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Ocean deoxygenation: Everyone's problem

Causes, impacts, consequences and solutions

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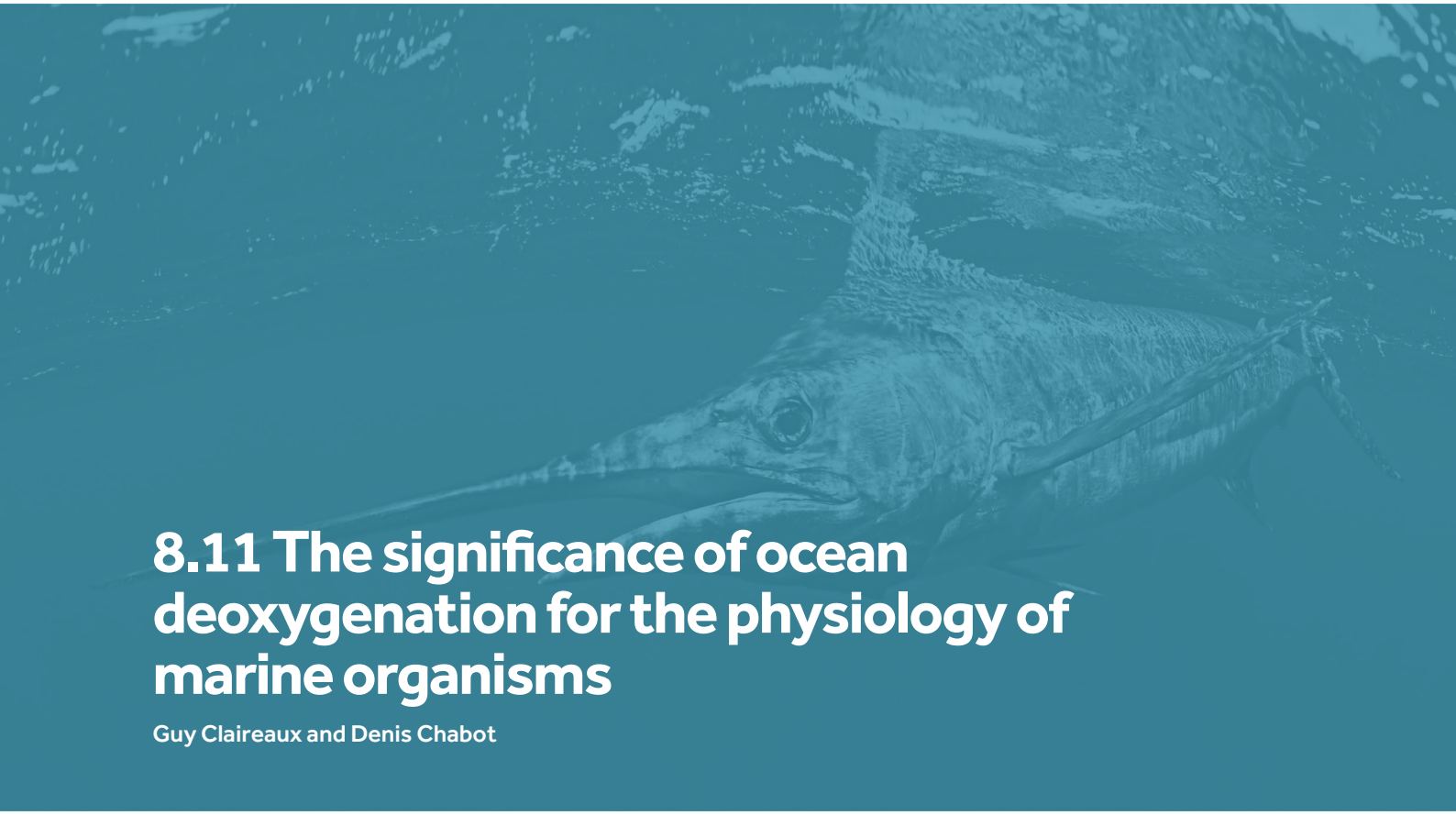

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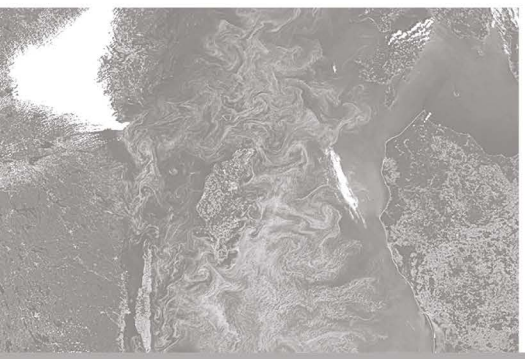

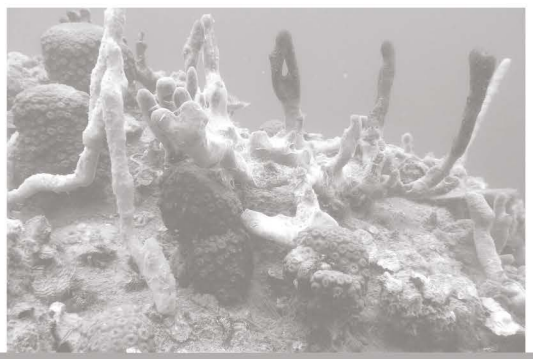

IUCN GLOBAL MARINE AND POLAR PROGRAMME

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8.11 The significance of ocean deoxygenation for the physiology of marine organisms

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Summary

- Breathing water is hard work, making the physiological performance and behavioural repertoire of marine organisms heavily dependent on their capacity to extract oxygen from the ambient sea water.
- There is no such thing as an oxygen threshold above which everything is fine and below which survival is at risk and conservation measures should be implemented. Ocean deoxygenation affects marine organisms as soon as it departs from full aeration, with downstream consequences on their activities and capacity to face natural contingencies. The target for conservation strategies should be, therefore, preserving the aeration of marine waters. This being said, it must be recognized that naturally hypoxic ecosystems exist in nature, supporting species with unique physiological and behavioural features. These poorly oxygenated ecosystems must be identified and preserved as they also contribute to biodiversity.
- Present-day deoxygenation of the ocean favours hypoxia tolerant species at the expense of hypoxia sensitive ones. This is illustrated by shifts in the species composition of marine communities.
- In the short term, marine organisms can respond to ocean deoxygenation through changes in their physiology and behaviour. Alteration in feeding behaviour and distribution pattern are classically observed, potentially leading to reduced growth and to more difficulties completing their life cycle.
- In the medium term, epigenetic processes may provide marine populations with a rapid way to acclimate to the rapidly changing oxygenation state. However, this developing field of biological sciences is too recent to fully evaluate the contribution of epigenetic responses to marine organisms' adaptation to ocean deoxygenation.
- Changes in the phenology (timing of life stage-specific events) of marine species, in relation with ocean deoxygenation have not been observed. However, deoxygenation generally co-occurs with other environmental disturbances (ocean warming and acidification) which are also liable to affect marine species' life-cycle. The lack of understanding of their interactions and synergies currently restricts our ability to assess marine populations' capacity to phenologically respond to ocean deoxygenation.
- In the long term, adaptation through natural selection may occur in species with short generation time. This is, however, more difficult to envisage in most commercial fish species which are characterized by long generation time. Between now and 2100, approximately 80 generations of sardine (*Sardina pilchardus*; age at first maturity: 1 year) but only 10-15 generations of Atlantic cod (*Gadus morhua*; age at first maturity: 5 to 8 years) will follow one another. These numbers of generations are relatively modest and cast some doubts on the capacity of commercial fish species in particular, to adapt to the fast-changing ocean conditions.
- Large inter-individual and inter-specific variation in tolerance to reduced oxygen availability exists in nature. This diversity in marine species' responses makes them challenging to comprehend. Moreover, synergies with other environmental stressors, whether natural or anthropogenic such as, ocean warming and acidification, add to this difficulty.
- Over the last 30 years, marine biologists and physiologists have made tremendous efforts to gain understanding of how marine animals respond to environmental conditions and, in particular, to reduced oxygen availability. Despite all these efforts there is still a long way to go and intensifying collaboration between physiologists, ecologists, modellers and managers is key to providing policy makers and marine resources' managers with fully operational, science-based information.

Ocean deoxygenation effect	Potential consequences
Reduced oxygen availability in the water ventilated over the respiratory surfaces (gills, skin).	• Reduced diffusion of oxygen across the epithelium of the respiratory organs (gill, skin). • Less oxygen transported to the cells by the internal circulatory fluid (blood, extracellular fluid).
Reduced oxygenation of the circulatory fluid.	• Reduced oxygen diffusion from the circulatory fluid into the cells. • Reduced oxygen availability in the cellular power houses (mitochondria).
Reduced oxygen diffusion into mitochondria.	• Reduced energy production in the form of ATP.
Reduced ATP production.	• Reduced capacity for activities. • Prioritization of functions by reallocating blood flow among the various organs. • Prioritization at the expense of non-essential (non-life sustaining) activities such as growth and reproduction.
Reduced growth and reproduction.	• Increased risk of predation. • Reduced survival. • Altered recruitment. • Altered population production (biomass) and demography.
Altered recruitment, production and demography.	• Altered ecosystem functioning. • Altered ecosystem services.

