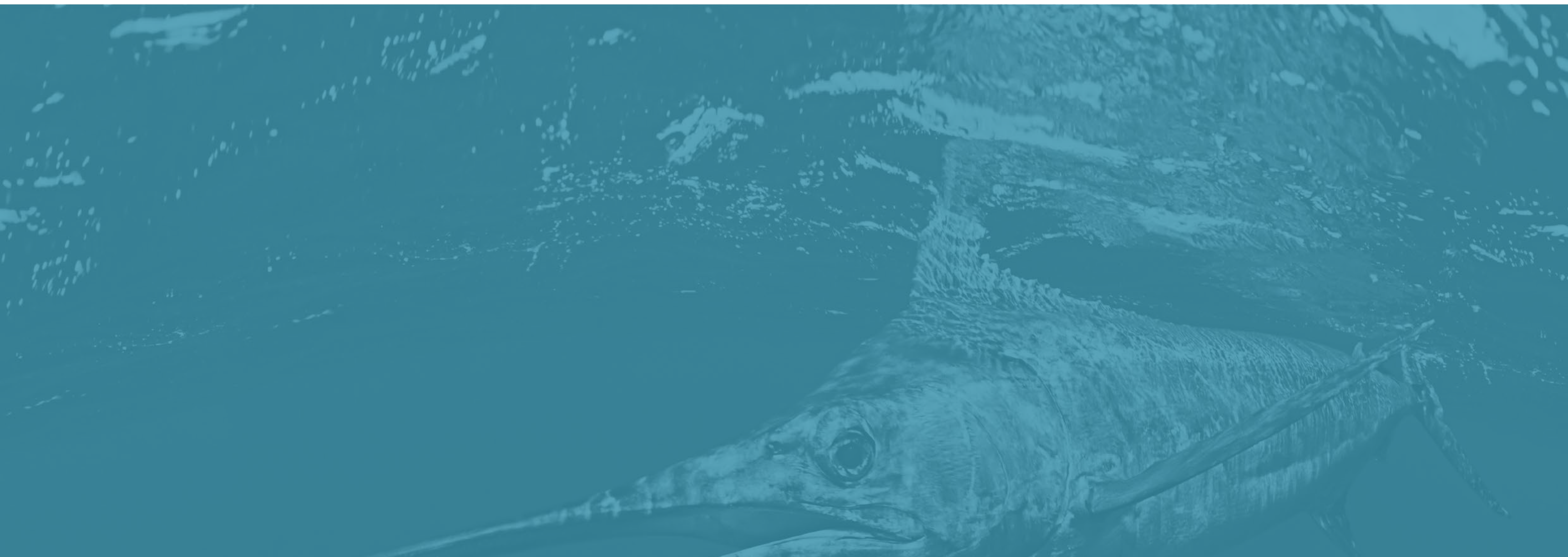

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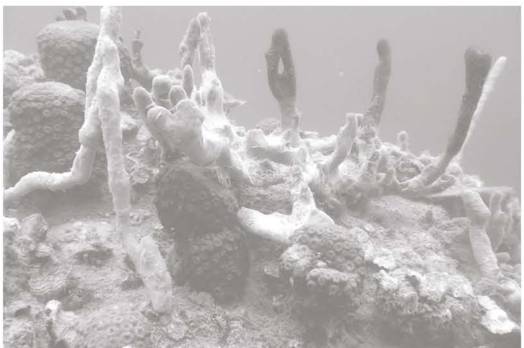

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Intergovernmental Oceanographic Commission

Sustainable Development Goals

8.4 The significance of ocean deoxygenation for continental margin mesopelagic communities

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Summary

- Global climate models predict global warming will lead to declines in midwater oxygen concentrations, with greatest impact in regions of oxygen minimum zones (OMZ) along continental margins. Time series from these regions indicate that there have been significant changes in oxygen concentration, with evidence of both decadal variability and a secular declining trend in recent decades. The areal extent and volume of hypoxic and suboxic waters have increased substantially in recent decades with significant shoaling of hypoxic boundary layers along continental margins.
- The mesopelagic communities in OMZ regions are unique, with the fauna noted for their adaptations to hypoxic and suboxic environments. However, mesopelagic faunas differ considerably, such that deoxygenation and warming could lead to the increased dominance of subtropical and tropical faunas most highly adapted to OMZ conditions.
- Denitrifying bacteria within the suboxic zones of the ocean's OMZs account for about a third of the ocean's loss of fixed nitrogen. Denitrification in the eastern tropical Pacific has varied by about a factor of 4 over the past 50 years, about half due to variation in the volume of suboxic waters in the Pacific. Continued long-term deoxygenation could lead to decreased nutrient content and hence decreased ocean productivity and decreased ocean uptake of carbon dioxide (CO_2). Deoxygenation could also lead to increased oceanic release of nitrous oxide (N_2O), a powerful greenhouse gas that is microbially produced in suboxic conditions.
- There are few time series to evaluate the impact of declining oxygen on the mesopelagic fauna of continental margins. However, in the California Current a broad suite of mesopelagic fishes has declined ~77%, highly correlated with a 22% decline in midwater oxygen concentrations. Several tropical-subtropical taxa noted for their adaptations to hypoxic conditions have increased in dominance. The Humboldt squid, adapted to preying on mesopelagic fishes in the hypoxic boundary layer, has dramatically increased its range and apparent abundance. Mesopelagic micronekton is a key trophic link between the zooplankton and a variety of predators: squids, tunas, sharks and other fishes, and a number of marine mammals and seabirds of special conservation interest, so a widespread decline in mesopelagic fishes could have profound consequences for global marine ecosystems and fisheries.

Ocean hypoxia effect	Potential consequences
Decreasing oxygen concentrations, expansion of suboxic and hypoxic waters.	• Biogeochemical consequences: increased denitrification, leading potentially to loss of nitrate and decreased ecosystem productivity. • Possible increased N_2O production, a powerful greenhouse gas, a positive feedback to global warming.
Shoaling of oxygen minimum zones and hypoxic boundary layers.	• Potential shoaling of deep scattering layers, leading to possible increased predation risk and declining abundance; decreased carbon sequestration by diel migrators. • Possible shifts in micronekton community composition toward taxa better adapted to suboxic conditions. • Range expansion of predators, such as Humboldt squid, adapted to hypoxia.
Decreased abundance of mesopelagic micronekton not adapted to more extreme hypoxic and suboxic conditions.	• Decreased prey available to a wide range of higher predators: fishes, squids, marine mammals and seabirds.

8.4.1 Introduction

Oxygen is a critical variable for the survival of marine organisms and as a determinant of the distribution and structure of marine communities. Declining oxygen concentrations are now a major issue in two somewhat distinct habitats: coastal waters subject to nutrient input from the land and hence to eutrophication and development of so-called "dead zones", and along continental margins in regions of high productivity and relatively sluggish circulation, which includes the major eastern boundary currents (EBC) and associated tropical oceans in the eastern Pacific, south-eastern Atlantic and northern Indian Oceans (Helly & Levin, 2004; Stramma et al., 2008) (Figure 8.4.1). The oxygen minimum zones (OMZ) in these regions along the continental margin are generally concentrated at mesopelagic depths, defined as 200 to 1000 m depth, where organic material settling out of the euphotic zone is predominantly consumed and metabolized (Robinson et al., 2010).

