Future Science Brief

Nº 10 June 2023

Ocean oxygen

The role of the Ocean in the oxygen we breathe and the threat of deoxygenation

European MARINE BOARD
Advancing Seas & Ocean Science

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This Future Science Brief is a result of the work of the European Marine Board Expert Working Group on Ocean oxygen. See Annex 1 for the list and affiliations of the Working Group members.

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Foreword

We all know that oxygen is a central element of life, and yet it comprises less than one-fifth of the volume of Earth's current atmosphere. This gas (O_2), that we all need to breathe, was not always present in the atmosphere, although oxygen was always present in compounds in the interior of the Earth. It has been a long Earth history before this gas appeared in the Ocean and accumulated in the atmosphere.

Oxygen is critical to the health of the planet. It affects the cycles of carbon, nitrogen and other key elements, and is a fundamental requirement for marine life from the seashore to the greatest depths of the Ocean. It is well known that the Ocean is afflicted by many stressors, from pollution and extractive activities, to Ocean acidification and global warming. However, the global loss of oxygen in the Ocean, also known as Ocean deoxygenation, has not yet gained as much public awareness. Deoxygenation is increasing in the coastal and open Ocean. Human-induced global warming and nutrient run-off from land are the main causes. Just like on land, having sufficient oxygen in the Ocean is of paramount importance to most living organisms. Therefore, the consequences of oxygen loss in the Ocean are extensive, and projections show that the Ocean will continue losing oxygen as global warming continues. Although there are still gaps in our knowledge, we know enough to be very concerned about the consequences of Ocean deoxygenation: the impacts might even be larger than from Ocean acidification or heat waves. Solutions to Ocean deoxygenation and mitigation strategies depend on sound knowledge and raising awareness – a main aim of this Future Science Brief.

In addition to understanding the multiple aspects and impacts of Ocean deoxygenation, another aim of this document is to explain the role of the Ocean in the oxygen we breathe. Because the Ocean produces approximately 50% of Earth's oxygen, sentences such as "every second breath we take comes from the Ocean" are commonly used to highlight the importance of the Ocean. However, the science behind this sentence is more complicated than it might seem at first glance, because of the time it has taken to produce the oxygen that has thus far accumulated in the atmosphere. And then there is the question of who do we actually mean with "we"? Is it humans, or all organisms on Earth? This document explains the role of the Ocean in Earth's oxygen production and accumulation, how the Earth became oxygenated, the modern oxygen cycle, the distribution of oxygen between land and Ocean, and the problem of Ocean deoxygenation.

The sense of urgency to improve Ocean health is reflected in the UN Decade of Ocean Science for Sustainable Development and the EU Mission: Restore our Ocean and Waters, and tackling the loss of oxygen in the Ocean is critical to achieving the aims of these two initiatives. This document will contribute to raising the necessary awareness and action. It will not be easy to reverse Ocean deoxygenation – but the consequences of inaction are far greater than the costs of action.

The Working Group on Ocean Oxygen kicked off in June 2022, after the European Marine Board decided that it was timely and necessary to write a document on Ocean oxygen. On behalf of the Members of EMB, I would like to sincerely thank the Members of the Ocean Oxygen Working Group for their enthusiasm and drive in producing this publication, particularly the Chairs Marilaure Grégoire and Andreas Oschlies. I would also like to thank the external reviewers for their valuable input, as well as the EMB Secretariat, and specifically the Science Officer Ana Rodriguez, for supporting the Working Group and coordinating the production of this document. Finally, I would like to thank the students Lucas Devisscher, Emma Losfeld and Anouk Hofman from the Artevelde University of Applied Sciences in Belgium for designing and creating the infographics used in this document to illustrate complex issues in a simple way.

Gilles Lericolais
Chair, European Marine Board
June 2023

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Executive summary

Oxygen is essential for the survival of most life on Earth. It is Earth's most abundant chemical element and is involved in numerous chemical reactions, including many biogeochemical cycles. Biogeochemical cycles are continuous loops that support life by cycling essential elements between Earth's living and non-living components, as well as between land and the Ocean. Most marine life also relies on oxygen to obtain energy. However, the Ocean is slowly losing oxygen (termed Ocean deoxygenation), mainly due to climate change and nutrient run-off from agriculture. Ocean deoxygenation promotes the production of the greenhouse gases nitrous oxide and methane, and is an increasing threat to marine life, the Ocean's ecosystems, and ultimately to humans, which all depend on a healthy Ocean.