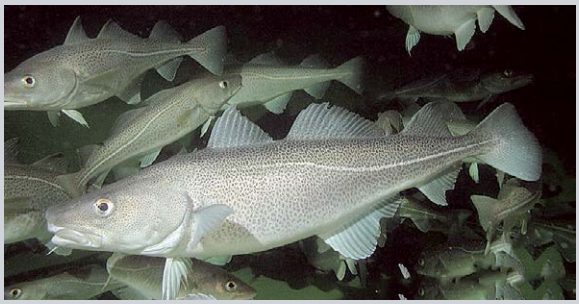
8.11.1 Introduction

For thousands of years, marine organisms have been a staple of the diet of many coastal human populations, as well as a determining factor of their health and wealth. Yet, proper knowledge about how environmental conditions influence the distribution and abundance of this important food source is relatively recent. As an example, only 70 years ago, a French naval historian presenting the state of scientific knowledge on the reproduction of Atlantic cod suggested that "*une certaine destruction est nécessaire, car, si tous les oeufs éclosaient et si tous les poissons arrivaient à l'état adulte, le monde serait mis en péril au bout de quelques générations et l'océan risquerait de se combler.*" [a certain destruction is necessary or, if all eggs hatched and if all fish grew to adult stage, the world would be in danger after a few generations and the oceans would be filled (translation by the authors)] (Lacroix, 1949). This poor perception of, and lack of basic knowledge about, how environmental conditions influence marine organisms appeared even more clearly in the late 1980s and early 1990s when population statistics and models did not anticipate the collapse of crucial fish stocks such as the Western Atlantic cod stocks (Atkinson et al., 1997; Chouinard & Fréchet, 1994; Rose et al., 1994, 2000; Taggart et al., 1994). Faulty models, poor data and non-science-based management decisions allowed for overfishing (Rose, 1997; Steele et al., 1992; Walters & Maguire, 1996), but the role of environmental variables was also mistakenly dismissed (Hutchings & Myers, 1994; Myers et al., 1996). Nowadays, fortunately, the key role played by the environment in determining marine organisms' activities and performance is taken more broadly into account, with large efforts being devoted to increasing current understanding of their physiology and behaviour (McKenzie et al., 2016). The recent controversy about the influence of ocean warming on fish body size and its possible ecological consequences provides a perfect illustration of the issues and challenges that the scientific community is facing in this regard (Cheung et al., 2013; Lefevre et al., 2017; Pauly & Cheung, 2017). In that case, the question was whether an unfavourable gill surface area to body mass ratio makes big fish less likely to survive global warming, shifting the composition of fish populations in favour of smaller individuals.

Among all the environmental factors that are liable to affect marine organisms, water temperature and oxygenation are certainly the most potent. With remarkable exceptions such as some sharks and tunas, as well as the opah (Figure 8.11.1), heat moves

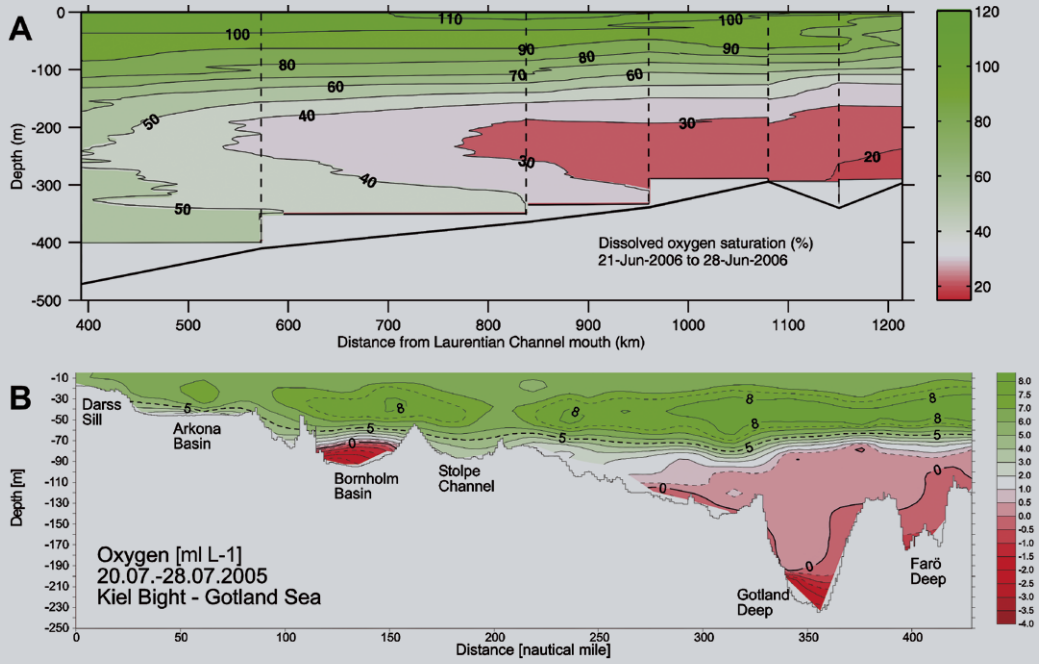
Box 8.11.1 A case study, the Atlantic cod

Atlantic cod (*Gadus morhua*) is a major source of food and wealth on both sides of the North Atlantic. In at least two regions of its distribution area, the Baltic Sea and the Gulf of Saint Lawrence, cod is faced with severely deoxygenated water (Chabot & Claireaux, 2008; Chabot & Gilbert, 2008) with oxygen levels less than 30% of air equilibration over extended areas. Physiologists have shown that 20-30% aerated water allows cod to meet minimal, life sustaining oxygen requirements but that it is not enough to cover the oxygen demand associated with activities such as feeding, escaping a predator or coping with a disease (Claireaux et al., 2000; Plante et al., 1998; Schurmann & Steffensen, 1997).



Box Figure 8.11.1.1 Atlantic cod (*Gadus morhua*). © Richard Larocque DFO.

Even when not life-threatening, water deoxygenation has a range of negative effects on cod. For instance, the growth rate of cod starts to decline as soon as ambient oxygenation drops below 70% of full aeration. This is due to decreased food consumption caused by a reduced ability to cover the additional demand for oxygen caused by digestion (Chabot & Dutil, 1999; Jordan & Steffensen, 2007). This is confirmed by laboratory experiments and field observations which show that cod avoid less than 70% saturated waters (Chabot & Dutil, 1999; Claireaux et al., 1995; Dutil et al., 2007; Herbert & Steffensen, 2005; Johansen et al., 2006; Schurmann & Steffensen, 1994).



Box Figure 8.11.1.2 Vertical profile of dissolved oxygen along a longitudinal transect in (A) the Estuary and Gulf of St. Lawrence and (B) the Baltic Sea. Note the different oxygen units and colour scales, A: from 0 to 100% sat; B: from 0 to 8 ml L^{-1}. Hypoxia is more severe in the Baltic Sea, with negative oxygen concentrations resulting from the combination of anoxia and elevated concentrations of hydrogen sulphide. Anoxia is not observed in the Estuary and Gulf of St. Lawrence. Modified from Fennel et al. (2008).

The Gulf of St. Lawrence is characterized by three deep channels (depth >175 m; Box Figure 8.11.1.2A) through which dense Northwest Atlantic water progresses upstream. As it moves towards the head of the channels, this already deoxygenated water (circa 60%) is further depleted of its oxygen due to the respiration by living organisms and decomposition of organic matter by micro-organisms (Genovesi et al., 2011; Gilbert et

al., 2005; Thibodeau et al., 2006). When reaching the head of the channels, the most extreme deoxygenation conditions are observed, with 18-25% of full saturation.

Since the 1980s, the distribution area of Atlantic cod in the Gulf of St. Lawrence has shrunk severely as a result of overfishing (Castonguay et al., 1999; Chouinard & Fréchet, 1994; Myers et al., 1996) combined with a very cold period which is suspected to have increased natural mortality (Dutil et al., 1999). In recent years, signs of recovery have been observed (DFO, 2017), but it is likely that the poor oxygenation of the deep waters will prevent cod from returning to their full historical distribution (Chabot, 2004; D'Amours, 1993; Gilbert et al., 2007).

