

Fish Ecology and Evolution in the World's Oxygen Minimum Zones and Implications of Ocean Deoxygenation

N.D. Gallo¹, L.A. Levin

Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, United States

¹Corresponding author: e-mail address: natalya.gallo@gmail.com

Contents

1. Introduction	2
2. Global Fish Exposure to Oxygen Minimum Zones	4
2.1 Depth of Upper and Lower OMZ Boundary	7
2.2 OMZ Thickness	8
2.3 Minimum O ₂ Levels in the OMZ Core	8
2.4 Local Temperature	9
2.5 Seasonality, Variability, and Biological Responses	10
3. Influence of Oxygen Minimum Zones on Demersal Fish Community Characteristics	12
3.1 Fish Oxygen Requirements Within OMZs	12
3.2 Composition of Demersal Fish Species in OMZs and OLZs	15
3.3 Regional Patterns in Space and Time	29
3.4 Effects of Oxygen on Fish CPUE, Biomass, and Density	42
3.5 Effects of Oxygen on Fish Diversity	45
3.6 Comparison of Trends Between Invertebrate and Demersal Fish Communities in OMZs	48
4. Behavioural and Physiological Adaptations Conferring Tolerance to Low O ₂ Environments	48
4.1 Responses of OMZ Fish Species to Severely Hypoxic Conditions	49
4.2 Critical Oxygen Level	54
4.3 Blood Adaptations to Hypoxic Conditions	54
4.4 Molecular Responses of Fish to Hypoxia	55
4.5 Metabolic Depression Under Hypoxic Conditions	56
4.6 Behavioural Adaptations	57
4.7 Life-History Trends	58
4.8 Feeding Strategies of Species Living in OMZs	59

5. Implications for a Warming Ocean and Expanding Oxygen Minimum Zones	60
5.1 Influences of Ocean Oxygen on Marine Communities Through Time	60
5.2 Ocean Deoxygenation	61
5.3 Implications for Fisheries Management	63
6. Conclusions	66
7. Advancing Understanding/Future Issues	67
Acknowledgements	68
References	69

Abstract

Oxygen minimum zones (OMZs) and oxygen limited zones (OLZs) are important oceanographic features in the Pacific, Atlantic, and Indian Ocean, and are characterized by hypoxic conditions that are physiologically challenging for demersal fish. Thickness, depth of the upper boundary, minimum oxygen levels, local temperatures, and diurnal, seasonal, and interannual oxycline variability differ regionally, with the thickest and shallowest OMZs occurring in the subtropics and tropics. Although most fish are not hypoxia-tolerant, at least 77 demersal fish species from 16 orders have evolved physiological, behavioural, and morphological adaptations that allow them to live under the severely hypoxic, hypercapnic, and at times sulphidic conditions found in OMZs. Tolerance to OMZ conditions has evolved multiple times in multiple groups with no single fish family or genus exploiting all OMZs globally. Severely hypoxic conditions in OMZs lead to decreased demersal fish diversity, but fish density trends are variable and dependent on region-specific thresholds. Some OMZ-adapted fish species are more hypoxia-tolerant than most megafaunal invertebrates and are present even when most invertebrates are excluded. Expansions and contractions of OMZs in the past have affected fish evolution and diversity. Current patterns of ocean warming are leading to ocean deoxygenation, causing the expansion and shoaling of OMZs, which is expected to decrease demersal fish diversity and alter trophic pathways on affected margins. Habitat compression is expected for hypoxia-intolerant species, causing increased susceptibility to overfishing for fisheries species. Demersal fisheries are likely to be negatively impacted overall by the expansion of OMZs in a warming world.



1. INTRODUCTION

Fish have been identified as one of the marine groups most sensitive to hypoxia (Vaquer-Sunyer and Duarte, 2008), however, tolerances can vary significantly across species based on evolutionary and environmental history. Oxygen minimum zones (OMZs) have been defined as areas where the dissolved oxygen content of the water drops below 0.5 mL L^{-1} or $22 \mu\text{mol kg}^{-1}$ or 7.5% saturation (Kamykowski and Zentara, 1990; Levin, 2003; Rogers, 2000) and conditions are considered severely hypoxic

(Hofmann et al., 2011). OMZs are typically treated as lacking demersal fish communities, however most OMZs have certain fish species that have evolved to tolerate the physiologically extreme conditions. For the fish community, these severely hypoxic conditions can give rise to physiological impairment, altered behaviour, reduced feeding, and habitat compression of nontolerant species, while generating food-rich settings that provide refuge from predators for tolerant species, leading to changes in community composition and altered predator–prey relationships along the margins (Keller et al., 2015; Koslow et al., 2011; Levin, 2003). In this way, oxygen gradients interact with other factors on continental margins to generate habitat heterogeneity (Gooday et al., 2010; Sellanes et al., 2010). To date, several studies have looked at megafaunal communities as a whole in specific OMZs. However, it is valuable to focus specifically on the role of OMZs in structuring fish communities and to examine generalities and differences across regions. This review focuses on studies from different OMZs (US West Coast, Namibia, Chile, Peru, Indian Ocean), with further exploration of unpublished and gray literature (Mexico, Central America, Chile) to extract available information about the presence, identity, abundance, and diversity of demersal fish in OMZs. In addition, this review will consider which fish live in OMZs, how they are able to do this through physiological and molecular adaptations, and how these adaptations have arisen through evolutionary time.

Section 2 of the review will focus on characteristics of OMZs that can give rise to different ecological responses in the demersal fish community. Section 3 of the review focuses on what is known regionally about fish communities in different OMZs and explores tolerant and intolerant species, changes in community composition, and changes in abundance and diversity across oxygen gradients. Section 4 of the review investigates the physiology and adaptations of fish species in hypoxic environments to look at which adaptations occur most commonly, whether certain orders or families appear to have greater ability to tolerate low-oxygen conditions, and if physiological adaptations of fish to low oxygen have arisen independently or share common origins. In Section 5, these previous sections are synthesized and discussed within the context of predicted climate-change driven decreases in global oxygen levels and the implications these changes may have for the demersal fish communities of continental margins that have OMZs. This review examines the OMZ as an interacting ecological zone within the continental margin ecosystem and provides an important foundation for understanding how demersal fish communities on the continental

margins are currently affected by OMZ conditions and how these communities may respond as OMZs expand with climate change.



2. GLOBAL FISH EXPOSURE TO OXYGEN MINIMUM ZONES

In the modern ocean, OMZ waters typically occur in the bathyal zone (100–1800 m) (Fig. 1) in areas with highly productive surface waters and poor midwater circulation (Wyrcki, 1962). OMZ waters underlie productive eastern boundary current regions including the Humboldt Current off Peru–Chile, the California Current off the US and Mexican West Coast, and the Benguela Current off southwestern Africa (Arntz et al., 2006). OMZ waters are also found in the Arabian Sea and Bay of Bengal in the Indian Ocean with monsoon-driven upwelling, in the eastern tropical Pacific, and in the North Pacific in the West Bering Sea and Gulf of Alaska (Helly and Levin, 2004; Kamykowski and Zentara, 1990; Paulmier and Ruiz-Pino, 2009). Severely hypoxic waters are also found in enclosed bodies of water such as the Baltic Sea, Black Sea, the Gulf of Aden, and the Red Sea (Kamykowski and Zentara, 1990), and in estuarine environments (Diaz and Rosenberg, 1995). Shallow-sill topographical depressions such as the Santa Barbara Basin and the Cariaco Trench can also have lower oxygen conditions than surrounding waters and can be anoxic or near anoxic at the bottom (Kamykowski and Zentara, 1990; Mead, 1963; Moffitt et al., 2014). While oxygen conditions are not low enough to be categorized as an OMZ, the shallow sills surrounding the Sulu Sea also give rise to unique low-oxygen conditions ($\sim 39 \mu\text{mol kg}^{-1}$) at abyssal depths (3000–5000 m) (Gordon et al., 2011), whereas OMZs typically occur at bathyal depths (Helly and Levin, 2004). Definitions and locations of hypoxic zones in different parts of the world have been thoroughly reviewed (Hofmann et al., 2011).

The total surface area of permanent OMZs in the world's oceans is $\sim 8\%$ of the total oceanic area and the calculated volume of OMZ waters is 10.3 million km^3 (Paulmier and Ruiz-Pino, 2009). Due to global circulation patterns, the northern hemisphere contains the greatest volume of the world's severely hypoxic water (Kamykowski and Zentara, 1990; Wyrcki, 1966) and 95% of the world's suboxic water ($< 5 \mu\text{mol kg}^{-1}$) is in the eastern tropical North Pacific (Deutsch et al., 2011). OMZs are composed of an upper boundary that is sensitive to seasonal fluctuations (Helly and Levin, 2004; Nam et al., 2015), followed by a low-oxygen core, and a more stable lower

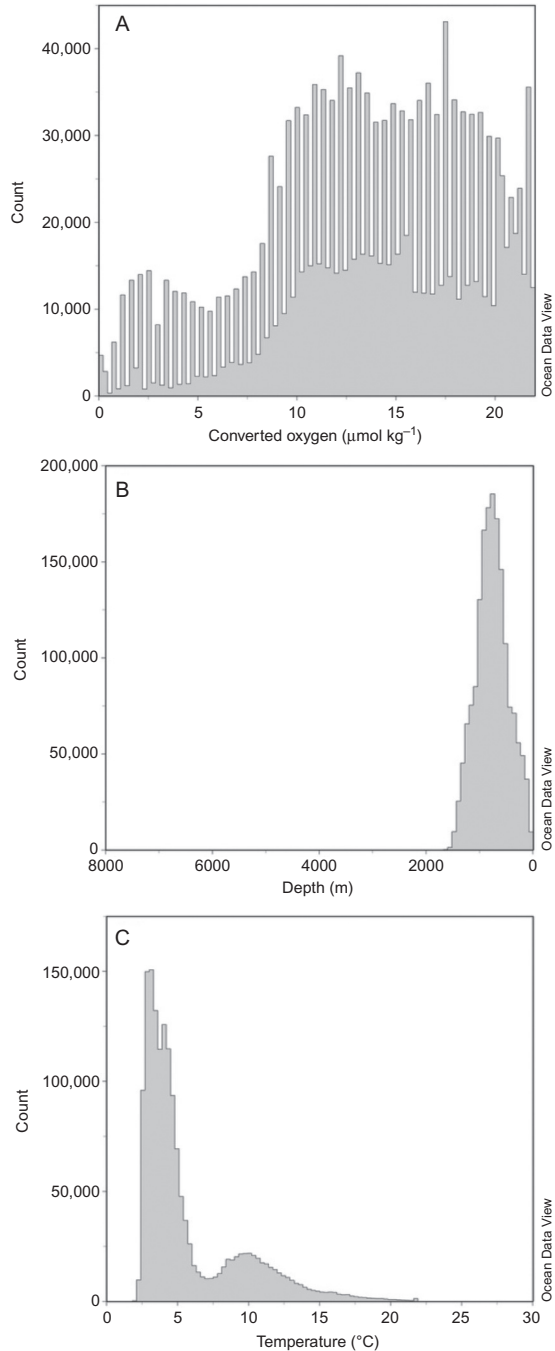


Fig. 1 Characteristics of the world's oxygen minimum zone (OMZ) waters where $\text{O}_2 \leq 22 \mu\text{mol kg}^{-1}$ with respect to (A) oxygen, (B) water depth, and (C) temperature, based on CTD profile data, downloaded from the World Ocean Database (Boyer et al., 2013) (1973–2009) and plotted using Ocean Data View 4.7.4 (Schlitzer, 2015).

boundary where oxygen concentrations begin to increase (Fig. 2A). Over- and underlying the OMZ is a transitional zone defined by Gilly et al. (2013) as the *oxygen limited zone* (OLZ) where oxygen concentrations are $22\text{--}60\ \mu\text{mol kg}^{-1}$ or $0.5\text{--}1.5\ \text{mL L}^{-1}$, this is also considered the hypoxic boundary at $<20\%$ oxygen saturation (Gray et al., 2002; Hofmann et al., 2011). Previous studies have also used alternative definitions of oxygen thresholds for OMZs (Gilly et al., 2013; Paulmier and Ruiz-Pino, 2009), but this review will consider systems with $\leq 22\ \mu\text{mol kg}^{-1}$ for clarity and consistency (Helly and Levin, 2004; Levin, 2003). This review does not focus on the mechanisms that give rise to and maintain OMZs, but several studies and reviews have looked at these questions in depth (Kamykowski and Zentara, 1990; Keeling et al., 2010; Moffitt et al., 2015b; Paulmier et al., 2006; Peña-Izquierdo et al., 2015; Rogers, 2000; Wyrki, 1962).

Oxygen Minimum Zone impact the pelagic community (Ekau et al., 2010; Gilly et al., 2013), but also the benthic community in areas where OMZs intersect the continental margins (Gooday et al., 2010; Helly and Levin, 2004; Levin, 2003; Levin et al., 2009). Globally, OMZs cover over

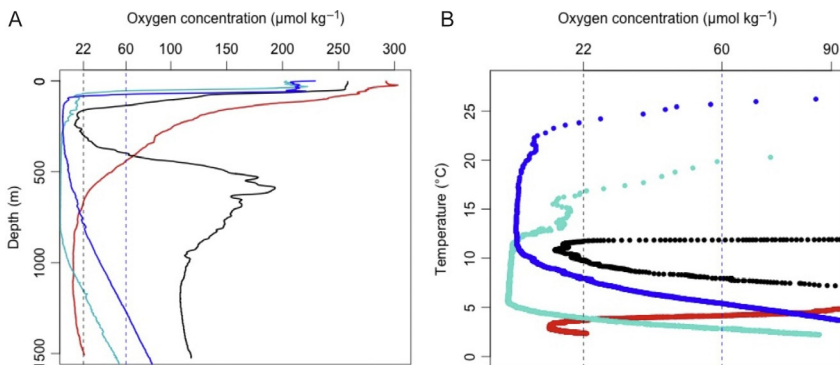


Fig. 2 Oxygen minimum zones (OMZs) in four regions exhibit differing characteristics with relation to (A) thickness, depth of upper and lower boundary, and minimum oxygen concentrations, and (B) local water temperature. *Blue* (*dark grey* in the print version) *dashed line* indicates oxygen limited zone (OLZ) boundary ($60\ \mu\text{mol kg}^{-1}$) and *black dashed line* indicates OMZ boundary ($22\ \mu\text{mol kg}^{-1}$)—*thick, deep, and cold* OMZ off Alaska ($58^\circ\ 5.898'\text{N}$, $147^\circ\ 47.778'\text{W}$), *turquoise* (*light grey* in the print version)—*very thick, shallow, and temperate* OMZ off Costa Rica and Nicaragua ($12^\circ\ 54.828'\text{N}$, $91^\circ\ 48.522'\text{W}$), *black*—*thin, shallow, and temperate* OMZ off central Chile ($32^\circ\ 59.880'\text{S}$, $72^\circ\ 59.880'\text{W}$), and *blue* (*dark grey* in the print version)—*thick, shallow, and very warm* OMZ in the Bay of Bengal ($16^\circ\ 37.800'\text{N}$, $91^\circ\ 56.700'\text{E}$). Conductivity–temperature–depth (CTD) profiles were downloaded from the World Ocean Database (Boyer et al., 2013) and plotted in R (R Core Team, 2012).

1.1 million km² of permanently hypoxic continental shelf and bathyal seafloor (Helly and Levin, 2004), and this area is expanding with climate change (Stramma et al., 2010). OMZs are areas of great benthic habitat heterogeneity due to the strong vertical zonation of dissolved oxygen, organic matter content, sediment type, as well as sulphide concentration (Levin et al., 2010) and play an important role in generating deep-sea biodiversity along the continental margins (Gooday et al., 2010; Levin, 2003; Rogers, 2000).

Globally OMZs exhibit notable geographic differences in the following characteristics that are ecologically and physiologically relevant for structuring the demersal fish community: the depth and seasonal variability of the upper and lower boundary, the thickness of the OMZ in the water column, the minimum oxygen levels observed within the OMZ core, the local temperature conditions present within the OMZ, and the geologic age of the ocean basin within which the OMZ occurs. These differences have been described in several papers (Arntz et al., 2006; Hofmann et al., 2011; Paulmier and Ruiz-Pino, 2009) and will be summarized here as they affect demersal fish communities.

2.1 Depth of Upper and Lower OMZ Boundary

Since increasing pressure with depth exerts an influence on continental margin zonation (Carney, 2005), and temperature also declines with increasing depth to 6000 m, the depth of the upper and lower boundary of the OMZ and OLZ is an important characteristic. The shallowest OMZs occur in the tropics, including in the Gulf of California, on the Pacific side of Mexico and Peru; in the northern Indian Ocean; and on the Namibian shelf (Helly and Levin, 2004). In the Humboldt and Benguela Current, the OMZ begins at shelf and upper slope depths (Arntz et al., 2006). These shallow OMZs can have their upper OMZ boundary at 50–100 m depth, meaning that severely hypoxic waters are close to the surface (at times within the euphotic zone) and impact shallower-water fish communities. For example, off the southwest coast of India near the city of Cochin, severely hypoxic OMZ conditions are found at 20 m depth mid-August through October (Banse, 1968). In contrast, the upper boundary of OMZs occurs deeper at higher latitudes. The upper boundary of the California Current OMZ begins at slope depths (400–500 m) (Arntz et al., 2006) and is found at deeper depths off Oregon, Washington, and Canada (600–700 m) than off California (Helly and Levin, 2004). Severely hypoxic waters can be found seasonally at inner shelf depths (20–50 m) in some of these areas such as off Oregon (Grantham et al., 2004;

Keller et al., 2010), or in eutrophic settings such as the Black Sea and Baltic Sea (Daskalov, 2003; Gooday et al., 2010).

The depth of the lower boundary of the OMZ in the California Current, Humboldt Current, and Benguela Current regions vary considerably (Arntz et al., 2006) with the lower boundary occurring at upper slope depths (200–400 m) off Chile and Namibia, and in contrast, extending deeper off Central America, Peru (500 m) and North America (900–1100 m) (Arntz et al., 2006). The lower boundary of the OMZ is also found deeper (>1000 m) in the southern Gulf of California, in the eastern tropical Pacific from 8° to 22°N, and in the northern Arabian Sea and Bay of Bengal (Helly and Levin, 2004). Most OMZ waters occur at depths shallower than 1500 m (Kamykowski and Zentara, 1990) (see Fig. 1).

2.2 OMZ Thickness

The thickness of OMZs (depth between upper and lower boundary) varies from 200 to 1200 m (Helly and Levin, 2004) (see Fig. 2), with the thickness and intensity influencing population dynamics along the continental margin. Thick OMZs likely act as greater barriers to gene flow, than shallow OMZs, and may play a greater role in speciation along continental margins (Rogers, 2000; White, 1988). Areas with thinner OMZs may allow some fish species to move out of low-oxygen conditions when circumstances become too severe or when they are undergoing a more energetically demanding life stage. Some of the thinnest OMZs (<300 m thick) include those off western Africa, off central Chile, off central North America, and in the West Bering Sea (Helly and Levin, 2004; Paulmier and Ruiz-Pino, 2009). The thickest OMZs (>1000 m) include those in the southern Gulf of California, in the eastern tropical North Pacific (>8°N), in parts of the North Pacific (~48–58°N), and in the northern Arabian Sea (Helly and Levin, 2004; Paulmier and Ruiz-Pino, 2009). In the N. Arabian Sea, the OMZ occurs between 100 and 1200 m (Murty et al., 2009) and is most intense off the coasts of Pakistan and west India (Slater and Kroopnick, 1984). Approximately 677,320 km² of deep seafloor is intercepted by OMZ waters in the Arabian Sea, making it one of the largest transects of deep seafloor affected by hypoxia in the world (Helly and Levin, 2004).

2.3 Minimum O₂ Levels in the OMZ Core

While OMZs are defined as having O₂ concentrations $\leq 22 \mu\text{mol kg}^{-1}$, the minimum oxygen levels encountered within the OMZ core vary (see

Fig. 2). The intensity of the OMZ core can give rise to different patterns of faunal zonation within the OMZ and can give rise to additional stressors. Biogeochemical changes, including denitrification, increased bioavailability of trace metals, and H_2S production begin to take place at suboxic conditions where oxygen concentrations fall below $5 \mu\text{mol kg}^{-1}$ (Paulmier and Ruiz-Pino, 2009), and these may all be additional stressors for the fish community. The OMZs originally thought to have the lowest core oxygen conditions include the northern Arabian Sea, the eastern north tropical Pacific, and the Gulf of California (Helly and Levin, 2004). However, a recent revolution in measurement technology for ultra low oxygen has revealed oxygen concentrations $<2 \mu\text{mol kg}^{-1}$ off Peru, Chile, Namibia, and elsewhere (Kavelage et al., 2014; Revsbech et al., 2009). The core of the eastern tropical Pacific is functionally anoxic, with oxygen concentrations in the OMZ core found to be $<0.1 \mu\text{mol kg}^{-1}$ between depths of 150 and 800 m (Tiano et al., 2014).

2.4 Local Temperature

The temperature characteristics of the OMZ are influenced by latitude, water masses, and boundary currents, which relate to the depth of the OMZ in the water column. Assembled data from all the world's OMZs reveal a bimodal distribution of temperature: while most OMZs have cold temperatures ($<6^\circ\text{C}$), some have much warmer conditions ($10\text{--}22^\circ\text{C}$) (Fig. 1C). Differences in temperature likely have physiological implications for the demersal fish communities that inhabit these regions. While many OMZs occur in tropical latitudes ($<25^\circ$), important exceptions include the OMZ off Central Chile and throughout the eastern North Pacific, including the seasonal OMZs in the West Bering Sea and Gulf of Alaska (Paulmier and Ruiz-Pino, 2009). Demersal fish living in OMZs with higher temperature conditions may be under greater hypoxia stress because metabolic rates and oxygen demand increase under warmer temperatures (Pörtner et al., 2006). In the Arabian Sea and Bay of Bengal (see Fig. 2B), temperatures are very warm. The lowest temperatures observed off the southwest coast of India near the city of Cochin where OMZ waters occur seasonally at 20 m were $20.9\text{--}22^\circ\text{C}$ and offshore at 50 m depth were $19.7\text{--}20.3^\circ\text{C}$ (Banse, 1968). Temperatures of $10\text{--}12^\circ\text{C}$ found at 800–1000 m off Pakistan and India (Cowie and Levin, 2009; Levin et al., 2013) are nearly twice as warm as other regional OMZs. A study using Argo floats in the Arabian Sea found that water temperatures at OMZ depths were

up to 25°C (Prakash et al., 2012). This contrasts greatly with the much colder local temperature conditions of the OMZ off the US West Coast, where OMZ temperatures are 4°C at 770 m off Oregon, 5–6°C at 500–525 m off California, and 3–4°C at 800 m off Alaska (see Fig. 2) (Levin et al., 2010). While oxygen remains above OMZ conditions ($\sim 39 \mu\text{mol kg}^{-1}$) in the Sulu Sea, these unique oxygen limited conditions in the abyssal zone (3000–5000 m) occur under uniformly warm temperatures (9.9°C) (Gordon et al., 2011).

2.5 Seasonality, Variability, and Biological Responses

Fish can respond to changes in oxygen across a range of timescales from rapid (hour to day) changes in gene expression (Gracey et al., 2001; Tiedke et al., 2014), to longer timescales through changes in the presence and density of specific species leading to altered community structure (Chu and Tunnicliffe, 2015; Keller et al., 2010; Wu, 2002). Natural variability of oxygen levels within OMZs may thus be physiologically and ecologically relevant. Oxygen variability in OMZs occurs on daily, seasonal, and interannual timescales. This appears to depend on latitude, water depth, the presence of monsoon-driven climatological changes, changes in the El Niño Southern Oscillation, and varying strengths of boundary currents and undercurrents (Nam et al., 2015). Greater seasonality in OMZs is noted at higher latitudes (Kamykowski and Zentara, 1990), and two seasonal OMZs have been identified in the West Bering Sea and the Gulf of Alaska where oxygen levels rise above OMZ levels during the summer (Paulmier and Ruiz-Pino, 2009). Off Central America, seasonality in the depth of the upper OMZ boundary has been observed with shoaling characteristic of November/December (Bianchi, 1991; Stromme and Saetersdal, 1988).

Oscillations of the upper boundary of OMZs are thought to be a widespread phenomenon (Murty et al., 2009), however the characteristic variance of the upper boundary is region-specific. At semi-diurnal and diurnal timescales, displacement of the OMZ upper boundary by internal tides has been observed on Volcano 7 in the Pacific Ocean (Wishner et al., 1995). Seasonal changes in upwelling intensity also gives rise to varying characteristics of the OMZ. The upper boundary of the OMZ exhibits more variability than the lower boundary, but both can be influenced by seasonal changes. Off Namibia, the strongest upwelling occurs in late winter (August) and spring (September–November) (Hamukuaya et al., 2001), leading to an expansion of low-oxygen zones. The diversity and distribution of the

demersal fish community on the Namibian shelf and upper slope was found to differ before (Winter 1987) and after (Summer 1988) the upwelling season, presumably due to the altered oxygen conditions (Mas-Riera et al., 1990). Off Oregon and Washington, low-oxygen water occurs at shallower depths during the late summer and fall and both catch per unit effort and total species richness have been positively correlated with bottom oxygen concentration (Keller et al., 2015). In the Southern California Bight, the upper boundary of the OMZ shoals during the spring and summer and is found deeper in the winter, due to upwelling and relaxation patterns that drive primary production and respiration (Send and Nam, 2012), as well as to increased advection of Pacific Equatorial Water in the core of the California Undercurrent during the summer (Nam et al., 2015).

Especially for the benthic communities, variability in oxygen conditions driven by undercurrent variability may also be important to consider since all eastern boundary currents have underlying counter-direction undercurrents, and the undercurrent typically overlaps with part of the depth of the OMZ. For example, Thiel (1978) reports that off Portugal and West Africa, the strongest undercurrent flow is observed at depths of 200–300 m (up to 30 cm s^{-1}) (Mittelstaedt, 1976), and the highest tidal activity is found in this range on the upper slope (Horn and Meincke, 1976). Strong seasonal variability of the California Undercurrent in terms of strength, depth, and direction likely contributes to deep-water oxygen variability along the continental margin in the Southern California Bight between 100 and 400 m depth (Bograd et al., 2015; Lynn and Simpson, 1987). These sources of environmental variability can influence the demersal fish community and illustrate that the upper boundary of the OMZ can be a dynamic environment.

In areas that experience strong seasonal monsoons, such as the Indian Ocean, OMZ variability may be even greater. Considerable monsoon-driven variability has been described in the Arabian Sea OMZ (Morrison et al., 1998, 1999; Prakash et al., 2012; Thiel, 1978). The depth of the OMZ off India is changed by the monsoon regime with oxygen-poor water shoaling up the continental shelf during the southwest monsoon (Banse, 1968), leading to decreased catches of fish and prawns by more than 75% from June to September (Sankaranarayanan and Qasim, 1968).