This Future Science Brief outlines the most recent science on Ocean oxygen, including the global oxygen cycle, current deoxygenation and the influence of the Ocean on the oxygen we breathe. It is not meaningful to discuss Ocean oxygen in isolation, therefore the full Earth oxygen system, including the Ocean and atmosphere, are considered. **Chapter 1** provides a general introduction to the importance of Ocean oxygen for life and the problem of deoxygenation. **Chapter 2** describes how oxygen got into the Earth's atmosphere, the feedbacks that stabilise oxygen concentrations, and the association of several mass extinctions with Ocean deoxygenation. It also examines whether the sentence commonly used in Ocean Literacy and science communication "every second breath we take comes from the Ocean" is scientifically accurate. **Chapter 3** covers the modern oxygen cycle, with an emphasis on oxygen in the Ocean. It also describes millennial to decadal natural variability in atmospheric and oceanic oxygen content. **Chapter 4** details current Ocean deoxygenation, including the mechanisms and degree of oxygen loss, effects on marine life and ecosystems, and impacts of deoxygenation on biogeochemical processes. **Chapter 5** explains the methods used to study oxygen and the strengths and limitations of modelling Ocean oxygen. **Chapter 6** discusses management, mitigation and adaptation needs to address Ocean deoxygenation. The final recommendations of this document are presented in **Chapter 7** and summarised below.

Recommendations for policy and management:

- Recognise Ocean deoxygenation as one of the major threats to marine ecosystems;
- Reduce and eventually reach net-zero anthropogenic emissions of greenhouse gases to stop upper Ocean deoxygenation;
- Limit run-off of nutrients and organic waste into the Ocean to reduce coastal deoxygenation and hypoxia (low oxygen conditions impacting marine life);
- Reduce stressors and increase protection of marine ecosystems, especially in deep-sea ecosystems, to increase resilience to deoxygenation;
- Include Ocean oxygen in future projections by intergovernmental bodies and in high-level frameworks for planetary health to spur action and societal awareness; and
- Promote the following statements on the role of the Ocean in the oxygen we breathe, to provide the most accurate information:
  - ✓ The Ocean produces ~50% of Earth's oxygen;
  - ✓ Every second breath taken by all life on Earth comes from the Ocean; and
  - ✓ Since the origin of life on Earth, the Ocean has provided most of the oxygen in the atmosphere, and is responsible for 6 of 7 breaths humans take.

Recommendations for funders, research and monitoring:

- Fund and perform coordinated research to better understand historical, current and future Ocean deoxygenation rates;
- Fund and perform targeted research to enhance understanding of the biological, chemical and physical processes controlling oxygen dynamics;
- Fund and increase Ocean oxygen observations and modelling efforts, and ensure that all oxygen data is compiled and shared, feeding into global databases, to accurately document and predict Ocean oxygen changes;
- Develop new low-power and low-cost oxygen sensors;
- Include oxygen in multiple stressor studies of marine environments;
- Fund and perform research to better understand how deoxygenation will impact marine life, from populations to ecosystems; and
- Fund and perform research to better understand the vulnerability of ecosystem services, our society and our economy to deoxygenation.

Credit: Sheila Heymans

Long Beach in Namibia. Ocean deoxygenation can impact the visual appeal of coasts and degrade water quality.

2021 United Nations Decade
2030 of Ocean Science
for Sustainable Development

Contribution to the UN Ocean Decade Challenges and Outcomes

This Future Science Brief and its recommendations support the following societal outcomes (O) and challenges (C) of the United Nations Decade of Ocean Science for Sustainable Development (Ocean Decade):