The Baltic Sea is a shallow body of water (average 55 m) with several deeper basins connected by channels (Box Figure 8.11.1.2B). Water exchange between the Baltic Sea and the North Sea is limited by sills situated in the Danish Strait where maximum depth varies between 7 and 18 m (Matthäus & Schinke, 1999). Baltic surface waters are brackish (salinity of 6-8 ‰) and they flow out into the North Sea unimpeded over the sills. Occasionally, denser oxygenated waters from the North Sea travel in the opposite direction, passing over the sills into the Baltic. Because of the sills, these inflows of oxygenated water only happen during strong and long-lasting westerlies (Matthäus & Schinke, 1999). Between inflows, oxygen progressively decreases in the deep basins, resulting in severe hypoxia or even anoxia (Matthäus & Schinke, 1999). During the period 1880 to 1976, inflow events occurred regularly. Since then, however, the number of major events has been decreasing, with only one per decade since the 1990s (Morholz et al., 2015). As a result, the deep basins of the Baltic Sea have been deoxygenated and even anoxic for most of the time since the 1970s (Fennel et al., 2008; Laine et al., 2007).

As in the Gulf of St. Lawrence, the presence of cod in the deep basins of the Baltic Sea is conditioned by the water oxygen level. During the 1960s and 1970s, these basins were relatively well oxygenated and were inhabited by cod (Laine et al., 2007; Uzars, 1994). During the 1980s, however, cod vacated the deep basins, switching from a benthic to a pelagic lifestyle and also diet (Tomkiewicz et al., 1998; Uzars, 1994). Moreover, deoxygenated water caused severe egg mortality (Nissling & Westin, 1991; Nissling et al., 1994; Wieland et al., 1994) as an oxygen level above 20% of full saturation is required for proper cod egg development. Since the 1980s, the reproductive volume available to Baltic cod has been shrinking and it is, nowadays, limited to the Bornholm Basin (MacKenzie et al., 2000).

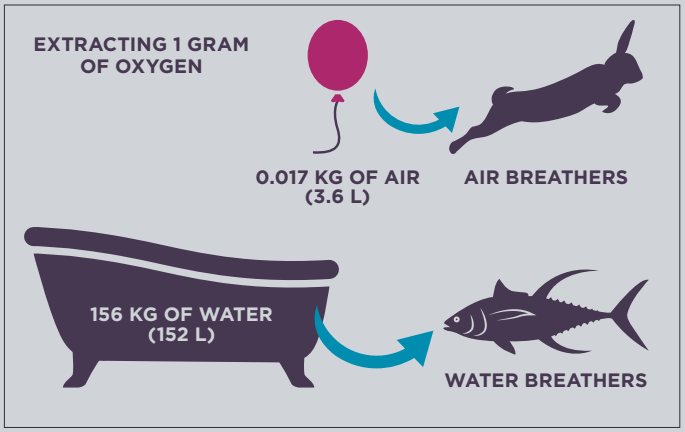
Figure 8.11.1 The opah (*Lampris guttatus*) has whole-body endothermy keeping it ~5 °C warmer than the surrounding environment. © Paulo Oliveira / Alamy stock photo.

so readily between the body of marine organisms and the surrounding water that their internal temperature is typically very close to that of the environment. The first consequence of this is that through controlling the rate of internal chemical reactions, water temperature sets the pace of ectotherms' metabolism and, therefore, influences all aspects of their physiology, behaviour and life cycle. As a result, water temperature is generally considered as the most pervasive dimension of oceanic creatures' ecological niche, as well as a key to understanding their distribution, migration and reproduction.

Beside adequate thermal conditions, the vast majority of marine animals also require properly oxygenated water to survive and thrive. Oxygen is required to fully extract and use the energy ingested as food or stored as reserves. By comparison, reactions that proceed without oxygen (anaerobic metabolic pathways) are approximately 15 times less efficient at accomplishing this task than processes which take place in the presence of oxygen

Box 8.11.2 Breathing in water

Breathing is much more difficult in water than in air. First, there is ~30 times less oxygen in sea water than in air (at 15 °C, 8.2 and 280 mg O_2 L^{-1} in water and air, respectively) (García & Gordon, 1992; Schmidt-Nielsen, 1997). Second, sea water is ~850 times denser and ~60 times more viscous than air (Chemical Rubber Company, 1984; Wiesenburg & Little, 1988). This means that water breathers must work harder than air breathers to move one litre of medium over their respiratory organs. Third, a much greater volume of water is required to extract the same quantity of oxygen than from air. For instance, to obtain 1 g of O_2 it takes 125 kg of sea water but only 0.0044 kg of air (ratio 28400:1). The most obvious consequence of this is that water breathers cannot afford to regulate their body temperature as this would require much more energy and oxygen. As a compensatory measure, water breathers are equipped with highly efficient respiratory systems which allow them to extract up to 80% of the oxygen present in the medium they breathe (Hughes & Shelton, 1962) while some air breathers barely reach 27% (Altman & Dittmer, 1971). As a result, the ratio of the mass of water to the mass of air that must be ventilated to extract 1 g of O_2 is 9176:1, or 156 kg of water for 0.017 kg of air (Box Figure 8.11.2.1).



Box Figure 8.11.2.1 Breathing in water: Relative ventilatory volume to extract 1 gram of oxygen in water breathers and air breathers.

(aerobic metabolic pathways; du Plessis et al., 2015). This multiplier effect of oxygen explains why, through evolution, marine species have developed a whole range of respiratory systems aimed at transferring oxygen from the ambient water into the cells. In many aquatic breathers, respiratory systems include gill arches which support gill lamellae. As water moves across the gills, a continuous positive O_2 pressure gradient allows the passive diffusion of O_2 from the water to the body fluids (Davis, 1975; Hofmann et al., 2011; Perry & McDonald, 1993). A more or less developed circulatory system then distributes O_2 among the various organs and tissues (Perry & McDonald, 1993). Once in the cell, oxygen is transferred to the cellular power houses, the mitochondria, where it is used to produce adenosine triphosphate (ATP), the chemical fuel of most cellular activities.

The fact that the temperature of oceanic waters fluctuates both spatially and temporally is a readily perceived phenomenon. Harder to envisage, however, is that the ocean's oxygen level also varies to a very large extent. The terms normoxic, hyperoxic, hypoxic and anoxic are classically used to describe a water mass with regard to its oxygen condition. A classic example to illustrate these terms is that of a tide pool situated high on a rocky shore. At high tide, the water in the pool is vigorously stirred and it is, therefore, fully aerated. This fully air-equilibrated or air-saturated water is termed normoxic (100% sat). At low tide, however, water oxygenation in that pool can vary greatly. During the day, for instance, photosynthesizing algae result in oxygen production that can elevate oxygenation well above air-saturation levels. In such a case, the water is described as being hyperoxic. During the night, in contrast, respiration by organisms present in the pool can drive the oxygen level below full air-saturation, resulting in hypoxic or even anoxic water as saturation reaches 0%.

Deoxygenated or hypoxic conditions are very common in aquatic ecosystems, occurring when dissolved oxygen is removed through respiratory or chemical processes

faster than it is replenished through, for example, exchange with the atmosphere, photosynthesis or advection of oxygen-rich water. In oceanic and coastal environments, stratification of the water column is the most commonly observed limiting factor for the diffusion of oxygen from the surface to deep layers. Eutrophication also leads to low levels of dissolved oxygen, as the increased primary production resulting from nutrient loading contributes to increased detritus deposition and oxygen consumption by the micro-organisms involved in their degradation (Bourgault et al., 2012; Breitburg et al., 2009; Cloern, 2001; Diaz & Rosenberg, 1995; Gray et al., 2002; Kemp et al., 2009; Rabalais, 2009; Rabalais et al., 2010; Zhang et al., 2010a). In the context of contemporary climate change and resulting ocean warming, it has also to be borne in mind that oxygen solubility in water is temperature dependent - the warmer the water the less oxygen it can dissolve. This close relationship between temperature and oxygen solubility is one reason why these two environmental factors will be considered jointly herein (McBryan et al., 2013).

The major effects of ocean deoxygenation on the physiology of marine organisms are explored, and implications in terms of conservation and management are identified. The section essentially focuses on fish, but the notions and concepts presented are broadly shared among all marine water breathers. Firstly, key mechanisms that make water-breathing organisms vulnerable to ocean deoxygenation are summarized. Secondly, the main physiological and behavioural responses of marine animals to ocean deoxygenation are highlighted and the resulting impacts on populations and communities are explored. Finally, key challenges and opportunities for conservation of marine species under deoxygenated marine water conditions are discussed.

8.11.2 Mechanisms of ambient oxygen effects: the case of a marine fish

One aspect of metabolism is to convert food material or stored reserves into a form of energy usable to power cellular activities. Adenosine triphosphate, or ATP, is used by virtually all forms of life to store and transfer energy. However, synthesizing ATP efficiently requires oxygen, which must be acquired from the environment (Nelson, 2016). Through evolution, the respiratory and circulatory systems of aquatic organisms have evolved to fulfil this function over a range of ambient oxygen levels which extends from above air saturation, down to levels below which oxygen-demanding activities are not sustained and death occurs (Chabot et al., 2016).