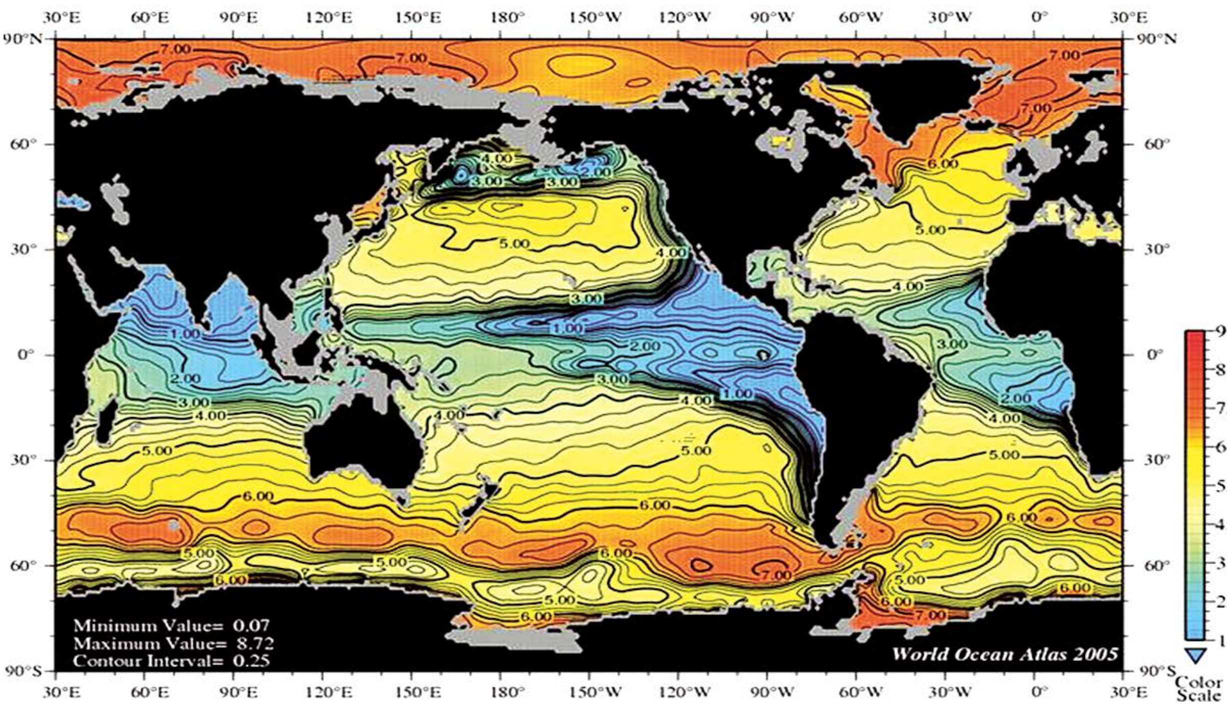

Figure 8.4.1 Annual mean oxygen concentration in ml L^{-1} at 200 m depth, showing the distribution of major OMZs in the tropical Atlantic, Pacific and Indian Oceans and along the major eastern boundary currents. From the World Ocean Atlas (2005).

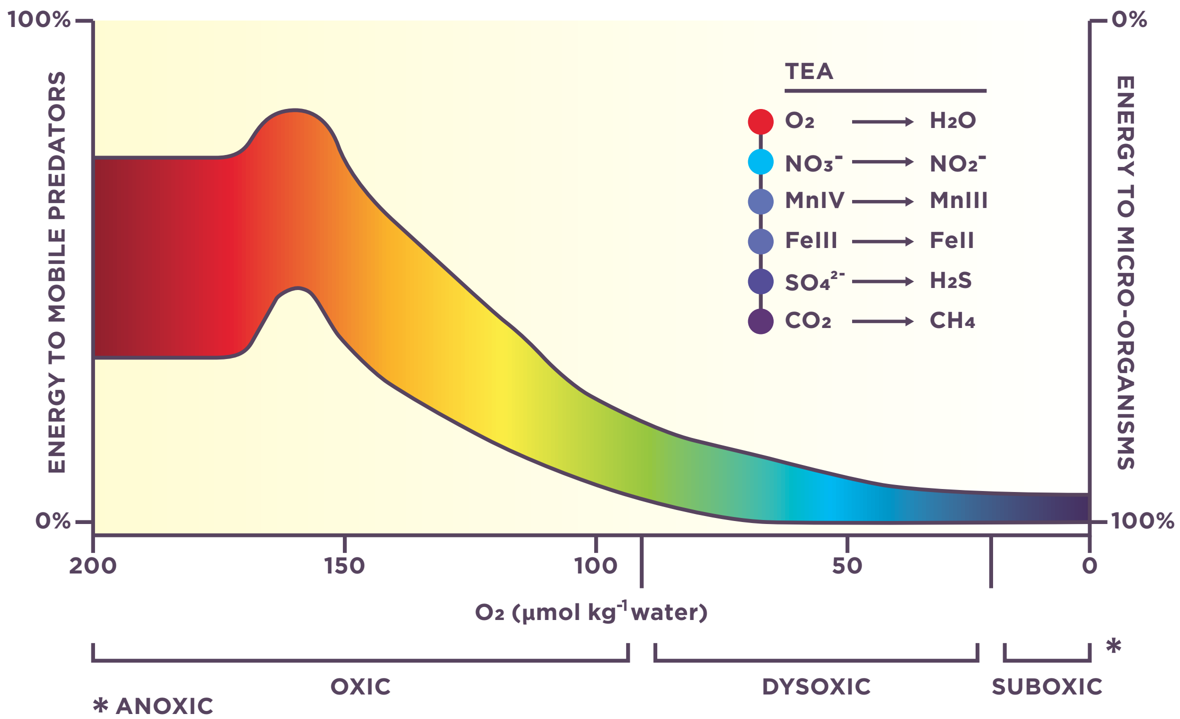

Figure 8.4.2 Oxic, dysoxic (or hypoxic) and anoxic states of the ocean are defined in relation to oxygen concentration, along with the dominant energetic pathways at each state. From Wright et al. (2012).

Oxygen concentrations < 2 ml O_2 L^{-1} are commonly defined as *hypoxic*, although many fishes, crustaceans and other metazoans exhibit physiological responses to oxygen concentrations considerably higher than this (Vaquer-Sunyer & Duarte, 2008). *Suboxic* conditions are often defined as oxygen concentrations < 0.1 ml O_2 L^{-1}, when microbial metabolism becomes predominantly anaerobic (Deutsch et al., 2011), whereas *anoxia* refers to the complete absence of oxygen (Figure 8.4.2). Classically, suboxia has been used as the criterion for determining the extent of OMZs (Paulmier & Ruiz-Pino, 2009), but higher organisms are strongly influenced by hypoxic conditions, so these waters will be considered in this review. Furthermore, there is considerable variation in the literature in defining the limits of hypoxia, suboxia, and OMZs, in large measure because organisms vary widely in their response to low-oxygen conditions (Vaquer-Sunyer & Duarte, 2008). OMZs are estimated to cover more than 1 million km^2 on the continental margins of the world ocean, defined as waters with oxygen concentration < 0.5 ml L^{-1} (Helly & Levin, 2004). On a volumetric basis, hypoxic waters are estimated to occupy 5% of the ocean's volume but are pervasive in the eastern Pacific and northern Indian Ocean between 100 and 1000 m depth (Deutsch et al., 2011), with a somewhat smaller, less intensely hypoxic zone in the upwelling regions of the eastern tropical Atlantic Ocean (Figure 8.4.1).