- **'A clean Ocean'** (O1) where we **'Understand and beat marine pollution'** (C1) by contributing to understanding the impacts of nutrient pollutants on ecosystems and to developing solutions to remove or mitigate them. This document outlines the direct link between land-based nutrient run-off and enhanced Ocean deoxygenation and hypoxia in coastal ecosystems, and its consequences on Ocean ecosystems and marine life.
- **A healthy and resilient Ocean'** (O2) where we **'Protect and restore ecosystems and biodiversity'** (C2) by contributing to understanding the effects of multiple stressors on Ocean ecosystems and to developing solutions considering future changing conditions. This document highlights the combined effects of deoxygenation, warming and acidification on marine life, stressing the need for studies on multiple stressors. Moreover, it elucidates how the deep Ocean will continue to lose oxygen for centuries, even if anthropogenic greenhouse gas emissions would be stopped today, highlighting the need for deep-sea ecosystem protection to enhance their resilience.
- **'A productive Ocean'** (O3) where a sustainable food supply allows to **'Sustainably feed the global population'** (C3) by highlighting how Ocean deoxygenation can lead to habitat compression and changes in food web structure, thereby impacting global fisheries, and influencing the development of solutions to supply food from the Ocean.
- **'A predicted Ocean'** (O4) where we need to **'Expand the Global Ocean Observing System'** (C7) by highlighting the need to include oxygen in all Ocean observing efforts.
- **'Unlock Ocean-based solutions to climate change'** (C5) by contributing to understanding the Ocean-climate nexus and the effects of climate change on the oxygen cycle. This document describes the oxygen cycle, its link to the carbon cycle and the effects of climate change on the oxygen cycle.

Knowledge on Ocean oxygen and the threat of Ocean deoxygenation is thus essential to achieve the objectives of the Ocean Decade.

Contribution to the EU Mission: Restore our Ocean and Waters

This Future Science Brief and its recommendations support the following three objectives (O) and one enabler (E) of the EU Mission: Restore our Ocean and Waters (Mission Ocean):

- **'Protect and restore marine and freshwater ecosystems and biodiversity'** (O1) by highlighting the threats of Ocean deoxygenation to marine life and ecosystems, and thus the importance of protection and restoration to increase resilience.
- **'Prevent and eliminate pollution'** (O2) by describing the direct link between anthropogenic nutrient run-off and hypoxia in coastal waters, which frequently leads to changes in marine animal community structure and mass mortality. These threats highlight the need to limit run-off of nutrients and organic waste into the Ocean.
- **'Make the sustainable blue economy carbon-neutral and circular'** (O3) by explaining the direct link between anthropogenic greenhouse gas emissions and Ocean deoxygenation, stressing the need to transition to a carbon-neutral economy.
- **'Promote a participatory governance based on public mobilisation and engagement'** (E2) by heightening awareness of the threat of Ocean deoxygenation to marine ecosystems, which is currently heavily under-communicated compared to similar stressors, such as Ocean acidification. Participatory governance and engagement will be key to increase public awareness.

Kelp below the sea surface in the Isle of Seil, Scotland. Coastal vegetative ecosystems, such as kelp beds, seagrass meadows, mangroves and tidal marshes may help to enhance oxygen levels locally through photosynthetic oxygen production.

EMB acknowledges that while the Working Group members writing this document and its recommendations represent diversity in European geographical location (see Annex I), professional background, and career level, their views do not represent ideas from other geographical locations and other forms of diversity and may therefore be biased. Although all authors are affiliated with European institutions, the document covers the global Ocean oxygen dynamics and the messages and recommendations are therefore relevant at the global scale.

1 Introduction

The sentence "every second breath you take comes from the Ocean" is commonly used in Ocean Literacy and science communication to highlight the importance of the Ocean for humans. Despite the widespread use of this phrase, there is growing debate among scientists about its accuracy. To avoid misleading the public, there is a need to clarify the science underpinning the actual connection between the oxygen reservoir in the atmosphere and oxygen production in the Ocean, including differences in timelines for marine- and terrestrially-produced oxygen. In contrast to the widely used "every second breath" sentence, there is little public awareness on the fact that the Ocean is currently losing oxygen, termed deoxygenation. This is of great concern, with likely significant detrimental effects on marine life, ecosystem functioning, and ultimately humans, and there is a need for heightened awareness about this threat.

Most life on Earth, including marine life, relies on oxygen for its survival. Oxygen is the most abundant element on Earth and is involved in many chemical reactions, including biogeochemical cycles of essential elements, such as carbon, sulphur, nitrogen and phosphorus. These cycles continuously loop essential elements between the living and non-living components of Earth. Biogeochemical cycles also connect the land and the Ocean. The Ocean is therefore essential to maintain the balance of biogeochemical cycles, and the whole Earth system. Biogeochemical cycles not only support life on Earth but are also vital for regulating Earth's climate and therefore have strong climatic, economic and societal relevance.