The concept of a limiting oxygen level curve (LOL-curve) is very useful to describe the gradual limitation imposed by declining ambient oxygen on a fish's ATP production and ensuing capacity for activities (Claireaux & Chabot, 2016; Neill & Bryan, 1991; Neill et al., 1994). The LOL-curve in an idealized fish is presented in Figure 8.11.2. The x-axis represents the range of oxygen levels that this fish may encounter in its environment. When expressed in terms of percentage of air-saturation, this range extends from more than 100% in a vegetated hyperoxic environment, to 0% (anoxia) as observed in a highly eutrophic water body. The y-axis represents, on an arbitrary scale, a range of observable metabolic rates, classically expressed as an oxygen uptake per unit of time and per unit of body mass. Note that, through evolution, respiratory and cardio-circulatory systems have evolved to maximize oxygen uptake when water is fully aerated (100% air saturation).

There are two important points on Figure 8.11.2: the standard metabolic rate (SMR) and the maximum sustainable metabolic rate (MMR). Briefly, SMR quantifies the minimum oxygen requirement to support life-sustaining activities and maintenance processes, whereas MMR estimates the maximum rate at which oxygen can be supplied to activities (Claireaux & Chabot, 2016). The area bounded by SMR and MMR indicate the confines within which an organism's activities must take place.

On the basis of this general framework, consider a typical fish living in a water body where oxygen availability gradually declines. At first (from point *a* to point *b*), the fish initial metabolic rate (*c.*220) is maintained by increasing water flow through the mouth and opercula (ventilation) and by augmenting blood flow in the gill lamellae (perfusion). At point b, however, these regulatory measures reach their limit and ambient oxygen availability becomes insufficient to sustain the fish's initial oxygen demand. Point *b* is termed the limiting oxygen level (LOL; *c.*25% air saturation). As the ambient oxygen level continues to fall, the fish then enters a second phase of the response, during which non-obligatory activities are progressively reduced to align the fish's metabolic oxygen demand with the availability of oxygen in the environment. This is achieved via behavioural adjustments such as, reduced swimming

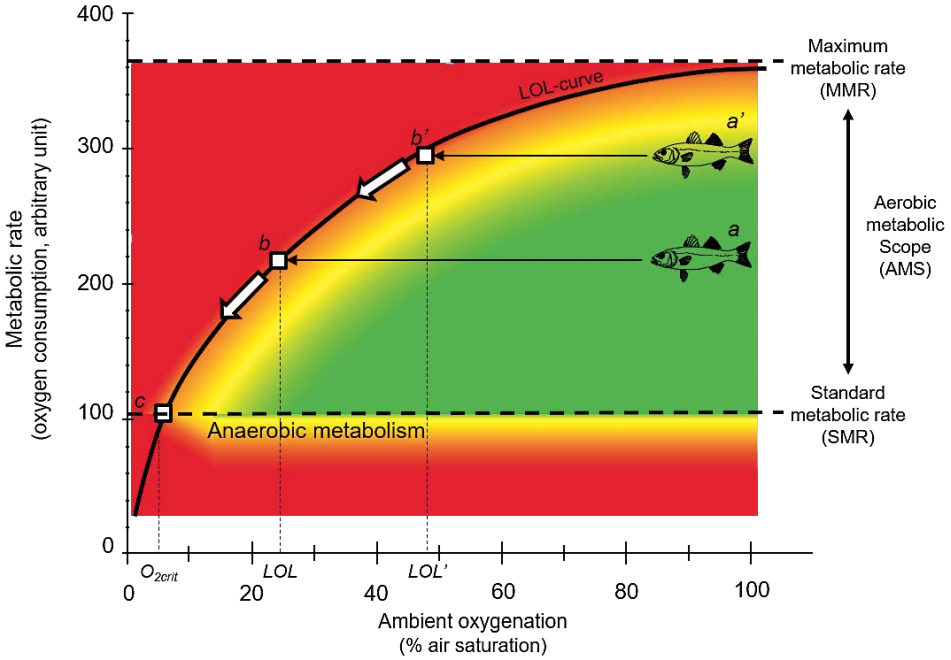


Figure 8.11.2 Influence of ambient oxygenation (% air saturation) upon the aerobic metabolic capacity of an idealized fish (unit less). MMR: maximum sustainable metabolic rate. SMR: standard metabolic rate. LOL-curve: continuum of limiting oxygenation levels. The vertical distance between the LOL-curve and SMR represents the aerobic metabolic scope at the ambient oxygen saturation considered. The series a-b-c and a'-b'-c figure the paths of change in metabolic rate in a hypothetical fish in two physiological states and exposed to a progressive deoxygenation of the surrounding water. a and a': initial metabolic rate in normoxia. b and b': indicate the points where the corresponding limiting oxygen levels are reached (LOL and LOL'). c: indicates the critical oxygen level (O_{2crit}) i.e. the minimum oxygen level required to sustain life sustaining activities (SMR).

activity (Domenici et al., 2000; Herbert & Steffensen, 2005; Poulsen et al., 2011; Schurmann & Steffensen, 1994) or reduced food ingestion (Buentello et al., 2000; Chabot & Dutil, 1999; Pichavant et al., 2000, 2001). As the fish's metabolic rate becomes oxygen dependent and "travels" from *b* to *c*, a redistribution of blood flow among tissues and organs is also observed (Axelsson et al., 2002), resulting in functional impairments such as reduced swimming capacity (Dutil et al., 2007) and slower digestion (Jordan & Steffensen, 2007; Zhang et al., 2010b). At point *c* (~8% air saturation), MMR equals SMR, i.e. only oxygen demand supporting short-term survival can be met. The oxygen level corresponding to point *c* is classically termed the critical oxygen saturation (O_{2crit}). If the ambient oxygen level declines below O_{2crit}, the fish will engage in anaerobic ATP synthesis and survival will then depend on its capacity to establish a proper balance between ATP demand and production.

If that same fish was now heavily engaged in digestion (*a'*), its oxygen demand would be 30% higher than previously (~300), making it more susceptible to reduced oxygen availability. In the event of a decline in ambient oxygen, that metabolic rate would indeed only be maintained until ~48% air saturation i.e. the corresponding LOL (*b'*). If water oxygen level was to decline below 48% air saturation, blood allocation to the digestive tract would then progressively be decreased and the animal's metabolic rate would follow the same path as before, dropping monotonically until O_{2crit} (*c*).

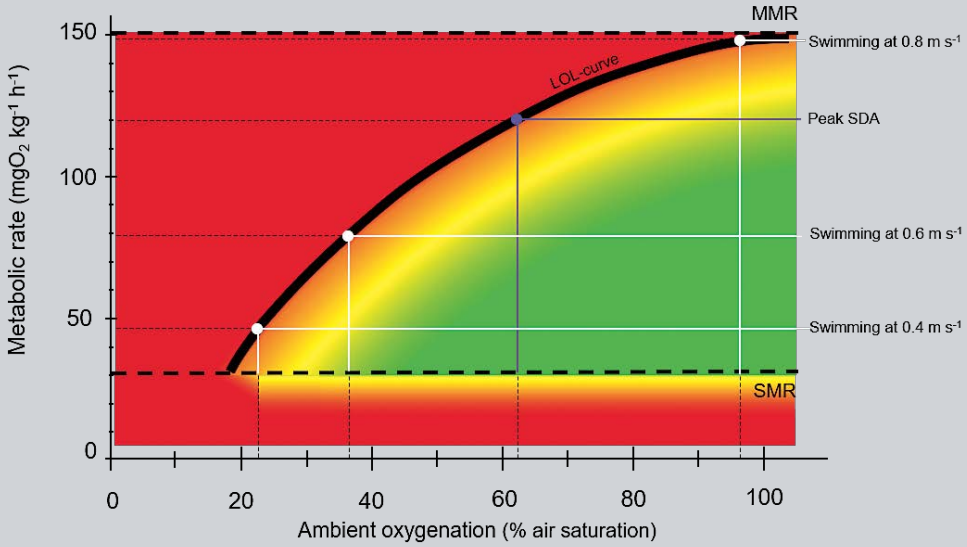
In summary, LOL values form a continuum, the LOL-curve (solid line in Figure 8.11.2), which extends from MMR measured in normoxia down to O_{2crit}. The vertical distance between the LOL-curve and SMR defines the aerobic metabolic scope (AMS), which delineates the metabolic boundaries within which all aerobic activities must be undertaken and are prioritized when ambient deoxygenation occurs (Fry, 1971). Note that activities include all energy-requiring work, which not only means mechanical work, but also growth, regulation of the internal milieu, gonad maturation, or fighting diseases and other stresses. The lower the ambient oxygen availability, the smaller AMS and, therefore, the lesser the capacity of fish to allocate oxygen to these activities. Reciprocally, the higher the metabolic demand for oxygen, the higher the corresponding LOL and, therefore, the sooner the limitation in case of decreasing oxygen availability in the environment i.e. LOL'>LOL on Figure 8.11.2. For this reason, Fry (1971) called dissolved oxygen a limiting factor for metabolic rate.