The El Niño Southern Oscillation (ENSO) influences the depth of the thermocline in eastern boundary current regions and thereby influences the characteristics of the OMZ. Off Peru, ENSO events can alter the depth of the upper boundary of the OMZ by nearly 100 m (Levin et al., 2002). In the

Humboldt Current System during an El Niño, the OMZ contracts due to changes at the OMZ upper boundary, which are driven by altered flow of the undercurrent (Arntz et al., 2006). The 1997–1998 El Niño reduced the amount of seafloor affected by the OMZ off Peru by approximately 69% (Helly and Levin, 2004), expanding local fisheries for hake, octopus, and scallop (Arntz et al., 2006). On the southern California shelf, El Niño also enhances oxygenation by reducing primary production (and subsequent respiration) while La Niña conditions do the opposite (Nam et al., 2011)—but few observations are made deeper within the OMZ. While the upper boundary of the OMZ is influenced by ENSO events, there is no indication that the lower boundary or zone below the OMZ is affected by ENSO, although some changes due to altered surface productivity are suggested (Arntz et al., 2006).



3. INFLUENCE OF OXYGEN MINIMUM ZONES ON DEMERSAL FISH COMMUNITY CHARACTERISTICS

Zonation of demersal fish communities has been well studied in areas without OMZs such as the northeast Atlantic and the Australian continental margins (Haedrich and Merrett, 1990; Koslow, 1993; Koslow et al., 1994); however, vertebrates frequently receive less focus than invertebrate community members in OMZ studies, either being left out entirely (Arntz et al., 2006) or being separated from the megafauna *sensu strictu* (Murty et al., 2009). Some OMZ regions such as the Gulf of California, the Pacific margin of Mexico, Central, and South America, and the Bay of Bengal remain grossly understudied; nonetheless, the infrequent descriptions of demersal fish communities in OMZs begin to shed light on some interesting and important patterns. This section will first introduce the oxygen requirements of fish and published hypoxia tolerances of fish within the context of OMZ oxygen conditions, and then identify some characteristic patterns illustrating how OMZs influence demersal fish communities, including changes in abundance and diversity, and the presence of edge effects and single fish species dominance at O_2 levels where most other megafauna are absent.

3.1 Fish Oxygen Requirements Within OMZs

Due to the physicochemical properties of gases in water, oxygen is much more limiting in water than in air. The lower availability of oxygen in water and the greater viscosity of water require that fish must be very efficient at extracting oxygen from the water. Hypoxic thresholds for fish have been

reviewed by Davis (1975), Gray et al. (2002), Vaquer-Sunyer and Duarte (2008), and Hofmann et al. (2011), and these studies have found that fish exhibit sublethal and lethal impacts of oxygen at higher thresholds than most invertebrate groups. Oxygen minimum zones represent some of the most hypoxic waters in the world and OMZ oxygen concentrations are lower than most lethal and sublethal oxygen concentrations determined for many fish species in the published literature. However, OMZs are not devoid of fish fauna, making them an opportune system to study how severe hypoxia influences the fish community and how fish adapt to these extreme conditions.

Fish exhibit a range of responses to hypoxia and responses vary with the severity of hypoxia (Davis, 1975). Sublethal responses occur first and include physiological, behavioural, or stress-induced responses. Specific oxygen thresholds can influence fish behaviour, metabolic rate, swimming ability, growth, circulatory dynamics, ventilation, gaseous exchange, blood O₂ saturation, sensitivity to toxins and other environmental stressors, and viability and development of eggs and larvae (Davis, 1975; Farrell and Richards, 2009; Nilsson, 2010; Richards, 2009). Reduced growth rate and food conversion efficiency is a sublethal impact of hypoxia, so growth has been suggested to be a useful criterion for hypoxia influence because it is an expression of the net product of metabolic functions (Davis, 1975). Gray et al. (2002) reported that growth of actively swimming fish is affected at oxygen levels of 183 $\mu\text{mol kg}^{-1}$.

The oxygen threshold at which oxygen becomes limiting for fish has been defined in many different ways in the literature and is species-specific (Davis, 1975; Hofmann et al., 2011). Of note, there is a research bias towards laboratory studies on Atlantic species (Chu and Tunnicliffe, 2015), which may be less hypoxia tolerant than Pacific species. The oxygen concentration at which a fish switches from being an oxyregulator (O₂ consumption independent of environmental O₂ levels) to an oxyconformer (O₂ consumption dependent on environmental O₂ levels), which is termed the critical oxygen tension (P_{crit}) (Richards, 2009, 2011), is considered to be a physiologically relevant hypoxia threshold. The metabolic index (ratio of O₂ supply to resting metabolic O₂ demand) has also been used to examine critical oxygen levels in marine environments, and this study found that conditions were only viable if they supported metabolic rates at least two to five times resting rates (Deutsch et al., 2015). Much higher hypoxia thresholds such as <50% O₂ saturation have also been used in the coastal literature, since sensitive species begin showing avoidance, reduced growth, and other signs of physiological stress below this level (Breitburg, 2002).

Based on a review of published literature on community responses to low-oxygen conditions, Hofmann et al. (2011) defined “mild hypoxia” to be $107 \mu\text{mol kg}^{-1}$, where sensitive species begin to show avoidance (Diaz and Rosenberg, 2008), “hypoxia” to be $61 \mu\text{mol kg}^{-1}$ where several studies have found that fish are absent (Gewin, 2010; Gray et al., 2002; Kemp et al., 2009; McClatchie et al., 2010), and “severe hypoxia” as $22 \mu\text{mol kg}^{-1}$ where mass mortality occurs and only highly adapted species are able to survive (Shaffer et al., 2009). One meta-analysis found that the average mean lethal concentration (LC_{50}) for marine benthic fish was $47.12 \pm 2.14 \mu\text{mol kg}^{-1}$, and the average mean sublethal concentration (SLC_{50}) was $134.92 \pm 11.93 \mu\text{mol kg}^{-1}$ (Vaquer-Sunyer and Duarte, 2008); however, the mean lethal concentrations and sublethal concentrations were calculated using data for only 23 and 15 species of fish respectively. Oxygen conditions in OMZs fall within the “severe hypoxia” category, while oxygen conditions within OLZs fall within the “hypoxia” category.

While oxygen is frequently reported as a concentration, it is important to keep in mind that the partial pressure of oxygen ($p\text{O}_2$) is the more physiologically relevant measurement since it provides the thermodynamic driving force for molecular transfer of oxygen across membranes (Hofmann et al., 2011). Temperature-dependent metabolic rate differences also need to be factored in because aerobic oxygen demand is greater under warmer temperatures (Brown et al., 2004; Deutsch et al., 2015), with the Q_{10} value of oxygen consumption for fish overall found to be 2.3 (Bridges, 1988). Blood–oxygen binding is also temperature sensitive (Mislan et al., 2015). Empirically, several studies have shown that lethal hypoxic conditions for fish are also reached much faster under warmer temperatures (Schurmann and Steffensen, 1992; Secor and Gunderson, 1998). This was not observed by Vaquer-Sunyer and Duarte (2011), but this contradictory result may be influenced by the manner of the meta-analysis and the range of physiological capacities of the fish species that were included in the analysis. The dependence of metabolic rate on environmental temperature suggests that fish living in “warm” OMZs (eg, in the Arabian Sea and Bay of Bengal) may be under additional stress relative to those living in colder or deeper OMZs such as in the California Current System (CCS). Approximating a Q_{10} value of 2 for fish, metabolic demand of demersal fish in the Bay of Bengal OMZ may be four times greater than in the Alaskan OMZ where temperatures at similar oxygen concentrations are 20°C colder (see Fig. 2).

Three additional factors make OMZs particularly inhospitable for fish and may contribute to greater hypoxia stress. While OMZs are very low

in oxygen, they also have high concentrations of $p\text{CO}_2$ and have been called carbon-maximum zones (Paulmier et al., 2011). For example, high $p\text{CO}_2$ (>1200 uatm.) and low pH (<7.6) are reported off California (Feely et al., 2008). As a result, OMZ fish are exposed to combined hypoxia–hypercapnia stress. High $p\text{CO}_2$ levels may have additional physiological consequences for respiration under low O_2 conditions because oxygen transport proteins are highly sensitive to pH (Rummer et al., 2013; Seibel and Walsh, 2003). High $p\text{CO}_2$ environmental conditions in other studies have induced a respiratory acidosis in fish, resulting in a decreased oxygen affinity and oxygen carrying capacity of haemoglobin due to the Root effect (Jensen and Weber, 1982, 1985; Jensen et al., 1993; Thomas, 1983). In certain fish species, blood pH can eventually be recovered over time through the exchange of Cl^- for HCO_3^- ions in the gills, leading to a phenomenal accumulation of HCO_3^- in the blood (Jensen and Weber, 1982). It is not known if OMZ fish also have high HCO_3^- levels to compensate for the high $p\text{CO}_2$ environment in which they live.

Because OMZs can have very old water (i.e. isolated from the surface via thermohaline circulation) that has experienced extensive remineralization, they are also high in nitrate and nitrite. Nitrite penetrates red blood cells and oxidizes haemoglobin to methaemoglobin, which cannot transport oxygen, thereby decreasing the blood capacitance and the blood arterial content (Jensen et al., 1987, 1993). Lastly, some OMZs such as off Namibia (Brüchert et al., 2009; Weeks et al., 2004) have high H_2S concentrations, which are usually toxic even in low concentrations because hydrogen sulphide inhibits cytochrome *c* oxidase in the mitochondria, thus blocking the last step of the respiratory chain where oxygen is the terminal electron receptor (Jensen et al., 1993). When exposed to H_2S , haemoglobin loses any oxygen that it is carrying and is transformed into sulphaemoglobin (van Assendelft, 1970). The interacting influence of high $p\text{CO}_2$, high nitrite and H_2S concentrations in OMZs can further make oxygen extraction more difficult for OMZ fish in an already oxygen limited environment. Thus, OMZ-tolerant fish species are truly physiologically remarkable.

3.2 Composition of Demersal Fish Species in OMZs and OLZs

Dissolved oxygen levels play a critical role in influencing megafaunal composition and community structure along the continental margins (Murty et al., 2009; Quiroga et al., 2009) and within submarine canyons (De Leo et al., 2012). Despite the characterization of fish as being relatively intolerant

of hypoxic conditions (Vaquer-Sunyer and Duarte, 2008), an assortment of demersal fish species are known from OMZs around the world (Hunter et al., 2011; Stein et al., 2006) (Fig. 3; Table 1). Since responses of demersal fish species to hypoxia are species-specific, a change in community

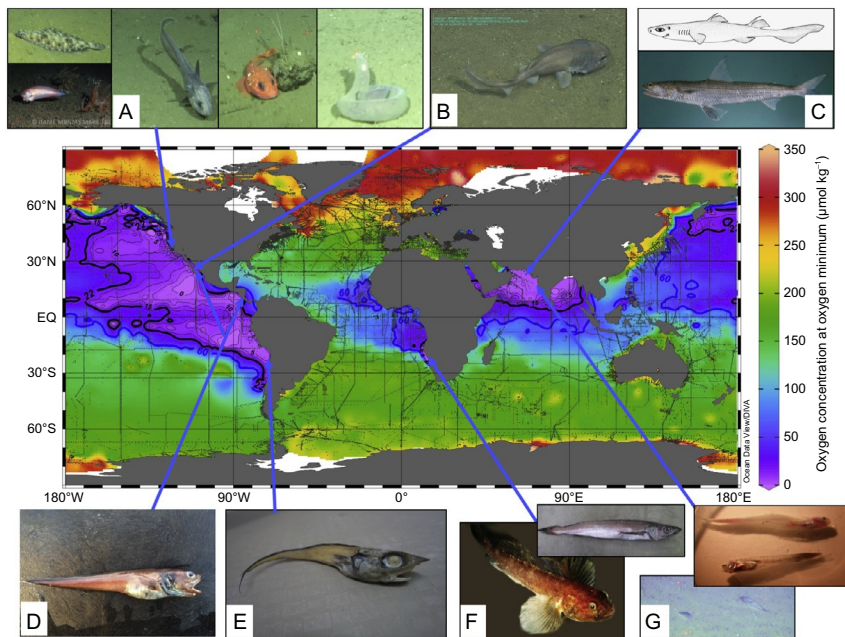


Fig. 3 Map of global spatial distribution of oxygen minimum zones (OMZs) with minimum oxygen concentrations ($\mu\text{mol kg}^{-1}$) within the water column and dominant resident demersal fish species known from each area. Thick blue (dark grey in the print version) contours show the spatial extent of oxygen limited zones ($\leq 60 \mu\text{mol kg}^{-1}$) and thick black contours show the spatial extent of oxygen minimum zones ($\leq 22 \mu\text{mol kg}^{-1}$). Data downloaded from the World Ocean Database (Boyer et al., 2013) (1973–2009) and plotted using Ocean Data View 4.7.4 and DIVA gridding software (Schlitzer, 2015). OMZ-adapted demersal fish species include: (A) in the Northeast Pacific—*Microstomus pacificus* (upper left), *Careproctus melanurus* (bottom left), *Nezumia liolepis* (middle left), *Sebastolobus alascanus* (middle right), and *Eptatretus deani* (right), (B) in the Gulf of California—*Cephalurus cephalus*, (C) on the Pakistan margin—*Centroscyllum ornatum* and *Saurida tumbil*, (D) in the Gulf of California and Central America—*Cherublemma emmelas*, (E) on the Chilean margin *Trachyrincus villegai*, (F) on the Namibian margin—*Sufflogobius bibarbatus* and *Merluccius capensis*, and (G) on the west Indian margin—*Bregmaceros* sp. and *Liparidae* sp. See Table 1 for citations. Photographs: SIO Triton ROV and UC Ship Funds (*M. pacificus*, *N. liolepis*, *S. alascanus*, *E. deani*, *Bregmaceros* sp.), MBARI (*C. cephalus*, *C. melanurus*), FAO (*C. ornatum*), H. Vestheim (*S. bibarbatus*), N.D. Gallo (*C. emmelas*, *T. villegai*), F.H. Van der Bank (*M. capensis*), J.E. Randall (*S. tumbil*), W.R. Hunter (*Liparidae* sp.).

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range ($\mu\text{mol kg}^{-1}$)	Citations
Myxiniformes						
Myxinidae						
<i>Eptatretus deani</i>	Black hagfish	US Pacific margin (northeastern Pacific)	366–2743	3.6–6.4	13.1–58.2	N.D. Gallo (unpublished data) and Day and Pearcy (1968)
<i>Eptatretus</i> sp.	Hagfish	Canada Pacific margin (northeastern Pacific)	890	3.6–4.0	10.5–15.3	Juniper et al. (2013)
Squaliformes						
Etmopteridae						
<i>Etmopterus</i> sp.	Lantern shark	Indian margin (Arabian Sea)	–	–	–	Hunter et al. (2011)
<i>Centroscyllium ornatum</i>	Ornate dogfish	Pakistan margin (Arabian Sea)	1000–1200	7.4–8.7	6.7–17.0	Murty et al. (2009)
Centrophoridae						
<i>Centrophorus granulosus</i>	Gulper shark	Yemen margin (Arabian Sea)	50–1440	5.2–12.9	13.3–212.7	Kukharev (2015)
Carcharhiniformes						
Scyliorhinidae						
<i>Apristurus brunneus</i>	Brown catshark	California margin (northeastern Pacific)	79–1448	2.9–5.4	13.1–70.9	N.D. Gallo (unpublished data)

Continued

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)—cont'd

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range ($\mu\text{mol kg}^{-1}$)	Citations
<i>Parmaturus xaniurus</i>	Filetail catshark	California margin to Gulf of California (northeastern Pacific)	88–1250	3.3–9.4	13.1–143.5	N.D. Gallo (unpublished data)
<i>Cephalurus cephalus</i>	Lollipop shark	Gulf of California	275–927	9.4	6.1	Aguirre-Villaseñor and Salas-Singh (2012)
<i>Halaehurus</i> spp.	Tiger catshark	Yemen margin (Arabian Sea)	–	–	13.3	Kukharev (2015)
<i>Cephalurus</i> sp. cf.	Catshark	Chilean margin (southeastern Pacific)	313–327	10.9–11.5	3.0–3.84	J. Sellanes Universidad Catolica del Norte (UCN) (unpublished data)
Proscylliidae						
<i>Eridacnis radcliffei</i>	Pygmy ribbontail catshark	Yemen margin (Arabian Sea)	71–766	–	13.3–174.9	Kukharev (2015)
Rajiformes						
Arhynchobatidae						
<i>Bathyraja interrupta</i>	Sandpaper skate	Oregon margin (northeastern Pacific)	64–1500	3.1–8.3	13.1–273.4	Day and Percy (1968)
<i>Bathyraja trachura</i>	Roughtail skate	Oregon margin (northeastern Pacific)	213–2550	1.6–7.0	18.4–156.2	Day and Percy (1968)
<i>Bathyraja</i> sp.	Skate	Indian margin (Arabian Sea)	–	–	–	Hunter et al. (2011)

Pleuronectiformes						
Pleuronectidae						
<i>Microstomus pacificus</i>	Dover sole	US Pacific margin (northeastern Pacific)	10–1370	2.9–11.5	13.1–318.9	Friedman et al. (2012) and Day and Pearcy (1968)
<i>Embassichthys bathybius</i>	Deep-sea sole	US and Canada Pacific margin (northeastern Pacific)	125–1800	2.4–6.4	13.1–54.3	N.D. Gallo (unpublished data), Day and Pearcy (1968), and Juniper et al. (2013)
<i>Lyopsetta exilis</i>	Slender sole	US and Saanich Inlet (northeastern Pacific)	25–800	4.2–8.7	14.0–244.6	Matabos et al. (2012) and Chu and Tunnicliffe (2015)
Paralichthyidae						
<i>Hippoglossina macrops</i>	Bigeye flounder	Chilean margin (southeastern Pacific)	34–580	10.6–16.5	22–83.5	J. Sellanes (UCN) (unpublished data)
Bothidae						
<i>Monolene maculipinna</i>	Pacific deep-water flounder	Costa Rica to Peru (eastern tropical Pacific)	205–384	13.0–27.5	16.2–175.4	Bianchi (1991)
Soleidae						
<i>Austroglossus microlepis</i>	West coast sole	Namibia to South Africa (southeastern Atlantic)	100–400	7.8–14.5	16.0–218.9	Hamukuaya et al. (2001)

Continued

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)—cont'd

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range ($\mu\text{mol kg}^{-1}$)	Citations
Anguilliformes						
Nettastomatidae						
<i>Facciolella equatorialis</i>	Dogface witch-eel	California margin (northeastern Pacific)	500–1000	6.2–8.2	9.2–47.7	N.D. Gallo (unpublished data)
<i>Nettastoma</i> sp.	Duckbill eel	Yemen margin (Arabian Sea)	–	–	13.3	Kukharev (2015)
Congridae						
<i>Congridae</i> sp.	Conger eel	Indian margin (Arabian Sea)	–	–	–	Hunter et al. (2011)
<i>Congridae</i> sp.	Conger eel	Pakistan margin (Arabian Sea)	1200	7.4	13.4–17.0	Murty et al. (2009)
Synphobranchidae						
<i>Synphobranchus</i> sp.	Cutthroat eel	Indian margin (Arabian Sea)	–	–	–	Hunter et al. (2011)
Serrivomeridae						
<i>Serrivomer</i> sp.	Sawtooth eel	Pakistan margin (Arabian Sea)	1100	8	9.4–11.2	Murty et al. (2009)

Notacanthiformes						
<i>Halosauridae</i>						
<i>Halosaurus</i> sp.	Halosaur	Pakistan margin (Arabian Sea)	1200	7.4	13.4–17.0	Murty et al. (2009)
<i>Notocanthidae</i>						
<i>Notocanthus</i> sp.	Deep-sea spiny eel	Pakistan margin (Arabian Sea)	1100	8	9.4–11.2	Murty et al. (2009)
Aulopiformes						
<i>Synodontidae</i>						
<i>Saurida tumbil</i>	Greater lizardfish	Pakistan margin (Arabian Sea)	4–700	11.0–26.6	4.9–206.5	Murty et al. (2009)
<i>Saurida undosquamis</i>	Brushtooth lizardfish	Yemen margin (Arabian Sea)	1–350	11.3–28.3	13.3–210.9	Kukharev (2015)
<i>Harpadon squamosus</i>	Lizardfish	Yemen margin (Arabian Sea)	–	–	13.3	Kukharev (2015)
Beryciformes						
<i>Trachichthyidae</i>						
<i>Hoplostethus</i> spp.	Roughy	Yemen margin (Arabian Sea)	–	–	13.3	Kukharev (2015)

Continued

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)—cont'd

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range ($\mu\text{mol kg}^{-1}$)	Citations
Perciformes						
Stichaeidae						
<i>Plectobranthus evides</i>	Bluebarred prickleback	Saanich Inlet (northeastern Pacific)	84–368	7.6–8.6	7.9–205.6	Chu and Tunnicliffe (2015) and Matabos et al. (2012)
Agonidae						
<i>Xeneretmus latifrons</i>	Blacktip poacher	US Pacific margin, Saanich Inlet (northeastern Pacific)	18–486	4.6–8.7	7.4–244.6	Chu and Tunnicliffe (2015) and Matabos et al. (2012)
<i>Bathylagonus nigripinnis</i>	Blackfin starsnout poacher	Canada Pacific margin (northeastern Pacific)	18–1290	3.0–8.3	10.5–201.7	Juniper et al. (2013)
Zoarcidae						
<i>Zoarcid</i> sp.	Eelpout	Canada Pacific margin (northeastern Pacific)	890	3.6–4	10.5–15.3	Juniper et al. (2013)
Serranidae						
<i>Diplctrum macropoma</i>	Mexican sand perch	Mexico to Peru (eastern tropical Pacific)	1–220	16.6–16.8	17.5–120.3	Bianchi (1991)
Trichiuridae						
<i>Trichiurus nitens</i>	Pacific cutlassfish	Mexico to Peru (eastern tropical Pacific)	160–250	13	17.5	Bianchi (1991)
<i>Lepturacanthus</i> spp.	Hairtail	Yemen margin (Arabian Sea)	–	–	13.3	Kukharev (2015)

Gobiidae

<i>Sufflogobius bibarbatus</i>	Bearded goby	Namibia and South Africa (southeastern Atlantic)	10–340	7.8–14.5	10.0–218.8	Hamukuaya et al. (2001) , Mas-Riera et al. (1990) , Utne-Palm et al. (2010) , and Salvanes et al. (2011)
--------------------------------	--------------	--------------------------------------------------	--------	----------	------------	-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------

Carangidae

<i>Trachurus trachurus capensis</i>	Horse mackerel	Gulf of Guinea to South Africa (southeastern Atlantic)	0–500	5.4–22.0	16–252.0	Hamukuaya et al. (2001)
<i>Carangidae</i> sp.	Carangid	Pakistan margin (Indian Ocean)	300	14.8	4.9–5.4	Murty et al. (2009)

Epigonidae

<i>Epigonus</i> sp.	Deep-water cardinalfish	Pakistan margin (Arabian Sea)	140	18.2	4.9	Murty et al. (2009)
---------------------	-------------------------	-------------------------------	-----	------	-----	-------------------------------------

Acropomatidae

<i>Synagrops adeni</i>	Aden splitfin	Yemen margin (Arabian Sea)	60–600	–	13.3	Kukharev (2015)
------------------------	---------------	----------------------------	--------	---	------	---------------------------------

Percophidae

<i>Bembrops caudimacula</i>	Opal fish	Yemen margin (Arabian Sea)	160–505	14.4–17.4	13.3–192.3	Kukharev (2015)
-----------------------------	-----------	----------------------------	---------	-----------	------------	---------------------------------

Centrolophidae

<i>Psenopsis cyanea</i>	Indian ruff	Yemen margin (Arabian Sea)	179–400	–	15.5–55.5	Kukharev (2015)
-------------------------	-------------	----------------------------	---------	---	-----------	---------------------------------

Continued

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)—cont'd

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range ($\mu\text{mol kg}^{-1}$)	Citations
<i>Scombridae</i>						
<i>Scomber australasicus</i>	Japanese mackerel	Yemen margin (Arabian Sea)	9–494	7.7–24.0	13.3–279.7	Kukharev (2015)
<i>Ophidiiformes</i>						
<i>Bythitidae</i>						
<i>Cataetyx rubrirostris</i>	Rubynose brotula	US Pacific margin (northeastern Pacific)	288–1000	4.9	9.0–20.6	N.D. Gallo (unpublished data)
<i>Ophidiidae</i>						
<i>Cherublemma emmelas</i>	Black brotula	Baja California to Northern Chile (eastern tropical Pacific)	15–902	6.1–20.4	3.9–219.6	Aguirre-Villaseñor and Castillo-Velázquez (2011), Bianchi (1991), and Stromme and Saetersdal (1988)
<i>Holcomycteromus</i> sp.	Cusk-eel	Indian margin (Arabian Sea)	–	–	–	Hunter et al. (2011)
<i>Brotulotaenia</i> sp.	Cusk-eel	Pakistan margin (Arabian Sea)	1000–1200	7.4–8.7	6.7–17.0	Murty et al. (2009)
<i>Genypterus maculatus</i>	Black cusk-eel	Chilean margin (southeastern Pacific)	82–328	9.2–11.8	17.9–50.9	Chilean Fisheries Development Program, FIP2004-09
<i>Genypterus blacodes</i>	Rock ling	Chilean margin (southeastern Pacific)	58–450	7.2–11.3	21.7–110.4	Chilean Fisheries Development Program, FIP2004-09

Gadiformes						
Macrouridae						
<i>Nezumia liolepis</i>	Smooth grenadier	Volcano 7 (eastern equatorial Pacific), US Pacific margin (northeastern Pacific)	450–1660	4.5–6.5	3.5–43.8	Friedman et al. (2012), Wishner et al. (1990, 1995), and Levin et al. (1991)
<i>Coryphaenoides acrolepis</i>	Strong-scaled rattail	Oregon margin (northeastern Pacific)	300–3700	1.7–6.9	18.8–158.8	Day and Pearcy (1968)
<i>Coryphaenoides pectoralis</i>	Pectoral rattail	Oregon margin (northeastern Pacific)	140–3500	1.8–4.6	17.1–256.4	Day and Pearcy (1968)
<i>Coryphaenoides sp.</i>	Grenadier	Indian margin (Arabian Sea)	–	–	–	Hunter et al. (2011)
<i>Trachyrincus villegai</i>	Grey grenadier	Northern Peru to Central Chile (southeastern Pacific)	250–980	–	2.6	Quiroga et al. (2009)
Merlucciidae						
<i>Merluccius productus</i>	North Pacific hake	US Pacific margin (northeastern Pacific), Saenich Inlet	3–1000	1.6–23.0	13.1–241.1	Chu and Tunnicliffe (2015)
<i>Merluccius angustimanus</i>	Panama hake	Mexico–Columbia (eastern tropical Pacific)	2–523	15.4–21.1	17.5–222.7	Bianchi (1991) and Stromme and Saetersdal (1988)