Although many of us take our richly oxygenated atmosphere for granted, there was very little free oxygen during most of Earth's 4.5-billion-year history. It was only when oxygen-producing cyanobacteria evolved that oxygen started to slowly accumulate in our atmosphere. The rise of oxygen is closely linked with the evolution of progressively more complex life-forms on Earth. Conversely, major drops in oxygen, especially in the Ocean, have been accompanied by global mass extinction events – with at least three of the five mass extinctions being linked to no oxygen (anoxia) in the Ocean.

The percentage of oxygen in our modern atmosphere has currently stabilised at ~21% and this stability is due to a balance in the global oxygen cycle, i.e. the processes that produce oxygen and consume it. Photosynthesis by plants on land and microscopic marine algae (called phytoplankton) in the Ocean produces roughly equal amounts of oxygen every year, leading to the notion that every second breath we take comes from the Ocean. But virtually all this oxygen is used shortly after by terrestrial and marine organisms, respectively, for respiration (i.e. the use of oxygen by animals, plants and microbes to produce energy). Therefore, understanding the role of the Ocean in the oxygen we breathe is more complicated than it might seem at first. In this document, we explain all components needed to understand this, including differences in timelines for marine- and terrestrially-produced oxygen.

In contrast to the relatively well-mixed atmosphere, oxygen in the Ocean exhibits strong spatial gradients. The surface of the Ocean is usually close to saturation (i.e. it has the maximum possible amount of dissolved oxygen at a given temperature). However, at intermediate depths, oxygen is supplied via Ocean circulation, and this supply cannot compensate for its consumption, creating persistent, natural, low oxygen areas, which have intensified and expanded in recent decades.

In addition to the decline in oxygen in naturally-occurring low oxygen areas, the whole Ocean has also been losing oxygen since the middle of the 20th century. This so-called Ocean deoxygenation is one of the most worrying changes occurring in marine ecosystems and yet it is heavily under-communicated. Global warming leads to oxygen loss, both directly, by reducing the amount of oxygen seawater can hold (i.e. reducing oxygen saturation levels), and indirectly, through changes in physical dynamics, such as intensifying stratification, which slows down Ocean circulation and reduces the transport of oxygen into the Ocean interior. The global Ocean oxygen content has decreased by more than two percent since the middle of the 20th century (Schmidtko *et al.,* 2017). Model projections for the end of this century predict a further decrease of several percent under both "business-as-usual" and "high mitigation" greenhouse gas emission scenarios (Bopp *et al.,* 2013).

Another major source of Ocean oxygen loss is eutrophication (i.e. nutrient enrichment) in coastal zones as a result of nutrient run-off from land. The increased application of fertilisers in agriculture has doubled the input of nutrients from land into the Ocean over the past half century. Eutrophication can lead to the development of very low oxygen conditions, ranging from hypoxia (reduced oxygen) to anoxia, with detrimental impacts on marine life.

The consequences of oxygen loss in the Ocean include decreased biodiversity, shifts in species distributions, displacement or reduction in fisheries resources, changes in biogeochemical cycling and mass mortalities. Low oxygen conditions also drive other chemical processes which produce greenhouse gases, toxic compounds and further degrade water quality. The degraded water quality directly affects marine ecosystems, but also indirectly impacts ecosystem services supporting local communities, regional economies and tourism. For instance, island communities that depend on coral reefs are increasingly subjected to deoxygenation, which has a detrimental impact on their livelihoods.

These changes are taking place on such a large scale that experts foresee that they will have implications for global biochemistry and climate, with a less productive Ocean and a lower capacity of both land and Ocean to serve as carbon sinks (Long *et al.,* 2019). The continued spread of deoxygenated areas in the Ocean is therefore of great concern, with potentially large impacts on biodiversity and human societies (Laffoley & Baxter, 2019). Raising awareness of the causes, impacts and solutions to Ocean deoxygenation is therefore critical. This document investigates the different mechanisms driving Ocean oxygen changes, their impacts and potential mitigation strategies.

Key terminology

Ocean deoxygenation refers to a decline in dissolved oxygen concentrations with time.

Oxygen Minimum Zone (OMZ) generally refers to regions that display persistent, low oxygen concentrations in vertical profiles, often found to occur naturally in the tropical Ocean at a depth of several tens to a few hundred metres.