Box 8.11.3 A case study, the European sea bass (*Dicentrarchus labrax*)

Understanding the limitations imposed by ocean deoxygenation on organisms' activities and performance has been a challenging issue since the very early days of animal physiology. In those days, gaining new knowledge about the mechanisms involved in hypoxia tolerance was the main objective. In recent decades, however, new challenges emerged, such as those related to the increasing pressure from human activities upon marine ecosystems. From this perspective, contemporary climate change and related ocean warming, acidification and deoxygenation are particularly hot topics for marine biologists. Faced with these new challenges, animal physiologists responded by adopting a drastic change in approach, moving from mechanistic (reductionist) orientated investigations to increasingly integrative studies aimed at understanding how the physiological influences of the environment propagate across the biological organization scale to eventually affect population-level (dynamic, production, evolution) and ecosystem-level (food web, biodiversity, resilience) processes. In this context, the notions of aerobic metabolic scope and limiting oxygen level proved to be effective tools (Claireaux & Lagardère, 1999; Claireaux & Lefrançois, 2007; Fry, 1947, 1971; Marras et al., 2015; Neill & Bryan, 1991; Neill et al., 1994).

Box Figure 8.11.3.1 European sea bass (*Dicentrarchus labrax*).
© imageBROKER / Alamy stock photo.

In the Atlantic Ocean, the distribution of the European sea bass (*Dicentrarchus labrax*; Box Figure 8.11.3.1) extends from the coast of Morocco to the South of Norway. The species is also present in the Mediterranean Sea as well as in the Black Sea. The sea bass is a eurytherm and euryhaline fish, capable of withstanding temperatures from 2 °C to 36 °C and salinities from 0‰ to 40‰. The sea bass is the target of commercial and recreational fisheries and Atlantic stocks are threatened, as indicated by the 32% lower total biomass in 2011-2012 compared with the three previous years. Accordingly, fishing restrictions have been put in place to preserve this stock (European Council Regulation, 2015).



Box Figure 8.11.3.2 Limiting effect of ambient oxygenation (% air saturation) upon the activities of 15 °C-acclimated European sea bass (*Dicentrarchus labrax*). Maximum sustainable metabolic rate (MMR) and standard metabolic rate (SMR) are indicated by the thick horizontal dotted lines. The thick solid line represents the limiting oxygen level-curve (LOL-curve) The thin white lines represent the metabolic rates associated with swimming at velocities of 0.4, 0.6 and 0.8 m s^{-1} and indicate the corresponding minimum oxygen level required to do so (LOL). The thin blue line represents the peak metabolic demand for oxygen following a full meal (specific dynamic action; SDA) and also indicate the corresponding LOL.

Box Figure 8.11.3.2 illustrates the limiting effect of ambient oxygenation on two ecologically crucial activities of the European sea bass: swimming and feeding. Swimming capacity is a key determinant of this top predator's ecological performance (Claireaux et al., 2006). When acclimated to a water temperature of 15 °C, the maximum swimming speed of a 200 g sea bass is approximately 80 cm s^{-1}. The oxygen demand to sustain such a swimming speed is approximately 300 mg O_2 h^{-1} kg^{-1}. Such a metabolic demand for oxygen can only be covered in fully aerated water (100% air saturation). As soon as ambient oxygenation departs from full aeration, sea bass maximum swimming velocity decreases, dropping to 60 cm s^{-1} at 37% saturation and to only 40 cm s^{-1} at 22% air saturation. The second most important activity considered in Box Figure 8.11.3.2 is feeding. A sea bass feeding maximally can ingest approximately 3% of its body mass in one meal. At 15 °C, digestion spreads over several days and will mobilize energy and, therefore, oxygen. The increased oxygen demand measured during digestion is termed the specific dynamic action (SDA) and it generally peaks 15-20 h post-feeding with peak oxygen demand during SDA attaining ~240 mg O_2 h^{-1} kg^{-1} (Lefrançois et al., 1998). The minimum ambient oxygen level necessary to allow such a rate of oxygen consumption is 60-65% air saturation. In a water body where the oxygenation level is less than 60% air saturation, sea bass cannot feed maximally, with consequences on growth and downstream impacts on size dependent performance such as, predator avoidance and reproductive capacity.

8.11.3 Responses of marine organisms to hypoxia

Over the past decades, the occurrence of hypoxic episodes in marine waters has increased drastically (Diaz & Rosenberg, 1995; Diaz, 2001), with an increase in the number of areas affected but also in the extension, severity and duration of these episodes (Breitburg et al., 2018; Chan et al., 2008; Conley et al., 2007;Stramma et al., 2008; Turner et al., 2008). Projections suggest that these circumstances will become even more common in the future (Breitburg et al., 2018; Keeling et al., 2010; Vaquer-Sunyer & Duarte, 2008).

As indicated earlier, coastal and oceanic waters are oxygenated from the surface, either directly, through oxygen transfer from the atmosphere, or from oxygen release by photosynthesising algae and phytoplankton. With the warming of the global ocean, however, surface waters absorb less oxygen due to reduced oxygen solubility (Carpenter, 1966). Moreover, when absorbed, the transfer of oxygen down the water column is made more difficult as warmer surface waters are lighter and are, therefore, less likely to sink and mix with deeper, colder water layers. In estuaries, where surface waters are generally less salty and therefore lighter than deeper water, the propensity to stratification is maximal, making benthic hypoxia an even more frequent event. This complex combination of biological and physical processes involving interactions between the "*four spheres*" (lithosphere, atmosphere, hydrosphere and biosphere) explains why ocean oxygenation is variable and why changes can stretch over years or even decades (Long et al., 2016), making them difficult to predict. There exist four levels of marine organisms' response to deoxygenation: species specific variation in tolerance, acclimation, epigenetics and adaptation.

8.11.3.1 Species specific variation in tolerance to deoxygenation

There is a broad variability in the capacity of marine species to tolerate ambient deoxygenation. Although there can be quite a bit of variation among the species of a given group, fishes and crustaceans are generally viewed as the most sensitive groups to hypoxia. At the other end of the spectrum, cnidarians, a phylum which includes the jellyfish, is among the most hypoxia tolerant animal groups. The overall winners are priapulids, a phylum of unsegmented marine worms (Vaquer-Sunyer & Duarte, 2008).

All the components of the oxygen cascade system, from oxygen extraction at the respiratory surface, through to it utilization for ATP production by mitochondria, are liable to display species-specific features which can explain the broad inter-specific differences in hypoxia tolerance. These differences not only concern aspects of ventilation and oxygen diffusion across respiratory epithelium, but also features of the circulatory system as well as the presence, nature and functioning characteristics of the respiratory pigments. These differences not only contribute to segregate marine organisms' ecological niche, but also set the boundaries of their capacity to cope with environmental deoxygenation.

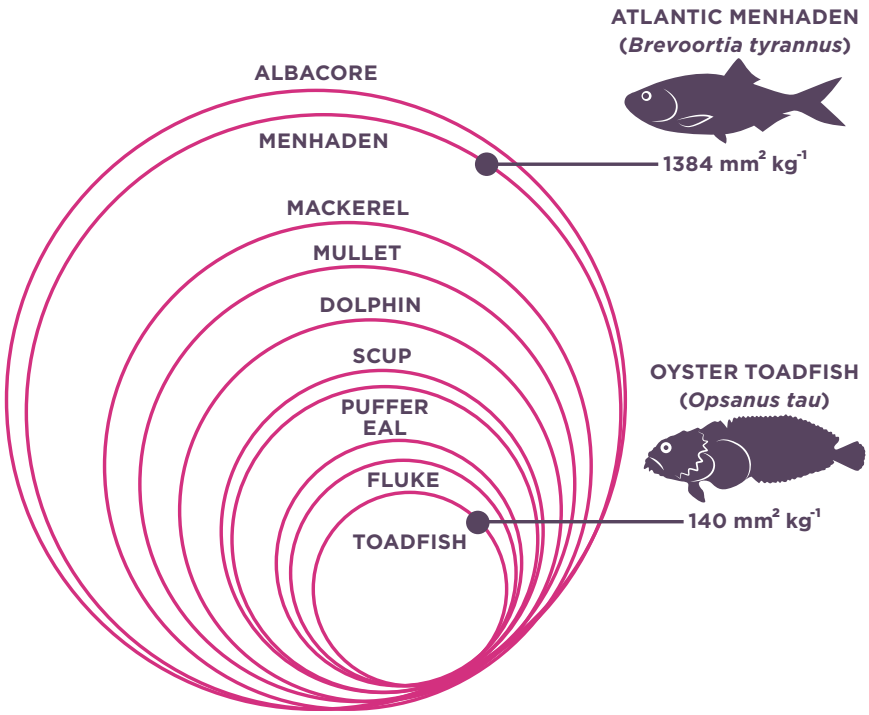


Figure 8.11.3 Relative gill areas of marine fishes (from Gray, 1954).