Continued

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)—cont'd

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range ($\mu\text{mol kg}^{-1}$)	Citations
<i>Merluccius capensis</i>	Cape hake	Angola to South Africa (southeastern Atlantic)	20–512	6.1–19.8	10.9–236.7	Hamukuaya et al. (2001), Mas-Riera et al. (1990), and Woodhead et al. (1998)
<i>Merluccius gayi gayi</i>	Whiting	Chilean margin (southeastern Pacific)	58–450	6.4–12.3	16.8–253.0	Chilean Fisheries Development Program, FIP2004–09
<i>Bregmacerotidae</i>						
<i>Bregmaceros bathymaster</i>	East Pacific codlet	Gulf of California (eastern tropical Pacific)	32–500	7.6–15.4	9.2–31.5	Davies et al. (2015)
<i>Bregmaceros cantori</i>	Striped codlet	Cariaco Trench, Venezuela to Brazil (western Atlantic)	450–846	14.2–26.9	4.0–222.7	Baird et al. (1973), Milliken and Houde (1984), and Love et al. (2004)
<i>Bregmaceros</i> sp.	Codlet	Indian margin (Arabian Sea)	540	12.1	0.34	Hunter et al. (2011)
<i>Bregmaceros</i> sp.	Codlet	Pakistan margin (Indian Ocean)	300	14.8	4.9–5.4	Murty et al. (2009)
<i>Moridae</i>						
<i>Physiculus roseus</i>	Rosy cod	Yemen margin (Arabian Sea)	277–510	–	13.3	Kukharev (2015)

Osmeriformes						
Argentinidae						
<i>Argentina aliciae</i>	Alice argentina	Nicaragua to Peru (eastern tropical Pacific)	73–300	13.8–17.1	16.2–46.4	Bianchi (1991)
Cottiformes						
Liparidae						
<i>Careproctus melanurus</i>	Blacktail snailfish	US Pacific margin (northeastern Pacific)	89–2286	1.8–7.2	13.1–133.0	Friedman et al. (2012), Day and Pearcy (1968), and Stein et al. (2006)
<i>Liparidae</i> sp.	Snailfish	Indian margin (Arabian Sea)	540	12.1	0.34	Hunter et al. (2011)
Scorpaeniformes						
Scorpaenidae						
<i>Pontinus sierra</i>	Speckled scorpionfish	Gulf of California to Panama (eastern tropical Pacific)	15–307	13.0–13.6	14.4–20.1	Bianchi (1991)
Sebastidae						
<i>Sebastolobus alascanus</i>	Shortspine thornyhead	US Pacific margin (northeastern Pacific)	54–1600	3.5–7.8	13.1–171.9	Friedman et al. (2012) and Day and Pearcy (1968)
<i>Sebastolobus altivelis</i>	Longspine thornyhead	US Pacific margin (northeastern Pacific)	201–1757	2.7–8.6	13.1–112.4	Friedman et al. (2012) and Day and Pearcy (1968)

Continued

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)—cont'd

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range ($\mu\text{mol kg}^{-1}$)	Citations
<i>Sebastes</i> sp.	Thornyhead	Canada Pacific margin (northeastern Pacific)	890	3.6–4	10.5–15.3	Juniper et al. (2013)
Anoplopomatidae						
<i>Anoplopoma fimbria</i>	Sablefish	US and Canada Pacific margin (northeastern Pacific)	175–2740	1.8–14.6	13.1–318.9	Friedman et al. (2012), Day and Pearcy (1968), and Juniper et al. (2013)
Triglidae						
<i>Chelidonichthys capensis</i>	Gurnard	Southeastern Atlantic and western Indian Ocean	10–390	6.1–20.5	16–222.3	Hamukuaya et al. (2001) and Mas-Riera et al. (1990)
Peristediidae						
<i>Satyrichthys adeni</i>	Yellowfinned searobin	Yemen margin (Arabian Sea)	71–378	7.9–17.3	13.3–213.1	Kukharev (2015)
Batrachoidiformes						
Batrachoididae						
<i>Aphos porosus</i>	Banded toadfish	Chilean margin (southeastern Pacific)	11–120	14.8–16.5	22–84.4	J. Sellanes (UCN) (unpublished data)

Order, family, species, common name, location, depth range (m), temperature range (°C), and oxygen range ($\mu\text{mol kg}^{-1}$), based on the Cited Literature, FishBase, and Encyclopedia of Life.

composition is observed along oxygen gradients as hypoxia-intolerant species are lost and tolerant species become abundant and dominate the community. Some studies of community shifts have been conducted across oxygen gradients (both with regard to latitude and depth) and insight has been gained from community changes during El Niño and La Niña conditions which greatly alter oxygenation. Based on previous research, we will focus at the regional level to categorize intolerant (those that show avoidance or mortality to severely hypoxic conditions) and tolerant (those inhabiting waters where $O_2 \leq 22 \mu\text{mol kg}^{-1}$) species. The names of known OMZ-dwelling fish species from around the world are compiled in [Table 1](#).

3.3 Regional Patterns in Space and Time

3.3.1 California Current Ecosystem

The US West Coast fish communities are among the best-studied on continental margins in part due to the extensive sampling by the National Oceanic and Atmospheric Administration (NOAA) Northwest Fisheries Science Center Groundfish Trawl Survey ([Keller et al., 2010, 2012, 2015](#)), research by the Monterey Bay Aquarium Research Institute (MBARI) ([Stein et al., 2006](#)) and the Scripps Institution of Oceanography on local OMZ communities, as well as the long-running oceanographic time-series from the California Cooperative Fisheries Investigation (CalCOFI) ([Netburn and Koslow, 2015](#)). Because the OMZ in the NE Pacific rarely reaches suboxic ($<5 \mu\text{mol kg}^{-1} O_2$) conditions, numerous demersal fish species are frequent inhabitants. In Monterey Canyon, California, six demersal and benthic fish species are present at ~ 450 – 1000 m water depths where the OMZ intercepts the continental margin ([Friedman et al., 2012](#)). These include the liparid, *Careproctus melanurus*, the sebastids, *Sebastes alascanus* and *Sebastes altivelis*, the anoplopomatid, *Anoplopoma fimbria*, the macrourid, *Nezumia liolepis*, and the pleuronectid *Microstomus pacificus*. These six species also occur in the OMZ off San Diego, California, at depths of ~ 450 – 800 m, in addition to the brotulid, *Cataetyx rubrirostris*, the nettastomatid, *Facciolella equatorialis*, the scyliorhinids, *Apristurus brunneus* and *Parmaturus xaniurus*, the pleuronectid, *Embassichthys bathybius*, and the myxinid, *Eptatretus deani* (N.D. Gallo et al., unpublished data). In the deeper OMZ off Oregon at 600 – 1100 m, the macrourids, *Coryphaenoides acrolepis* and *Coryphaenoides pectoralis*, the pleuronectids, *M. pacificus* and *E. bathybius*, the sebastids, *S. alascanus* and *S. altivelis*, the liparid, *C. melanurus*, the anoplopomatid, *A. fimbria*, the myxinid, *Eptatretus* sp., and the arhynchobatids, *Bathyraja interrupta* and *Bathyraja trachura*, were

found to be common community members (Day and Percy, 1968). *Microstomus pacificus*, occupies the greatest depth range (57–1217 m) of any fish species on the US West Coast (Keller et al., 2015), showing tolerance to a broad range of temperature, pH, oxygen, and pressure conditions.

In an analysis of the probability of occurrence of four mainly non-OMZ-dwelling Eastern Pacific demersal fish species, the chimaera, *Hydrolagus collieri*, and the pleuronectid, *Eopsetta jordani*, were found to be sensitive to near-bottom oxygen concentration, while the sebastid, *Sebastes elongatus*, and pleuronectid, *M. pacificus* showed no changes in probability of occurrence in relation to bottom oxygen concentrations (Keller et al., 2015). The lack of response from *S. elongatus* is surprising given that rockfish are thought to be sensitive to hypoxia, however this species is not found within the OMZ and may be sensitive to severely hypoxic conditions but not oxygen concentrations in its native depth range. High rockfish (*Sebastes* sp.) mortalities were observed off Oregon during an incursion of hypoxic water onto the inner shelf (<70 m) (Grantham et al., 2004). The pleuronectid, *Hippoglossus stenolepis*, also appears to be intolerant of OMZ conditions and exhibits an apparent minimum dissolved oxygen threshold of $\sim 39 \mu\text{mol kg}^{-1}$ (Sadorus et al., 2014).

Several studies from Canada have also shown responses of the demersal fish community to changes in oxygen as well as considerable tolerance to hypoxia. Due to the presence of a shallow-water sill and high productivity in the Saanich Inlet, the inlet becomes seasonally hypoxic, and changes are observed in the epibenthic community at 100 m (Chu and Tunnicliffe, 2015; Matabos et al., 2012). More than half of the variance in the entire epibenthic species assemblage was explained by components of the oxygen regime (Chu and Tunnicliffe, 2015). The pleuronectid, *Lyopsetta exilis*, was abundant during severely hypoxic ($\text{O}_2 < 22 \mu\text{mol kg}^{-1}$) conditions when bacterial mats were present (Chu and Tunnicliffe, 2015; Matabos et al., 2012). Interestingly, *L. exilis* is a common species along the entire US Pacific margin but, does not occur within the OMZ off California or Oregon, even though it commonly inhabits severely hypoxic waters in Saanich Inlet. This is likely because its distribution along the US Pacific margin is being set by other environmental factors (depth, temperature, prey availability) or their interaction with hypoxia tolerance (Vaquer-Sunyer and Duarte, 2011). The bathymasterid, *Ronquilus jordani*, the cottid, *Scorpaenichthys marmoratus*, the pleuronectid, *Lepidopsetta bilineata*, the stichaeidid, *Lumpenus sagittal*, the paralichthyid, *Citharichthys* sp., and the gadid *Theragra chalcogramma* all appeared only after oxygen content increased

to $>22 \mu\text{mol kg}^{-1}$ (Chu and Tunnicliffe, 2015; Matabos et al., 2012). Differing results were found by Chu and Tunnicliffe (2015) and Matabos et al. (2012), for the presence of the stichaeid, *Plectobranchnus evides*, the agonid, *Xeneretmus latifrons*, and the merlucciid, *Merluccius productus* under severely hypoxic conditions ($\text{O}_2 < 22 \mu\text{mol kg}^{-1}$) in the Saanich Inlet, with their presence being noted by Chu and Tunnicliffe (2015), and absence noted by Matabos et al. (2012). Rockfish (*Sebastes* sp.) were only present during the highest oxygen periods ($\sim 88\text{--}131 \mu\text{mol kg}^{-1}$) and were absent when conditions were severely hypoxic (Matabos et al., 2012). Interestingly, oxygen appears to also control species interactions. For example, Doya et al. (2016) noted that squat lobster–pleuronectid interactions may be mediated by oxygenation in Saanich Inlet.

At a deeper site (890 m) off Canada in Barkley Canyon, the NEPTUNE observatory recorded the presence of the following fish species living under severely hypoxic conditions ($\text{O}_2 \sim 10.5\text{--}15.3 \mu\text{mol kg}^{-1}$) within the OMZ core: the anoplopomatid, *A. fimbria*, the myxinid, *Eptatretus* sp., an unidentified zoarcid, the agonid, *BathYGONUS nigripinnis*, the sebastid, *Sebastolobus* sp., and the pleuronectid, *E. bathybius* (Juniper et al., 2013). Of these, *A. fimbria* was the only fish species present consistently during the year-long study, while other species were more sporadic (Juniper et al., 2013).

3.3.2 Eastern Tropical Pacific—Gulf of California

The Gulf of California, which hosts an extension of the NE Pacific OMZ, is an interesting area for studying the influence of severe hypoxic conditions on the demersal fish community due to the presence of a very thick OMZ with a shallow upper boundary in the southern Gulf of California. The few published studies that are available document several fish species living at very low-oxygen levels, such as the ophidiid, *Cherublemma emmelas*, at $\sim 5.7\text{--}8.8 \mu\text{mol kg}^{-1}$ (Aguirre-Villaseñor and Castillo-Velázquez, 2011), and the scyliorhinid, *Cephalurus cephalus*, living at $\sim 6.1 \mu\text{mol kg}^{-1}$ (Aguirre-Villaseñor and Salas-Singh, 2012) (Fig. 3). Additional demersal fish distributions in the Gulf of California are provided by Fischer et al. (1995), but oxygen values are not given for the observations; however, based on the depth distributions provided (Fischer et al., 1995) and the known hydrography of the Gulf of California (Aguirre-Villaseñor and Salas-Singh, 2012), there are likely many other fish species living under OMZ conditions. Larval midwater fish habitats in the Gulf of California are known to be affected by the steep oxygen gradients, with shallow hypoxic conditions partitioning

groups of fish species but not affecting total larval fish abundance (Davies et al., 2015), and interestingly, the highest larval fish species richness was observed within the subsurface hypoxic habitat ($\sim 8.8\text{--}43.8 \mu\text{mol kg}^{-1}$), which was dominated by the codlet, *Bregmaceros bathymaster* (Davies et al., 2015).

3.3.3 Eastern Tropical Pacific—Volcano 7

Volcano 7 is an inactive seamount at $13^{\circ}23' \text{ N}$ and $102^{\circ}27' \text{ W}$, which rises from a depth of 3400 m to 730 m and penetrates the OMZ (72–1302 m) in the eastern tropical Pacific with the lowest oxygen levels present at the summit ($\sim 3.5\text{--}3.9 \mu\text{mol kg}^{-1}$) (Wishner et al., 1990, 1995). The lowest megafaunal abundances (including fish) on the seamount were observed at the uppermost region when oxygen was $\sim 3.5\text{--}3.9 \mu\text{mol kg}^{-1}$, while the highest megafaunal abundances (including fish) were observed at only slightly higher oxygen levels of $\sim 4.8\text{--}7 \mu\text{mol kg}^{-1}$. This illustrates the non-linearity of community responses to small changes in environmental oxygen conditions. The only megafauna observed on the upper summit of Volcano 7 were the macrourid, *N. liolepis*, (49.2% of the megafauna community), and solitary sessile coelenterates (Levin et al., 1991). Just below the upper summit, where oxygen levels were slightly higher ($\sim 5.7 \mu\text{mol kg}^{-1}$) and where the range in oxygen levels was greater due to internal tide oscillations (Wishner et al., 1990, 1995), diversity of the megafauna community increased and *N. liolepis*, anemones, galatheid crabs, serpulid polychaetes, sponges, and ophiuroids dominated the community (Levin et al., 1991). *Nezumia liolepis* was the only megafauna species consistently observed on both the upper and lower summit, but abundances were much higher on the lower summit, with 1.8 individuals m^{-2} being the maximum density observed (Wishner et al., 1990).

3.3.4 Eastern Tropical Pacific—Mexico and Central America

The Pacific Coast of Mexico is a very data-poor region, even though the thick and intense OMZ likely exerts a strong influence on the demersal fish communities along the margin. Off Central America, the OMZ can be 1200 m thick with an upper boundary that can be as shallow as 50 m (Bianchi, 1991; Wyrki, 1966) and temperatures at the upper boundary are relatively warm ($\sim 15^{\circ}\text{C}$) (Bianchi, 1991; Levin et al., 2015) (see Fig. 2B). OMZ conditions were typically found at the edge of the continental shelf and upper slope throughout the year (Stromme and Saetersdal, 1988). Oxygen concentrations at the OMZ core are much lower than in the core of the US West Coast or Alaskan OMZ (see Fig. 2A).

Bianchi (1991) examined how environmental conditions structure demersal assemblages using data from 348 trawls spanning 10–500 m depths, along 685 nautical miles of coastline including the shelf and slope edge of southern Mexico, Guatemala, El Salvador, Honduras, Nicaragua, and northern Costa Rica. This study found that the assemblage characterized as living at the lowest oxygen concentrations encountered in the study ($O_2 \sim 17.5 \pm 4.4 \mu\text{mol kg}^{-1}$, $T = 13 \pm 1^\circ\text{C}$) was characterized by the highest abundances of individuals and the highest biomass, with much of the biomass due to galatheid crustaceans. Several demersal fish species were also common community components in this OMZ assemblage and included the argentiniid, *Argentina aliciae*, the serranid, *Diplectrum macropoma*, the merlucciid, *Merluccius angustimanus*, the trichiurid, *Trichiurus nitens*, the scorpaenid, *Pontinus sierra*, and the bothid, *Monolene maculipinna* (Bianchi, 1991). *Diplectrum macropoma* was the only demersal fish species that was unique to the OMZ community and not part of the other seven identified assemblages (Bianchi, 1991). Demersal fish species that are present in the assemblage that is characterized by oxygen limited conditions ($O_2 \sim 30.6 \pm 4.4 \mu\text{mol kg}^{-1}$), but are absent from the OMZ assemblage and may be intolerant of OMZ conditions include the stromateid, *Peprilus snyderi*, the batrachoidid, *Porichthys nautopaedium* (now *P. margaritatus*), the triglid, *Prionotus quiescens* (now *P. stephanophrys*), the synodontid, *Synodus evermanni*, the ogocephalid, *Zalietes elater*, and the paralichthyid, *Citharchthys platophrys* (Bianchi, 1991). Additional sampling carried out outside of Nicaragua in deeper water (300–350 m) found that demersal species assemblages associated with OMZ conditions exhibited low faunal diversity, but the ophidiid, *C. emmelas*, and the merlucciid, *M. angustimanus*, were some of the only species present under these conditions (Stromme and Saetersdal, 1988), suggesting high hypoxia tolerance. Most demersal fish species that form important fisheries off Central America, including butterfish (*Peprilus* spp.), sea bass (*Hemanthias* sp. and *Diplectrum euryplectrum*), snapper (*Lutjanus* sp.), and grunts (*Pomadasyd* sp. and *Orthopristis* sp.), are not components of the OMZ assemblage (Stromme and Saetersdal, 1988), suggesting that fisheries resources here may be particularly vulnerable to habitat compression within the relatively narrow zone above the OMZ, as severely hypoxic waters expand with climate change.

3.3.5 Humboldt Current Ecosystem—Peru and Chile

There has been more historical focus on the influence of ENSO events and changes in oxygenation on the pelagic community in the Humboldt Current System than the demersal community because the pelagic fish

community is very important economically. At present, the western coast of South America produces more fish per unit area than any other region in the world ocean (Montecino and Lange, 2009). Industrial demersal fisheries are comparatively small in the Humboldt Current System, making up <1% of total fish landings in Peru (Montecino and Lange, 2009). However, there are some demersal fish species including the macrourid, *Macruronus magellanicus*, the merlucciids, *Merluccius gayi gayi* and *Merluccius gayi peruanus*, the arhynchobatid, *Raja chilensis* (now *Sympterygia lima*), the ophidiids, *Gerypteris* spp., and the paralichthyids, *Paralichthys* spp. and *Hippoglossina* sp., that are commonly landed off Peru and Chile (Montecino and Lange, 2009). The hake fishery in Peru (*Merluccius gayi peruanus*) has recently shown a significant decline, attributed both to overfishing and population vulnerability to environmental stress (Ballón et al., 2008; Guevara-Carrasco and Leonart, 2008; Montecino and Lange, 2009). Fish scales and osseous skeletal materials in laminated sediment cores have been used as a proxy for studying changes in fish abundances in the Peruvian and Chilean OMZ over historical time (Díaz-Ochoa et al., 2009; Milessi et al., 2005). While these cores shed light on historical changes for pelagic species, relatively few data are available about the demersal communities because scales and skeletal materials from small pelagics dominate the cores (Díaz-Ochoa et al., 2009; Milessi et al., 2005).

The OMZ in the eastern South Pacific is thickest (>600 m) and shallowest (<150 m) off Peru, and the upper boundary shoals near the coast extending into the euphotic zone in some places (Fuenzalida et al., 2009). As a result, the demersal fish community off Peru is likely intimately shaped by the steep oxygen gradients and severely hypoxic conditions, but there are few published studies of this community. A study of benthic biomass changes across oxygen and depth gradients for filamentous bacteria, macrobenthos, and demersal fish catch was carried out at 65 stations spanning 35–359 m and oxygen conditions from ~ 9.2 to $68.7 \mu\text{mol kg}^{-1}$ (Rosenberg et al., 1983). Macrobenthic biomass peaked at $\sim 26.3 \mu\text{mol kg}^{-1}$ and then declined with decreasing oxygen levels. Demersal fish catches appeared to peak between ~ 35 and $17.5 \mu\text{mol kg}^{-1}$, and fish catches were positively correlated to high macrobenthic biomass ($p < 0.001$), but negatively correlated to the occurrence of filamentous bacteria ($p < 0.01$) that occur in severely hypoxic environments (Rosenberg et al., 1983). Additional analysis of data in Rosenberg et al. (1983) indicate no significant difference between demersal fish catch for areas where $\text{O}_2 > 22 \mu\text{mol kg}^{-1}$ ($519.76 \pm 197.90 \text{ kg}/20 \text{ min}$) and where $\text{O}_2 < 22 \mu\text{mol kg}^{-1}$ ($315.52 \pm 258.98 \text{ kg}/20 \text{ min}$), but that variance in

catches increases in the severely hypoxic areas. Below $15.3 \mu\text{mol kg}^{-1}$, demersal fish catches were much lower ($<100 \text{ kg}/20 \text{ min}$) for all samples (Fig. 4B) (Rosenberg et al., 1983). Unfortunately, no data were given in Rosenberg et al. (1983) about the composition of these catches and it is likely that the composition of the fish community differs at the severely hypoxic sites. Based on the published latitudinal and bathymetric distribution of a number of fish species off Peru and Chile (Fischer et al., 1995; Sielfeld and Vargas, 1999) in areas and depths where severely hypoxic conditions are known (Fuenzalida et al., 2009; Helly and Levin, 2004), there are likely

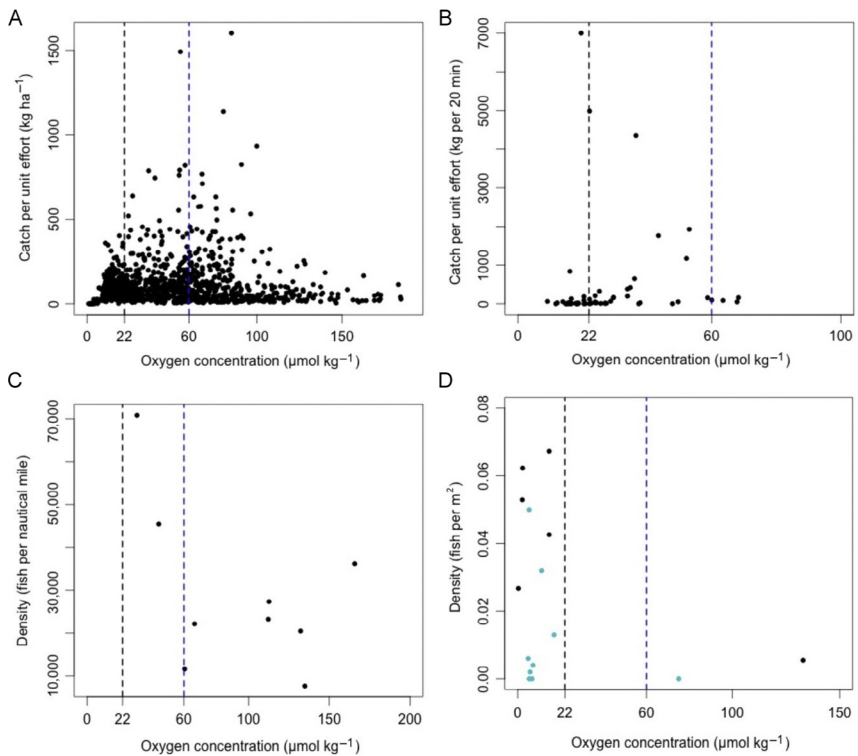


Fig. 4 Changes in fish catch per unit effort (CPUE) or density with oxygen concentrations ($\mu\text{mol kg}^{-1}$) in four different oxygen minimum zone (OMZ) regions: (A) US West Coast from Keller et al. (2015), (B) Peruvian margin from Rosenberg et al. (1983), (C) Namibian margin from Mas-Riera et al. (1990), (D) Arabian Sea including data from Murty et al. (2009) (turquoise; light grey in the print version) from the Pakistan margin and Hunter et al. (2011) (black) from the west Indian margin. Blue (dark grey in the print version) dashed line indicates the oxygen limited zone (OLZ) boundary ($60 \mu\text{mol kg}^{-1}$) and black dashed line indicates the OMZ boundary ($22 \mu\text{mol kg}^{-1}$).

many demersal fish species in the Humboldt Current System that are highly adapted to living under severe hypoxia.

A study using Agassiz trawls at depths ranging from 120 to 2201 m at three locations off Chile, found that depth and dissolved oxygen levels were the main factors responsible for influencing megafaunal changes along the shelf and slope (Quiroga et al., 2009). Where oxygen levels fell below $\sim 6.66 \mu\text{mol kg}^{-1}$, megafaunal species were nearly absent, however one species of macrourid, *Trachyrincus villegai*, was captured in the OMZ at 317 m ($\text{O}_2 \sim 2.6 \mu\text{mol kg}^{-1}$) (Quiroga et al., 2009) (Table 1; Fig. 3). Interestingly, this species was only observed at this one OMZ core station and was not captured during any additional trawls in higher oxygen conditions suggesting that it may be an OMZ specialist. Compared to the distribution of demersal fish species along oxygen gradients on the US margin, it appears the Chilean fish community is relatively depauperate based on the findings of Quiroga et al. (2009); even sites outside of the OMZ exhibited lower species richness and abundance. However, this may also be an artefact of the different trawl types used for sampling off Chile and off the United States.

New unpublished trawl data (J. Sellanes, Universidad Catolica del Norte, personal communication, 22 January 2016) off Coquimbo, Chile ($\sim 30^\circ\text{S}$), reveal that three additional demersal fish species inhabit the Chilean OMZ (depth $\sim 50\text{--}300$ m, $\text{O}_2 \sim 2.2\text{--}22.0 \mu\text{mol kg}^{-1}$): the paralichthyid, *Hippoglossina macrops*; the batrachoidid, *Aphos porosus*; and the scyliorhinid, *Cephalurus* sp. cf. Unpublished trawl data from 2004 from the Chilean Fisheries Development Program (IFOP, 2005), spanning $29\text{--}42^\circ\text{S}$ and depths $58\text{--}450$ m, reveal three demersal fisheries species also inhabiting the Chilean OMZ ($\text{O}_2 \sim 16.9\text{--}22.0 \mu\text{mol kg}^{-1}$): the merlucciid, *Merluccius gayi gayi*; and the ophidiids, *Genypterus maculatus* and *Genypterus blacodes*. Therefore, further research may show that demersal fish are also well represented in the Chilean OMZ benthic community.

Changes in the benthic community due to increased oxygenation during El Niño events also offer insight into the sensitivity of certain species to hypoxia. During El Niño, the merlucciid, *Merluccius gayi peruanus*, which usually lives north of Chimbote, Peru, due to the low-oxygen conditions in the south, extends its distribution southward and beyond the slope margin, and switches to a demersal life style because of the improved oxygen and food conditions at the seafloor (Arntz et al., 2006; Espino, 1999; Espino et al., 1985; Wosnitza-Mendo and Espino, 1986). The sciaenid, *Sciaena deliciosa*, also migrate offshore and feed on anchovies that have a deeper depth distribution during El Niño conditions (Arntz and Tarazona,

1989). ENSO-driven changes in the meiofauna and macrofauna communities (Gutierrez et al., 2008; Levin et al., 2002; Sellanes et al., 2007) may also give rise to different prey availability for demersal fish during El Niño conditions.