Oxygen Deficient Zone (ODZ) refers to regions where oxygen concentrations are below critical threshold values, thereby impacting marine life and/or biogeochemistry. ODZs can occur naturally in particularly intense Oxygen Minimum Zones (OMZs). Throughout this document we will use ODZs as an overarching term for low oxygen regions, because OMZs refer to the shape of the vertical profile, not to the absolute level of oxygen concentrations.

A herring shoal in Scotland, UK. The consequences of oxygen loss in the Ocean include decreased biodiversity, shifts in species distributions and displacement or reduction in fisheries resources.

2 History of the oxygen cycle on Earth

This chapter presents the history of the oxygen cycle on Earth, including what type of life existed before there was oxygen in our atmosphere, how the Earth became oxygenated, and how that changed life on Earth. It also discusses the relationship between mass extinctions and Ocean deoxygenation. Furthermore, it explains the mechanisms that maintain the balance of oxygen in the atmosphere and historical tipping points. Finally, the amount of atmospheric oxygen originating from land and the Ocean is presented, and the question of whether every second breath we take comes from the Ocean is discussed.

The key messages from this chapter are:

- During most of Earth's 4.5-billion-year history, there was virtually no free oxygen in our atmosphere (i.e. it was anoxic);
- The Great Oxidation Event (GOE) occurred ca. 2.4 billion years ago and was a tipping point in the history of atmospheric oxygen. Oxygen-producing cyanobacteria (i.e. blue-green algae) evolved and oxygen started accumulating in the atmosphere, radically changing the chemistry and biology of Earth;
- Eukaryotes (i.e. organisms that have cells with a nucleus) evolved in an Ocean with oxygenated surface water, anoxic deep waters and atmospheric oxygen levels likely 1-10% of present levels;
- The Paleozoic Oxygenation Event (POE) was another tipping point, which occurred ca. 400 million years ago and was associated with the evolution of land plants;
- Numerous feedbacks stabilise the oxygen content of the atmosphere;
- Three out of five mass extinctions were associated with Ocean deoxygenation; and
- 86% of the oxygen humans breathe (or six out of seven breaths we take) originated from the Ocean over geological time scales.

2.1 History of oxygen and its relationship to life

2.1.1 Life before oxygen

The Earth is 4.5 billion years old and contained virtually no free oxygen (in its O_2 gas form) in the atmosphere or the Ocean for the first ca. 2 billion years (during the Hadean Eon and the Archean Eon, Figure 2.1 and 2.2; an eon is the largest geological time unit) - although oxygen (O) was always present in compounds in the interior of the Earth. Life evolved around 3.7 billion years ago (during the Archean Eon) (Rosing, 1999), but was anaerobic, i.e. it neither produced nor used oxygen. Organisms producing methane and organisms metabolising sulphate evolved 3.5 billion years ago (Shen *et al.*, 2001). These are both important biological processes today that help control the biogeochemical cycling of carbon and sulphur. Despite the evolution of these organisms, the rates of primary production on the anoxic Earth, including the Ocean, was likely considerably lower than today (Canfield *et al.*, 2006). Only very simple life forms existed with a species diversity likely substantially lower than today.

2.1.2 Oxygenation of Earth

The chemistry and biology on land and in the Ocean changed profoundly with the evolution of oxygen-producing cyanobacteria, which produce oxygen and organic matter (i.e. matter composed of carbon-based compounds) through photosynthesis (Box 2.1), and spread to all aquatic environments receiving sunlight. The timing of cyanobacterial evolution is unclear, but they certainly evolved by 2.4 billion years ago (during the Proterozoic Eon, Figure 2.1 and 2.2) when a dramatic increase in oxygen occurred in the atmosphere, called the Great Oxidation Event (GOE) (Figure 2.1). The spread of cyanobacteria increased biological primary production on the Earth by several orders of magnitude. This was beneficial to all life on Earth, feeding the anaerobic life in sediments and marine waters that were still mostly anoxic. The introduction of oxygen into the environment allowed the evolution of aerobic metabolism (i.e. energy production or consumption using oxygen), which dramatically increased the complexity of marine ecosystems.