Deoxygenation of the global ocean is commonly predicted by global ocean climate models as the consequence of a decrease in oxygen solubility and deep-water ventilation in a warmer, more stratified ocean (Gruber, 2011; Keeling et al., 2010; Matear & Hirst, 2003; Oschlies et al., 2008). These predictions are consistent with the contraction and expansion of OMZs observed (based on proxies) during glacial-interglacial periods in the past 200 kyr (Falkowski et al., 2011; Galbraith et al., 2004), although the relationship may not be straightforward (Jaccard & Galbraith, 2012). However, recent climate models appear to underestimate the extent of deoxygenations due to climate warming, with projections of a 2-4% loss in oceanic oxygen content from 1870 to 2100 (Bopp et al., 2013; Levin, 2018). However, syntheses of global observations indicate an average 2% global loss of oxygen in the open ocean over just the past 50 years (Helm et al., 2011; Schmidtko et al., 2017), with substantially greater losses, in the order of 20%, in the eastern tropical Pacific, the North Pacific, and Southern Ocean (Levin, 2018) (Figure 8.4.3). The largest trends are often observed in the naturally oxygen-depleted OMZs along continental margins, where oxygen concentrations are at threshold levels for many organisms. The volume of anoxic water has quadrupled and the area of ocean with hypoxic water (< 1.5 ml O_2 L^{-1}) at 200 m depth has increased by 4.5 million km^2, an area roughly the size of the European

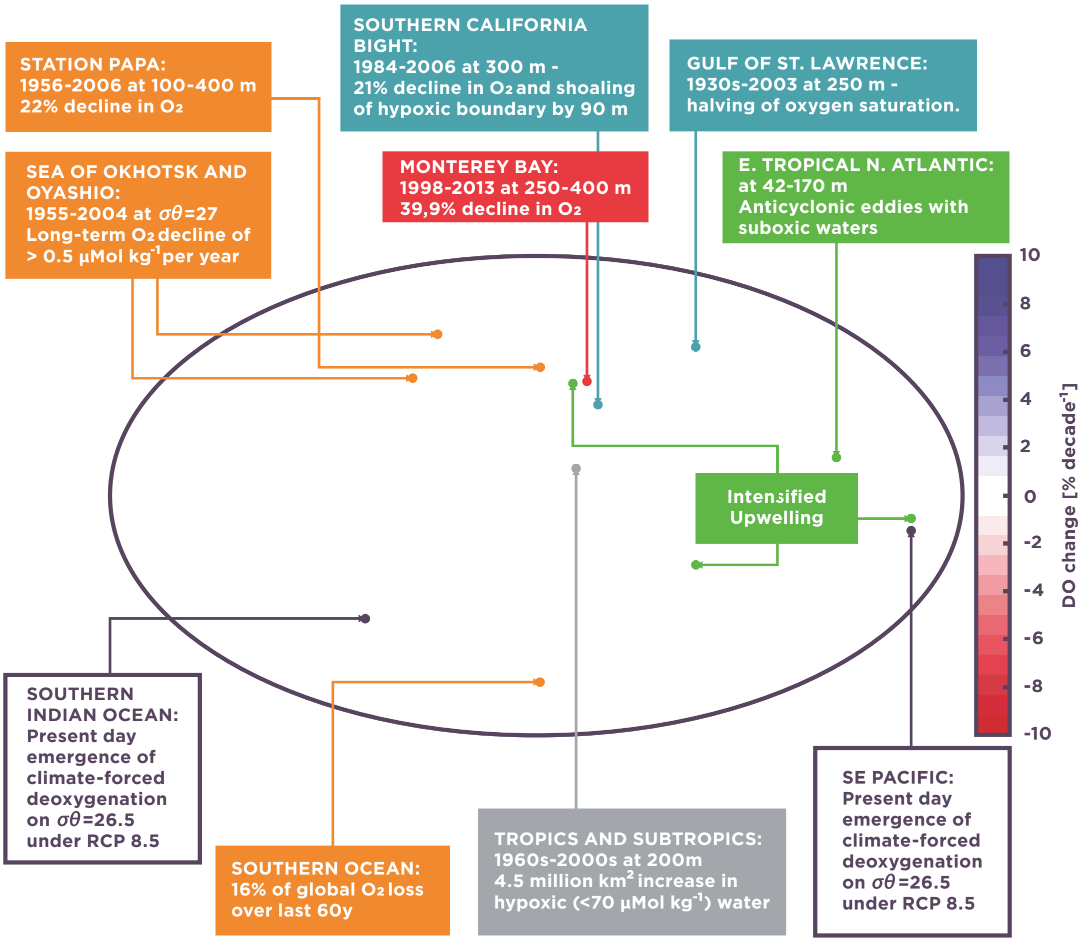

Figure 8.4.3 Summary findings of the primary long-term records of open ocean deoxygenation at mesopelagic depths superimposed on the percentage change in dissolved oxygen per decade since 1960 (from Schmidtko et al., 2017). The colour of the text boxes indicates the potential primary drivers: orange: solubility and stratification; red: oxygen decline in source waters; blue: circulation-driven changes; green: intensified upwelling; grey: uncertain causes; white: climate warming impact apparent due to low natural variability. Abbreviations: σθ, density surface; RCP, representative concentration pathway. From Levin (2018).

Union, over the past 50 years (Beitburg et al., 2018). Over this period, the hypoxic boundary layer (HBL) has shoaled approximately 100 m in the Gulf of Alaska and southern California Current, where midwater oxygen time series extend back more than 50 years (Bograd et al., 2008; Whitney et al., 2007).

Marine metazoans generally exhibit strong oxygen-level constraints, so it is expected that declining oxygen levels and the expansion of zones with critical oxygen levels will have significant impacts on the physiology, distribution, abundance and general ecology of the marine fauna in these regions (Ekau et al., 2010; Stramma et al., 2010; Vaquer-Sunyer & Duarte, 2008).

As Gruber (2011) notes, the ocean today faces a triad of threats: acidification, warming, and deoxygenation. These are linked causally – CO_2 build-up causes both global warming and ocean acidification and warming in turn leads to deoxygenation – and they may also work synergistically in their ecological impacts. Deoxygenation and acidification also tend to be correlated in the ocean, since oxygen consumption by marine organisms produces CO_2 that in turn leads to a decline in ocean pH. However, each of these stressors has its own unique physiological and ecological impacts. This review will focus on the impact of deoxygenation, while noting potential synergistic impacts.

8.4.2 Definition of species groups

In considering the impacts of deoxygenation on the mesopelagic fauna of continental margins, the full range of the fauna from microbes to higher predators will be considered.

Microbial activity is closely associated with oxygen content, groups with differing metabolisms being found in well-oxygenated, hypoxic and anoxic waters. At suboxic concentrations ($[O_2] < 0.1$ ml L^{-1}) anaerobic processes dominate, such as denitrification and anaerobic ammonium oxidation. These processes in the OMZs are responsible for removing about a third of the fixed nitrogen in the global ocean, the remainder occurring in the anaerobic sediments (Sarmiento & Gruber, 2006). In nutrient-depleted ocean waters, certain photosynthetic cyanobacteria, such as *Trichodesmium* and *Prochlorococcus,* are able to fix atmospheric nitrogen (N_2) to ammonium and are responsible for approximately half of the ocean's photosynthetic production. However, the ocean's nitrogen cycle is in approximate balance, so an equivalent amount of nitrate and ammonium is converted back to gaseous nitrogen. This microbially-mediated process occurs only under suboxic conditions, either in the water column in OMZs or within the sediments.

This review will focus on the zooplankton, micronekton and nekton, particularly those mesopelagic taxa (principally crustaceans, squids and fishes) that interact with low-oxygen waters and are impacted by them. These groups are defined primarily along a size spectrum, with the zooplankton ranging in size from approximately 2 mm to 2 cm. As their name implies, they are largely advected by the ambient currents, although they are able to migrate on a diel or seasonal basis to depths of several hundred metres or more. The micronekton (roughly 2 – 20 cm in length) are dominated by small fishes, with squids and larger pelagic crustaceans comprising a significant fraction (Figure 8.4.4). They feed predominantly at the second trophic level and are able to carry out diel migrations of several hundred to 1000 m. The nekton (0.2 – 2 m) consist predominantly of fish and squid, predators on the micronekton.