3.3.6 Benguela Current Ecosystem—Namibia

In the Benguela Current, only a small part of the Namibian coastline is exposed to OMZ conditions, unlike the widespread OMZs in the California Current, Humboldt Current, and Indian Ocean (Fig. 3). The lowest averaged seafloor values of dissolved oxygen are $<13.1 \mu\text{mol kg}^{-1}$ and occur on the inner shelf immediately north of Walvis Bay (Dingle and Nelson, 1993). Both north and south of Walvis Bay, oxygen concentrations increase above $43.8 \mu\text{mol kg}^{-1}$. Several studies off Namibia have shown that oxygen levels play a major role in determining the composition and distribution of the demersal fish community and that certain fish assemblages are specifically present at low-oxygen levels (Hamukuaya et al., 2001; Mas-Riera et al., 1990). On the shelf and upper slope, five distinct assemblages were observed based on multiple bottom trawl samples collected during the years 1992–1996, and spanning $17\text{--}29^\circ\text{S}$ along the Namibian coastline at depths between 50 and 600 m (Hamukuaya et al., 2001). Teleosts were the dominant demersal taxa (92–96%), followed by chondrichthyans (2–6%), and invertebrates (1–3%) (Hamukuaya et al., 2001). Analysis of trawl data indicated four clear assemblages along the shelf and upper slope and revealed a clear spatial correlation between the distribution of low-oxygen levels and the distribution of the northern shelf assemblage. The northern shelf assemblage was composed of the merlucciid, *Merluccius capensis*, the gobiid, *Nematogobius bibarbatus* (now *Sufflogobius bibarbatus*), and the triglid, *Chelidonichthys capensis*; these species made up 76–80%, 12–17%, and 2–3% of the community respectively (Hamukuaya et al., 2001). Following the upwelling season when oxygen levels $<43.8 \mu\text{mol kg}^{-1}$ expanded to cover the region, this northern shelf assemblage expanded its distribution into deeper water from 50–280 m to 50–346 m (Mas-Riera et al., 1990). This community also exhibited responses to seasonal (Macpherson and Gordo, 1992) and interannual (Hamukuaya et al., 2001) variability, with the northern and central shelf assemblages expanding into deeper water during the Benguela Niño (1993 and 1995) (Hamukuaya et al., 2001).

Other dominant species that were present off Namibia where O_2 levels were $<22 \mu\text{mol kg}^{-1}$, included the carangid, *Trachurus trachurus capensis*, and the soleid, *Austroglossus microlepis* (Hamukuaya et al., 2001). *Sufflogobius*

bibarbatus and *A. microlepis* are also known to occur off South Africa at similar depths but under higher oxygen conditions (Roel, 1987). Species that were excluded from these severely hypoxic regions off Namibia, but were dominant within the OLZ included the sparid, *Dentex macrophthalmus*, the albulid, *Pterothrissus belloci*, the acropomatid, *Synagrops microlepis*, the chlorophthalmid, *Chlorophthalmus atlanticus*, the lophiid, *Lophius vomerinus*, and the sebastid, *Helicolenus dactylopterus* (Mas-Riera et al., 1990). The incredible hypoxia tolerance of *S. bibarbatus*, and the keystone role this species may have in the hypoxic Namibian shelf ecosystem, have been noted in several studies (Salvanes et al., 2011; Utne-Palm et al., 2010).

Hypoxia-intolerant fish species have also been noted in the Benguela Current. The merlucciid, *Merluccius paradoxus*, the zeid, *Zeus capensis*, and the scyliorhinid, *Holohalaelurus regani*, contract their range to the more southern area during the upwelling season when oxygen levels on the northern shelf are low and expand northward prior to the upwelling season when oxygen levels are higher (Mas-Riera et al., 1990), suggesting that they are sensitive to low-oxygen concentrations ($<43.8\text{--}65.6\ \mu\text{mol kg}^{-1}$). Mortality was observed for the soleid, *Solea bleekeri*, the sebastid, *H. dactylopterus*, the sciaenid, *Argyrosomus* sp., the scyliorhinid, *Haploblepharus pictus*, the sparid, *Pachymetopon blochii*, and the clinid, *Clinus* sp., during hypoxic events occurring during March–May of 1997 (Arntz et al., 2006). However, it is difficult to attribute these directly to hypoxia intolerance given that sulphide (H_2S) eruptions frequently accompany hypoxic events on the inner shelf off Namibia. Hake have also been observed to show avoidance behaviour during these hypoxic events and typically migrate offshore (Arntz et al., 2006; Bailey et al., 1985). The two dominant species of hake in the Benguela Current (*M. capensis* and *M. paradoxus*) exhibit different tolerances to low-oxygen conditions. *Merluccius capensis* is dominant in areas with extremely low-oxygen concentrations, and can tolerate oxygen concentrations as low as $\sim 10.9\ \mu\text{mol kg}^{-1}$ (Woodhead et al., 1998), while *M. paradoxus* is dominant at similar depths but in areas where oxygen levels are $>65.6\text{--}87.5\ \mu\text{mol kg}^{-1}$ (Mas-Riera et al., 1990). Future research could use these two congeneric species to identify adaptations that confer hypoxia tolerance in *Merluccius*.

In contrast to oxygen conditions off Namibia, the shelf and upper slope of Angola does not experience $\text{O}_2 < 43.8\ \mu\text{mol kg}^{-1}$ and the deep continental slope assemblage ($\sim 350\text{--}550\ \text{m}$) identified living under OLZ conditions was composed of the merlucciid, *Merluccius polli*, the albulid, *P. belloci*, the ogcocephalid, *Dibranchius atlanticus*, the macrourid, *Malacocephalus occidentalis*, the acropomatid, *S. microlepis*, the chlorophthalmid, *C. atlanticus*,

the solenocerid, *Solenocera africana*, the morid, *Laemonema* sp., the trichiurid, *Benthodesmus tenuis*, and the centrophorid, *Centrophorus granulosus* (Bianchi, 1992). In South Africa, oxygen conditions are also higher than off Namibia and shelf and upper slope communities do not experience OMZ conditions (Smale et al., 1993) (see Fig. 3).

3.3.7 Northern Indian Ocean—Arabian Sea

The Arabian Sea can be divided oceanographically into areas north and south of 15°N, each with considerable difference in fish composition (Madhupratap et al., 2001). In the north, the OMZ occurs at a shallower depth than in the south, which may give rise to some of these differences. Nearly all landings of Bombay duck (the synodontid, *Harpadon nehereus*) which makes up 7% of total landings in the Arabian Sea, and the majority of croakers, eels, elasmobranchs, catfish, and threadfins, are caught north of 15°N (Madhupratap et al., 2001). In contrast, the majority of perches and flatfish are caught south of 15°N (Madhupratap et al., 2001).

The influence of monsoon-driven, low-oxygen conditions on near-shore, demersal fisheries species on the west coast of India received significant attention in the 1950–1970s (Banse, 1959, 1968; Carruthers et al., 1959). Off Cochin in the Arabian Sea, the deoxygenation of near-bottom water during the SW monsoon resulted in the regular disappearance of demersal fishes on the shelf and the area covering the middle and outer shelf between Cochin and Karachi became unprofitable for trawling (Banse, 1968). Paired hydrographic and trawl data from the shelf off Cochin showed that demersal fish disappeared within several days from the shallower part of the shelf (<20 m) with the onset of the SW monsoon (~June), suggesting that the fish were rapidly escaping upwelling-driven low-oxygen conditions (Banse, 1959). The acropomatid, *Synagrops japonicus*, a typically abundant species (>1000 lbs per haul) and an important fisheries species, was noted to have changed its distribution, thus avoiding upwelled hypoxic waters off Cochin (Banse, 1959). Oxygen concentrations below ~22 $\mu\text{mol kg}^{-1}$ appeared to be critical to this change in distribution (Banse, 1959, 1968), suggesting that the species is not tolerant to OMZ conditions but sometimes inhabits areas within the OLZ. Other fish that appear to be sensitive to upwelled, severely hypoxic conditions include the cynoglossid, *Cynoglossus macrostomus*, which disappears from shore along the Malabar Coast during the onset of the SW monsoon and returns to shore by midwater after the monsoon has passed (George, 1958). *Cynoglossus macrostomus* appears to wait out the severely hypoxic conditions by moving into deeper areas during the

monsoon months (Khan and Nandakumaran, 1993). The habitat of the gobiid, *Trypauchen vagina*, has also been documented to become compressed to inshore, shallower waters at the onset of monsoon conditions (Seshappa, 1953). Upon relaxation of upwelling, and return to oxygen-rich conditions, favourable trawling conditions were observed to become rapidly re-established within days (Banse, 1959) indicating that these fish respond quickly to oxygen changes and return to their preferred habitat when preferable oxygen conditions are re-established. Of note, mortality was observed off Cochin during the flood tide in the peak of the upwelling season, when dead fish were reported to float into the harbour of Cochin, and it was thought that the fish were being trapped in the deoxygenated, upwelled water (Banse, 1968).

While fish do not appear to be tolerant of OMZ conditions in the shallower ecosystems of the Arabian Sea, in deeper water fish are important components of the margin community. A study conducted on the Pakistan margin using photographic transects through the OMZ at nine depths (140, 300, 400, 700, 900, 1000, 1100, 1200, and 1850 m) revealed that while benthic invertebrates (megafauna *sensu stricto*) were entirely absent in the OMZ core and lower transition zone (300–900 m, $O_2 \sim 5.3\text{--}6.6 \mu\text{mol kg}^{-1}$), fish and natant decapods were fairly common at 300 m, and fish were the only metazoan megafauna seen in photographs from 700 m ($O_2 \sim 5.3 \mu\text{mol kg}^{-1}$) (Murty et al., 2009). Eleven fish species were observed on the Pakistan margin OMZ: the bregmacerotid, *Bregmaceros* sp.; the ophiidiid, *Brotulotaenia* sp.; an unidentified carangid, *Carangidae* sp.; the halosaur, *Halosaurus* sp.; the notocanthid, *Notocanthus* sp.; the synodontid, *Saurida tumbil*; the serrivomerid, *Serrivomer* sp.; the epigonid, *Epigonus* sp.; Actinopterygii sp.; the congrid, *Congridae* sp.; the etmopterid, *Centroscyllium ornatum* (Murty et al., 2009) (Table 1). A study conducted using video footage from the west Indian margin at depths between 530 and 2000 m, identified the following fish taxa living within or just below the OMZ: the liparid, *Liparidae* sp.; the ophiidiid, *Holcomycteronus* sp.; the macrourid, *Coryphaenoides* sp.; the congrid, *Congridae* sp.; the synaphobranchid, *Synaphobranchus* sp.; the etmopterid, *Etmopterus* sp.; the arhynchobatid, *Bathyraja* sp. (Hunter et al., 2011). The study also listed *Gobiidae* sp., however this was a misidentification and was really a bregmacerotid, *Bregmaceros* sp., (L.A. Levin, personal observation, 20 July 2015). *Liparidae* sp. and *Bregmaceros* sp. were the resident fish fauna within the OMZ core (Hunter et al., 2011). Contrary to common expectation, such observations suggest that these fish species may be some of the most hypoxia-tolerant megafauna on the margins of the Arabian Sea.

In the northwestern Arabian Sea, off Yemen, several permanent demersal fish OMZ inhabitants were described by [Kukharev \(2015\)](#) including the synodontids, *Saurida undosquamis* and *Harpadon squamosus*, the trichiurid, *Lepturacanthus* spp., the peristediid, *Satyrichthys adeni*, the acropomatid, *Syngnagrops adeni*, the percophid, *Bembrops caudimacula*, the morid, *Physiculus roseus*, the nettastomatid, *Nettastoma* sp., the trachichthyid, *Hoplostethus* spp., the centrophorid, *C. granulosus*, the scyliorhinid, *Halaehurus* spp., and the prosylliid, *Eridacnis radcliffei*. [Kukharev \(2015\)](#) notes that two species also diurnally migrate into the OMZ from shallower depths, including the centrolphid, *Psenopsis cyanea*, and the scombrid, *Scomber australasicus*.

In the Sea of Oman, severely hypoxic water is found at shallower depths during the summer and fall ($22 \mu\text{mol kg}^{-1}$ boundary at ~ 130 m) and deeper during the winter and spring ($22 \mu\text{mol kg}^{-1}$ boundary at ~ 180 m). Near-shore, the OMZ upper boundary can occur even shallower (~ 90 m) and over 70% of the Omani shelf can be covered by OMZ conditions ([Piontkovski and Al-Oufi, 2014](#)). Oxygen depletion in Omani coastal waters has resulted in periodic fish kills, with the frequency of fish kill incidences increasing in the fall in the western Arabian Sea ([Piontkovski et al., 2012](#)). Seasonal oxycline shoaling during the summer and fall also results in habitat compression for myctophids and artisanal fisheries species ([Piontkovski and Al-Oufi, 2014](#)). Habitat compression of fisheries species results in increased fisheries landings and there was a significant relationship found between the depth of the $\sim 87.5 \mu\text{mol kg}^{-1}$ oxygen boundary and the total landings of sailfish, with landings increasing in a nonlinear fashion due to habitat compression for the species as the oxycline shoaled ([Piontkovski and Al-Oufi, 2014](#)). Demersal fish species also appeared to exhibit habitat compression and were found to be concentrated closer to the coast during the low-oxygen conditions of the fall. Demersal species were widely distributed on the shelf during the higher oxygen conditions characteristic of the winter monsoon ([Piontkovski and Al-Oufi, 2014](#)). Shoaling of severely hypoxic waters during the fall was hypothesized to have led to the displacement of the shelf fish community and to changes in demersal fish species diversity. Diversity was almost twice as high in March (38 unique species observed) when oxygen was higher, in comparison to November (22 unique species observed) when oxygen was lower ([McIlwain et al., 2011](#)). Most species were either present in lower abundances or absent in the lower oxygen conditions in November, with the carangid, *Decapterus russelli*, which was previously a dominant species, showing dramatic declines in abundance ([McIlwain et al., 2011](#)). In contrast, several species including the agonid, *Holapogon maximus*; the carangid,

Carangoides sp. (identified as *Carangoides* sp. 2); the muraenid, *Gymnothorax* spp.; the nemipterid, *Nemipterus japonicus*; the serranid, *Epinephelus epistictus*; and the triakid, *Iago omanensis*, increased in abundance during the low-oxygen conditions (McIlwain et al., 2011), which may indicate that they are more tolerant of these severely hypoxic conditions. McIlwain et al. (2011) noted that oxygen was not measured during the course of their study but that comparisons were made using hydrographic data from other studies in the area in which seasonal oxygen measurements were made.

3.3.8 Northern Indian Ocean—Bay of Bengal

To our knowledge, no scientific studies have focused on the role of oxygen gradients in structuring the demersal fish community in the Bay of Bengal, which has a thick OMZ (Fig. 2). This represents a large data gap in our knowledge. The OMZ on the East Indian margin extends from 100 to 900 m, and O_2 is $<15.3 \mu\text{mol kg}^{-1}$ in the OMZ core (Raman et al., 2015). Reports describing demersal resources have been produced by the Food and Agriculture Administration of the United Nations (Nishida and Sivasubramaniam, 1986) but paired data on environmental variables and demersal community composition are not available. Based on the identified depth distribution (300–600 m) and the known hydrography of the region, it is probable that the chlorophthalmid, *Chlorophthalmus* sp., the peristediid, *Peristedion* sp., the acropomatids, *Acropoma* sp. and *Synagrops* sp., the synodontid, *Saurida* sp., the nomeids, *Cubiceps* sp. and *Psenes* sp., the centrolophid, *Palinurichthys* sp., the scyliorhinid, *Haploblepharus* sp., the carcharhinid, *Scoliodon* sp., the sphyrnid, *Sphyrna* sp., the squatinid, *Squatina* sp., the nettastomatid, *Nettastoma* sp., and unidentified triacanthodids and priacanthids reside within the OMZ in severely hypoxic conditions in the Bay of Bengal (Nishida and Sivasubramaniam, 1986).

3.4 Effects of Oxygen on Fish CPUE, Biomass, and Density

In reviewing the available studies on demersal fish communities in OMZs, the relationship between oxygen levels and demersal fish density, biomass, or catch per unit effort (CPUE) is variable (Fig. 4). In many regions, studies find a decrease in demersal fish density, biomass, or CPUE with decreasing oxygen levels, although this effect is typically nonlinear with greater reductions happening below certain oxygen thresholds. This oxygen threshold is region-specific and likely influenced by the geologic history of the area, the local depth, and temperature of the OMZ, and the demersal fauna present in that area.

Along the entire US Pacific Coast, the CPUE of demersal fish species exhibited significant positive relationships with near-bottom oxygen concentrations (Keller et al., 2015). Near-bottom oxygen concentrations exert a stronger influence on demersal fish CPUE at lower oxygen concentrations ($\text{DO} < \sim 60 \mu\text{mol kg}^{-1}$) (Keller et al., 2015), implying a nonlinear response of community biomass to oxygen concentration. Bottom oxygen concentration explained up to 84% of the variation in biomass for individual species and 31–69% of the depth-specific variation in biomass along a hypoxic gradient off Oregon (Keller et al., 2010). Off Peru, CPUE of demersal fish catches decreases strongly when oxygen levels falls below $15.3 \mu\text{mol kg}^{-1}$ (Rosenberg et al., 1983). Between Bombay and Karachi in the Indian Ocean, CPUE of commercially exploited fishes also appears to be positively related to the oxygen content of the near-bottom water and during the southwest monsoon and postmonsoon seasons when oxygen declines, the entire shelf < 50 m off the west coast of India and Pakistan may be devoid of exploitable concentrations of the demersal fish species (Banse, 1968). Similarly, in the Baltic, bottom trawling becomes unprofitable when low-oxygen conditions result in cod either moving away or moving into the midwater (Berner and Schemainda, 1957).

Other studies have indicated that there is variability in the influence of oxygenation on fish density. The highest densities of fish observed by Murty et al. (2009) on the Pakistan margin in the Arabian Sea were observed at 300 m within the OMZ core, where oxygen levels were $5.36 \mu\text{mol kg}^{-1}$ and the temperature was 14.8°C . At this depth, the community was composed of, in order of dominance, the synodontid, *Saurida tumbil*, the bregmacerotid, *Bregmaceros* sp., and the carangid, *Carangidae* sp., and the total density was $0.05 \text{ individuals m}^{-2}$ (Murty et al., 2009). In the northwest Arabian Sea on the Yemen margin, high biomass populations of demersal fish were also found in the OMZ (Kukharev, 2015). In contrast, on the Indian margin of the Arabian Sea, the OMZ core community at 530 m depth ($\text{O}_2 \sim 0.34 \mu\text{mol kg}^{-1}$) was characterized by low densities of fish ($0.02\text{--}0.03 \text{ individuals m}^{-2}$), with liparids being one of the community members present in the OMZ core (Hunter et al., 2011). The Indian margin is a much higher-energy area with more mineral input from rivers and may not provide the same level of food as on the Pakistan margin. Within the lower boundary of the OMZ (800–1100 m), fish densities increased and were approximately two times higher than within the OMZ core (Hunter et al., 2011). Off Hawaii, where oxygen concentrations do not reach OMZ conditions, the general pattern was also a reduction in demersal fish

abundances at intermediate depths where oxygen conditions were lowest ($\sim 30.6 \mu\text{mol kg}^{-1}$) (De Leo et al., 2012).

Interesting anomalies of very high demersal fish catches for areas with low-oxygen concentrations have also been reported. The largest catch included in the analysis of Banse (1968) (539 lb of commercially important fish caught in 45 min) was obtained at an oxygen concentration of $\sim 21 \mu\text{mol kg}^{-1}$. Increased landings off Bombay have been reported at the start of the northeast monsoon when OMZ conditions are found inshore at 35 m depth (Carruthers et al., 1959). Off Namibia, the highest demersal fish densities were obtained in the regions with the lowest oxygen concentrations, with $\sim 70,000$ fish/nautical mile captured by trawl in an area where the mean oxygen concentration was $\sim 31.1 \mu\text{mol kg}^{-1}$ and ranged from ~ 0 to $74.4 \mu\text{mol kg}^{-1}$ (Mas-Riera et al., 1990). In the Sea of Oman, fisheries landings also increase as oxyclines shoal and low-oxygen conditions are found at shallower depths (Piontkovski and Al-Oufi, 2014). High densities of demersal fish have also been described near Volcano 7 at very low oxygen conditions ($4.8\text{--}7 \mu\text{mol kg}^{-1}$) (Levin et al., 1991; Wishner et al., 1995) and in the Gulf of California (N.D. Gallo, unpublished data). These high-density regions tend to be dominated by single species. Food tends to be plentiful in these environments, in the form of phytodetritus and meiofauna, which generally tolerate extremely low oxygen levels (Levin, 2003). Other OMZ studies conducted off northern Chile (Quiroga et al., 2009) do not provide evidence for these zones of greater density in the demersal fish community (Quiroga et al., 2009), known as *edge effects* (Mullins et al., 1985), but it is possible that the depth where edge effects of certain species would be observed were missed by the sampling. Continuous sampling across oxygen gradients using an ROV, submersible, or photosled, is more likely to detect edge effects than spatially separated trawl sampling, as edge effects can occur in response to very small, but physiologically relevant, changes in $p\text{O}_2$.

High-density areas surrounding low-oxygen regions are also observed in coastal and estuarine “dead zones”. Organisms avoided lethal oxygen thresholds by aggregating at short distances from the edge of the hypoxic zone in the Gulf of Mexico (Craig, 2012). This aggregation was particularly apparent for finfish, which are considered relatively intolerant of oxygen stress, and the result was an increase in fish biomass in areas surrounding the hypoxic zone (Craig, 2012). Breitburg (2002) found that while demersal fish harvest decreased in areas of persistent, year-round hypoxia or anoxia in the water column, areas that only had seasonal hypoxia in the semi-enclosed European Seas were characterized by high fish harvest. It is important to keep in mind

that increased organic matter is a confounding factor in severely hypoxic zones, and that total benthic standing stock is positively related to increased organic matter (Thiel, 1978), so some of these high-density patterns may be due to organic enrichment of the benthic community and others due to habitat compression from hypoxic conditions. In coastal and estuarine systems, the relationship between fish abundance and hypoxia is not straightforward because hypoxia is often eutrophication-driven, which can give rise to elevated fish abundances in the overlying, better-oxygenated surface waters (Breitburg, 2002). This mosaic of low-oxygen waters in close proximity to highly oxygenated, productive waters in coastal systems has prevented the decrease in abundance of fish expected if just considering the low-oxygen concentration of the bottom waters (Breitburg, 2002; Breitburg et al., 2009). Given that the studies on demersal fish communities in OMZs are relatively limited, additional studies may help resolve the relationship between oxygen and abundance patterns.

3.5 Effects of Oxygen on Fish Diversity

In general, demersal fish species diversity decreases with decreasing oxygen conditions across regions, but specific oxygen thresholds that induce this change are region-specific. Species richness exhibited significant positive relationships with near-bottom oxygen concentrations within the hypoxic region off Oregon (Keller et al., 2010) and along the entire US Pacific coast (Keller et al., 2015). Near-bottom oxygen concentrations exert a stronger influence on species richness at lower oxygen concentrations ($\text{DO} < \sim 60 \mu\text{mol kg}^{-1}$) (Keller et al., 2015), implying a nonlinear response of community biomass to oxygen concentration. In the seasonally hypoxic Saanich Inlet, higher fish species richness was observed during periods of higher oxygen concentration, while single-species dominance by *L. exilis* was typically characteristic of severely hypoxic conditions (Matabos et al., 2014). Increased homogenization and decreased species richness in the Saanich Inlet under severely hypoxic conditions was also observed by Chu and Tunnicliffe (2015).

In the Benguela Current off Namibia, the low oxygen, central shelf demersal fish assemblage was characterized by the lowest diversity and high dominance by a few species, compared to the other four identified assemblages (Hamukuaya et al., 2001). This study found a positive relationship between oxygen saturation and demersal fish species diversity, where diversity increases but appears to reach a threshold between oxygen

concentrations of 43.8–65.6 $\mu\text{mol kg}^{-1}$ (Hamukuaya et al., 2001). Beyond this, oxygen levels did not seem to affect demersal fish community diversity. Mas-Riera et al. (1990) also found that oxygen conditions exerted a strong influence over demersal fish community diversity off Namibia. The lowest values for Shannon–Weiner diversity index (H') obtained during the study (based on 146 trawl samples taken along the shelf and upper slope of Namibia) were obtained for the northern shelf association which was characterized by the lowest oxygen conditions, whereas the highest values for diversity were observed for the transitional subcommunity; diversity was 2.5 times higher even though it was immediately adjacent to the low-oxygen northern shelf association. Similarly, in the southern shelf region, an increase in oxygen led to a noticeable increase in diversity (Mas-Riera et al., 1990). Mas-Riera et al. (1990) also notes that off northwest Africa the diversity of the shelf and upper slope demersal fish fauna (Roel et al., 1985) is higher than that found off Namibia, which could be due to the strong upwelling intensity and OMZ conditions found off Namibia.

In the Chilean OMZ, fish species richness was low, with one species observed by Quiroga et al. (2009) in northern Chile and no species observed in central Chile. Quiroga et al. (2009) found that species richness increased below the OMZ with three species observed at 365 m off Concepcion (central Chile) and nine species observed at 864–895 m off Antofagasta northern Chile. Unpublished trawl data from report FIP2004–09 from the Chilean Fisheries Development Program (IFOP, 2005), spanning 29–42°S, depths 58–450 m, and $\text{O}_2 \sim 16.9\text{--}253.1 \mu\text{mol kg}^{-1}$, also show lower fish species richness within the Chilean OMZ (see Fig. 5C), but higher species richness (2–5 species in the OMZ) than observed by Quiroga et al. (2009). Within the Pakistan margin OMZ, the greatest fish species richness with a total of four species was observed at depths below the OMZ core (1100 and 1200 m) where oxygen levels began to increase to 11.17 and 16.97 $\mu\text{mol kg}^{-1}$ (Murty et al., 2009). However, high species richness with a total of three unique species was also observed at 300 m where oxygen levels were much lower (5.36 $\mu\text{mol kg}^{-1}$) (Murty et al., 2009).