Increased atmospheric oxygen liberated many micro-nutrients contained in rocks through weathering, which were delivered to the Ocean through rivers. Phosphorus is one of the nutrients that were delivered to the Ocean. Because it is essential for life, it gave an extra boost to marine phytoplankton growth and thus primary production (Bekker & Holland, 2012). Similarly, dissolved silicate also reached the Ocean from the weathering of rocks and is an essential nutrient for diatom growth (i.e. a type of phytoplankton that forms the base of many modern oceanic and coastal food webs).

During the GOE, the surface mixed layer of the Ocean (i.e. the surface waters which are well mixed by wind, and other processes, typically covering the first tens of metres of the Ocean) became oxygenated and allowed the efficient cycling of elements because oxygen plays a central role in the biogeochemical cycling of many elements. For example, organic matter produced by cyanobacteria from carbon dioxide (CO_2) and water (H_2O) created oxygen (O_2), that could be rapidly respired back to carbon dioxide and water (Box 2.1). Similarly, nitrogen (N) could now also be efficiently recycled and this allowed another key nutrient for life, nitrate (NO_3), to accumulate in the surface of the Ocean (Cheng *et al.*, 2019).

Box 2.1 Mechanisms of biological oxygen production and consumption through photosynthesis and respiration

Oxygen (O_2) is produced through photosynthesis and consumed through aerobic respiration, which includes decomposition by microbes.

Photosynthesis is a process whereby oxygen is produced by cyanobacteria, plants and algae, using sunlight, water and carbon dioxide (CO_2) to produce organic matter. This process of organic matter production is called “primary production”. Both on land and in the Ocean, photosynthesis is responsible for virtually all biological primary production. The equation for photosynthesis is:

Sunlight Energy + Water + Carbon Dioxide → Organic matter + Oxygen

(Aerobic) respiration is the process whereby living organisms produce energy from organic matter and oxygen. In humans and other animals this involves breathing oxygen and eating (i.e. consuming organic matter). Microbes respire (aerobically) when they use oxygen to decompose organic matter, thereby producing energy. The equation for aerobic respiration is:

Organic matter + Oxygen → Carbon Dioxide + Water + Energy

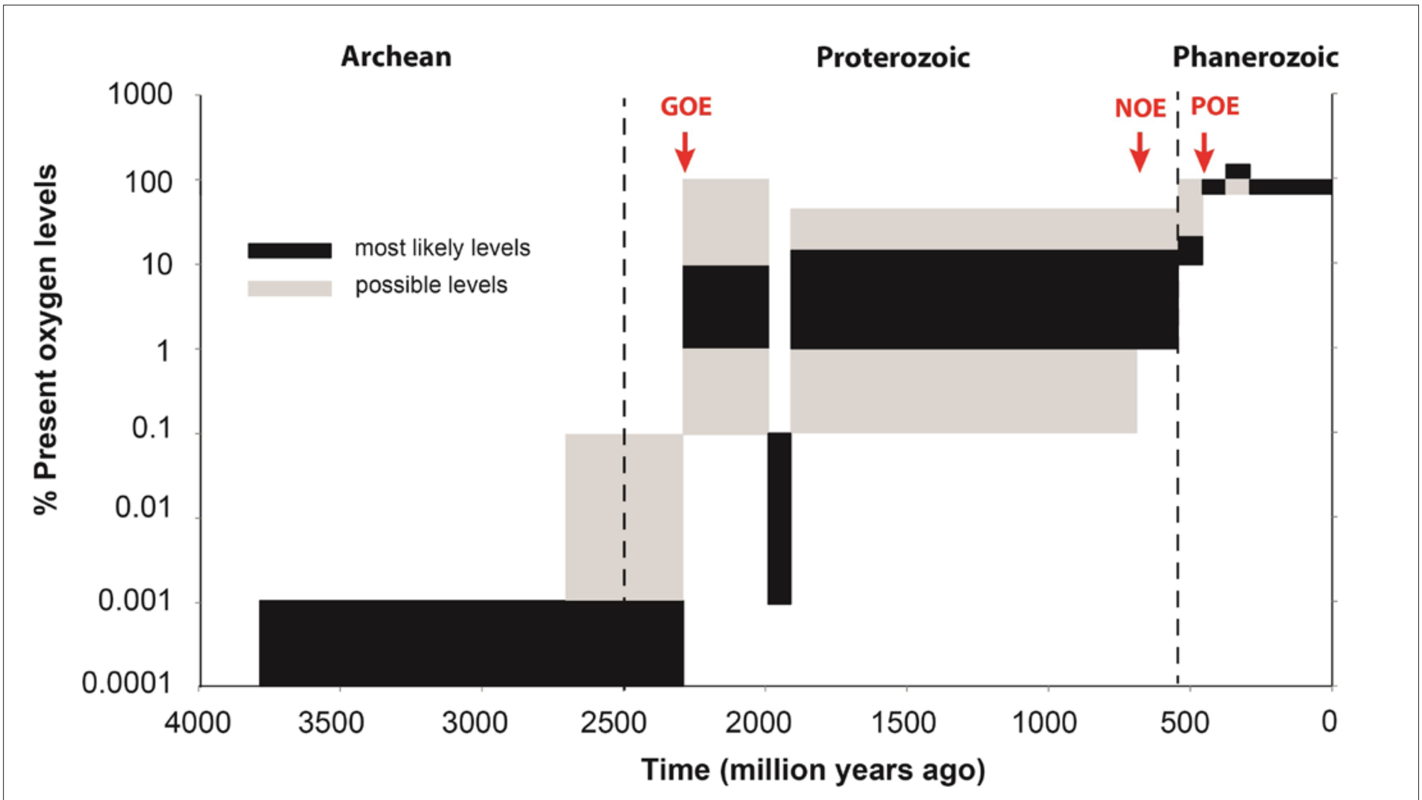


Figure 2.1 History of atmospheric oxygen since the formation of Earth 4.5 billion years ago. Oxygen levels are expressed in percentage of present atmospheric oxygen levels. The black shaded areas denote the most likely oxygen levels at the time (based on most scientific studies), whereas the the grey shaded areas indicate the range of uncertainty (i.e. possible oxygen levels based on some studies). Note that the percentage oxygen levels are represented on a logarithmic scale to show the very wide range of values; the oxygen level values therefore do not increase linearly. GOE = Great Oxygenation Event; NOE= Neoproterozoic Oxygenation Event; POE = Paleozoic Oxygenation Event.

2.1.3 The emergence of eukaryotes

Although oxygen accumulated in the atmosphere and the Ocean after the GOE, levels of oxygen were likely much lower than today, probably around 1-10% of present values. However, the exact values remain uncertain and they might have been considerably higher or lower (see grey bands in Figure 2.1). While the surface mixed layer of the Ocean would have been in equilibrium with the atmosphere, the waters directly above the seabed were mostly anoxic. Anoxia was probably also common below the surface mixed layer of the Ocean (Guilbaud *et al.,* 2015). The deep-sea, however, could have been mildly oxygenated depending on where the deep water formed and on patterns of Ocean circulation. Eukaryotes, including eukaryotic algae, first evolved in this unevenly oxygenated Ocean, with the earliest fossil evidence dating back to 1.7-1.6 billion years ago (Knoll *et al.,* 2006).

It is unknown if more advanced marine eukaryote ecosystems first emerged at the same time as algae and eukaryotic grazers (1.7-1.6 billion years ago), but by 750 million years ago they were certainly present (Zumberge *et al.,* 2019). Animals, which first evolved in the Ocean, also likely appeared around this time. Sponges are thought to be one of the first animal groups that evolved on Earth, and the first possible sponge fossils are around 600 million years old (Yin *et al.,* 2015).