The mesopelagic fauna is highly diverse with three-fold more mesopelagic than epipelagic fish taxa in the global ocean (Koslow, 2007) (Figure 8.4.5). The most diverse family of mesopelagic fishes are the myctophids or lanternfishes (Figure 8.4.6), with some 240 species (Nelson, 2006). They are plankton feeders, but unlike the silvery plankton feeders in epipelagic waters (e.g. sardines, anchovies, mackerels), myctophids are highly adapted to life in the so-called "twilight zone," with dark skins, large eyes, and numerous photophores or light organs (hence their name, "lanternfish"). However, the mesopelagic fauna encompasses a range of ecological and physiological strategies. A key family of mesopelagic fishes, the hatchetfishes (Figure 8.4.7), mostly inhabits the upper mesopelagic zone above ~500 m depth and typically has reflective scales as camouflage in these better-lit waters and has upward-directed eyes and mouth to pick out its prey against the downwelling light. On the other hand, one of the most abundant vertebrates on the planet, the fish *Cyclothone,* typically inhabits the deeper mesopelagic and bathypelagic, and its eyes are highly reduced (Figure 8.4.8).

The mesopelagic micronekton largely comprises the Deep Scattering Layer (DSL), so-called for its distinct signature on echo sounders. This is often, but not necessarily, associated with the HBL above the core of the OMZ and is noted for its diel migration into near-surface waters to feed at night (Bianchi et al., 2013; Netburn & Koslow, 2015) (Figure 8.4.9). However, a significant proportion of the DSL remains permanently at depth (Williams & Koslow, 1997), and these groups have markedly different physiological and life history strategies (Childress et al., 1980). Many lanternfishes are among the diel migrators whereas *Cyclothone* and hatchetfishes are generally among the non-migrators. In regions with the most strongly developed OMZ, where hypoxic waters may extend to within 200 m of the surface, a specialized mesopelagic fauna has evolved

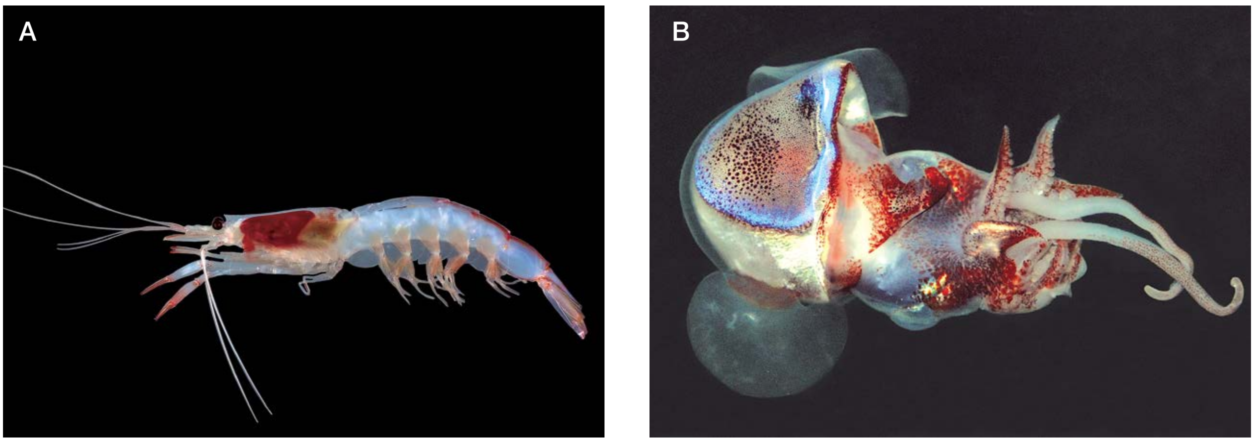

Figure 8.4.4 A) *Pasiphaea* sp. - a decapod shrimp; B) *Stoloteuthis* sp. - a bobtail squid. © Alex Rogers IUCN/NERC Seamounts Project.

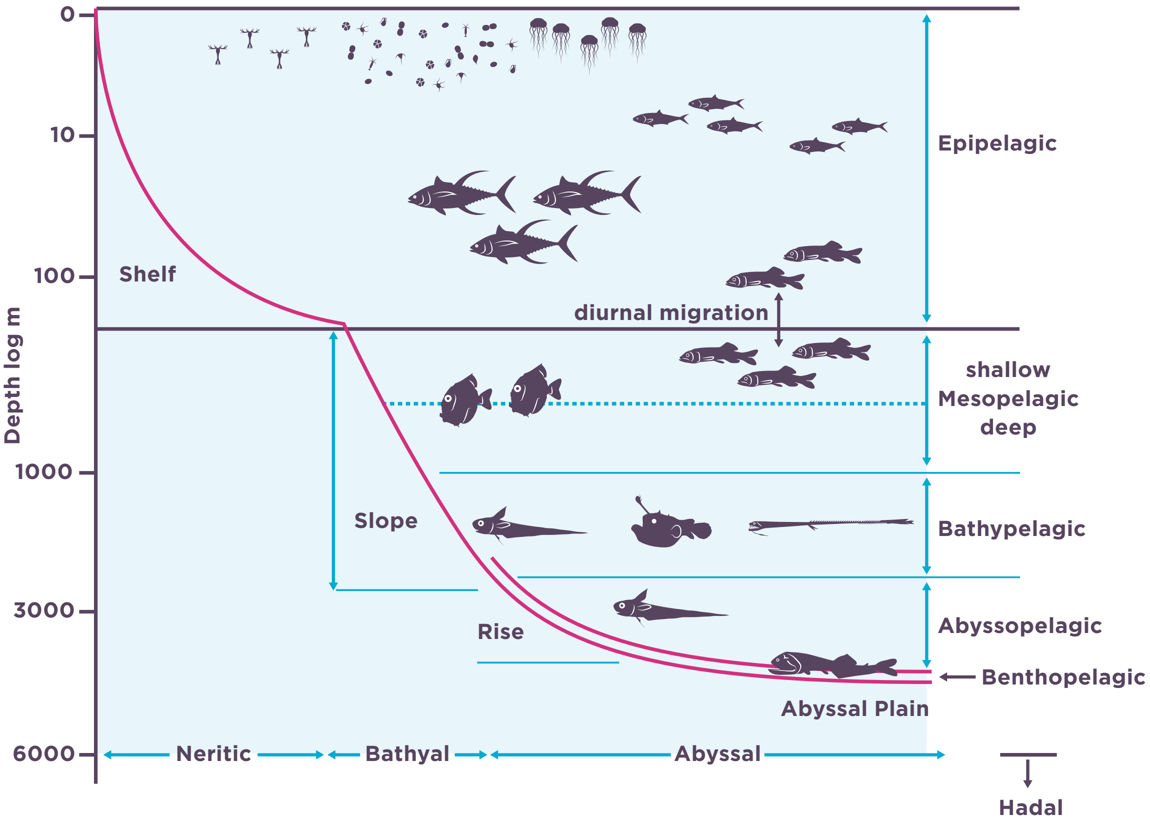

Figure 8.4.5 Schematic showing the zonation of pelagic and benthic faunas through the water column.

capable of descending into suboxic and anoxic waters during the day and migrating to the surface at night to re-oxygenate and feed (Childress & Seibel, 1998; Seibel, 2011). There does not appear to be a resident metazoan community in anoxic waters. However, mesopelagic zooplankton may be associated with the lower boundary of the OMZ as well as the upper boundary (Wishner et al., 2013).

8.4.3 Trends and impacts

8.4.3.1 Microbial communities

The mesopelagic zone has been termed the biogeochemical engine for the world's ocean: ~90% of the organic carbon that is exported from near-surface waters is consumed and metabolised back to CO_2 there, accounting for about 30% of the ocean's total CO_2 production (Robinson et al., 2010). A significant but still uncertain proportion of this water-column metabolism is carried out by the zooplankton and micronekton, but the bulk is generally considered to be carried out by the microbial community. The composition and metabolic functioning of the water-column microbial community is sensitive to ambient oxygen concentrations, with respiration dominated by dissolved oxygen where its concentration is greater than 10 - 20 µmol O_2 kg^{-1} sea water (= 0.25 – 0.5 ml O_2 L^{-1}), since oxygen provides the greatest free energy yield, followed progressively by nitrate (NO_3), manganese, iron, sulphate, and finally CO_2 (Figure 8.4.2; Wright et al., 2012).