The surface of respiratory organs must be large enough to allow sufficient oxygen extraction from the water to sustain downstream activities. The link between oxygen extraction capacity and life style is especially clear in fish (Figure 8.11.3). When species of approximately the same body mass are compared, there is indeed a definite difference as illustrated by the streamlined, active menhaden (*Brevoortia tyrannus*) which has a gill surface area nearly ten times that of the sluggish toadfish (*Opsanus tau*) (Figure 8.11.4). The ecological significance of this relationship is twofold as it also implies that organisms with high metabolic demands for oxygen are also those that will be limited the most in case of ambient deoxygenation. As a result, gill surface area to body mass ratio is a convenient proxy to compare hypoxia tolerance among marine organisms (Childress & Seibel, 1998). Mass for mass, animals with large gills will tend to be more active but also less tolerant to hypoxia than fish with small gills.

The inter-specific variability in hypoxia tolerance affects both the position and shape of the LOL-curve, as well as the value of the O_{2crit} (Figure 8.11.2), with lower values of the latter being generally observed in intertidal species in comparison with fast swimming pelagic species (Richards & Lau, 2017). This difference is believed to represent an adaptation to hypoxic conditions, a more common feature of intertidal and coastal ecosystems. As previously discussed, the lower O_{2crit}, the lower the oxygen threshold below which life sustaining activities are no longer covered aerobically and survival is at risk.

Blood oxygen affinity is also a primary determinant of hypoxia tolerance in marine organisms (Farrell & Richards, 2009; Mandic et al., 2009; Wells, 2009). It is generally quantified as P_{50}, which is the partial pressure of oxygen at which blood is 50% saturated with oxygen. Blood with a high affinity for oxygen has a low P_{50}, while animals with blood with a low P_{50} are more hypoxia tolerant. Tunas, for example, are active pelagic fish living in well aerated water bodies. Their blood oxygen affinities are relatively low, with P_{50} values ranging from 2 to 3 kPa (Brill & Bushnell, 1991; Jones et al., 1986; Lowe et al., 2000). The lugworm (*Arenicola marina*) (Figure 8.11.5), on the other hand, is endemic to shallow intertidal ecosystems chronically affected by severe hypoxic episodes and its blood has 20 times more affinity for oxygen than tunas, with a P_{50} of 0.1 to 0.2 kPa (Everaarts, 1986).

8.11.3.2 Acclimation

It is important that the concepts of acclimation and adaptation are defined. Adaptation is understood as the evolutionary process by which, through natural selection, a population's gene pool changes to accommodate new environmental conditions (Ownby et al., 2002). Acclimation, on the other hand, results from

behavioural, physiological, phenological and epigenetic adjustments made by an organism to minimize the effects of environmental disturbance.

8.11.3.2.1 Behaviour

Behaviour is the first line of defence when environmental conditions depart from optimum. Mobile organisms have the capacity to avoid hypoxic waters and this is generally associated with comparably higher oxygen thresholds than in less mobile and, *a fortiori,* sessile species. For example, fishes have been reported to move higher in the water column when bottom waters become hypoxic (Claireaux et al., 1995; Wu, 2002), and fishes and invertebrates can leave an area that has become hypoxic (Bell & Eggleston, 2005). These behavioural changes aiming at ensuring short term survival can have significant ecological implications. When exposed to progressive hypoxia, mullets (*Liza aurata* and *Mugil cephalus*) (Figure 8.11.6) perform aquatic surface respiration by which they rise to the surface to ventilate in the well-oxygenated layer of water in contact with air (Lefrançois et al., 2009; Shingles et al., 2005). However, although providing an advantage in hypoxic habitats, surfacing also exposes fish to significantly increased risks of predation by birds (Domenici et al., 2007; Kersten et al., 1991; Kramer et al., 1983). Similarly, crustaceans have been reported moving to shallower areas to avoid hypoxic bottom waters, making them more vulnerable to predators (Bell et al., 2003). Furthermore, organisms moving out of hypoxic waters may occur in increased density in well aerated environments, intensifying inter- and intra-specific competition (Eby & Crowder, 2002; Eby et al., 2005). If these indirect costs become too high, and hypoxia is not too severe, marine organisms may also remain in hypoxic water instead of avoiding it (Bell & Eggleston, 2005). Another illustration of the ecological consequences of environmental hypoxia is that hypoxic water layers may act as predation refuges for forage species from active, oxygen-demanding predators which are thus less capable of active predation in deoxygenated water (Altieri, 2008; Anjos et al., 2008; Hedges & Abrahams, 2015).

Fast-moving organisms do not necessarily show a broader behavioural repertoire than those with restricted mobility. A whole range of behavioural responses have indeed been observed in benthic species. Polychaetes, annelids, crustaceans, bivalves, priapulids and anemones, for instance, leave their burrows and

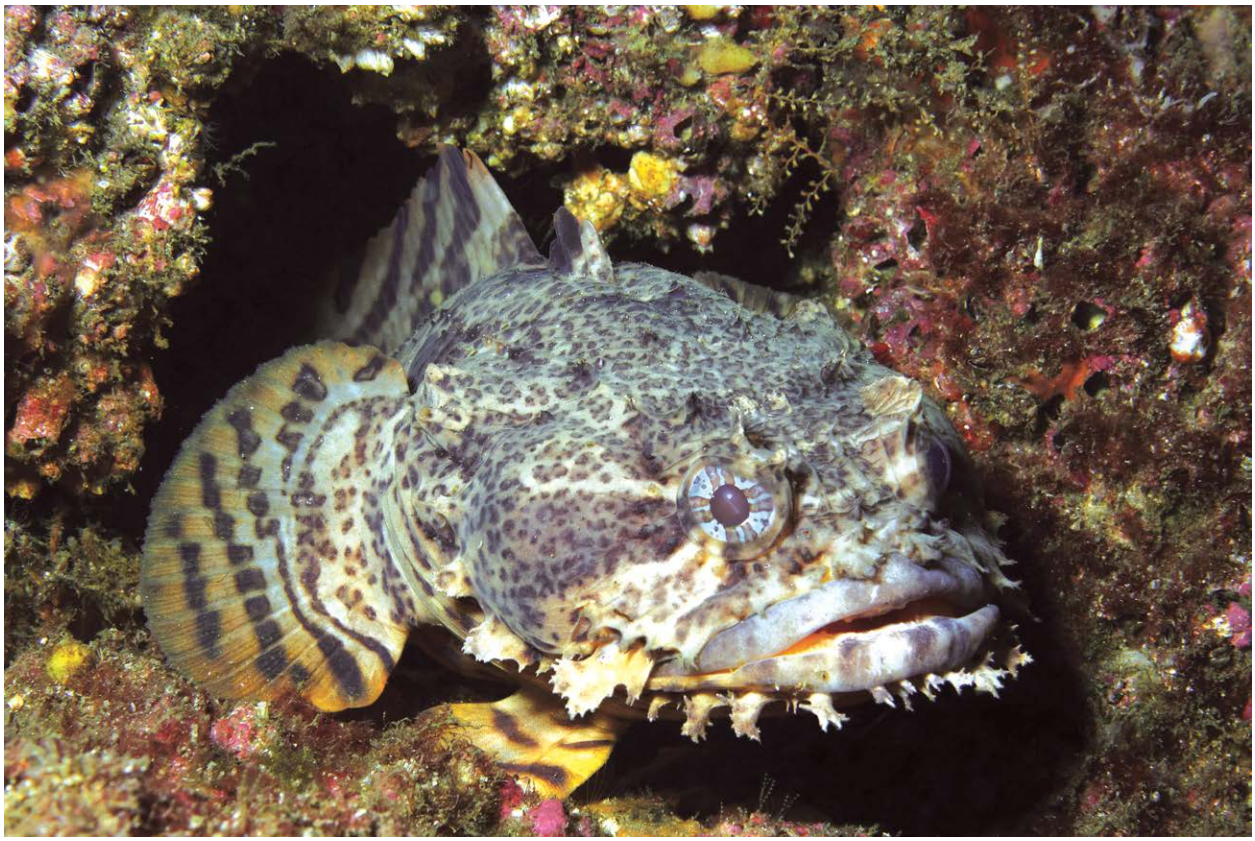


Figure 8.11.4 The oyster toadfish (*Opsanus tau*) waits in its lair. © YAY Media AS / Alamy stock photo.