The demersal fish species richness in different OMZs appears to vary, from few species observed off Chile (Quiroga et al., 2009; Table 1) to more than 15 demersal fish species known from the US West Coast OMZ (Day and Percy, 1968; Friedman et al., 2012; Keller et al., 2015; N.D. Gallo, unpublished data) (Table 1). However, these differences may be due to some regions being understudied and additional research may reveal more hypoxia-tolerant species living in these areas. At a regional scale, OMZs may lead to

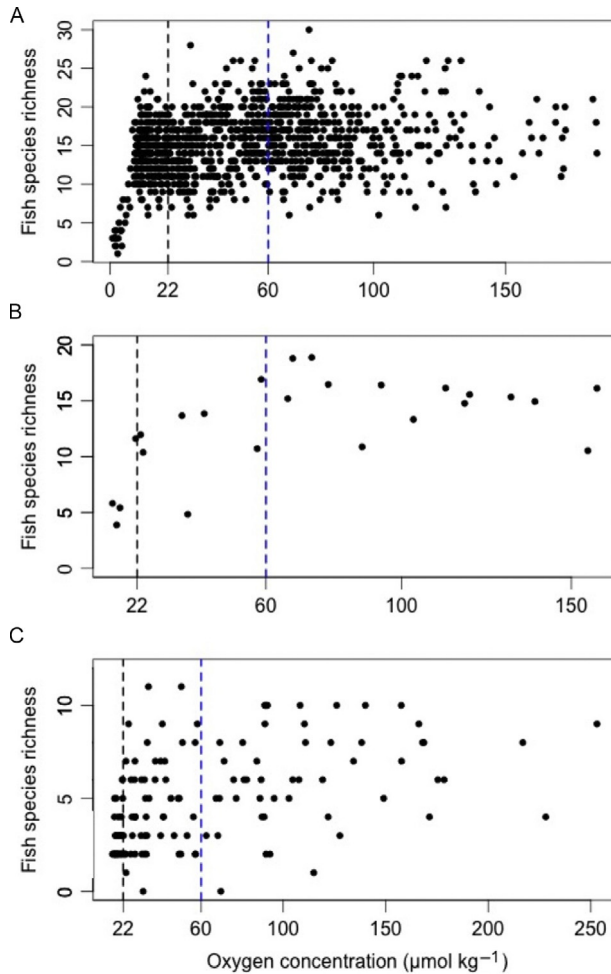


Fig. 5 Changes in fish species richness with oxygen concentrations ($\mu\text{mol kg}^{-1}$) (A) off the US West Coast from Keller et al. (2015), (B) off the Namibian coast from Hamukuaya et al. (2001), data extracted using Web Plot Digitizer, and (C) off the Chilean coast (29–42°S and depths 58–450 m) from unpublished data by the Chilean Fisheries Development Program (IFOP, 2005). Blue (dark grey in the print version) dashed line indicates the oxygen limited zone (OLZ) boundary ($60 \mu\text{mol kg}^{-1}$) and black dashed line indicates the oxygen minimum zone (OMZ) boundary ($22 \mu\text{mol kg}^{-1}$).

enhanced biodiversity by acting as barriers to gene flow and creating strong gradients which exert selective pressure on specific physiological traits (Rogers, 2000; White, 1988). Studies on how the expansion and contraction of OMZs over geologic time may have influenced the evolution of closely related slope and shelf demersal fish species such as the sebastids, *S. alascanus* and

S. altivelis, off the US West Coast, the pleuronectids, *M. pacificus* and *E. bathybius*, off the US West Coast, and the merlucciids, *M. capensis* and *M. paradoxus*, off Namibia, as well as others, would be informative.

3.6 Comparison of Trends Between Invertebrate and Demersal Fish Communities in OMZs

Invertebrates often provide food for demersal fish, so it is informative to ask whether fish patterns in OMZs mirror those of sediment-dwelling invertebrates. Metazoan meiofauna in general have been found to be more tolerant of hypoxic conditions than macrofauna (Josefson and Widbom, 1988; Levin et al., 1991; Rogers, 2000) with nematodes dominating the meiofauna under low-oxygen conditions (Diaz and Rosenberg, 1995; Gooday et al., 2010; Levin et al., 1991). For the most part, it appears that trends in the demersal fish community resemble trends for meio, macro, and invertebrate megafauna across oxygen gradients, although the oxygen thresholds governing changes in diversity and abundance of the fish community are different (Gooday et al., 2010). One of the interesting findings is that extremely hypoxia-tolerant demersal fish species appear to be able to live under oxygen conditions where most nonvertebrate megafauna are absent or extremely rare due to the severely hypoxic conditions (Murty et al., 2009). This suggests that fish in these areas may be preying on macrofauna or meiofauna. Changes in distribution can lead to shifts in the relative importance of a specific species and give rise to altered carbon flow pathways in the food web (Breitburg, 2002). Similar to the high-density edge effects observed for the demersal fish community in some areas under severely hypoxic conditions, abundant macrobenthic communities have also been reported at low-oxygen concentrations from off Peru, California, Volcano 7, and Oman (Levin et al., 1991, 2000; Mullins et al., 1985; Rosenberg et al., 1983).



4. BEHAVIOURAL AND PHYSIOLOGICAL ADAPTATIONS CONFERRING TOLERANCE TO LOW O₂ ENVIRONMENTS

There are many definitions of hypoxia (Hofmann et al., 2011) and the body of literature on adaptations suggests that there are multiple ways to become hypoxia tolerant. This is consistent with the fact that hypoxia tolerance has evolved independently many times in fishes (Friedman et al., 2012; Mandic et al., 2009). Multiple pieces have been written about the

mechanisms underlying molecular responses of an organism to oxygen limitation (Davis, 1975; Farrell and Richards, 2009; Kramer, 1987; Nilsson, 2010; Pollock et al., 2007; Rankin and Jensen, 1993; Richards, 2009; Wells, 2009; Wu, 2002, 2009), which can arise both from insufficient oxygen in the environment, as well as insufficient oxygen supply due to high active metabolic rate. Fish are exposed to hypoxic conditions in several environments, including tide pools, river mouths, ice-covered lakes, eutrophic estuaries, or enclosed bodies of water, and OMZs. Most previous studies and reviews have focused on Amazonian, estuarine, lake, and tidepool fishes to understand hypoxia sensitivity and tolerance, and few have looked at the adaptations of fish living under naturally occurring, chronic, severely hypoxic conditions such as OMZs. While some fish die when exposed to low-oxygen waters, such as the high mortality of rockfish reported off Oregon during the upwelling of OMZ waters onto the shelf (Grantham et al., 2004), others live in OMZ environments and have evolved the capacity to survive under severely hypoxic conditions (Friedman et al., 2012). Behavioural, morphological, and molecular adaptations to hypoxia will be briefly reviewed here in order to better understand some of the patterns of changes in abundance and diversity of the fish community under OMZ conditions that have been previously explored in this chapter. Understanding which adaptations confer tolerance to hypoxia is important to understanding which fish species will be resilient to living in a more oxygen-deficient future ocean.

4.1 Responses of OMZ Fish Species to Severely Hypoxic Conditions

Two theoretical, not mutually exclusive mechanisms have been proposed in the literature as methods of coping with reduced oxygen availability: increased oxygen extraction from the environment (through increased gill surface area, ventilation behaviour, increased oxygen affinity in respiratory pigments, or other molecular changes), or reduced oxygen demand (through metabolic suppression or anaerobic metabolism) (Childress and Seibel, 1998; Friedman et al., 2012; Seibel, 2011). Known behavioural, morphological, and physiological adaptations of OMZ demersal fish species are listed in Table 2.

Response of hypoxia-tolerant cellular systems to lack of oxygen occurs in two phases: defense and rescue (Hochachka et al., 1996). The first step includes suppressing ATP-demand and ATP-supply pathways by down-regulating protein synthesis through translational arrest, and downregulating

Table 2 Physiological, Behavioural, and Morphological Adaptations of Demersal Fish Species to Life Under Severely Hypoxic Conditions Found in Oxygen Minimum Zones

	Description	Citation
Behavioural adaptations		
<i>Sluggish movement</i>		
<i>Sebastes alascanus</i>	Sluggish movement	Yang et al. (1992) and Friedman et al. (2012)
<i>Increased ventilation rate</i>		
<i>Sufflogobius bibarbatus</i>	Increased ventilation rate	Salvanes et al. (2011)
<i>Interactions with sediment</i>		
<i>Bregmaceros</i> sp.	Bury themselves into sediment	Hunter et al. (2011)
<i>Cherublemma emmelas</i>	Bury head into sediment	N.D. Gallo (unpublished data)
<i>Anoplopoma fimbria</i>	Crash body into sediment	L.A. Levin (unpublished data)
<i>Sufflogobius bibarbatus</i>	Bury themselves into sediment	Salvanes et al. (2011)
Reproductive adaptations		
<i>Microstomus pacificus</i>	Ontogenetic migration	Hunter et al. (1990)
<i>Sebastes alascanus</i>	Ontogenetic migration	Day and Pearcy (1968)
<i>Anoplopoma fimbria</i>	Ontogenetic migration	Day and Pearcy (1968)
<i>Careproctus melanurus</i>	Embryos and larvae develop in crab gill cavity	Peden and Corbett (1973) and Somerton and Donaldson (1998)
Morphological adaptations		
<i>Increased gill surface area</i>		
<i>Careproctus melanurus</i>	High gill surface area	Friedman et al. (2012)
<i>Anoplopoma fimbria</i>	High gill surface area	Friedman et al. (2012)
<i>Microstomus pacificus</i>	High gill surface area	Friedman et al. (2012)
<i>Nezumia liolepis</i>	High gill surface area	Friedman et al. (2012)
<i>Cephalurus cephalus</i>	High gill surface area	Compagno (1984)
<i>Change in muscle composition</i>		
<i>Microstomus pacificus</i>	Gelatinous white muscle	Hunter et al. (1990)

Table 2 Physiological, Behavioural, and Morphological Adaptations of Demersal Fish Species to Life Under Severely Hypoxic Conditions Found in Oxygen Minimum Zones—cont'd

	Description	Citation
Change in swimbladder		
<i>Bregmaceros cantori</i>	Daily increase in mass and volume of swimbladder	Love et al. (2004)
Physiological adaptations		
Enzymatic changes		
<i>Sebastes alascanus</i>	Blood and heart LDH enzymatic adaptations, low aerobic enzymatic activity	Yang et al. (1992) and Friedman et al. (2012)
<i>Sebastes altivelis</i>	Low aerobic enzymatic activity	Friedman et al. (2012)
<i>Careproctus melanurus</i>	High aerobic enzymatic activity	Friedman et al. (2012)
<i>Anoplopoma fimbria</i>	High aerobic enzymatic activity, loss of bNHE, modified Root effect	Friedman et al. (2012) and Rummer et al. (2010)
<i>Microstomus pacificus</i>	Decrease in anaerobic capacity	Vetter et al. (1994)
Increase in haemoglobin		
<i>Saurida tumbil</i>	Bright red gills with presumed high haemoglobin concentration	Murty et al. (2009)
<i>Cherublemma emmelas</i>	Bright red gills with presumed high haemoglobin concentration	N.D. Gallo (unpublished data)

ion-channel ATP use by channel arrest (Hochachka et al., 1996). It is thought that cells that are not hypoxia-tolerant are not able to recover from this translational arrest of protein synthesis, while hypoxia-tolerant cells respond to extended periods of hypoxia by activating “rescue” mechanisms that begin to upregulate the expression of several key proteins, thus allowing low-level metabolic activity but with dramatically reduced ATP turnover rates (Hochachka et al., 1996). Haeme-based proteins that are known to sense changes in oxygen tension in numerous organisms are thought to be the oxygen sensors responsible for detecting hypoxic conditions and

subsequently activating hypoxia-dependent transcription factors (Bunn and Poyton, 1996). In fish, as well as in mammals, a heterodimeric transcription factor called hypoxia-inducible factor 1 (HIF-1), regulates target genes that are activated in hypoxic conditions (Semenza, 1998). While research has not been conducted to identify this response in OMZ fish species, it is the fundamental cellular response to hypoxia, and is likely to occur in these fish.

In one of the few studies on hypoxia adaptations of demersal fish to OMZ conditions, Friedman et al. (2012) examined the demersal fish present in the US West Coast OMZ, and compared the gill surface area and white muscle enzyme activities to conspecifics not found in the OMZ. Of the four orders of fish studied (Scorpaeniformes, Pleuronectiformes, Cottiformes, and Gadiformes) types of adaptations differed, suggesting flexibility in evolving hypoxia tolerance. The pleuronectid, *M. pacificus*, had a gill surface area 1.8–3 times larger than conspecifics that occupied higher oxygen areas on the continental shelf, increasing oxygen extraction ability (Friedman et al., 2012). Several studies have also noted that as *M. pacificus* migrates into the OMZ, it undergoes an increase in water content and the muscle tissue becomes more gelatinous, resulting in a ~20% decrease in caloric density per gram wet weight (Hunter et al., 1990; Vetter et al., 1994). These morphological adaptations may be key to the very broad depth distribution (57–1217 m) of *M. pacificus* that extends through the whole OMZ (Keller et al., 2015).

Increasing gill surface area under hypoxic conditions appears to be a common adaptation across different orders of fish and also is a relatively plastic trait (Chapman et al., 2000; Nilsson, 2007; Sollid et al., 2003), with changes to the lamellar surface area of the gills able to occur as rapidly as 12–24 h (Matey et al., 2008). *Nezumia liolepis*, a macrourid known to live under OMZ conditions both in the US West Coast OMZ and near Volcano 7 (Wishner et al., 1990, 1995), also had increased gill surface area (Friedman et al., 2012). Larger gill surface area appears to also be an adaptation in cartilaginous fish, and the large head and expanded gills of the scyliorhinid, *C. cephalus*, are thought to be an adaptation to the severely hypoxic conditions in the Gulf of California (Compagno, 1984).

In contrast, other OMZ species in the order Scorpaeniformes exhibit enzymatic adaptations to OMZ conditions. The sebastid, *S. alascanus*, has specific blood and heart enzyme adaptations that allowed for greater reliance on anaerobic metabolism (Yang et al., 1992). However, enzymatic substrates for aerobic metabolism have been found to be reduced in both the sebastids, *S. alascanus* and *S. altivelis*, suggesting low aerobic activities under OMZ conditions (Friedman et al., 2012). The two congeneric *Sebastobolus* species

were not found to have increased gill surface area (Friedman et al., 2012), suggesting they adapt to hypoxic conditions primarily through behavioural modifications and reduced enzymatic activity, and not through morphological adaptations. While increased reliance on anaerobic metabolism has been proposed as a mechanism for maintaining cellular energy demand under hypoxia, this requires large glycogen stores (Vornanen et al., 2009), an opportunity to repay the oxygen debt, and a strategy for eliminating lactic acid. Some freshwater fish species including the cyprinids, *Carassius auratus*, *C. caraccius*, and *Rhodeus amarus*, have evolved efficient ways to eliminate toxic end products through ethanol excretion (Vornanen et al., 2009). Migrating myctophids in the Arabian Sea have also been described as utilizing alcohol dehydrogenase to excrete ethanol (Torres et al., 2012). However, increased reliance on anaerobic metabolism is likely more beneficial for fish living in environments where they are exposed to periodic hypoxia and not chronic hypoxia, therefore is likely not an important adaptation of demersal fish living in OMZs. No evidence of increased lactate dehydrogenase activity or increase in anaerobic poise was observed in the seabastids, *S. alascanus* or *S. altivelis*, in response to OMZ conditions (Vetter and Lynn, 1997). Anaerobic capacity was found to decrease in response to OMZ conditions in the pleuronectid, *M. pacificus* (Vetter et al., 1994).

The two most active and mobile OMZ-dwelling species examined by Friedman et al. (2012) were the liparid, *C. melanurus* and the anoplomatid, *A. fimbria*. These species exhibited large gill surface area and high aerobic enzymatic activity, documented through a high concentration of malate dehydrogenase (MDH) and citrate synthase (CS) enzymes, which are within the citric acid cycle and are utilized during aerobic metabolism (Friedman et al., 2012). Unfortunately, a liparid from outside of the OMZ was not available for comparison with *C. melanurus*, and *A. fimbria* was present both outside of, and within the OMZ, so interpretation of these results as OMZ adaptations is more difficult. A separate study by Rummer et al. (2010) did find that *A. fimbria* had specialized adaptations to tolerate hypoxic conditions, based on the magnitude of its Root effect. The Root effect is a pH-dependent reduction in haemoglobin-oxygen carrying capacity and is hypothesized to have evolved to enhance tissue oxygen delivery in fish (Rummer et al. 2013). Rummer et al. (2010) found that *A. fimbria* exhibits a Root effect that most closely resembles that of a hypoxia-tolerant cyprinid, *Cyprinus carpio*, as opposed to a Root effect characteristic of other studied Scorpaeniformes. This suggests that *A. fimbria* has evolved both morphological and physiological adaptations to hypoxic conditions.

4.2 Critical Oxygen Level

The critical oxygen level (P_{crit}) is the partial pressure of oxygen ($p\text{O}_2$) at which a fish transitions from being an oxyregulator (oxygen consumption rate is independent of environmental oxygen conditions) to being an oxyconformer (where oxygen consumption rate becomes dependent on environmental oxygen conditions) (Richards, 2011), and is an important concept in considering the oxygen niches of demersal fish. At P_{crit} , aerobic scope (the difference between maximum metabolic rate and standard metabolic rate) is zero, meaning that energy can no longer be used for locomotion, reproduction, or growth (Farrell and Richards, 2009; Pörtner and Peck, 2010; Pörtner et al., 2010). Hypoxia-tolerant fish have been found to have lower critical oxygen levels than hypoxia-intolerant fish. Mandic et al. (2009) found that hypoxia tolerance was phylogenetically independently associated with enhanced oxygen extraction capacity in sculpins. Routine oxygen consumption rate, mass-specific gill surface area, and whole-blood haemoglobin oxygen-binding affinity (P_{50}) accounted for 75% of the variation in P_{crit} (Mandic et al., 2009). Species with a low P_{crit} had low routine metabolic rates, a large gill surface area, and high whole-blood haemoglobin oxygen binding affinity (Mandic et al., 2009). However, P_{crit} alone does not appear to be a perfect predictor of hypoxia tolerance of fish (Speers-Roesch et al., 2013). The critical oxygen level identified for *S. bibrabatus*, the bearded goby that lives in severely hypoxic conditions off Namibia, was $5.45 \pm 0.22\%$ of air saturation ($\sim 10 \mu\text{mol kg}^{-1}$), but the gobies tolerated levels of $< 0.3 \mu\text{mol kg}^{-1}$ dissolved oxygen for 4.5 h without any equilibrium loss or decrease in escape responsiveness (Salvanes et al., 2011).

4.3 Blood Adaptations to Hypoxic Conditions

Differences in fish haemoglobins have also been proposed as physiological strategies allowing fish to survive in changing environments. Fish living in low-oxygen environments were found to have higher haemoglobin oxygen affinities than fish living in higher oxygen environments (Powers, 1980; Wells, 2009). The intrinsic haemoglobin oxygen affinity is genetically determined, meaning that changes must take place over generations, but physiological plasticity can be provided by regulating intracellular concentrations of allosteric modifier molecules (Powers, 1980), thus giving rise to faster modifications to decreased environmental oxygen. The presence of multiple haemoglobins in fishes (Powers, 1980) may allow fish to quickly respond to

altered environmental conditions. Decreasing red blood cell organic phosphate levels also leads to an increase in haemoglobin oxygen affinity due to the influence of ATP on the Bohr effect (Powers, 1980). Differences in the lactate dehydrogenase (LDH) phenotype have also been shown to increase haemoglobin oxygen affinity through differing regulation of intraerythrocyte ATP concentration (Powers, 1980; Powers et al., 1979).

Increasing haematocrit or haemoglobin levels is also a physiological adaptation to hypoxic conditions in certain species. The freshwater cyprinid, *Pimephales promelas*, was found to increase haematocrit levels in response to hypoxic conditions (MacLeod and Smith, 1966), and the bright red gills of *Saurida tumbil* living in the Arabian Sea OMZ on the Pakistan margin were hypothesized to be due to high haemoglobin concentrations (Murty et al., 2009). *Cherublemma emmelas* collected from the Gulf of California OMZ also had very bright red gills and likely have high haemoglobin concentrations (N.D. Gallo, unpublished data). Higher oxygen extraction capacity due to increased haemoglobin concentration, increased haemoglobin-oxygen affinity, and decreased red cell ATP concentration, are also hypoxia adaptations of the eel *Anguilla anguilla* (Wood and Johansen, 1972). The haemoglobin oxygen dissociation curve shifts to the left in hypoxia-tolerant species (Wells, 2009; Wood and Johansen, 1972) and high oxygen affinity of haemoglobin, may be a consistent adaptation to low-oxygen conditions. Interestingly, midwater deep scattering layer fishes that live in Eastern Tropical Pacific OMZ conditions were found to have surprisingly low haemoglobin affinities for oxygen (Douglas et al., 1976). For fish living under OMZ conditions, based on the Bohr effect, it would be beneficial to tightly regulate levels of CO₂ at the gill and tissue. Having low CO₂/high pH at the gills would shift the blood oxygen dissociation curve to the left, thus increasing haemoglobin oxygen affinity and oxygen uptake. Having high CO₂/low pH at the tissue would shift the blood oxygen dissociation curve to the right, thus allowing for more oxygen offloading to the tissues. Studies with OMZ fish species are needed to test this.

4.4 Molecular Responses of Fish to Hypoxia

Molecular responses are also recognized as determining the hypoxia tolerance of different fish species, but these results are usually based on short-term hypoxia exposure, are biased towards fresh or shallow-water species, and may not be as informative for the chronic hypoxia experienced by OMZ demersal fish species. Gracey et al. (2001) found that the gobiid, *Gillichthys*

mirabilis, which lives in low-oxygen burrows in estuarine environments, survives hypoxia by altering gene expression in a tissue-specific manner, down-regulating genes for protein synthesis and locomotion, while upregulating genes for anaerobic ATP production and gluconeogenesis. Exposure of two fish that naturally live in the Elbe estuary, the percid, *Gymnocephalus cernuus*, and the pleuronectid, *Platichthys flesus*, to hypoxic conditions resulted in large tissue-specific gene expression changes in myoglobin, neuroglobin, and caspase 3, along with an increase in respiratory pigment levels in the gills (Tiedke et al., 2014). Changes in globin expression under hypoxic conditions have also been observed in freshwater zebrafish (Roesner et al., 2006) and goldfish (Roesner et al., 2008). These molecular changes in gene-expression channel energy to essential metabolic processes while increasing oxygen extraction capability. In a comparison of two closely related sculpins, the hypoxia-tolerant intertidal *Oligocottus maculosus* and the hypoxia-intolerant subtidal *Blepsias cirrhosis*, Mandic et al. (2014) found that while a number of genes showed a similar hypoxia-induced transcription pattern in both species, the difference in hypoxia tolerance between the species may partly be explained by a large set of genes involved in fatty acid oxidation and oxidative phosphorylation that showed divergent transcriptional patterns in response to hypoxic conditions. The genes in the conserved hypoxia response in the two species were involved in glycolysis and apoptosis (Mandic et al., 2014). Hypoxia inducible factor (HIF) is the transcription factor that results in hypoxia-mediated changes in gene expression (Semenza, 1998). Extremely hypoxia-tolerant fish such as the grass carp, *Ctenopharyngodon idellus*, may also have novel isoforms of key proteins, such as HIF-1 alpha, that may confer greater hypoxia tolerance through differential hypoxia-specific transcriptional and translational regulation (Law et al., 2006). To the knowledge of the authors, no studies have looked at molecular gene responses of OMZ fish species to oxygen stress.

4.5 Metabolic Depression Under Hypoxic Conditions

Metabolic depression is an important component of the hypoxia response, and hypoxia-tolerant animals are thought to extend their period of survival under severely hypoxic conditions through a depression of basal metabolic rate (Richards, 2010). For this reason, evolutionary lineages of fish that naturally have lower basal metabolic rates or live in deep-sea, food-poor, or cold-water conditions, may be pre-adapted for survival under severely hypoxic conditions. A consistent trend of decreasing metabolic enzyme activity

with depth has been found across 61 species of demersal fish (Drazen et al., 2015). Recently, a physiological trade-off was found between hypoxia tolerance and aerobic exercise capacity in four species of fresh and shallow-water centrarchids (Crans et al., 2015), but similar studies have not been conducted for OMZ fish.

4.6 Behavioural Adaptations

Avoidance, altered breathing, decreased feeding, and altered phototaxis are all reported behaviours of fish in response to low oxygen (Davis, 1975). Altering breathing behaviour either by hyperventilation, increasing breathing frequency or stroke volume, or by switching from periodic or episodic breathing to continuous breathing are all possible fish responses to hypoxia (Perry, 2011). Hyperventilation during hypoxia also produces a respiratory alkalosis, leading to an elevation of red blood cell pH and increasing the affinity of haemoglobin for oxygen by the Bohr effect, and increasing O₂ uptake (Brauner and Randall, 1998; Perry, 2011). Salvanes et al. (2011) found that the gobiid living in the Namibian OMZ, *S. bibarbatius*, is able to tolerate hypoxic conditions for long periods by increasing ventilation rate.

Oxygen minimum zone-tolerant fish may also have habitat-specific behavioural adaptations including selection of microhabitats and semi-diurnal, diurnal, and seasonal migrations. For example, OMZ species such as the sebastids, *S. alascanus* and *S. altivelis*, may preferentially utilize microhabitats that are exposed to greater water flow (eg, presence of rocks or mounds that modify and increase turbulence and flow). Orientation into the current or selection of microhabitats with greater water flow over respiratory surfaces would increase the gas exchange rate (Brewer and Hofmann, 2014). While it is unclear what the physiological significance of the behaviour is, several OMZ fish species have been observed interacting with the sediment in unexpected ways. *Bregmaceros* sp. were observed burying themselves into the sediment in the Arabian Sea OMZ core (Hunter et al., 2011). In the Gulf of California OMZ core, ophiidiids of the species *C. emmelas* were observed with their heads buried in the sediment (N.D. Gallo, unpublished data). In the Namibian OMZ, *S. bibarbatius* also associates closely with the sediment, burying into it when in danger, despite the high concentrations of methane and hydrogen sulphide in the sediments (Salvanes et al., 2011). The anoplomatid, *A. fimbria*, has also been observed ramming its head into the sediment in the OMZ on the California and Oregon margin (L.A. Levin, unpublished data).

There are also reports of fish exhibiting sluggish behaviour, decreased feeding, and higher disease susceptibility and a lowered immune response in fish exposed to oxygen conditions slightly above lethal conditions (Shepard, 1955). To the knowledge of the authors, no studies have looked at how OMZ conditions influence the immune responses of demersal fish species living in OMZs, and it is possible that fish living under OMZ conditions may be more disease and parasite prone due to a lowered immune response. Grenadiers living in the Gulf of California OMZ appear to have higher external parasite loads than grenadiers observed in other areas (L.A. Kuhnz, MBARI, personal communication, 8 September 2015).

4.7 Life-History Trends

Different stages in the life history of a species can have different tolerances to hypoxia. In the shallow-water marine sparid, *Pagrus major*, metabolic rates were highest and hypoxia tolerance was lowest during metamorphosis (Ishibashi et al., 2005). Within a species, smaller individuals can have a higher tolerance to low-oxygen levels compared with their larger counterparts (Burlison et al., 2001; Cerezo and Garcia, 2004; Pörtner and Knust, 2007; Robb and Abrahams, 2003). During the monsoon-driven shoaling of severely hypoxic waters on the Omani shelf, greater abundances of small individuals of the nemipterid, *Parascopis aspinosa*, and the triakid, *I. omanensis*, were observed. In the same area, an observed trend of decreasing length with depth for several fish species including the serranid, *E. epistictus*, and the lutjanid, *Pristipomoides filamentosus*, was also attributed to the greater sensitivity of larger individuals to hypoxia (McIlwain et al., 2011). Merrett and Marshall (1980) note that the slope fish community off northwest Africa differed from the fish fauna characteristic of the non-upwelling western North Atlantic fish community in that the dominant species in the African slope community were found to be of smaller mean size and there was no evidence of the “bigger-deeper” phenomenon (Mettett and Haedrich, 1997). Interestingly, an opposite pattern is seen off the US West Coast, where most OMZ-dwelling demersal fish species, including the sebastid, *S. alascanus*, the pleuronectid, *M. pacificus*, and the anoplopomatid, *A. fimbria*, undergo an ontogenetic migration with larvae in surface waters, juveniles settling at shallower depths, and the largest and oldest individuals present within the OMZ (Day and Pearcy, 1968; Hunter et al., 1990). The relationship between hypoxia tolerance and body size is not simple, however, and a recent review found that body size had

little or no impact on the ability of fish to take up oxygen during hypoxic conditions, but that larger individuals may be at an advantage when anaerobic metabolism is employed because small individuals reach lethal levels of anaerobic end products faster (Nilsson and Ostlund-Nilsson, 2008).