These latter forms of microbial metabolism occur predominantly in the ocean's OMZs. Denitrification, the conversion of nitrate (NO_3), a key nutrient, to nitrite (NO_2) and then to gaseous nitrous oxide (N_2O) and finally

Figure 8.4.6 Lanternfish *Lepidophanes guentheri.* Note its various types of light organs, including photophores along its ventral surface that provide countershading so it can be seen less easily from below against downwellinig light and its "flashlight" organs in front of its eyes. © Solvin Zankl / Alamy stock photo.

Figure 8.4.7 A hatchetfish, *Agryropelecus affinis.* Inhabiting the upper mesopelagic, it has reflective scales and upward-directed eyes and mouth to detect prey overhead against the downwelling light. © Paulo Oliveira / Alamy stock photo.

molecular nitrogen (N_2) is particularly critical to oceanic biogeochemistry, because it involves loss of NO_3, a limiting nutrient, from ocean waters, which must be balanced by nitrogen fixation if oceanic productivity is not to decline. The production of N_2O is also of interest because it is a powerful greenhouse gas, some 300-fold more powerful than CO_2. The ocean accounts for about a third of natural N_2O emissions, much of which comes from the OMZs and HBLs. Expanding and shoaling pools of hypoxic and suboxic water could increase the ocean's production and release of N_2O (Codispoti, 2010). The OMZs account for approximately a third of the ocean's loss of fixed nitrogen (Sarmiento & Gruber, 2006).

Modelling studies indicate that the annual rate of denitrification in the eastern tropical North Pacific has varied by a factor of 4 over the past 50 years. About half of this is due to a two-fold variation in the volume of suboxic water in the Pacific, with the other half due to changes in microbial metabolism related to basin-scale variation in the depth of the thermocline, which affects microbial metabolism through the availability of organic matter (a shoaling suboxic layer contains more organic matter) and the influence of temperature on metabolic rates (Deutsch et al., 2011). Deutsch et al. (2014) use the $\delta^{15}N$ signal in sediment cores from anoxic basins off southern and Baja California to reconstruct a time series for denitrification in the California Current since 1850. (Denitrification preferentially removes the lighter ^{14}N isotope leaving behind nitrate enriched in ^{15}N, which is taken up by the phytoplankton and subsequently deposited in seafloor sediments.) The time series indicates that the OMZ and denitrification declined for much of the 20th century, prior to their expansion at the end of the century. This is linked to decadal

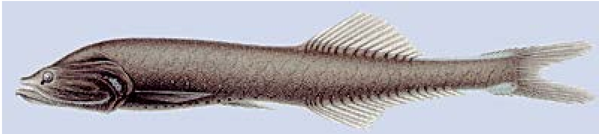

Figure 8.4.8 *Cyclothone acclinidens,* an abundant fish of the lower mesopelagic and bathypelagic with dark pigmentation and reduced eyes. © Welter-Schultes.

cycles in the intensity of the trade winds, which drive upwelling, productivity, and thermocline depth. This work indicates that variability in the trade winds, surface productivity and the depth of the thermocline, all of which influence oxygen consumption through microbial metabolism, may be as important as climate warming in their influence on oceanic oxygen concentration. Over the past several hundred thousand years, however, there has been a close correspondence between the $\delta^{15}N$ signal and glacial-interglacial cycles, with greater denitrification and apparently enhanced OMZs during periods of warming and contraction of OMZs during cooler periods. The trend over recent decades has been toward an expansion of the ocean's suboxic volume and hence greater denitrification. The potential long-term impact of this trend is a decline in the nitrate content of the world's ocean; as a key limiting nutrient, decreased nitrate could lead to a decrease in marine productivity and decreased uptake of carbon by the global ocean. Whether decreased nitrate regeneration in the ocean might be compensated by changes in oceanic nitrogen fixation remains unknown. Also uncertain are the relative impacts and interactions of trade wind/thermocline variability and climate warming on the pools of suboxic and hypoxic waters in the OMZs and HBLs of the world ocean, given that the tropical OMZs appear most sensitive to varying thermocline depth and its influence on microbial metabolism, whereas the extra-tropical HBLs may be most influenced by the effect of warming on oxygen solubility and water-column stratification, which inhibits the mixing of oxygen into deeper waters.

8.4.3.2 Zooplankton

Crustacean zooplankton, such as copepods and euphausiids, often carry out diel vertical migrations to avoid predators. Like fish, these crustaceans have varying tolerance for hypoxia: some taxa show little tolerance while others undergo metabolic suppression on the order of 40-80% and are able to vertically migrate in and out of hypoxic water in regions with a shallow HBL, such as the eastern Tropical Pacific or Humboldt Current (Seibel et al., 2016; Wishner et al., 2013). A distinct assemblage of crustaceans is also notable in