Figure 8.11.5 Lugworm (*Arenicola marina*) casts. © John M Baxter.

tubes, or reduce their burial depth, in the presence of hypoxia (Dyer et al., 1983; Nestlerode & Diaz, 1998; Neuenfeldt et al., 2009; Nilsson & Rosenberg, 1994; Pihl et al., 1992). Bivalves can also stretch their siphon upward into the water column to reach waters with higher oxygen concentration (Jorgensen, 1980). Some echinoderms stand immobile on their arm tips with the central disk elevated to avoid the hypoxic bottom water (Baden et al., 1990) while some gastropods can climb structures to reach waters with higher oxygen concentration (Vaquer-Sunyer & Duarte, 2008). Even sessile organisms can avoid frequently occurring or chronic hypoxia by avoiding them as larvae, before settling (positive oxytaxis; Lagos et al., 2015).

8.11.3.2.2 Physiology

The full coverage of the species-specific characteristics of oxygen homeostasis in marine organisms is beyond the scope of the present section. A general framework can, however, be laid down. Through evolution, a suite of physiological systems has developed to ensure optimal cellular oxygenation and downstream ATP production (Nilsson & Östlund-Nilsson, 2008). This physiological infrastructure for oxygen delivery includes an entry (respiratory surfaces), a transport vehicle (a circulatory fluid, with or without respiratory pigments, possibly included in red blood cells), sets of highways and secondary roads (the vasculature) and a propulsion device (the heart). Moreover, regulatory mechanisms are provided by endocrine and neural pathways, the complexity of which increases with the accuracy of species-specific homeostatic requirements. When fish, for instance, are exposed to acute hypoxia, they reduce their heart rate, elevate gill vascular resistance, hyperventilate and increase ventilatory amplitude (Burleson & Smatresk, 1990 a, b; Burleson et al., 1992; Randall, 1982). Key to these reflex regulatory responses is oxygen-sensing which occurs through specialized chemoreceptor cells (Coolidge et al., 2008), the location of which is still a topic of active research. In fish, for instance, oxygen chemoreceptors have been located in the brain (Smatresk et al., 1986), the vasculature (Randall, 1982), the buccal and gill cavities (Milsom et al., 2002) and the gills (Burleson & Milsom, 1993; Laurent & Dunel, 1980; Reid & Perry, 2003; Sundin et al., 2000). It has also been shown that the receptors in the gills sense oxygen in the water flow as well as within the gill vasculature itself (Randall, 1982).

Metabolic adjustments to cope with reduced oxygen availability have also been reported, resulting in reduced

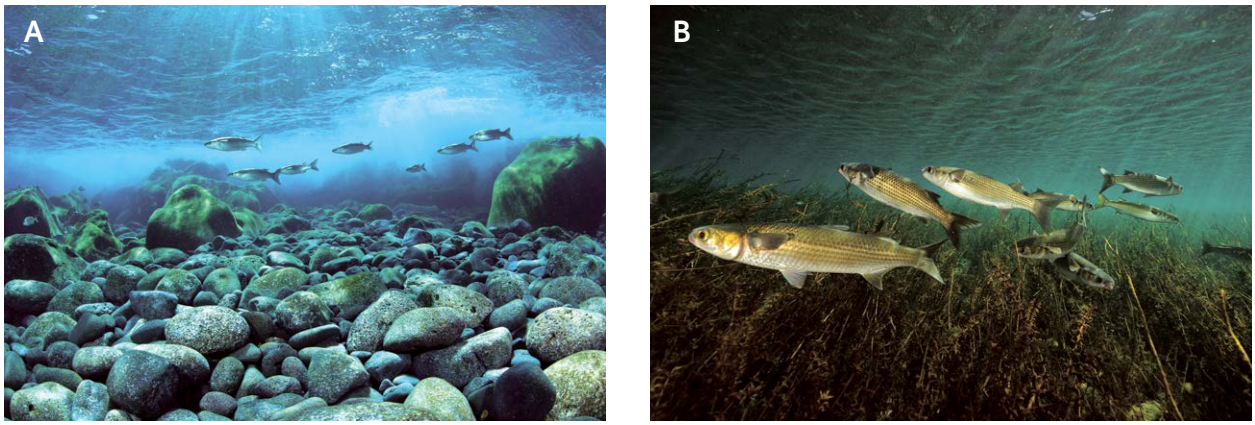


Figure 8.11.6 (A) Golden grey mullet *Lisa aurata* in the surf breaking on the shore. © Nature Picture Library / Alamy stock photo; (B) Flathead grey mullet *Mugil cephalus*. © Mark Conlin / Alamy stock photo.

activity (echinoderms and fish; Diehl et al., 1979; Herbert & Steffensen, 2005; Johansen et al., 2006) reduced feeding activity (fish, crustaceans, molluscs, and polychaetes; Bell et al., 2003; Chabot & Dutil, 1999; Llanso & Diaz, 1994; Tamai, 1993) and reduced metabolic rates (cnidarians and crustaceans; Harper & Reiber, 1999; Rutherford & Thuesen, 2005). Shifts to anaerobic metabolism over time scales of hours to days have also been reported in bivalves (Brooks et al., 1991; De Zwaan et al., 1993), polychaetes (Grieshaber and Volkel, 1998), oligochaetes (Dubilier et al., 1997), echinoderms (Ellington, 1975), and crustaceans (Anderson et al., 1994). Metabolic depression has also been reported in fish (Bickler & Buck, 2007). For a review see Vaquer-Sunyer and Duarte (2008) and Keeling *et* al. (2010). It has also been shown that hypoxia is an endocrine disruptor in fish, impairing reproduction (Wu et al., 2003). For instance, in the Gulf of Mexico, gonadal growth is impaired at hypoxic sites in both females and males Atlantic croaker (*Micropogonias undulatus*; Thomas & Rahman, 2018). At the cellular level, the effects of hypoxia are mediated by a family of proteins, the hypoxia inducible factors (HIF). These proteins, and in particular HIF-1, act as transcription factors and are regulated in the absence of oxygen. In fish it has been shown that hypoxia exposure which resulted in HIF-1 induction during embryogenesis are associated with enhanced hypoxia tolerance in subsequent developmental stages (Robertson et al., 2014).

8.11.3.2.3 Phenology

The life cycles of marine organisms are synchronized with periodic (e.g. tidal, seasonal) changes in their environment in such a way that their various phases e.g. hatching, metamorphosis or settlement, occur under the most favourable conditions. This synchronization process is highly species-specific and occurs through an organism's sensitivity to environmental cues such as temperature, light or food availability (Edwards & Richardson, 2004). Through this process, the spawning season, for instance, is synchronized with ocean temperature so that the development of the early life stages takes place under the most favourable combination of salinity, temperature and food conditions (Asch, 2015; Greve et al., 2005; Koeller et al., 2009; Poloczanska et al., 2013).

To our knowledge, however, there exists no published report documenting phenological responses of marine species to environmental oxygen levels. Local episodes of hypoxia generally co-occur with other environmental disturbances which are also liable to trigger shifts in marine species' life-cycle. The lack of understanding of these interactions, their synergies and their impact on an organism's physiology clearly contributes to restrict present ability to assess a marine population's capacity to phenologically respond to ongoing ocean deoxygenation (McBryan et al., 2013).

8.11.3.2.4 Epigenetics

In marine organisms, embryonic and larval life stages are commonly associated with critical changes in morphology, physiology and behaviour, usually coupled with shifts in habitat and diet. During that period, environmental conditions strongly influence the development of embryos and larvae, affecting not only the performance of these young stages but also having consequences for later life stages (Vanderplancke, 2014; Zambonino et al., 2013, 2017). Moreover, being characterized by fast growth and rapid cell division, early life stages are also prone to epigenetic remodelling (Perera & Herbstman, 2011).

Figure 8.11.7 Zebrafish (*Danio rerio*). © Ian Grainger / Shutterstock.com

Epigenetics proposes that, through fine-tuned molecular mechanisms (DNA methylation, histone modification and non-coding RNA-associated gene silencing), environmental cues such as diet, past environmental conditions, exposure to contaminants or diseases can affect gene activation and expression. It also suggests that these functional modifications of the genes can accumulate throughout an organism's lifetime and, most importantly, can be passed onto the next generation. Epigenetics therefore makes the transition between phenotypic plasticity and genetic adaptation. For example, a beneficial transgenerational effect of parental hypoxic exposure on hypoxia tolerance of offspring has been demonstrated in the zebrafish (*Danio rerio*; Ho & Burggren, 2012) (Figure 8.11.7). This involvement of epigenetic mechanisms in the production of phenotypic diversity is crucial because it presents new possibilities for species to rapidly respond to ongoing climate change and resulting ocean deoxygenation (Donelson et al., 2012). Negative epigenetic effects are also possible, such as reproductive impairments in future generations of medaka (*Oryzias melastigma*), a small fish inhabiting shallow lagoons and swamps, after parents were exposed to hypoxia (Wang et al., 2016). However, research on environmental and evolutionary epigenetics is at an early stage and its integration into evolutionary theory is far from possible at this time.