Reproductive and early life-history strategies may also function as adaptations to hypoxic conditions. For example, the peak spawning period of Malabar sole off India occurs after the low-oxygen monsoon period (Khan and Nandakumaran, 1993). While liparids are known to deposit eggs on a variety of biogenic substrates, including bivalve shells (DeMartini, 1978), polychaete tubes (Marliave and Peden, 1989), and sponges (Chernova, 2014), certain liparids have a unique reproductive strategy involving sexual parasitism of lithodid crabs (Somerton and Donaldson, 1998). *C. melanurus*, an OMZ-dwelling liparid off the US West Coast, lays its eggs in the gill cavity of the Brown Box Crab (*Lopholithodes foraminatus*; Peden and Corbett, 1973), which may increase oxygenation of the eggs during early development. Development is an energetically costly process requiring high oxygen levels; reduced larval growth, retarded development and deformities of embryos are all common features of early development in hypoxic conditions (Alderdice et al., 1958; Kajimura et al., 2005). While 98% of the spawning biomass of the OMZ-dwelling pleuronectid, *M. pacificus*, in central California is found within the OMZ, larvae and juveniles inhabit the upper water column and settle on the upper slope (Hunter et al., 1990). In contrast, young *S. altivelis* are found within the OMZ core off San Diego (N.D. Gallo, unpublished data).

4.8 Feeding Strategies of Species Living in OMZs

Low oxygen conditions have been linked with lower proportions of carnivory in the polychaete community due to high mobility and metabolic demand (Sperling et al., 2013), raising the possibility that carnivory in demersal fish living in OMZs may also be selected against. Fish living under severely hypoxic conditions may select food from the surrounding environment that is less metabolically costly to either obtain or digest, and may be more reliant on detrital production, as opposed to predation at higher trophic levels. *S. bibarbatu*s off Namibia have been found to consume jellyfish and sulphidic diatomaceous mud, thus transferring otherwise “dead-end” resources back into the food chain (Utne-Palm et al., 2010). Based on isotopic signatures, jellyfish, which may represent an easy food to digest, contributed 17–60% of the diet of *S. bibarbatu*s (Utne-Palm et al., 2010), while

gut content analysis showed that polychaetes, euphausiids, and amphipods were also important diet components (Cedras et al., 2011). Fish experiencing oxygen stress may also feed less (Farrell and Richards, 2009), as has been observed using gut content analysis for *S. alascanus* in the OMZ core in the Southern California Bight (N.D. Gallo, unpublished data). In estuarine systems, seasonal hypoxia is known to influence the trophic structure of the benthic community by diverting energy from consumers to microbes (Baird et al., 2004; Diaz and Rosenberg, 2008).



5. IMPLICATIONS FOR A WARMING OCEAN AND EXPANDING OXYGEN MINIMUM ZONES

5.1 Influences of Ocean Oxygen on Marine Communities Through Time

The geologic record is rich with evidence of widespread changes in marine oxygen conditions through time (Jacobs and Lindberg, 1998; Jenkyns, 2010; Moffitt et al., 2014, 2015a,b; Norris et al., 2013; White, 1988). Historical changes in marine oxygen conditions, and the expansion and contraction of OMZs through time, likely played an important role in the evolution and modern-day distribution of deep-sea species, as well as the diversity patterns observed in bathyal and abyssal deep-sea fauna today (Armstrong, 1996; Jeppsson, 1990; Rogers, 2000; White, 1988). Major extinctions or radiations of marine fauna are associated with periods of widespread marine anoxia or the return to fully oxygenated conditions (Moffitt et al., 2015a; Rogers, 2000). Increases in atmospheric oxygen around 400 million years ago were correlated with the radiation of large predatory fish, which required higher oxygen conditions (Dahl et al., 2010). The expansion of oxygen minima during the mid and late Cretaceous, Eocene, and Miocene periods are thought to have promoted widespread episodes of allopatric speciation at intermediate depths (500–2500 m) (White, 1988). The Cretaceous/Paleogene Event, during which OMZs significantly expanded and an oceanic anoxic event occurred (White, 1988), produced a major shift in the functional diversity of the coastal bony fish community. Aerobically active predatory fishes, similar to modern tuna, billfish, and jacks, exhibited particularly large losses (Friedman, 2009), while fishes in the true open ocean, far from coastal OMZs, were more resilient to the extinction event (Sibert et al., 2014).

Rogers (2000) describes the transition between a warm, oxygen-poor (S-phase) and cool, oxygen-rich (P-phase) ocean. Modern-day ocean conditions are characteristic of a P-phase ocean, with deep, cold circulation

originating from the poles, a well-oxygenated deep ocean, and disjunct mid-water OMZs. In the past, transitions to a warm (S-phase) ocean were accompanied by major extinction events of deep-sea fauna and an upslope migration by the bathyal fauna into better-oxygenated conditions on the shelf. In contrast, invasion and colonization of the abyssal zone is hypothesized to have taken place during the transition to “cool” (P-phase) conditions. There is a parabolic distribution of fish and invertebrate species diversity with depth, which peaks in the bathyal zone (Rex and Etter, 2010; White, 1988). Extinctions of abyssal fauna and repeated speciation events of the bathyal fauna during these transitions from P to S-phase oceans are hypothesized to explain the observed high bathyal species diversity and the comparatively low diversity and young age of the abyssal fish fauna in today’s oceans (Rogers, 2000; White, 1988).

In some cases, margins with OMZs may actually have higher species diversity across the entire margin due to repeated speciation events, as OMZs expanded and contracted through geologic time (Rogers, 2000). For example, Merrett and Marshall (1980) estimate that the fish diversity along the continental margin off northwest Africa is likely to be about two times greater than that of a similar depth range in the temperate western North Atlantic, based on comparison to data from Cohen and Pawson (1977) from the western North Atlantic. Interestingly, the fossil record shows that several of the demersal fish families known from OMZs (Ophidiidae, Bythiidae, Macrouridae, Scorpaenidae, Notacanthidae) appeared within a relatively short time (83–50 Ma) (Patterson, 1993). Other families that appeared during this time were Moridae and Trachichthyidae, which are typically deep-sea species that likely also have lower basal metabolic rates. Future studies should examine how past conditions in ocean oxygenation influenced the evolution of the demersal fish fauna known from today’s OMZs.

5.2 Ocean Deoxygenation

As oceans warm due to anthropogenic climate change, the oceans lose oxygen in a process known as ocean deoxygenation (Keeling et al., 2010). Long-term ocean monitoring shows that oxygen concentrations in the ocean have declined during the 20th century (Stramma et al., 2010; Whitney et al., 2007), and the Intergovernmental Panel for Climate Change 5th Assessment Report predicts that it is likely that large decreases in oceanic dissolved oxygen will occur during the 21st century (Ciais et al., 2013). The possible

implications of expansion of low-oxygen waters have long been recognized (Kamykowski and Zentara, 1990) and Redfield et al. (1963) stated that the margin of safety against anoxia development in the deep ocean is not large, and that significant areas exist in the Pacific Ocean where oxygen is nearly exhausted.

Areas that are already low in oxygen, such as naturally occurring OMZs, are particularly vulnerable to changes in the global ocean oxygen inventory. For example, a 1°C warming throughout the upper ocean is predicted to increase the volume of hypoxic areas by 10% and triple the volume of sub-oxic waters (Deutsch et al., 2011). The volume and spatial extent of OMZs is predicted to increase with anthropogenic ocean warming and related changes to oceanic circulation (Keeling et al., 2010). Model and observational data show that coastal upwelling-favourable winds in poleward portions of eastern boundary upwelling systems have increased, leading to lower oxygen and lower pH conditions for those margins (Garcia-Reyes et al., 2016). Over the last half-century, vertical expansions of OMZ boundaries and declining core oxygen values have already been documented in the eastern tropical Atlantic and the equatorial Pacific with consequences for marine organisms (Stramma et al., 2008, 2010). The emergence of anoxic conditions (Chan et al., 2008) and OMZ expansion have been documented in the California Current System, with hypoxic waters shoaling vertically by up to 90 m from 1984–2006 (Bograd et al., 2008).

Decreases in ocean oxygen are accompanied by increasing ocean temperatures and decreasing ocean pH. As oceanic temperatures warm with climate change, oxygen consumption rates at depth increase (Stramma et al., 2008). The combined effects of warming and oxygen loss this century are projected to reduce the upper ocean's metabolic index (ratio of O₂ supply to resting metabolic O₂ demand) by ~20% globally and by ~50% in northern high-latitude regions, forcing poleward and vertical contraction of metabolically viable habitats and species ranges (Deutsch et al., 2015). Climate models predict substantial warming and deoxygenation throughout most of the upper ocean (Bopp et al., 2013; Keeling et al., 2010) and the Pacific is prone to some of the largest reductions in metabolic index, driven by its larger projected fractional decrease in oxygen (Deutsch et al., 2015).

Habitat compression, sublethal, and lethal impacts are all potential responses of fishes to low-oxygen conditions (Ekau et al., 2010). Fish species that live in today's OMZs may experience range expansions as severely hypoxic waters expand while hypoxia-intolerant species will likely exhibit range contractions (Gilly et al., 2013). Habitat compression due to OMZ

expansion has already been documented for pelagic billfish in the tropical northeast Atlantic (Prince et al., 2010; Stramma et al., 2011) and in the Pacific Oceans (Prince and Goodyear, 2006), as well as for midwater fish in the southern California Current ecosystem (Koslow et al., 2011), but has not yet been documented for demersal fish species in the published literature. However, the shoaling of hypoxic waters above the OMZ in the Southern California Bight has reduced the habitat of rockfish in the Cowcod Conservation Area (McClatchie et al., 2010). Range contractions and expansions of fish species may result in changes to the continental margin food web, and may also affect fisheries yield. The expansion of hypoxic zones is also predicted to lead to a decrease in biodiversity in the affected habitats (Levin et al., 2009).

5.3 Implications for Fisheries Management

Upwelling ecosystems are some of the world's most productive ecosystems and the intermediate zone between the intertidal and the upper boundary of the OMZ is of utmost importance for both artisanal and demersal fisheries (Arntz et al., 2006). Although some OMZ-adapted fish species, including the sebastids *S. alascanus* and *S. altivelis* (Vetter, 1996), the pleuronectid, *M. pacificus* (Vetter et al., 1994), the anoplopomatid, *A. fimbria* (Norse et al., 2012) (Fig. 6), and the merlucciid, *M. capensis* (Mas-Riera et al., 1990) are commercially important species, in most areas, many commercially important fish species are excluded from these severely hypoxic zones (Arntz et al., 2006). Muscular tissue is more calorically expensive to maintain (Hunter et al., 1990), and therefore most muscular, aerobically active fish species that are preferred fisheries items will be excluded from OMZs. Although the pleuronectid, *M. pacificus*, is a fisheries species and is adapted to OMZ conditions, individuals living within the OMZ become more gelatinous (Hunter et al., 1990) and these individuals are no longer profitable to land because they are more difficult to fillet (C. Meng, Captain of F/V Noah's Ark, personal communication, 21 July 2014). In the Arabian Sea on the West Coast of India, reductions in fish catch due to the upwelling of low-oxygen water during the southwest monsoon have been reported by multiple studies (Banse, 1959, 1968). Fish species living in OMZs also tend to be longer-lived species, such as the sebastid, *S. alascanus*, which is reported to live over 100 years (Butler et al., 1995), so different considerations for sustainable fisheries management apply (Mettett and Haedrich, 1997; Norse et al., 2012). Considerations of bycatch are also important.

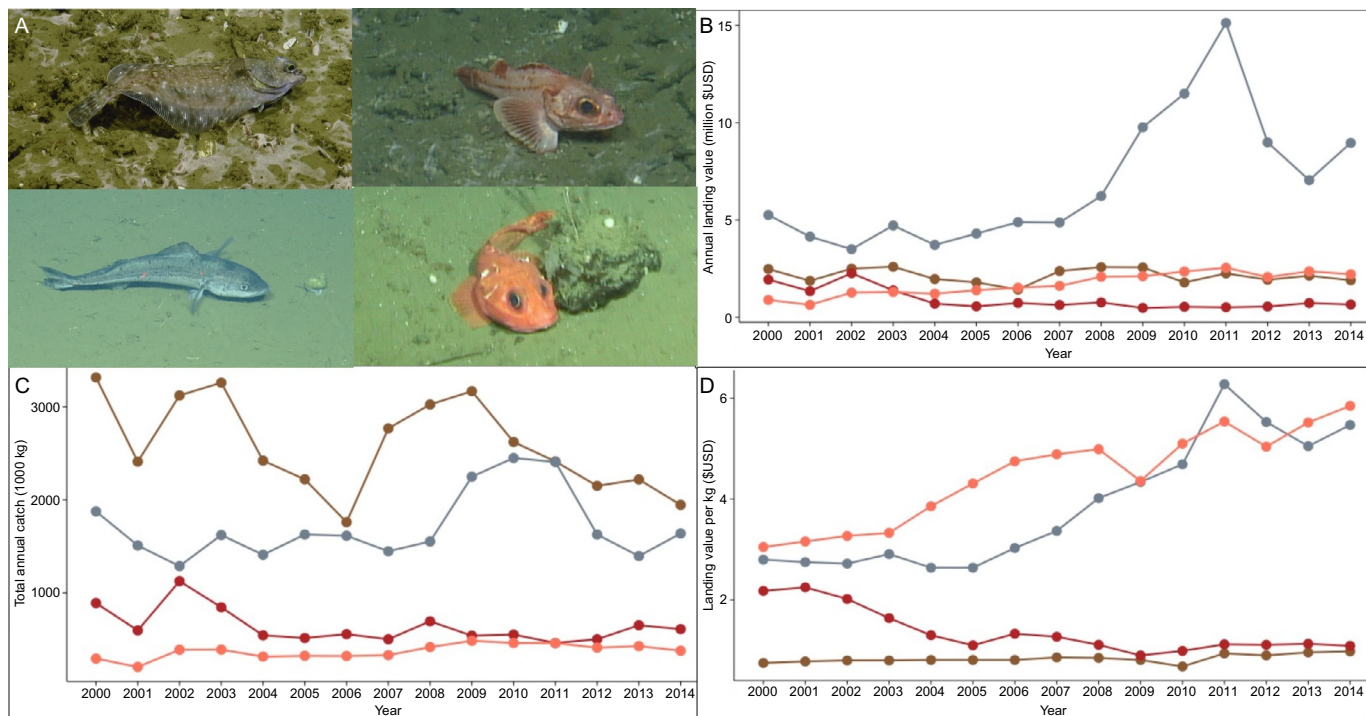


Fig. 6 Several oxygen minimum zone (OMZ) adapted fish species are economically important in the United States, including (A) *Microstomus pacificus* (upper left), *Sebastolobus altivelis* (upper right), *Anoplopoma fimbria* (lower left), and *Sebastolobus alascanus* (lower right). California fisheries landing data from 2000–2014 for *M. pacificus* (brown; dark grey in the print version), *A. fimbria* (grey), *S. alascanus* (orange; light grey in the print version), and *S. altivelis* (maroon; dark grey in the print version) showing (B) annual landing value in millions of \$USD, (C) total annual catch in thousands of kg, and (D) landing value per kg (\$USD). Data were assembled from the California Department of Fish and Wildlife annual California commercial landings reports. During this period, *M. pacificus* and *A. fimbria* make up the greatest mass of landings, *S. alascanus* and *A. fimbria* are the most profitable per kg, and *A. fimbria* is the most economically important OMZ-dwelling demersal fisheries species with an annual landing value in California of up to \$15 million USD. Photographs: E/V Nautilus (*M. pacificus*, *S. altivelis*, and *A. fimbria*), SIO Triton ROV UC Ship Funds (*S. alascanus*).

While the reproductive biomass of *M. pacificus* occurs within the OMZ at depths of 500–900 m where these fish are very gelatinous and not profitable for landing, reproductive individuals are still captured as bycatch by trawlers fishing for *S. alascanus* and *S. altivelis* at these depths (C. Meng, Captain of F/V Noah's Ark, personal communication, 21 July 2014).

Many important fisheries species including *Sebastes* sp. off the US West Coast (Grantham et al., 2004; McClatchie et al., 2010) and butterfish (*Peprilus* spp.), sea bass (*Hemanthias* sp. and *D. euryplectrum*), snapper (*Lutjanus* sp.), and grunts (*Pomadasys* sp. and *Orthopristis* sp.) off Central America (Stromme and Saetersdal, 1988) are hypoxia intolerant and not components of the OMZ assemblage. The general pattern that emerges is that demersal fisheries are likely to be negatively impacted overall by the expansion of OMZs in a warming world. While the immediate impacts may be regional increases in catches due to habitat compression for intolerant species, overall, the decreased habitat may negatively impact the population dynamics of the fisheries species. In the Southern California Bight Cowcod Conservation Area, an 18% habitat loss for rockfish due to hypoxia exposure is predicted over 20 years (McClatchie et al., 2010), showing that these changes can occur relatively quickly.

Expanding OMZs can also reduce prey availability for fisheries species. The CalCOFI ichthyoplankton time-series (1951–2008) indicates that decreasing oxygen levels in the CCS is correlated with a marked decline (~63%) in the region's mesopelagic fishes which serve as a major food web link to higher trophic levels (Koslow et al., 2011). Bioacoustic and trawl sampling on CalCOFI cruises have also shown that dissolved oxygen concentrations off southern California are key in determining the depth of the lower boundary of the deep scattering layer which includes fish and invertebrate prey (Netburn and Koslow, 2015). At a global scale, seawater oxygen concentration is the best single predictor of the migration depth of the diel vertical migrating community and migration depth is shallower in regions with OMZs (Bianchi et al., 2013). These findings have important implications for altered benthopelagic coupling in an ocean with thicker and more intense OMZs. OMZ expansion will also reduce infaunal invertebrate biodiversity at depths of 200–1500 m on upwelling margins, potentially altering trophic support of demersal and benthic fishery species (Sperling et al., 2016).

Fisheries management should take into consideration how climate-change driven ocean impacts such as warming, ocean acidification, ocean oxygen loss, and altered productivity patterns influence the environmental

carrying capacity and available ranges of the fisheries species of interest. Ecosystem-based fisheries management needs to incorporate oxygen availability into vulnerability assessments, spatial management, and marine protected area designation. In developing countries, there is a real need for additional oceanographic monitoring to address these changes in real time. Biological time-series, which are currently greatly lacking (Koslow and Couture, 2013), will be key to understanding how altered oceanographic conditions influence demersal and pelagic fish populations and communities in a warming ocean.



6. CONCLUSIONS

Globally, OMZs and OLZs are important oceanographic features in the Pacific, Atlantic, and Indian Ocean, and are characterized by severely hypoxic conditions, which are physiologically challenging for supporting demersal fish communities. Oxygen minimum zone thickness, depth of the OMZ upper boundary, minimum oxygen levels within the OMZ core, local temperatures, and diurnal, seasonal, and interannual oxycline variability differ regionally, with the thickest and shallowest OMZs occurring in the tropics. Although most fish are not hypoxia-tolerant, some fish species are and have evolved physiological, behavioural, and morphological adaptations that allow them to live under the severely hypoxic, hypercapnic, and at times sulphidic, conditions found in OMZs. At least 77 representative demersal fish species in 44 families and 16 orders, including Scorpaeniformes, Gadiiformes, Pleuronectiformes, Cottiformes, Ophidiiformes, Anguilliformes, Perciformes, Notacanthiformes, Aulopiformes, Osmeriformes, Carcharhiniformes, Squaliformes, Rajiformes, Myxiniformes, Batrachoidiformes, and Beryciformes, have been reported living in OMZs. No single fish family or genus has been able to exploit all OMZs. However, each region has its own set of OMZ-adapted demersal fish species, illustrating that evolutionary adaptation to OMZ conditions has occurred multiple times in multiple groups. The severely hypoxic conditions in OMZs lead to decreased demersal fish diversity, but fish density and biomass trends are variable and dependent on region-specific thresholds. A trend of decreasing density under severely hypoxic conditions, with nonlinear declines in density observed under lower oxygen conditions, appears when more data are available for a region. In data-poor areas, this trend may be masked by the presence of edge effects (high-density bands of a single-species living close to a physiological threshold). Demersal fish tend to follow similar patterns as

meiofauna, macrofauna, and invertebrate megafauna in OMZs (Gooday et al., 2010), however, in OMZs with extremely low-oxygen conditions (Arabian Sea, Gulf of California), demersal fish may be present even when most invertebrate megafauna are excluded (Murty et al., 2009). Therefore, some OMZ-adapted fish species may be more hypoxia-tolerant than OMZ-adapted invertebrates, contrary to expectation. It is likely that region-specific oxygen thresholds are critical in determining shifts in demersal fish density and diversity, though a more in-depth analysis with additional data is needed to specify these thresholds, and different regions will likely be characterized by different thresholds.

Oxygen minimum zones represent a fascinating place to study the physiological and ecological consequences of oxygen-limiting environments; moreover there is a timely, practical importance to understanding how they influence demersal fish communities. Expansions and contractions of OMZs in the past have affected fish evolution and diversity (Friedman, 2009; Rogers, 2000; Sibert et al., 2014; White, 1988). Current patterns of ocean warming, along with alterations in circulation and productivity patterns, are leading to oxygen loss in many marine ecosystems (Deutsch et al., 2011; Garcia-Reyes et al., 2016; Keeling et al., 2010). Areas with OMZs have experienced oxygen declines, leading to the expansion and shoaling of OMZs (Bograd et al., 2008; Stramma et al., 2008, 2010). These changes are expected to lead to decreases in demersal fish community diversity, changes in species composition, and altered trophic pathways on affected margins. Habitat compression is expected for hypoxia-intolerant species (McClatchie et al., 2010), causing increased susceptibility to overfishing for fisheries species. The general pattern suggests that demersal fisheries are likely to be negatively impacted overall by the expansion of OMZs in a warming world. Ecosystem-based fisheries management needs to incorporate oxygen availability into vulnerability assessments, spatial management, and marine protected area designation.



7. ADVANCING UNDERSTANDING/FUTURE ISSUES

Our review of the scientific literature shows that some areas such as the continental shelf and margin of Central and South America and the Bay of Bengal remain poorly studied and limited information is available on how oxygen gradients influence demersal fish community structure and function. Demersal fish are important components of the benthic community and more work is warranted on how oxygen gradients shape demersal fish

assemblages and influence carbon transfer in these understudied, severely hypoxic regions. Additional research should determine at which pO_2 thresholds the greatest amount of species turnover occurs, and how these thresholds are influenced by local temperatures and CO_2 , since these will be ecologically relevant considerations for predicting changes in the demersal fish community under climate change scenarios. In order to sustainably manage demersal fisheries in areas with expanding OMZs, there will be a need to integrate information on changes in environmental oxygen levels with data on species-specific hypoxia tolerances (P_{crit} , aerobic scope, metabolic index, $P_{50}-pO_2$ at which 50% of the blood is oxygenated), which give rise to the oxygen niche of a species (Deutsch et al., 2015; Mislan et al., 2015; Pörtner and Knust, 2007; Pörtner and Peck, 2010; Pörtner et al., 2010). Recent technological advances in using satellite archival tags to measure in situ dissolved oxygen concentrations in the natural environment occupied by the individual (Coffey and Holland, 2015) may be highly informative in determining the environmental niche of the species. These environmental and physiological data must then be considered from an ecological framework, to understand how species interactions and food web dynamics, including predator and prey abundances, may be affected. Additional research is needed on the adaptations of OMZ-specialized fish to the extreme environments in which they live, which include chronic severely hypoxic and hypercapnic, and at times sulphidic, conditions. Most studies on molecular responses and adaptations of fish to hypoxia have focused on freshwater, estuarine, or intertidal fish species, with none known to the authors focusing on OMZ-adapted fish. Knowledge regarding how OMZ-adapted species cope under these conditions may improve our understanding of which species may be tolerant or vulnerable to future climate change impacts.

ACKNOWLEDGEMENTS

We thank an anonymous reviewer, R. Burton (SIO), and E. Sibert (SIO) for comments on the chapter. We thank B. Yannicelli (Centro de Estudios Avanzados en Zonas Aridas), J. Sellanes (UCN), J. Barry (MBARI), J.A. Koslow (SIO), H.J. Walker (SIO), and L. Kuhnz (MBARI) for helpful discussions and content used in this review. We thank A. Keller for providing data from the NOAA Northwest Fisheries Science Center Groundfish Trawl Survey. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. DGE-1144086 to N.D.G. Further exploration of unpublished fisheries literature from the Chilean Fisheries Development Program (IFOP) project FIP2004-09 was made possible through support by CONICYT Programa de Cooperacion Internacional

Graduate Research Opportunities Worldwide CONICYT-NSF Codiga Proyecto Grow 14001 to N.D.G. L.L acknowledges support from NSF-EAR 1324095. Any opinion, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

REFERENCES

- Aguirre-Villaseñor, H., Castillo-Velázquez, R., 2011. New depth record of *Cherublemma emmelas*, black brotula (Ophidiiformes: Ophidiidae) from the Gulf of California. Mexico. *Rev. Mex. Biodivers.* 82 (2), 713–715 (in spanish).
- Aguirre-Villaseñor, H., Salas-Singh, C., 2012. New records of the lollipop catshark *Cephalurus cephalus* (Scyliorhinidae) from the Gulf of California. Mexico. *Rev. Mex. Biodivers.* 83 (1), 298–300 (in spanish).
- Alderdice, D.F., Wickett, W.P., Brett, J.R., 1958. Some effects of temporary exposure to low dissolved oxygen levels on Pacific salmon eggs. *J. Fish. Res. Board Can.* 15, 229–249.
- Armstrong, H.A., 1996. Biotic recovery after mass extinction: the role of climate and ocean-state in the post-glacial (Late Ordovician—Early Silurian) recovery of the conodonts. In: Hart, M.B. (Ed.), *Biotic Recovery from Mass Extinction Events*, vol. 102. Geological Society Special Publication, pp. 105–117.
- Arntz, W.E., Tarazona, J., 1989. Effects of El Niño 1982–83 on benthos, fish and fisheries off the South American Pacific coast. In: Glynn, P.W. (Ed.), *Global Ecological Consequences of the 1982–83 El Niño-Southern Oscillation*. Oceanographic Series, 52. Elsevier, Amsterdam, pp. 323–360.
- Arntz, W.E., Gallardo, V.A., Gutierrez, D., Isla, E., Levin, L.A., Mendo, J., Neira, C., Rowe, G.T., Tarazona, J., Wolff, M., 2006. El Niño and similar perturbation effects on the benthos of Humboldt, California, and Benguella Current upwelling ecosystems. *Adv. Geosci.* 6, 243–265.
- Bailey, G.W., de Beyers, C.J., Lipschitz, K., 1985. Seasonal variation of oxygen deficiency in waters off southern South West Africa in 1975 and 1976 and its relation to the catchability and distribution of the cape rock lobster *Jasus lalandii*. *S. Afr. J. Mar. Sci.* 3, 197–214.
- Baird, R.C., Wilson, D.F., Milliken, D.M., 1973. Observations on *Bregmaceros nectabanus* Whitley in the anoxic, sulfurous water of the Cariaco Trench. *Deep-Sea Res.* 1 20, 503–504.
- Baird, D., Christian, R.R., Peterson, C.H., Johnson, G.A., 2004. Consequences of hypoxia on estuarine ecosystem function: energy diversion from consumers to microbes. *Ecol. Appl.* 14, 805–822.
- Ballón, M., Wosnitza-Mendo, C., Guevara-Carrasco, R., Bertrand, A., 2008. The impact of overfishing and El Niño on the condition factor and reproductive success of Peruvian hake, *Merluccius gayi peruanus*. *Prog. Oceanogr.* 79, 300–307.
- Banse, K., 1959. On upwelling and bottom-trawling off the southwest coast of India. *J. Mar. Biol. Ass. India* 1, 33–49.
- Banse, K., 1968. Hydrography of the Arabian Sea shelf of India and Pakistan and effects on demersal fishes. *Deep Sea Res. Oceanogr. Abstr.* 15, 45–48.
- Berner, M., Schemainda, R., 1957. Über den Einfluss der hydrographischen Situation—insbesondere des Durchluftungszustandes—auf die vertikale Verteilung und den Fang der Laichdorschscharme im Bornholmbecken. *Z. Fisch. N.F.* 6, 331–342.
- Bianchi, G., 1991. Demersal assemblages of the continental shelf and slope edge between the Gulf of Tehuantepec (Mexico) and the Gulf of Papagayo (Costa Rica). *Mar. Ecol. Prog. Ser.* 73, 121–140.