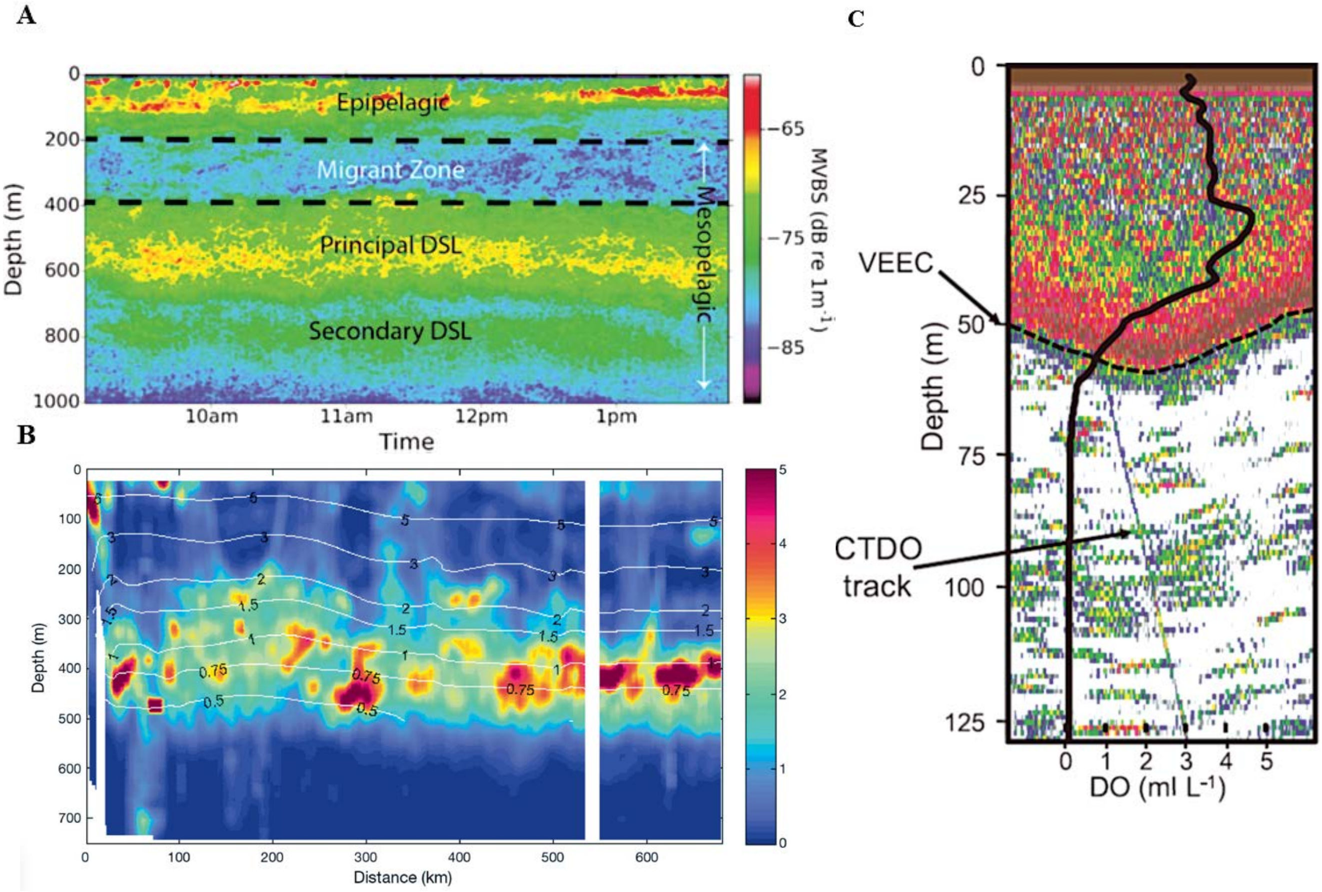

Figure 8.4.9 A) Echogram from the south-west Indian Ocean (28.8ºS, 47.3ºE). The colour bar is mean volume backscattering strength (MVBS, dB re 1 m^{-1} (from Proud et al., 2017). B) Composite daytime echogram from 6 onshore-offshore transects of a CalCOFI cruises off southern California, with isolines of oxygen concentration (in ml O_2 L^{-1}). (From Koslow et al., 2011). C) Echogram from off Peru showing the vertical extent of anchovetta in relation to dissolved oxygen concentration. (From Bertrand et al., 2010.).

forming a secondary peak in biomass in the oxycline at the base of the OMZ (Saltzman & Wishner, 1997; Wishner et al., 1995, 2013). Although pteropods have been considered prime candidates to be affected by ocean acidification because of their aragonite shells, the physiology of pteropod taxa that migrate into the OMZ, unlike that of non-migrators, does not appear to be affected by elevated CO_2 (i.e. acidity) levels, presumably because they naturally encounter comparable conditions in the OMZ (Maas, 2012). However, while various authors have speculated how deoxygenation may affect crustacean or pteropod zooplankton (Ekau et al., 2010; Seibel et al., 2016; Stramma et al., 2010) (Figure 8.4.10), no studies have linked zooplankton time series of abundance with changing oxygen conditions.

Gelatinous zooplankton appear to be less stressed by hypoxic conditions than fishes and crustaceans, and several authors have speculated that jellyfish and ctenophore blooms may be facilitated by hypoxic conditions, as well as by other anthropogenic perturbations, such as overfishing (Purcell et al., 2013; Richardson et al., 2009). Mesopelagic gelatinous plankton are typically too fragile to be sampled with nets and were very poorly known before developments in underwater video technology revealed that they play a major role in mesopelagic ecology (Robison, 2004) (Figure 8.4.11). However, time series of gelatinous zooplankton are few and often flawed, and the issue of current trends in their abundance remains uncertain (Condon et al., 2012).

8.4.3.3 Micronekton

Oxygen concentration is a critical factor influencing the physiology, behaviour, and ecology of metazoans within the mesopelagic. Although mass mortality events due to low-oxygen conditions are not observed offshore as in coastal regions (e.g. Chan et al., 2008), active swimming activity and high-cost physiological functioning, such as vision, are impaired at low oxygen concentrations (McCormick & Levin, 2017).

Figure 8.4.10 Deep-sea pteropod *Clio recurva.* © Solvin Zankl / Alamy stock photo.

In regions without an OMZ, the micronekton are predominantly distributed in daytime in DSLs throughout the mesopelagic zone down to approximately 1000 m depth (Proud et al., 2017; Williams & Koslow, 1997). However, in regions with a deep OMZ (depths > ~500 m), a primary DSL is situated in the HBL, above the core of the OMZ (Figure 8.4.9) (Bianchi et al., 2013; Koslow et al., 2011); DSLs are largely absent from within the OMZ. Thus, organisms apparently seek refuge from predation during daylight hours utilizing the lack of both light and oxygen within the HBL, and they avoid the suboxic conditions below the HBL (Netburn & Koslow, 2015). However, where the OMZ shoals above mesopelagic depths, epipelagic organisms, such as anchovy, are tightly constrained from entering suboxic waters, but mesopelagic taxa in these regions have evolved various adaptations to such conditions and enter the OMZ during daylight hours, migrating at night into

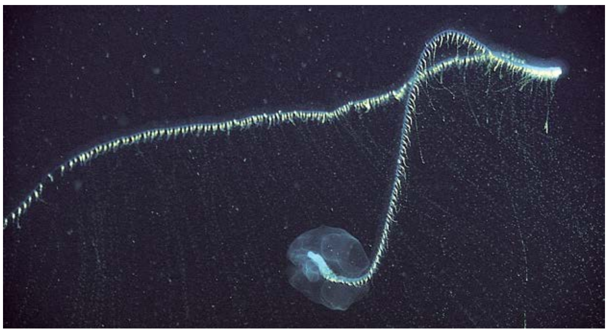

Figure 8.4.11 The mesopelagic siphonophore, *Praya dubia*, sometimes termed, "the curtain of death" can be several tens of metres in length. © S. Haddock, MBARI.

near-surface waters to oxygenate and feed (Cornejo & Koppelman, 2006).

The morphological, physiological and behavioural adaptations of mesopelagic organisms to low-oxygen conditions include increased gill area, respiratory proteins with high oxygen affinities, and the ability to reduce activity levels (e.g. observations of apparent torpor in certain myctophids (Barham, 1966)) and suppress metabolic activity (Seibel, 2011; Seibel et al., 2016). As a result of this suite of adaptations, the biomass and diversity of zooplankton and micronekton integrated through the water column is not significantly reduced until oxygen concentrations approach suboxic levels (Childress & Seibel, 1998). And while species richness can be markedly reduced in suboxic conditions, overall mesopelagic fish biomass may remain substantial (Gjøsaeter, 1984; Gjøsaeter & Kawaguchi, 1980). However, taxa differ markedly in their distributions in relation to oxic, hypoxic and suboxic waters and in their adaptations to such conditions. It should be noted that although many mesopelagic taxa conduct diel vertical migrations and can re-oxygenate at night in near-surface waters, many taxa do not, and non-migrators exhibit metabolic rates approximately an order of magnitude lower than migratory taxa (Childress et al., 1980).

Some of the dominant taxa that have evolved specialized adaptations to live within the HBL or partially within the OMZ have ranges that may extend over several water masses or biogeographic provinces where there is a contiguous OMZ. Thus, the ranges of the myctophid *Triphoturus mexicanus,* the gonostomatid *Cyclothone signata,* and the phosichthyid *Vinciguerria lucetia* extend from the southern California Current across the Eastern Tropical Pacific to the Humboldt Current (Moser, 1996). The hypoxia-tolerant euphausiid, *Euphausia exima,* and the copepod, *Rhincalanus nasutus* also follow this distributional pattern (Brinton, 1962; Castro et al., 1993; Ekau et al., 2010; Seibel et al., 2016).