8.14.3.3 Adaptation

Adaptation is taken to mean the evolutionary process by which natural selection affects, over generations, the gene pool of a population so that this population remains adapted to its environment (Ownby et al., 2002).

Table 8.11.1 Generation time in some marine organisms (after Heron, 1972 in Anderson, 1981)

Organism	Order of magnitude of generation time
Bacteria	Few hours
Ciliates	Few days
Rotifers	1 to 3 weeks
Planktonic crustaceans	1 to 6 months
Bivalves	1 to 3 years
Commercial fish	1 to 10 years

While behavioural and physiological adjustments can be made within seconds to hours in case of changes in the environmental conditions, adaptation occurs over generations. Thus, a species' generation time will strongly determine its capacity to adapt to rapidly changing conditions - the shorter the generation time the higher the potential for rapid evolutionary adaptation (Table 8.11.1).

The pattern of the selective pressure is also a key determinant of the rate of a species' evolutionary process. Unfortunately, interactions between natural variability and anthropogenic climate change make it difficult to project future oxygenation conditions in the ocean. Even more open to conjecture are future oxygenation conditions in shallow coastal waters, where continental and marine biogeochemical processes are particularly intricate. As a result, the patterns of natural selection in these environments are particularly difficult to establish and marine organisms' evolutionary capacity to adapt to these new conditions is still uncertain. Between now and 2100, for instance, approximately 80 generations of sardine (Figure 8.11.8A) (*Sardina pilchardus*; age at first maturity: 1 year) but only 10-15 generations of Atlantic cod (Figure 8.11.8B) (age at first maturity: 5 to 8 years) will occur. If the complexity of the physiological infrastructure involved in homeostasis is considered, these numbers of generations are relatively modest and cast some doubts on the capacity of commercial fish species in particular, to adapt to the fast changing ocean conditions.

8.11.4 Interactions with other environmental drivers

With global climate change, ocean warming is combining with ocean deoxygenation and acidification (Altieri & Gedan, 2015; Stortini et al., 2017) and this combination is likely to have synergetic impacts on marine ecosystems.

The interaction between warming and deoxygenation is perceived to be both strong and worrisome as both drivers are likely to co-occur in many coastal areas. As already mentioned, the vast majority of marine organisms are ectotherms, which means that their body temperature is that of the environment. Thus, ocean warming increases their metabolic rate and, therefore, will increase their need for oxygen. At the same time, oxygen solubility decreases as temperature increases (García & Gordon, 1992), making it more difficult for these species to meet their increased oxygen requirement.

Respiration is the main cause of environmental deoxygenation, and because respiration releases carbon dioxide (CO_2) in a nearly equivalent amount as to that of consumed oxygen (respiratory quotient *c.*0.8), environmental hypoxia generally occurs together with increased dissolved CO_2 (hypercapnia). However, CO_2 not only dissolves but also chemically reacts with water, altering its carbonate chemistry and lowering its pH. Consequently, deoxygenated deep waters are generally more acidic than oxygenated, surface waters (Burnett, 1997; Gobler et al., 2014; Melzner et al., 2012; Mucci et al., 2011). Note that the contemporary increase in anthropogenic CO_2 release in the atmosphere, and its diffusion into the ocean, potentially aggravates marine hypercapnia and the resulting acidification of marine waters.

Published reports suggest that early life-stages of bivalves display additive effects (increased mortality, reduced growth) when facing acidification and deoxygenation combined (Gobler et al., 2014). Similarly, two species of

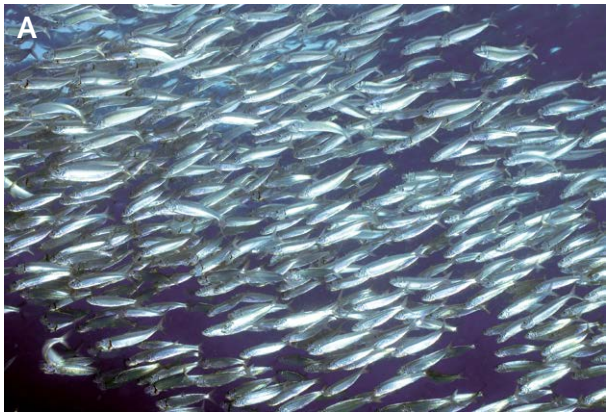


Figure 8.11.8 (A) Sardines (*Sardinia pilchardus*). © BIOSPHOTO / Alamy stock photo; (B) Atlantic cod (*Gadus morhua*). © Paulo Oliveira / Alamy stock photo.

silversides (*Menidia menidi*a and *Menidia beryllina*) have been shown to resort to surface respiration at a higher ambient oxygenation when pH is decreased, indicating lower hypoxia tolerance under acidified conditions (Miller et al., 2016). In cephalopods, environmental hypercapnia affects blood oxygen transport capacity because of the sensitivity of the oxygen-transporters (haemocyanin) to internal acid-base disequilibrium (Seibel, 2016). With rare exceptions (Cochran & Burnett, 1996; Gobler et al., 2014; Miller et al., 2016), published values of hypoxia tolerance have been typically obtained in CO_2 / pH conditions prevailing in surface waters. These values most likely underestimate the true sensitivity of marine species to ambient deoxygenation (Cochran & Burnett, 1996).

The gills of marine organisms are a multi-tasking organ involved in breathing, osmoregulation, acid-base regulation, feeding and excretion. Due to this functional linkage, a strong interaction between ion, water and gas exchange exists, termed the osmo-respiratory compromise (Claireaux & Dutil, 1992). Consequently the increased ventilation (water) and perfusion (blood) of the gills observed when oxygen availability is reduced, result in increased transepithelial movements of water and ions, putting additional load on homeostasis-related energy expenditure. This tight relationship between osmoregulation and ventilation pivots on a complex, species-specific and delicately tuned functional trade-off which remains to be fully investigated (Evans et al., 2005).

Contaminants, parasites and disease can also modulate the capacity of marine organisms to face environmental deoxygenation. Gills, for instance, are particularly vulnerable to water-borne contaminants (Farrell et al., 2004). Moreover, it has been shown that hypoxia reduced the ability of fish to metabolize contaminants and increased ROS production and resulting oxidative damage (Chiedek et al., 2007; Kreitsberg et al., 2013; Mustafa et al., 2012). Parasitized sticklebacks, *Gasterosteus aculeatus* and *Pungitius pungitius* displayed surface respiration at a higher level of dissolved oxygen than healthy individuals (Giles, 1987; Smith & Kramer, 1987). Eastern oyster *Crassostrea virginica* are also more prone to infection during hypoxic events, and it has been proposed that this is due to reduced immune competency (Breitburg et al., 2015). Increased susceptibility to disease and parasites during hypoxic episodes has also been demonstrated in fish (Boleza et al., 2001; Plumb et al., 1976).

8.11.5 Conclusions / Recommendations

As environmental conditions change in the ocean, so does the distribution of habitats that marine species can occupy (Cooke et al., 2014; Huey et al., 2012; Marras et al., 2015; McKenzie et al., 2016). Marine organisms respond to ocean deoxygenation in a number of ways, with physiological, behavioural and epigenetic adjustments, changes in distribution and, possibly, phenology, to evolutionary adaptation. The diversity of these potential responses, and their variability within and among species, makes them challenging to comprehend. Moreover, synergies with other existing pressures, whether natural or resulting from human activities such as, ocean warming and acidification, add to this difficulty. It is therefore crucial that the currently available knowledge base is increased and conveyed to policymakers and the general public to ensure that scientifically sound mitigation and conservation strategies are designed, agreed upon and implemented.

As has been seen, the constraints imposed on marine organisms by dwindling oxygen availability are relatively well understood. However, the propagation of their effects across biological organizational levels remains insufficiently understood to allow reliable projections of impacts upon marine ecosystems' structure, function and services. Over the last 30 years, marine biologists and physiologists have made tremendous efforts to overcome this sticking point, gaining a mechanistic, cause and effect, understanding how marine animals respond to reduced oxygen availability, and hence offering to enrich available models (Deutsch et al., 2015; Holt & Jørgensen, 2015; Jørgensen et al., 2012; Marras et al., 2015; Peck et al., 2016; Rose et al., 2018). Unfortunately, the contribution of this new knowledge to marine resource management is still largely incomplete and greater collaborations between physiologists, ecologists, modellers and managers are required if policy decisions with regard to fisheries management or marine protected areas, for example, are to be fully supported with science-based information (Bianucci et al., 2016; McKenzie et al., 2016; Stortini et al., 2017).

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