- Bianchi, G., 1992. Demersal assemblages of the continental shelf and upper slope of Angola. *Mar. Ecol. Prog. Ser.* 81, 101–120.
- Bianchi, D., Galbraith, E.D., Carozza, D.A., Mislan, K.A.S., Stock, C.A., 2013. Intensification of open-ocean oxygen depletion by vertically migrating animals. *Nat. Geosci.* 6, 545–548.
- Bograd, S.J., Castro, C.G., Lorenzo, E.D., Palacios, D.M., Bailey, H., Gilly, W., Chavez, F.P., 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. *Geophys. Res. Lett.* 35, L12607.
- Bograd, S.J., Pozo Buil, M., Di Lorenzo, E., Castro, C.G., Schroeder, I.D., Goericke, R., Anderson, C.R., Benitez-Nelson, C., Whitney, F.A., 2015. Changes in source waters to the Southern California Bight. *Deep-Sea Res. II* 112, 42–52.
- Bopp, L., Resplandy, L., Orr, J.C., Doney, S.C., Dunne, J.P., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Séférian, R., Tjiputra, J., Vichi, M., 2013. Multiple stressors of ocean ecosystems in the 21st century: projects with CMIP5 models. *Biogeosciences* 10, 6225–6245.
- Boyer, T.P., Antonov, J.I., Baranova, O.K., Coleman, C., Garcia, H.E., Grodsky, A., Johnson, D.R., Locarnini, R.A., Mishonov, A.V., O'Brien, T.D., Paver, C.R., Reagan, J.R., Seidov, D., Smolyar, I.V., Zweng, M.M., 2013. *World Ocean Database 2013*, NOAA Atlas NESDIS 72, Levitus, S. (Ed.), Mishonov, A. (Technical Ed.), Silver Spring, MD, 209 pp.
- Brauner, C.J., Randall, D.J., 1998. The linkage between oxygen and carbon dioxide transport. In: Perry, S.F., Tufts, B. (Eds.), *Fish Physiology. Fish Respiration*, 17. Academic Press, New York, pp. 283–319.
- Breitbart, D., 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. *Estuaries* 25 (4B), 767–781.
- Breitbart, D.L., Hondorp, D.W., Davias, L.A., Diaz, R.J., 2009. Hypoxia, nitrogen, and fisheries: integrating effects across local and global landscapes. *Annu. Rev. Mar. Sci.* 1, 329–349.
- Brewer, P.G., Hofmann, A.F., 2014. A plea for temperature in descriptions of the oceanic oxygen status. *Oceanography* 27, 160–167.
- Bridges, C.R., 1988. Respiratory adaptations in intertidal fish. *Am. Zool.* 28, 79–96.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Towards a metabolic theory of ecology. *Ecology* 85, 1771–1789.
- Brüchert, V., Currie, B., Peard, K.R., 2009. Hydrogen sulphide and methane emissions on the central Namibian shelf. *Progr. Oceanogr.* 83, 169–179.
- Bunn, H.F., Poyton, R.O., 1996. Oxygen sensing and molecular adaptation to hypoxia. *Physiol. Rev.* 76, 839–885.
- Burleson, M.L., Wilhelm, D.R., Smatresk, N.J., 2001. The influence of fish size on the avoidance of hypoxia and oxygen selection by largemouth bass. *J. Fish Biol.* 59 (5), 1336–1349.
- Butler, J.L., Kastle, C., Rubin, K., Heijnis, D.K.-H., Jacobson, L., Andrews, A., Wakefield, W.W., 1995. Age determination of shortspine thornyhead, *Sebastes alascanus*, using otolith sections and ^{210}Pb : ^{226}Ra ratios: Administrative Report. National Marine Fisheries Service Southwest Fisheries Science Center, La Jolla.
- Carney, R.S., 2005. Zonation of deep biota on continental margins. *Oceanogr. Mar. Biol.* 43, 211–278.
- Carruthers, J.N., Gogate, S.S., Naidu, J.R., Laevastu, T., 1959. Shorewards upslope of the layer of minimum oxygen off Bombay: its influence on marine biology, especially fisheries. *Nature* 183, 1084–1087.
- Cedras, R.B., Salvanes, A.-G.V., Gibbons, M.J., 2011. Investigations into the diet and feeding ecology of the bearded goby *Sufflogobius bibarbatus* off Namibia. *Afr. J. Mar. Sci.* 33, 313–320.

- Cerezo, J., Garcia, B., 2004. The effects of oxygen levels on oxygen consumption, survival and ventilatory frequency of sharpsnout sea bream (*Diplodus puntazzo* Gmelin, 1789) at different conditions of temperature and fish weight. *J. Appl. Ichthyol.* 20, 488–492.
- Chan, F., Barth, J.A., Lubchenco, J., Kirincich, A., Weeks, H., Peterson, W.T., Menge, B.A., 2008. Emergence of anoxia in the California Current large marine ecosystem. *Science* 319, 920.
- Chapman, L., Galis, F., Shinn, J., 2000. Phenotypic plasticity and the possible role of genetic assimilation: hypoxia-induced trade-offs in the morphological traits of an African cichlid. *Ecol. Lett.* 3, 387–393.
- Chernova, N.V., 2014. New species of the genus *Careproctus* (Liparidae) from the Kara Sea with notes on spongiophilia, reproductive commensalism between fishes and sponges (Rosellidae). *J. Ichthyol.* 54 (8), 501–512.
- Childress, J.J., Seibel, B.A., 1998. Life at stable low oxygen: adaptations of animals to oceanic oxygen minimum layers. *J. Exp. Biol.* 201, 1223–1232.
- Chu, J.W.F., Tunnicliffe, V., 2015. Oxygen limitations on marine animal distributions and the collapse of epibenthic community structure during shoaling hypoxia. *Glob. Change Biol.* 21 (8), 2989–3004.
- Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., Jones, C., Le Quéré, C., Myneni, R.B., Piao, S., Thornton, P., 2013. Carbon and other biogeochemical cycles. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK/NY, USA.
- Coffey, D.M., Holland, K.N., 2015. First autonomous recording of in situ dissolved oxygen from free-ranging fish. *Anim. Biotelem.* 3, 47.
- Cohen, D.M., Pawson, D.L., 1977. Observations from the DSRV Alvin on populations of benthic fishes and selected larger invertebrates in and near DWD-106: Baseline report of environmental conditions in deepwater dumpsite 106. U.S. Department of Commerce, NOAA, Dumpsite Evaluation Report 77-1, 2, Biological characteristics.
- Compagno, L.J.V., 1984. Species catalogue. Sharks of the world. An annotated and illustrated catalogue of sharks species known to date. Part. 2. Carcharhiniformes. *FAO Fish. Synop.* 4, 251–655.
- Cowie, G.L., Levin, L.A., 2009. Benthic biological and biogeochemical patterns and processes across an oxygen minimum zone (Pakistan margin, NE Arabian Sea). *Deep Sea Res. II* 56, 261–270.
- Craig, J.K., 2012. Aggregation on the edge: effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the Northern Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 445, 75–95.
- Crans, K.D., Pranckevicius, N.A., Scott, G.R., 2015. Physiological tradeoffs may underlie the evolution of hypoxia tolerance and exercise performance in sunfish (Centrarchidae). *J. Exp. Biol.* 218, 3264–3275.
- Dahl, T.W., Hammarlund, E.U., Anbar, A.D., Bond, D.P.G., Gill, B.C., Gordon, G.W., Knoll, A.H., Nielsen, A.T., Schovsbo, N.H., Canfield, D.E., 2010. Devonian rise in atmospheric oxygen correlated to the radiations of terrestrial plants and large predatory fish. *PNAS* 107, 17911–17915.
- Daskalov, G., 2003. Long-term changes in fish abundance and environmental indices in the Black Sea. *Mar. Ecol. Prog. Ser.* 255, 259–270.
- Davies, S.M., Sanchez-Velasco, L., Beier, E., Godinez, V.M., Barton, E.D., Tamayo, A., 2015. Three-dimensional distribution of larval fish habitats in the shallow oxygen minimum zone in the Eastern Tropical Pacific Ocean off Mexico. *Deep-Sea Res. I* 101, 118–129.

- Davis, J.C., 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. *J. Fish. Res. Bd. Can.* 32 (12), 2295–2332.
- Day, D., Percy, W., 1968. Species associations of benthic fishes on the continental shelf and slope off Oregon. *J. Fish. Res. Bd. Can.* 25 (12), 2665–2675.
- De Leo, F.C., Drazen, J.C., Vetter, E.W., Rowden, A.A., Smith, C.R., 2012. The effects of submarine canyons and the oxygen minimum zone on deep-sea fish assemblages off Hawaii. *Deep-Sea Res. I* 64, 54–70.
- DeMartini, E.E., 1978. Apparent paternal care in *Liparis fucensis* (Pisces: Cyclopteridae). *Copeia* 1978 (3), 537–539.
- Deutsch, C., Brix, H., Ito, T., Frenzel, H., Thompson, L., 2011. Climate-forced variability of ocean hypoxia. *Science* 333, 336–339.
- Deutsch, C., Ferrel, A., Seibel, B., Pörtner, H.-O., Huey, R.B., 2015. Climate change tightens a metabolic constraint on marine habitats. *Science* 348, 1132–1136.
- Diaz, R., Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanogr. Mar. Biol.* 33, 245–303.
- Diaz, R.J., Rosenberg, R., 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321, 926–929.
- Díaz-Ochoa, J.A., Lange, C.B., Pantoja, S., De Lange, G.J., Guttierrez, D., Munoz, P., Salamanca, M., 2009. Fish scales in sediments from off Callao, central Peru. *Deep-Sea Res. II* 56, 1124–1135.
- Dingle, R.V., Nelson, G., 1993. Sea-bottom temperature, salinity and dissolved oxygen on the continental margin off south-western Africa. *S. Afr. J. Mar. Sci.* 13, 33–49.
- Douglas, E.L., Friedl, W.A., Pickwell, G.V., 1976. Fishes in oxygen-minimum zones: blood oxygenation characteristics. *Science* 191, 957–959.
- Doya, C., Aguzzi, J., Chatzievangelou, D., Costa, C., Company, J.P., Tunnicliffe, V., 2016. The seasonal use of small-scale space by benthic species in a transiently hypoxic area. *J. Mar. Syst.* 154 (B), 280–290.
- Drazen, J.C., Friedman, J.R., Condon, N.E., Aus, E.J., Geringer, M.E., Keller, A.E., Clarke, M.E., 2015. Enzyme activities of demersal fishes from the shelf to the abyssal plain. *Deep-Sea Res. I* 100, 117–126.
- Ekau, W., Auel, H., Pörtner, H.-O., Gilbert, D., 2010. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences* 7, 1669–1699.
- Espino, M., 1999. “El Niño 1997–98”: su efecto sobre el ambiente y los recursos pesqueros del Peru. In: Tarazona, J., Castillo, E. (Eds.), *El Niño 1997–98 y su impacto sobre los ecosistemas marino y terrestre*. *Rev. Per. Biol.*, vol. Extraordinario, pp. 97–109 (in spanish).
- Espino, M., Benites, C., Maldonado, M., 1985. Situacion de la poblacion de merluza durante “El Niño”. In: Arntz, W.E., Landa, A., Tarazona, J. (Eds.), *El Niño. Su impacto en la fauna marina*. *Bol. Inst. Mar Peru-Callao spec. vol.*, pp. 159–162 (in spanish).
- Farrell, A., Richards, J., 2009. Defining hypoxia: an integrative synthesis of the responses of fish to hypoxia. *Fish Physiol.* 27, 487–503.
- Feely, R.A., Sabine, C.L., Hernandez-Ayon, J.M., Ianson, D., Hales, B., 2008. Evidence for upwelling of corrosive “acidified” water onto the continental shelf. *Science* 320, 1490–1492.
- Fischer, W., Krupp, F., Schneider, W., Sommer, C., Carpenter, K.E., Niem, V.H., 1995. GuiaFAO para la identificacion de especies para los fines de la pesca. In: *Pacifico centro-oriental. Vertebrados—Parte 1 vol. I–III*. FAO, Rome, pp. 1–1813.
- Friedman, M., 2009. Ecomorphological selectivity among marine teleost fishes during the end-Cretaceous extinction. *PNAS* 106 (13), 5218–5223.
- Friedman, J.R., Condon, N.E., Drazen, J.C., 2012. Gill surface area and metabolic enzyme activities of demersal fishes associated with the oxygen minimum zone off California. *Limnol. Oceanogr.* 57 (6), 1701–1710.

- Fuenzalida, R., Schneider, W., Garcés-Vargas, J., Bravo, L., Lange, C., 2009. Vertical and horizontal extension of the oxygen minimum zone in the eastern South Pacific Ocean. *Deep-Sea Res. II* 56, 992–1003.
- García-Reyes, M., Sydemann, W.J., Schoeman, D.S., Rykaczewski, R.R., Black, B.A., Smit, A.J., Bograd, S.J., 2016. Under pressure: climate change, upwelling, and eastern boundary upwelling ecosystems. *Front. Mar. Sci.* 2 (109). <http://dx.doi.org/10.3389/fmars.2015.00109>.
- George, P.C., 1958. Sole Fisheries. Fisheries of the West Coast of India. Central Marine Fisheries Research Station, Mandapam Camp, pp. 51–54.
- Gewin, V., 2010. Dead in the water. *Nature* 466, 812–814.
- Gilly, W.F., Beman, J.M., Litvin, S.Y., Robison, B.H., 2013. Oceanographic and biological effects of shoaling of the oxygen minimum zone. *Annu. Rev. Mar. Sci.* 5, 393–420.
- Gooday, A.J., Bett, B.J., Escobar, E., Ingole, B., Levin, L.A., Neira, C., Raman, A.V., Sellanes, J., 2010. Habitat heterogeneity and its influence on benthic biodiversity in oxygen minimum zones. *Mar. Ecol.* 31, 125–147.
- Gordon, A.L., Tessler, Z.D., Villanoy, C., 2011. Dual overflows into the deep Sulu Sea. *Geophys. Res. Lett.* 38, L18606.
- Gracey, A.Y., Troll, J.V., Somero, G.N., 2001. Hypoxia-induced gene expression profiling in the euryoxic fish *Gillichthys mirabilis*. *PNAS* 98 (4), 1993–1998.
- Grantham, B.A., Chan, F., Nielsen, K.J., Fox, D.S., Barth, J.A., Huyer, A., Lubchenko, J., Menge, B.A., 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature* 429, 749–754.
- Gray, J.S., Wu, R.S.S., Or, Y.Y., 2002. Effects of hypoxia and organic enrichment on the coastal marine environment. *Mar. Ecol. Prog. Ser.* 238, 249–279.
- Guevara-Carrasco, R., Leonart, J., 2008. Dynamics and fishery of the Peruvian hake: between nature and man. *J. Mar. Syst.* 71, 249–259.
- Gutierrez, D., Enriquez, E., Purca, S., Quipuzcoa, L., Marquina, R., Flores, G., Graco, M., 2008. Oxygenation episodes on the continental shelf of central Peru: remote forcing and benthic ecosystem response. *Prog. Oceanogr.* 79, 177–189.
- Haedrich, R.L., Merrett, N.R., 1990. Little evidence for faunal zonation or communities in deep sea demersal fish faunas. *Prog. Oceanogr.* 24, 239–250.
- Hamukuaya, H., Bianchi, G., Baird, D., 2001. The structure of demersal assemblages off Namibia in relation to abiotic factors. *S. Afr. J. Mar. Sci.* 23, 397–417.
- Helly, J.J., Levin, L.A., 2004. Global distribution of naturally occurring marine hypoxia on continental margins. *Deep-Sea Res. I* 51, 1159–1168.
- Hochachka, P.W., Buck, L.T., Doll, C.J., Land, S.C., 1996. Unifying theory of hypoxia tolerance: molecular/metabolic defense and rescue mechanisms for surviving oxygen lack. *PNAS* 93, 9493–9498.
- Hofmann, A.F., Peltzer, E.T., Walz, P.M., Brewer, P.G., 2011. Hypoxia by degrees: establishing definitions for a changing ocean. *Deep-Sea Res. I* 58, 1212–1226.
- Horn, W., Meincke, J., 1976. Note on the tidal current field in the continental slope area off Northwest Africa. *Mem. Soc. Roy. Sci. Liege* 6 (10), 31–42.
- Hunter, J., Butler, J., Kimbrell, C., Lynn, E., 1990. Bathymetric patterns in size, age, sexual maturity, water content, and caloric density of Dover sole, *Microstomus pacificus*. *CalCOFI Rep.* 31, 132–144.
- Hunter, W.R., Oguri, K., Kitazato, H., Ansari, Z.A., Witte, U., 2011. Epi-benthic mega-faunal zonation across an oxygen minimum zone at the Indian continental margin. *Deep-Sea Res. I* 58, 699–710.
- IFOP, 2005. Proyecto FIP No 2004-09: Evaluación hidroacústica de merluza común, año 2004. Chilean Fisheries Development Program. Unpublished Report FIP 2004-09. <http://www.fip.cl/Archivos/Hitos/Informes/infinal%202004-09.pdf>. (in spanish).

- Ishibashi, Y., Inoue, K., Nakatsukasa, H., Ishitani, Y., Miyashita, S., Murata, O., 2005. Ontogeny of tolerance to hypoxia and oxygen consumption of larval and juvenile red sea bream, *Pagrus major*. *Aquaculture* 244, 331–340.
- Jacobs, D.K., Lindberg, D.R., 1998. Oxygen and evolutionary patterns in the sea: onshore/offshore trends and recent recruitment of deep-sea faunas. *PNAS* 95, 9396–9401.
- Jenkyns, H.C., 2010. Geochemistry of oceanic anoxic events. *Geochem. Geophys. Geosyst.* 11, Q03004.
- Jensen, F.B., Weber, R.E., 1982. Respiratory properties of tench blood and hemoglobin. Adaptation to hypoxic-hypercapnic water. *Molec. Physiol.* 2, 235–250.
- Jensen, F.B., Weber, R.E., 1985. Kinetics of the acclimational responses of tench to combined hypoxia and hypercapnia I and II. *J. Comp. Physiol.* 156B, 197–211.
- Jensen, F.B., Andersen, N.A., Heisler, N., 1987. Effects of nitrite exposure on blood respiratory properties, acid-base and electrolyte regulation in the carp (*Cyprinus carpio*). *J. Comp. Physiol.* 157B, 533–541.
- Jensen, F.B., Nikkinmaa, M., Weber, R.E., 1993. Environmental perturbations of oxygen transport in fishes: causes, consequences and compensations. In: Rankin, J.C., Jensen, F.B. (Eds.), *Fish Ecophysiology*. Chapman & Hall, London, pp. 161–179.
- Jeppsson, L., 1990. An oceanic model for lithological and faunal changes tested on the Silurian record. *J. Geol. Soc. Lond.* 147, 663–674.
- Josefson, A.B., Widbom, B., 1988. Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin. *Mar. Biol.* 100, 31–40.
- Juniper, S.K., Matabos, M., Mihaly, S., Ajayamohan, R.S., Gervais, F., Bui, A.O.V., 2013. A year in Barkley Canyon: a time-series observatory study of mid-slope benthos and habitat dynamics using the NEPTUNE Canada network. *Deep-Sea Res.* II 92, 114–123.
- Kajimura, S., Aida, K., Duan, C., 2005. Insulin-like growth factor-binding protein-1 (IGFBP-1) mediates hypoxia-induced embryonic growth and developmental retardation. *PNAS* 102, 1240–1245.
- Kalvelage, T., Lavik, G., Jensen, M.M., Revsbech, N.P., Schunck, H., Loescher, C., Desai, D.K., LaRoche, J., Schmitz-Streit, R., Kuzpers, M.M.M., 2014. Aerobic microbial respiration in oceanic oxygen minimum zones. *Geophys. Res. Abstr.* 16, EGU2014–EGU8109.
- Kamykowski, D., Zentara, S., 1990. Hypoxia in the world ocean as recorded in the historical data set. *Deep-Sea Res.* I 37, 1861–1874.
- Keeling, R.F., Kortzinger, A., Gruber, N., 2010. Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci.* 2, 199–229.
- Keller, A.A., Simon, V., Chan, F., Wakefield, W.W., Clarke, M.E., Barth, J.A., Kamikawa, D., Fruh, E.L., 2010. Demersal and invertebrate biomass in relation to an offshore hypoxic zone along the US West Coast. *Fish. Oceanogr.* 19 (1), 76–87.
- Keller, A., Wallace, J., Horness, B., 2012. Variations in eastern North Pacific demersal fish biomass based on the US west coast groundfish bottom trawl survey (2003–2010). *Fish. Bull.* 110, 205–222.
- Keller, A.A., Ciannelli, L., Wakefield, W.W., Simon, V., Barth, J.A., Pierce, S.D., 2015. Occurrence of demersal fishes in relation to near-bottom oxygen levels within the California Current large marine ecosystem. *Fish. Oceanogr.* 24 (2), 162–176.
- Kemp, W.M., Testa, J.M., Conley, D.J., Gilbert, D., Hagy, J.D., 2009. Temporal responses of coastal hypoxia to nutrient loading and physical controls. *Biogeosciences* 6 (12), 2985–3008.
- Khan, M.F., Nandakumaran, K., 1993. Population dynamics of Malabar sole *Cynoglossus macrostomus* Norman along Calicut coast. *Indian J. Fish.* 40 (4), 225–230.
- Koslow, J., 1993. Community structure in North Atlantic deep-sea fishes. *Prog. Oceanogr.* 31, 321–338.

- Koslow, J.A., Couture, J., 2013. Comment: follow the fish. *Nature* 502, 163–164.
- Koslow, J., Bulman, C., Lyle, J., 1994. The mid-slope demersal fish community off south-eastern Australia. *Deep-Sea Res. I* 41, 113–141.
- Koslow, J.A., Goericke, R., Lara-Lopez, A., Watson, W., 2011. Impact of declining intermediate-water oxygen on deepwater fishes in the California Current. *Mar. Ecol. Prog. Ser.* 436, 207–218.
- Kramer, D., 1987. Dissolved oxygen and fish behavior. *Environ. Biol. Fishes* 18 (2), 81–92.
- Kukharev, N.N., 2015. On fish aggregations in the oxygen minimum zones in the North-Western Arabian Sea. *Труды ЮгНИРО*, Т. 53, 149–172 (in Russian).
- Law, S.H.W., Wu, R.S.S., Ng, P.K.S., Yu, R.M.K., Kong, R.Y.C., 2006. Cloning and expression analysis of two distinct HIF- α isoforms—gcHIF-1 α and gcHIF-4 α —from the hypoxia-tolerant grass carp, *Ctenopharyngodon idellus*. *BMC Mol. Biol.* 7, 15.
- Levin, L.A., 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanogr. Mar. Biol.* 41, 1–45.
- Levin, L.A., Huggett, C.L., Wishner, K.F., 1991. Control of deep-sea benthic community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean. *J. Mar. Res.* 49, 763–800.
- Levin, L.A., Gage, J.D., Martin, C., Lamont, P.A., 2000. Macro-benthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea. *Deep-Sea Res. II* 47, 189–226.
- Levin, L.A., Gutierrez, D., Rathburn, A., Neira, C., Sellanes, J., Munoz, P., Gallardo, V., Salamanca, M., 2002. Benthic processes on the Peru margin: a transect across the oxygen minimum zone during the 1997–98 El Niño. *Prog. Oceanogr.* 53, 1–27.
- Levin, L., Ekau, W., Gooday, A., 2009. Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences* 6, 2063–2098.
- Levin, L.A., Mendoza, G.F., Gonzalez, J.P., Thurber, A.R., Cordes, E.E., 2010. Diversity of bathyal macrofauna on the northeastern Pacific margin: the influence of methane seeps and oxygen minimum zones. *Mar. Ecol.* 31, 94–110.
- Levin, L.A., McGregor, A.L., Mendoza, G.F., Woulds, C., Cross, P., Witte, U., Gooday, A.J., Cowie, G., Kitazato, H., 2013. Macrofaunal colonization across the Indian margin oxygen minimum zone. *Biogeosciences* 10, 7161–7177.
- Levin, L.A., Mendoza, G.F., Grupe, B.M., Gonzalez, J.P., Jellison, B., Rouse, G., Thurber, A.R., Warren, A., 2015. Biodiversity on the rocks: macrofauna inhabiting authigenic carbonate at Costa Rica methane seeps. *PLoS One* 10, e0131080.
- Love, R.H., Fisher, R.A., Wilson, M.A., Nero, R.W., 2004. Unusual swimbladder behavior of fish in the Cariaco Trench. *Deep-Sea Res. I* 51, 1–16.
- Lynn, R.J., Simpson, J.J., 1987. The California current system: the seasonal variability of its physical characteristics. *J. Geophys. Res.* 92 (C12), 12947–12966.
- MacLeod, J.C., Smith Jr., L.L., 1966. Effect of pulpwood fiber on oxygen consumption and swimming endurance of the fathead minnow, *Pimephales promelas*. *Trans. Am. Fish. Soc.* 95, 71–84.
- Macpherson, E., Gordo, A., 1992. Trends in the demersal fish community off Namibia from 1983 to 1990. *S. Afr. J. Mar. Sci.* 12, 635–649.
- Madhupratap, M., Nair, K.N.V., Gopalakrishnan, T.C., Haridas, P., Nair, K.K.C., Venugopal, P., Gauns, M., 2001. Arabian Sea oceanography and fisheries of the west coast of India. *Curr. Sci.* 81 (4), 355–361.
- Mandic, M., Todgham, A.E., Richards, J.G., 2009. Mechanisms and evolution of hypoxia tolerance in fish. *Proc. R. Soc. B* 276 (1657), 735–744.
- Mandic, M., Ramon, M.L., Gracey, A.Y., Richards, J.G., 2014. Divergent transcriptional patterns are related to differences in hypoxia tolerance between the intertidal and the subtidal sculpins. *Mol. Ecol.* 23, 6091–6103.