There are few time series of mesopelagic fishes to assess the impacts of changing oxygen conditions on ecological time scales. However, using larval fish abundance as a proxy for spawning stock biomass, Koslow et al. (2011) report a strong correlation (r = 0.75) between mid-depth oxygen concentration and the abundance of 24 mesopelagic fish taxa, which dominated the first principal component (PC1) of the CalCOFI ichthyoplankton time series extending back to 1951. Since 1984, midwater oxygen concentrations

SECTION 8.4

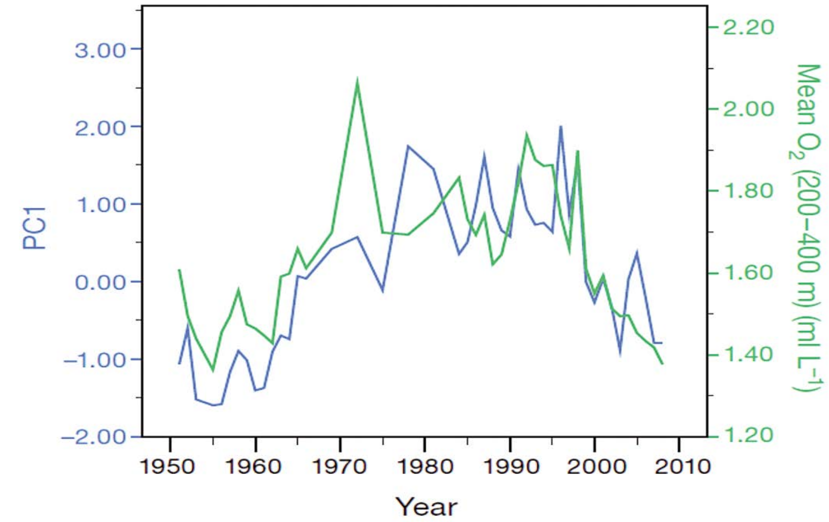

Figure 8.4.12 Time series, from the CalCOFI surveys (1951 – 2008) off southern California, of annual mean oxygen concentration at 200 – 400 m depth (green) and the first principal component (PC1) from analysis of the ichthyoplankton (blue). Twenty-four mesopelagic taxa loaded significantly on PC1. The correlation between the oxygen and PC1 time series is 0.75. From Koslow et al. (2011).

declined approximately 20%, leading to a concomitant shoaling of the OMZ by 41 m on average and up to 90 m in some regions of the Southern California Bight (Bograd et al., 2008). Over this period, the average abundance of the 24 mesopelagic fishes that loaded significantly on PC1 declined 63% (Figure 8.4.12). One hypothesized mechanism was increased predation, due to the mesopelagic fauna being more vulnerable to visual predation as the DSL followed the shoaling HBL: ambient light levels experienced by the DSL in the HBL would increase by an estimated 2.5 and 7-fold, respectively, with a 41 or 90 m shoaling of the HBL, assuming a constant light extinction coefficient with depth (Koslow et al., 2011). However, a recent study based on a circumglobal research cruise found that the depth of the DSL in the global ocean varied by about 400 m depending upon oxygen conditions (whether there was an OMZ or HBL and its depth and intensity) but that the DSL appeared to be tracking particular light levels rather than oxygen concentrations (Aksnes et al., 2017). Light extinction was significantly higher in hypoxic or suboxic waters, apparently due to bacterial production of coloured dissolved organic matter under low-oxygen conditions. The dramatic decline in abundance of mesopelagic fishes in the southern California Current (CC) may also be the result of a shift in the region's fauna. The southern CC is an ecotone, a region of mixing between two water masses and their associated mesopelagic faunas: the cool CC flowing equatorward and a warm water countercurrent extending northward from the equatorial tropical Pacific. The region has warmed in recent years, and the once-dominant cool-water mesopelagic fishes have substantially declined while warm-water taxa, such as the Mexican lampfish (*T. mexicanus*) and Panama lightfish (*V. lucetia*) have dramatically increased (Koslow et al., 2019). This suggests that warming and deoxygenation may lead to a shift in the relative distributions of mesopelagic faunas more or less tolerant of hypoxic and suboxic conditions. Whether this will lead to an overall increase or decrease in mesopelagic fish biomass is an open question: a recent study found an increase in mesopelagic fish biomass off Baja California since 1998 concomitant with declining midwater oxygen levels, primarily due to increases in warm-water affinity taxa, such as the Mexican lampfish and Panama lightfish (Koslow et al., 2019).

8.4.3.4 Nekton

There appear to be winners as well as losers as a result of a shoaling HBL. The enhanced susceptibility to predation of small planktivorous mesopelagic fishes has led to increased populations of several of their predators. Two rockfish taxa (*Sebastes goodei* and *S. diploproa*) that prey on midwater fishes were virtually the only fishes that showed a significant opposite trend to the mesopelagic fishes off southern California (Koslow et al., 2011). Most striking has been the range expansion of the jumbo or Humboldt squid (*Dosidocus gigas*) over the entire California Current since the early 2000s and the dramatic expansion of its fishery from virtually non-existent 25 years ago to becoming the largest invertebrate fishery in the world (630,000 t in 2009) (Figure 8.4.13) (Gilly et al., 2013). The Humboldt squid has a number of physiological and behavioural adaptations that support its role as a particularly

Figure 8.4.13 Humboldt squid fishery © Amanda Cotton / Alamy stock photo.

active and voracious predator on mesopelagic fishes in the HBL, including reduced rapid jetting, metabolic suppression and having a form of haemocyanin that enhances oxygen binding (Gilly et al., 2012; Rosa & Seibel, 2010; Seibel, 2011; Stewart et al., 2014). Modelling indicates that enhanced availability of mesopelagic prey due to a shoaling HBL is likely a strong driver of the Humboldt squid's range expansion (Stewart et al., 2014).

A shoaling HBL appears to enhance the foraging of other visual predators on mesopelagic fishes. Prince and Goodyear (2006) show that the foraging depth of large, active predatory fishes, such as marlin and sailfish, is restricted by the HBL. Where there is a shallow HBL, such as in the eastern tropical Pacific, these fishes are significantly larger at age than in areas where such a layer is absent, such as in the western North Atlantic, presumably because foraging is more efficient where the foraging habitat is highly restricted. On the other hand, these fishes are more vulnerable to fishing gear where their habitat is compressed.

8.4.3.5 Ecosystem consequences

The biomass of mesopelagic fishes, and hence their role in marine ecosystems and biogeochemistry, were substantially underestimated in the past when their abundance was estimated predominantly from sampling with small research trawls (e.g. Gjøsaeter & Kawaguchi, 1980). Avoidance of such samplers by midwater fishes has now been clearly demonstrated (Kaartvedt et al., 2012), and recent studies based on acoustics (or, preferably, acoustics combined with net sampling) indicate that mesopelagic fish biomass is approximately an order of magnitude higher than previously estimated (Koslow et al., 1997), in the order of 10 billion tonnes globally (Irigoien et al., 2014), approximately two orders of magnitude greater than global marine fishery landings (Pauly & Zeller, 2016). The diel vertical migration of mesopelagic fishes, which involves a large fraction of this community feeding in near-surface waters and transporting and metabolising the material at midwater depths, may contribute significantly to carbon sequestration and the global carbon cycle and, indeed, to the metabolic processes leading to the HBL (Bianchi et al. ,2013; Davison et al., 2013). A significant decline in the mesopelagic fish community due to climate warming and deoxygenation could diminish the ocean's rate of carbon sequestration, a potential positive feedback to climate warming. A shoaling of the DSL in response to a shoaling HBL could also influence carbon sequestration, since a shallower DSL increases the recycling of its metabolic and waste products at mesopelagic depths and their potential return to near-surface waters.

Mesopelagic fishes are predominantly at the third trophic level and are key consumers of zooplankton production and key prey for a variety of squids, fishes, marine mammals and birds on continental margins and in the open ocean (Beamish et al., 1999; Brodeur et al., 1999; Brodeur & Yamamura, 2005). While much of mesopelagic fish production is consumed by other mesopelagic predators, such as squids, viperfishes and dragonfishes (Sutton & Hopkins, 1996) (Figure 8.4.14), it is not surprising given their enormous biomass that they comprise a significant component of the diet of many commercial species (e.g. tunas, salmon, and walleye pollock in the North Pacific) and species of special conservation interest such as a variety of marine mammals, including elephant and fur seals and whales (Beamish et al., 1999; Brodeur et al., 1999; Brodeur & Yamamura, 2005; Cherel et al., 2008). A significant decline in this group could therefore have a significant impact on global marine ecosystem productivity.

It should be noted that the observed decline in mesopelagic fishes associated with deoxygenation off southern California is counter to the recent prediction that mesopelagic fishes globally may significantly increase by approximately 17% over the coming century (Proud et al., 2017). This prediction, based on a simple model that examined the potential impacts of a warming ocean and a shoaling DSL, failed to assess the model against observed trends (e.g. Koslow et al., 2011) that ran counter to model predictions. Although the paper proposed a model for the biogeography of the global ocean's mesopelagic zone, there were no data from any of the ocean's major eastern boundary currents, OMZ regions or the northern North Pacific Ocean.

Few studies have examined changes in the biodiversity of mesopelagic communities in relation to deoxygenation. In the southern California Current, species richness in the CalCOFI ichthyoplankton time series was most closely correlated with the diversity of the mesopelagic community, which was in turn significantly correlated with temperature, due to the influx of the highly diverse warm-water affinity (tropical-sub-tropical) mesopelagic fauna during relatively warm periods (Koslow et al., 2017).

This influx of tropical-subtropical affinity mesopelagic fishes (e.g. *V. lucetia* and *T. mexicanus*) adapted to a shallow HBL has increased dramatically off southern California in recent years. Comparing the period 2011 – 2015 with the period prior to 2004, overall larval fish abundance declined by almost 50% due to the decline in cool-water dominant taxa, but the abundance of warm-water mesopelagic taxa increased 73%. The rank-order of abundance of the two most abundant warm-water affinity mesopelagic fishes, the Panama lightfish and Mexican lampfish, rose from 10 and 19 to six and seven, respectively, between these periods. The tropical-subtropical fish taxa that dominate the mesopelagic fish community in the region from Baja California to the northern Humboldt Current off Peru are thus becoming increasingly dominant off southern California as the OMZ there has shoaled (Koslow et al., 2019). These trends are consistent with predictions

Figure 8.4.14 (A) Sloane's viperfish *Chauliodus sloani* © Paulo Oliveira / Alamy stock photo; (B) Scaleless black dragonfish *Melanostomias biseriatus* © Nature Picture Library / Alamy stock photo.

based on palaeo-oceanographic patterns, that growing hypoxia will be associated with the increased dominance of fishes particularly well adapted to such conditions (Rogers, 2000).

This section has focused considerably on the California Current, in large measure because there are no time series for mesopelagic fish abundance and community dynamics from elsewhere. The extent to which patterns and trends in the southern California Current can be generalized is unclear; as noted, that region is an ecotone, where cool-water and warm-water affinity faunas meet, so changes in abundance may reflect distributional shifts at the edge of species ranges rather than large-scale trends. The ecosystem consequences of deoxygenation on continental margin mesopelagic communities are poorly understood, and comparative studies from other regions of the impacts of deoxygenation on mesopelagic fish communities is a high priority.

To date, ecosystem models have not adequately examined the potential impacts of deoxygenation on mesopelagic communities of continental margins in regions with OMZs. Ainsworth et al. (2011) stated as their objective to examine across five regions off the west coast of North America the impacts of deoxygenation, along with acidification, changes in primary production, range shifts and the size structure of the zooplankton. However, mesopelagic fishes were represented in only one of the five regional models, and even in that model the model domain only extended to ~1280 m depth. As a result, the biomass of mesopelagic fishes in that model (Field et al., 2006) was only about a third as high as in a model that treats the entire California Current domain (Davison et al., 2015). As noted above, Proud et al. (2017) failed to test and validate their recent model against existing time series and was based on few or no data from regions with significant OMZs. It is encouraging that recent models for the California Current (e.g. Marshall et al., 2017) have incorporated realistic biomass levels for mesopelagic fishes within an Atlantis modelling structure; the use of such a model to examine the potential impacts of deoxygenation would be extremely valuable. However, the value of such models would be considerably enhanced by a better understanding of the behavioural and physiological response of key taxa from different water types to varying OMZ and HBL characteristics. In regions, such as the California Current, where cool- and warm-water affinity mesopelagic faunas overlap, are they found at similar depths and similar oxygen and light levels? What are the metabolic and productivity costs of descending into hypoxic or suboxic water? If fishes or other organisms undergo metabolic suppression when they remain during the day in suboxic water, does this limit their growth potential or, alternatively, does it enhance growth efficiency? Improved modelling of the impacts of deoxygenation must depend, at least in part, on a better understanding of the underlying physiology and ecology.

It is noteworthy that over the history of the planet, low-oxygen conditions appear to have considerably influenced the evolution of deep sea fishes, leading both to extinctions and the generation of biodiversity. Periods of highly anoxic conditions when the ocean was warm and highly stratified appear to be associated with extinction events in the deep sea, while the separation of populations by well-developed OMZs may also enable allopatric speciation over evolutionary time scales and hence the high species diversity at bathyal (mesopelagic) depths presently observed (Rogers, 2000; White, 1987).

8.4.3.6 Societal consequences

Societal consequences follow from the biogeochemical and ecosystem consequences. As described above, an expansion of the ocean's suboxic zones would have a significant impact on denitrification, leading potentially to decreased productivity in EBCs and tropical regions noted for their high levels of fish production.

The ecological consequences of deoxygenation appear highly complex, including the potential decline of a broad range of mesopelagic micronekton, the range expansion of certain OMZ specialist taxa including both mesopelagic fishes and predators (e.g. the Humboldt squid), which will influence both the abundance and availability of prey for a suite of visual predators. Some of these impacts could have further follow-on impacts. For example, the Humboldt squid feeds voraciously on commercial species, such as Pacific hake, as well as on mesopelagic fishes (Stewart et al., 2014). And today, the Humboldt squid is itself a valued commercial species. To evaluate the societal consequences of these ecological effects would require a reasonably sophisticated modelling exercise that can evaluate the influence of changing prey availability on predator feeding efficiency, and the flow-on to society of a number of first- and second-order effects and their potential non-linear interactions. The recent Atlantis model that evaluated the impact of ocean acidification on the fisheries ecosystem of the California Current System would be a possible candidate for such a study if refocused on deoxygenation (Marshall et al., 2017): Atlantis models can potentially examine the flow-on of ocean change to biochemical, ecosystem, and societal impacts. To better address the impacts of deoxygenation and other aspects of climate change on mesopelagic communities, the deep sea should be recognized by the United Nations Framework Convention on Climate Change (UNFCCC) (Levin & Le Bris ,2015).

8.4.4 Conclusions

Distinct ecological communities of microbes, zooplankton, micronekton and predators are adapted to living within the oxygen-limited mesopelagic waters along continental margins, most notably in regions with OMZs. These organisms exhibit a variety of morphological, physiological and behavioural adaptations to inhabiting the HBL and even the OMZ in regions where the OMZ shoals above mesopelagic depths. Oxygen levels and the depth of the HBL and OMZ have exhibited strong fluctuations over the past ~70 years for which there are a few good time series.

Although these appear to be related in part to decadal-scale forcing, global climate models predict a secular decline in oxygen concentrations at intermediate water depths and there is already ample evidence of such a global trend. It is widely speculated that such changes could have significant consequences for the distribution and abundance of these and other marine mesopelagic communities. Off southern California, there is evidence that mesopelagic fishes have experienced several-fold changes in abundance since 1951, highly correlated with shifts in oxygen concentration and the depth of the HBL but also linked with sea temperatures, the ENSO cycle and Pacific Decadal Oscillation.

Based on current revised estimates for the abundance of the mesopelagic micronekton, this ecological community likely contributes far more to the global carbon cycle as well as to global food webs than previously recognized. Given the high level of uncertainty and its high global importance, high priority needs to be given to understanding the impact of global climate change and deoxygenation on mesopelagic ecosystems along continental margins, particularly where OMZs predominate. There is an urgent need for an expanded network of time series for mesopelagic communities (Koslow & Couture, 2013) and for modelling studies that incorporate our best current understanding of these ecosystems.

8.4.5 References

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