- Marliave, J.B., Peden, A.E., 1989. Larvae of *Liparis fucensis* and *Liparis callyodon*: is the “cottoid bubblemorp [sic]” phylogenetically significant? *Fish. Bull.* 87, 735–743.
- Mas-Riera, J., Lombarte, A., Gordo, A., Macpherson, E., 1990. Influence of Benguela upwelling on the structure of demersal fish populations off Namibia. *Mar. Biol.* 182, 175–182.
- Matabos, M., Tunnickliffe, V., Juniper, S.K., Dean, C., 2012. A year in hypoxia: epibenthic community responses to severe oxygen deficit at a subsea observatory in a coastal inlet. *PLoS One* 7, e45626.
- Matabos, M., Bui, A.O.V., Mihaly, S., Aguzzi, J., Juniper, S.K., Ajayamohan, R.S., 2014. High-frequency study of epibenthic megafaunal community dynamics in Barkley Canyon: a multi-disciplinary approach using the NEPTUNE Canada network. *J. Mar. Syst.* 130, 56–68.
- Matey, V., Richards, J.G., Wang, Y., Wood, C.M., Rogers, J., Davies, R., Murray, B.W., Chen, X.-Q., Du, J., Brauner, C.J., 2008. The effect of hypoxia on gill morphology and ionoregulatory status in the Lake Qinghai scaleless carp, *Gymnocypris przewalskii*. *J. Exp. Biol.* 211, 1063–1074.
- McClatchie, S., Goericke, R., Cosgrove, R., Auad, G., Vetter, R., 2010. Oxygen in the Southern California Bight: multidecadal trends and implications for demersal fisheries. *Geophys. Res. Lett.* 37, L19602.
- McIlwain, J.L., Harvey, E.S., Grove, S., Shiell, G., Al-Oufi, H., Al-Jardani, N., 2011. Seasonal changes in a deep-water fish assemblage in response to monsoon-generated upwelling events. *Fish. Oceanogr.* 20 (6), 497–516.
- Mead, G., 1963. Observations on fishes caught over the anoxic waters of the Cariaco Trench, Venezuela. *Deep-Sea Res. Oceanogr. Abstr.* 10, 251–257.
- Merrett, N., Marshall, N., 1980. Observations on the ecology of deep-sea bottom-living fishes collected off northwest Africa (08°–27°N). *Prog. Oceanogr.* 9, 185–244.
- Mettett, N.R., Haedrich, R.L., 1997. *Deep-Sea Demersal Fish and Fisheries*, first ed. Chapman and Hall, London.
- Milessi, A.C., Sellanes, J., Gallardo, V.A., Lange, C.B., 2005. Osseous skeletal material and fish scales in marine sediments under the oxygen minimum zone off northern and central Chile. *Estuar. Coast. Shelf Sci.* 64, 185–190.
- Milliken, D.M., Houde, E.D., 1984. A new species of Bregmacerotidae (Pisces), *Bregmaceros cantori*, from the Western Atlantic Ocean. *Bull. Mar. Sci.* 35 (1), 11–19.
- Mislan, K.A.S., Dunne, J.P., Sarmiento, J.L., 2015. The fundamental niche of blood-oxygen binding in the pelagic ocean. *Oikos*. <http://dx.doi.org/10.1111/oik.02650>.
- Mittelstaedt, F., 1976. On the currents along the Northwest African coast south of 22°N. *Dt. Hydrogr. Z.* 29 (3), 97–117.
- Moffitt, S.E., Hill, T.M., Ohkushi, K., Kennett, J.P., Behl, R.J., 2014. Vertical oxygen minimum zone oscillations since 20 ka in Santa Barbara Basin: a benthic foraminiferal community perspective. *Paleoceanography* 29, 44–57.
- Moffitt, S.E., Hill, T.M., Roopnarine, P.D., Kennett, J.P., 2015a. Response of seafloor ecosystems to abrupt global climate change. *PNAS* 112 (15), 4684–4689.
- Moffitt, S.E., Moffitt, R.A., Sauthoff, W., Davis, C.V., Hewett, K., Hill, T.M., 2015b. Paleoclimatological insights on recent oxygen minimum zone expansion: lessons for modern oceanography. *PLoS One* 10 (1), e0115246.
- Montecino, V., Lange, C.B., 2009. The Humboldt Current System: ecosystem components and processes, fisheries, and sediment studies. *Prog. Oceanogr.* 83, 65–79.
- Morrison, J.M., Codispoti, L.A., Gaurin, S., Jones, B., Magnhnani, V., Zheng, Z., 1998. Seasonal variation of hydrographic and nutrient fields during the US JGOFS Arabian Sea Process Study. *Deep-Sea Res. II* 45, 2053–2102.
- Morrison, J., Codispoti, L., Smith, S., 1999. The oxygen minimum zone in the Arabian Sea during 1995. *Deep-Sea Res. II* 46, 1903–1931.

- Mullins, H.T., Thompson, J.B., McDougall, K., Vercoutere, T.L., 1985. Oxygen–minimum zone edge effects: evidence from the central California coastal upwelling system. *Geology* 13, 491–494.
- Murty, S.J., Bett, B.J., Gooday, A.J., 2009. Megafaunal responses to strong oxygen gradients on the Pakistan margin of the Arabian Sea. *Deep-Sea Res. II* 56, 472–487.
- Nam, S.H., Kim, H.-J., Send, U., 2011. Amplification of hypoxic and acidic events by La Niña conditions on the continental shelf off California. *Geophys. Res. Lett.* 38, L22602.
- Nam, S.H., Takeshita, Y., Frieder, C.A., Martz, T., Ballard, J., 2015. Seasonal advection of Pacific equatorial water alters oxygen and pH in the Southern California Bight. *J. Geophys. Res. Oceans* 120, 5387–5399.
- Netburn, A.N., Koslow, J.A., 2015. Dissolved oxygen as a constraint on daytime deep scattering layer depth in the southern California current ecosystem. *Deep-Sea Res. I* 104, 149–158.
- Nilsson, G.E., 2007. Gill remodeling in fish—a new fashion or an ancient secret? *J. Exp. Biol.* 210, 2403–2409.
- Nilsson, G.E., 2010. *Respiratory Physiology of Vertebrates. Life With and Without Oxygen*. Cambridge University Press, Cambridge, pp. 1–334.
- Nilsson, G.E., Ostlund-Nilsson, S., 2008. Does size matter for hypoxia tolerance in fish? *Biol. Rev. Camb. Philos. Soc.* 83, 173–189.
- Nishida, T., Sivasubramaniam, K., 1986. Atlas of Deep Water Demersal Fishery Resources in the Bay of Bengal. Bay of Bengal programme: development of small-scale fisheries, UN FAO, pp. 1–17.
- Norris, R.D., Turner, S.K., Hull, P.M., Ridgwell, A., 2013. Marine ecosystem responses to Cenozoic global change. *Science* 341, 492–498.
- Norse, E.A., Brooke, S., Cheung, W.W.L., Clark, M.R., Ekeland, E., Froese, R., Gjerde, K.M., Haedrich, R.L., Heppell, S.S., Morato, T., Morgan, L.E., Pauly, D., Sumaila, R., Watson, R., 2012. Sustainability of deep-sea fisheries. *Mar. Pol.* 36, 307–320.
- Patterson, C., 1993. An overview of the early fossil record of acanthomorphs. *B. Mar. Sci.* 52 (1), 29–59.
- Paulmier, A., Ruiz-Pino, D., 2009. Oxygen minimum zones (OMZs) in the modern ocean. *Prog. Oceanogr.* 80, 113–128.
- Paulmier, A., Ruiz-Pino, D., Garçon, V., Fariás, L., 2006. Maintaining of the Eastern South Pacific Oxygen Minimum Zone (OMZ) off Chile. *Geophys. Res. Lett.* 33, L20601.
- Paulmier, A., Ruiz-Pino, D., Garçon, V., 2011. CO₂ maximum in the oxygen minimum zone (OMZ). *Biogeosciences* 8, 239–252.
- Peden, A.E., Corbett, C.A., 1973. Commensalism between a liparid fish, *Careproctus sp.*, and the lithodid box crab, *Lopholithodes foraminatus*. *Can. J. Zool.* 51 (5), 555–556.
- Peña-Izquierdo, J., van Sebille, E., Pelegri, J.L., Sprintall, J., Mason, E., Llanillo, P.J., Machin, F., 2015. Water mass pathways to the North Atlantic oxygen minimum zone. *J. Geophys. Res. Oceans* 120. <http://dx.doi.org/10.1002/2014JC010557>.
- Perry, S., 2011. Respiratory responses to hypoxia in fish. In: Farrell, A.P. (Ed.), *Encyclopedia of Fish Physiology: From Genome to Environment*. Academic Press, Amsterdam, pp. 1751–1756.
- Piontkovski, S., Al-Oufi, H., 2014. Oxygen Minimum Zone and fish landings along the Omani Shelf. *J. Fish. Aquat. Sci.* 9, 294–310.
- Piontkovski, S., Al-Gheilani, H.M.H., Jupp, B.P., Al-Azri, A.R., Al-Hashmi, K.A., 2012. Interannual changes in the Sea of Oman ecosystem. *Open Mar. Biol. J.* 6, 38–52.
- Pollock, M., Clarke, L., Dube, M., 2007. The effects of hypoxia on fishes: from ecological to physiological effects. *Environ. Rev.* 14, 1–14.

- Pörtner, H.O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315, 95–97.
- Pörtner, H.O., Peck, M.A., 2010. Climate change effects on fish and fisheries: towards a cause- and -effect understanding. *J. Fish Biol.* 77, 1745–1779.
- Pörtner, H.O., Bennett, A.F., Bozinovic, F., Clarke, A., Lardies, M.A., Lucassen, M., Pelster, B., Schiemer, F., Stillman, J.H., 2006. Trade-offs in thermal adaptation: the need for a molecular to ecological integration*. *Physiol. Biochem. Zool.* 79 (2), 295–313.
- Pörtner, H.O., Schulte, P.M., Wood, C.M., Schiemer, F., 2010. Niche dimensions in fishes: an integrative view. *Physiol. Biochem. Zool.* 83 (5), 808–826.
- Powers, D., 1980. Molecular ecology of teleost fish hemoglobins: strategies for adapting to changing environments. *Am. Zool.* 20, 139–162.
- Powers, D.A., Greaney, G.S., Place, A.R., 1979. Physiological correlation between lactate dehydrogenase genotype and haemoglobin function in killifish. *Nature* 277, 240–241.
- Prakash, S., Nair, T.M.B., Bhaskar, T.V.S.U., Prakash, P., Gilbert, D., 2012. Oxycline variability in the central Arabian Sea: an argo-oxygen study. *J. Sea Res.* 71, 1–8.
- Prince, E.D., Goodyear, C.P., 2006. Hypoxia-based habitat compression of tropical pelagic fishes. *Fish. Oceanogr.* 15, 451–464.
- Prince, E.D., Luo, J., Goodyear, C.P., Hoolihan, J.P., Snodgrass, D., Orbesen, E.S., Serafy, J.E., Ortiz, M., Schirripa, M.J., 2010. Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes. *Fish. Oceanogr.* 19, 448–462.
- Quiroga, E., Sellanes, J., Arntz, W.E., Gerdes, D., Gallardo, V.A., Hebbeln, D., 2009. Benthic megafaunal and demersal fish assemblages on the Chilean continental margin: the influence of the oxygen minimum zone on bathymetric distribution. *Deep-Sea Res. II* 56, 1112–1123.
- R Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN: 3-900051-07-0.
- Raman, A.V., Damodaran, R., Levin, L.A., Ganesh, T., Rao, Y.K.V., Nanduri, S., Madhusoodhanan, R., 2015. Macrobenthos relative to the oxygen minimum zone on the East Indian margin, Bay of Bengal. *Mar. Ecol.* 36, 679–700.
- Rankin, J.C., Jensen, F.B., 1993. *Fish Ecophysiology*. Chapman and Hall, London, pp. 1–421.
- Redfield, A.C., Ketchum, B.H., Richards, F.A., 1963. The influence of organisms on the composition of sea-water. In: Hill, M.N. (Ed.), *The sea*, vol. 2. Interscience, New York, pp. 26–77.
- Revsbech, N.P., Larsen, L.H., Gundersen, J., Dalsgaard, T., Ulloa, O., Thamdrup, B., 2009. Determination of ultra-low oxygen concentrations in oxygen minimum zones by the STOX sensor. *Limnol. Oceanogr. Methods* 7, 371–381.
- Rex, M.A., Etter, R.J., 2010. *Deep-Sea Biodiversity: Pattern and Scale*. Harvard University Press, Cambridge, MA. 354 pp.
- Richards, J., 2009. Metabolic and molecular responses of fish to hypoxia. *Fish Physiol.* 27, 443–485.
- Richards, J., 2010. Metabolic rate suppression as a mechanism for surviving environmental challenge in fish. *Prog. Mol. Subcell. Biol.* 49, 113–139.
- Richards, J.G., 2011. Physiological, behavioral and biochemical adaptations of intertidal fishes to hypoxia. *J. Exp. Biol.* 214, 191–199.
- Robb, T., Abrahams, M.V., 2003. Variation in tolerance to hypoxia in a predator and prey species: an ecological advantage of being small? *J. Fish Biol.* 62, 1067–1081.
- Roel, B.A., 1987. Demersal communities off the west coast of South Africa. *Af. J. Marine Sci.* 5, 575–584.
- Roel, B.A., Rucabado, J., Lloris, D., Leonart, J., 1985. Las comunidades de peces demersales del afloramiento de Africa occidental (Sahara y Namibia). In: Bas, C., Margalef, R., Rubies, P. (Eds.), *Simposio internacional sobre las areas de afloramiento mas importantes*

- del oeste africano (Cabo Blanco y Benguela). Instituto Investigaciones Pesqueras, Barcelona, pp. 691–700 (in spanish).
- Roesner, A., Hankeln, T., Burmester, T., 2006. Hypoxia induces a complex response of globin expression in zebrafish (*Danio rerio*). *J. Exp. Biol.* 209, 2129–2137.
- Roesner, A., Mitz, S.A., Hankeln, T., Burmester, T., 2008. Globins and hypoxia adaptation in the goldfish, *Carassius auratus*. *FEBS J.* 275, 3633–3643.
- Rogers, A.D., 2000. The role of the oceanic oxygen minima in generating biodiversity in the deep sea. *Deep-Sea Res. II* 47, 119–148.
- Rosenberg, R., Arntz, W.E., Chuman de Flores, E., Flores, L.A., Carbjal, G., Finger, I., Tarazona, J., 1983. Benthos biomass and oxygen deficiency in the upwelling system off Peru. *J. Mar. Sci.* 41, 263–279.
- Rummer, J.L., Roshan-Moniri, M., Balfry, S.K., Brauner, C.J., 2010. Use it or lose it? Sablefish, *Anoplopoma fimbria*, a species representing a fifth teleostean group where bNHE associated with the red blood cell adrenergic stress response has been secondarily lost. *J. Exp. Biol.* 213, 1503–1512.
- Rummer, J.L., McKenzie, D.J., Innocenti, A., Supuran, C.T., Brauner, C.J., 2013. Root effect hemoglobin may have evolved to enhance general tissue oxygen delivery. *Science* 340, 1327–1329.
- Sadorus, L.L., Mantua, N.J., Essington, T., Hickey, B., Hare, S., 2014. Distribution patterns of Pacific halibut (*Hippoglossus stenolepis*) in relation to environmental variables along the continental shelf waters of the US West Coast and southern British Columbia. *Fish. Oceanogr.* 23 (3), 225–241.
- Salvanes, A.G.V., Utne-Palm, A.C., Currie, B., Braithwaite, V.A., 2011. Behavioural and physiological adaptations of the bearded goby, a key fish species of the extreme environment of the northern Benguela upwelling. *Mar. Ecol. Prog. Ser.* 425, 193–202.
- Sankaranarayanan, V.N., Qasim, S.Z., 1968. The influence of some hydrographical factors on the fisheries of the Cochin area. *Bull. Nat. Inst. Sci. India* 38, 846–853.
- Schlitzer, R., 2015. *Ocean Data View*. <http://odv.awi.de>.
- Schurmann, H., Steffensen, J.F., 1992. Lethal oxygen levels at different temperatures and the preferred temperature during hypoxia of the Atlantic cod, *Gadus morhua*. *J. Fish Biol.* 41, 927–934.
- Secor, D.H., Gunderson, T.E., 1998. Effects of hypoxia and temperature on survival, growth, and respiration of juvenile Atlantic Sturgeon, *Acipenser oxyrinchus*. *Fish. Bull.* 96 (3), 603–613.
- Seibel, B.A., 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *J. Exp. Biol.* 214, 326–336.
- Seibel, B.A., Walsh, P.J., 2003. Biological impacts of deep-sea carbon dioxide injection inferred from indices of physiological performance. *J. Exp. Biol.* 206, 641–650.
- Sellanes, J., Quiroga, E., Neira, C., Gutiérrez, D., 2007. Changes of macrobenthos composition under different ENSO cycle conditions on the continental shelf off central Chile. *Cont. Shelf Res.* 27, 1002–1016.
- Sellanes, J., Neira, C., Quiroga, E., Teixido, N., 2010. Diversity patterns along and across the Chilean margin: a continental slope encompassing oxygen gradients and methane seep benthic habitats. *Mar. Ecol.* 31, 111–124.
- Semenza, G.L., 1998. Hypoxia-inducible factor 1: master regulator of O₂ homeostasis. *Curr. Opin. Genet. Dev.* 8 (5), 588–594.
- Send, U., Nam, S., 2012. Relaxation from upwelling: the effect on dissolved oxygen on the continental shelf. *J. Geophys. Res.* 117, C04024.
- Seshappa, G., 1953. Observations on the physical and biological features of the inshore sea bottom along the Malabar coast. *Proc. Nat. Inst. Sci. India* 19, 257–279.

- Shaffer, G., Olsen, S.M., Pedersen, J.O.P., 2009. Long-term ocean oxygen depletion in response to carbon dioxide emissions from fossil fuels. *Nat. Geosci.* 2, 105–109.
- Shepard, M.P., 1955. Resistance and tolerance of young speckled trout (*Salve linus fontinalis*) to oxygen lack, with special reference to low oxygen acclimation. *J. Fish. Res. Board Can.* 12, 387–446.
- Sibert, E.C., Hull, P.M., Norris, R.D., 2014. Resilience of Pacific pelagic fish across the Cretaceous/Palaeogene mass extinction. *Nat. Geosci.* 7, 667–670.
- Sielfeld, W., Vargas, M., 1999. Review of marine fish zoogeography of Chilean Patagonia (42°–57°S). *Sci. Mar.* 63, 451–463.
- Slater, R.D., Kroopnick, P., 1984. Controls on dissolved oxygen distribution and organic carbon deposition in the Arabian Sea. In: Haq, B.U., Milliman, J.D. (Eds.), *Geology and Oceanography of the Arabian Sea and Coastal Pakistan*, pp. 305–312.
- Smale, M.J., Roel, B., Badenhorst, A., Field, J.G., 1993. Analysis of the demersal community of fish and cephalopods on the Agulhas Bank, South Africa. *J. Fish Biol.* 43, 169–191.
- Sollid, J., De Angelis, P., Gundersen, K., Nilsson, G.E., 2003. Hypoxia induces adaptive and reversible gross morphological changes in crucian carp gills. *J. Exp. Biol.* 206, 3667–3673.
- Somerton, D.A., Donaldson, W., 1998. Parasitism of the golden king crab, *Lithodes aequispinus*, by two species of snailfish, genus *Careproctus*. *Fish. Bull.* 96, 871–884.
- Speers-Roesch, B., Mandic, M., Groom, D.J.E., Richards, J.G., 2013. Critical oxygen tensions as predictors of hypoxia tolerance and tissue metabolic responses during hypoxia exposure in fishes. *J. Exp. Mar. Biol. Ecol.* 449, 239–249.
- Sperling, E.A., Frieder, C.F., Raman, A.V., Girguis, P.R., Levin, L.A., Knoll, A.H., 2013. Oxygen, ecology, and the Cambrian radiation of animals. *PNAS* 110 (33), 13446–13451.
- Sperling, E.A., Frieder, C.A., Levin, L.A., 2016. Biodiversity response to natural gradients of multiple stressors on continental margins. *Proc. R. Soc. B.* 283, 20160637.
- Stein, D.L., Drazen, J.C., Schlining, K.L., Barry, J.P., Kuhnz, L., 2006. Snailfishes of the central California coast: video, photographic and morphological observations. *J. Fish Biol.* 69, 970–986.
- Stramma, L., Johnson, G.C., Sprintall, J., Mohrholz, V., 2008. Expanding oxygen-minimum zones in the tropical oceans. *Science* 320, 655–658.
- Stramma, L., Schmidtko, S., Levin, L.A., Johnson, G.C., 2010. Ocean oxygen minima expansions and their biological impacts. *Deep-Sea Res.* I 57, 587–595.
- Stramma, L., Prince, E.D., Schmidtko, S., Luo, J., Hoolihan, J.P., Visbeck, M., Wallace, D.W.R., Brandt, P., Kortzinger, A., 2011. Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nat. Clim. Change* 2, 33–37.
- Stromme, T., Saetersdal, G., 1988. Final report: surveys of the fish resources on the Pacific Shelf from Colombia to Southern Mexico, 1987. pp. 1–94. NORAD/UNDP/FAOPROGRAMME.
- Thiel, H., 1978. Benthos in upwelling regions. In: Boje, R., Tomczak, M. (Eds.), *Upwelling Ecosystems*. Springer-Verlag, Berlin, pp. 124–138.
- Thomas, S., 1983. Changes in blood acid–base balance in trout (*Salmo gairdneri* Richardson) following exposure to combined hypoxia and hypercapnia. *J. Comp. Physiol.* 152, 53–57.
- Tiano, L., Garcia-Robledo, E., Dalsgaard, T., Devol, A.H., Ward, B.B., Ulloa, O., Canfield, D.E., Revsbech, N.P., 2014. Oxygen distribution and aerobic respiration in the north and south eastern tropical Pacific oxygen minimum zones. *Deep-Sea Res.* I 94, 173–183.

- Tiedke, J., Thiel, R., Burmester, T., 2014. Molecular responses of estuarine fish to hypoxia: a comparative study with ruffe and flounder from field and laboratory. *PLoS One* 9 (3), e90778.
- Torres, J.J., Grigsby, M.D., Clarke, M.E., 2012. Aerobic and anaerobic metabolism in oxygen minimum layer fishes: the role of alcohol dehydrogenase. *J. Exp. Biol.* 215, 1905–1914.
- Utne-Palm, A.C., Salvanes, A.G.V., Currie, B., Kaartvedt, S., Nilsson, G.E., Braithwaite, V.A., Stecyk, J.A.W., Hundt, M., van der Bank, M., Flynn, B., Sandvik, G.K., Klevjer, T.A., Sweetman, A.K., Brüchert, V., Pittman, K., Peard, K.R., Lunde, I.G., Strandabø, R.A.U., Gibbons, M.J., 2010. Trophic structure and community stability in an overfished ecosystem. *Science* 329, 333–336.
- Van Assendelft, O.W., 1970. Spectrophotometry of Haemoglobin Derivatives. Royal Vangorcum, Assen, Netherlands. 152 pp.
- Vaquer-Sunyer, R., Duarte, C.M., 2008. Thresholds of hypoxia for marine biodiversity. *PNAS* 105, 15452–15457.
- Vaquer-Sunyer, R., Duarte, C.M., 2011. Temperature effects on oxygen thresholds for hypoxia in marine benthic organisms. *Glob. Change Biol.* 17, 1788–1797.
- Vetter, R.D., 1996. Bathymetric demography and niche separation of thornyhead rockfish: *Sebastes alascanus* and *Sebastes altivelis*. *Can. J. Fish. Aquat. Sci.* 53, 600–609.
- Vetter, R.D., Lynn, E.A., 1997. Bathymetric demography, enzyme activity patterns, and bioenergetics of deep-living scorpaenid fishes (genera *Sebastes* and *Sebastes*): paradigms revisited. *Mar. Ecol. Prog. Ser.* 155, 173–188.
- Vetter, R.D., Lynn, E.A., Garza, M., Costa, A.S., 1994. Depth zonation and metabolic adaptation in Dover sole, *Microstomus pacificus* and other deep-living flatfishes: factors that affect the sole. *Mar. Biol.* 120, 145–159.
- Vormanen, M., Stecyk, J.A.W., Nilsson, G.E., 2009. The anoxia-tolerant crucian carp (*Carassius carassius* L.). In: Richards, J.G., Farrell, A.P., Brauner, C.J. (Eds.), *Fish physiology*. In: Hypoxia, vol. 27. Elsevier, Amsterdam, pp. 397–441.
- Weeks, S.J., Currie, B., Bakun, A., Peard, K.R., 2004. Hydrogen sulphide in the Atlantic Ocean off southern Africa, implications of a new view based on SeaWiFS satellite imagery. *Deep-Sea Res. I* 51, 153–172.
- Wells, R.M.G., 2009. Blood-gas transport and hemoglobin function: adaptations for functional and environmental hypoxia. *Fish Physiol.* 27, 255–299.
- White, B.N., 1988. Oceanic anoxic events and allopatric speciation in the deep sea. *Biol. Oceanogr.* 5, 243–259.
- Whitney, F.A., Freeland, H.J., Robert, M., 2007. Persistently declining oxygen levels in the interior waters of the eastern subarctic Pacific. *Prog. Oceanogr.* 75, 179–199.
- Wishner, K., Levin, L., Gowing, M., Mullineaux, L., 1990. Involvement of the oxygen minimum in benthic zonation on a deep seamount. *Nature* 346, 57–59.
- Wishner, K., Ashjian, C., Gelfman, C., 1995. Pelagic and benthic ecology of the lower interface of the Eastern Tropical Pacific oxygen minimum zone. *Deep-Sea Res. I* 42, 93–115.
- Wood, S., Johansen, K., 1972. Adaptation to hypoxia by increased HbO₂ affinity and decreased red cell ATP concentration. *Nat. New Biol.* 237, 278–279.
- Woodhead, P.M., Hamukuaya, H., O'Toole, M.J., McEnroe, M., 1998. Effects of oxygen depletion in shelf waters on hake populations off central and northern Namibia. In: Shannon, V., O'Toole, M.J. (Eds.), *International Symposium, Environmental Variability in the South East Atlantic*. National Marine Information and Research Centre, Namibia.

- Wosnitza-Mendo, C., Espino, M., 1986. The impact of El Niño on recruitment of the Peruvian hake (*Merluccius gayi peruanus*). *Meeresforsch* 31, 47–51.
- Wu, R.S.S., 2002. Hypoxia: from molecular responses to ecosystem responses. *Mar. Pollut. Bull.* 45, 35–45.
- Wu, R., 2009. Effects of hypoxia on fish reproduction and development. *Fish Physiol.* 27, 79–141.
- Wyrcki, K., 1962. The oxygen minima in relation to ocean circulation. *Deep-Sea Res.* I 9, 11–23.
- Wyrcki, K., 1966. Oceanography of the eastern equatorial Pacific Ocean. *Oceanogr. Mar. Biol.* 4, 33–68.
- Yang, T.H., Lai, N.C., Graham, J.B., Somero, G.N., 1992. Respiratory, blood and heart enzymatic adaptations of *Sebastolobus alascanus* (Scorpaenidae: Teleostei) in the oxygen minimum zone: a comparative study. *Biol. Bull.* 183, 490–499.