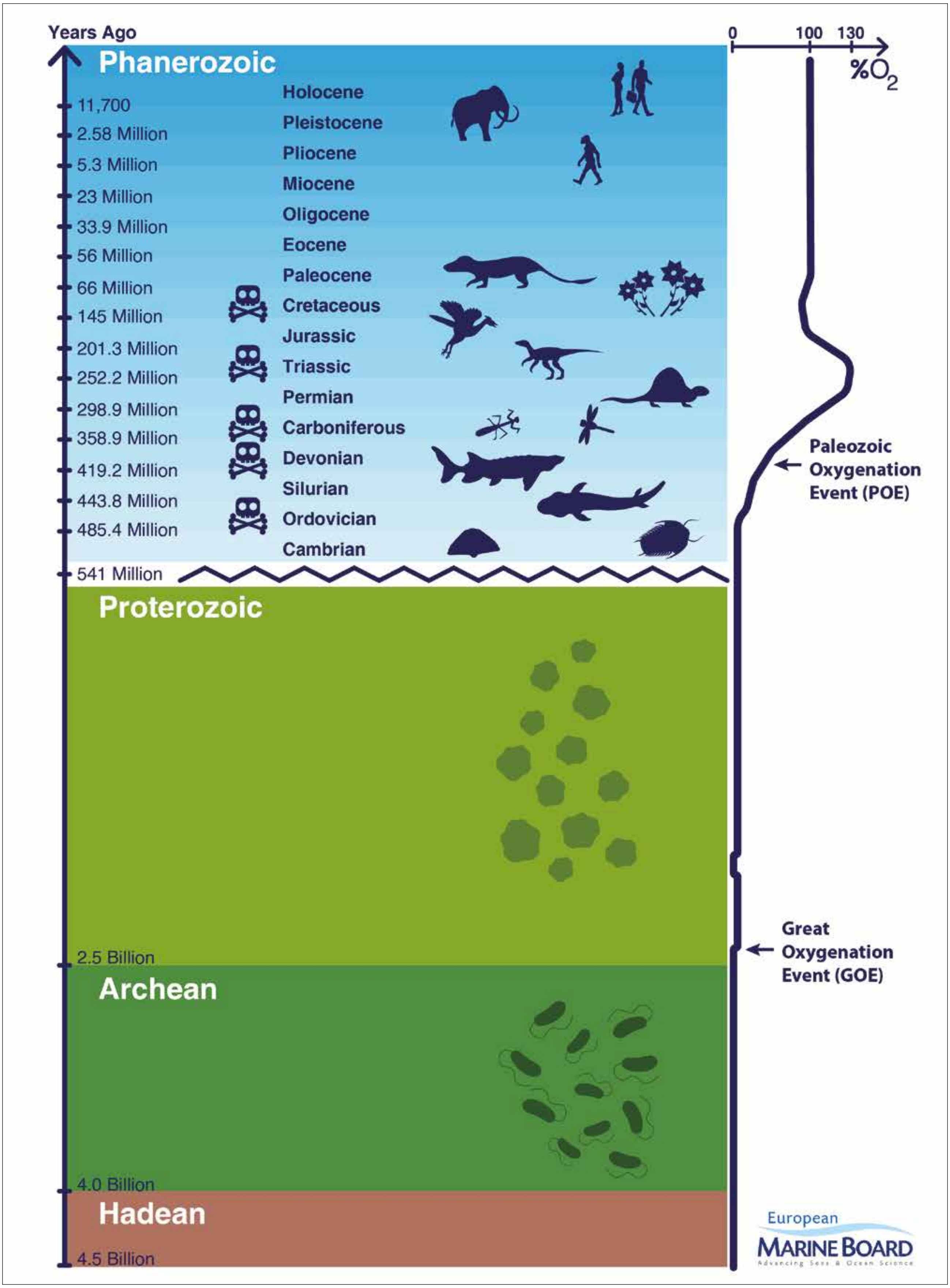
There is a longstanding hypothesis that the rise in atmospheric oxygen concentrations enabled animal evolution. This hypothesis is supported by the rise in animal evolution around 650-700 million years ago in what is known as the Neoproterozoic Oxygenation Event (NOE) (Figure 2.1) (Och & Shields-Zhou, 2012). However, the atmosphere and Ocean might have accumulated sufficient oxygen for the earliest animals as far back as 1.7 billion years ago (Canfield *et al.,* 2021), long before the NOE. In addition, evidence for the NOE is not as straightforward as for the GOE. Atmospheric oxygen might have not reached modern-like levels until about 400 million years ago during the Paleozoic Oxygenation Event (POE) - another tipping point in the history of atmospheric oxygen - when land plants evolved and proliferated (Dahl *et al.,* 2010) (Figure 2.1 and 2.2). The relationship between oxygen dynamics and animal evolution is, therefore, still unclear.

2.1.4 Mass extinctions and Ocean deoxygenation

Deep-sea and seabed anoxia remained common in the Phanerozoic Eon (the current eon, covering the last 551 million years), well after animals first evolved (Sperling *et al.,* 2021). Deep-sea anoxia probably persisted due to low atmospheric oxygen levels, but it might also be due to different configurations of continents, which led to different patterns of deep-water circulation (Pohl *et al.,* 2022).

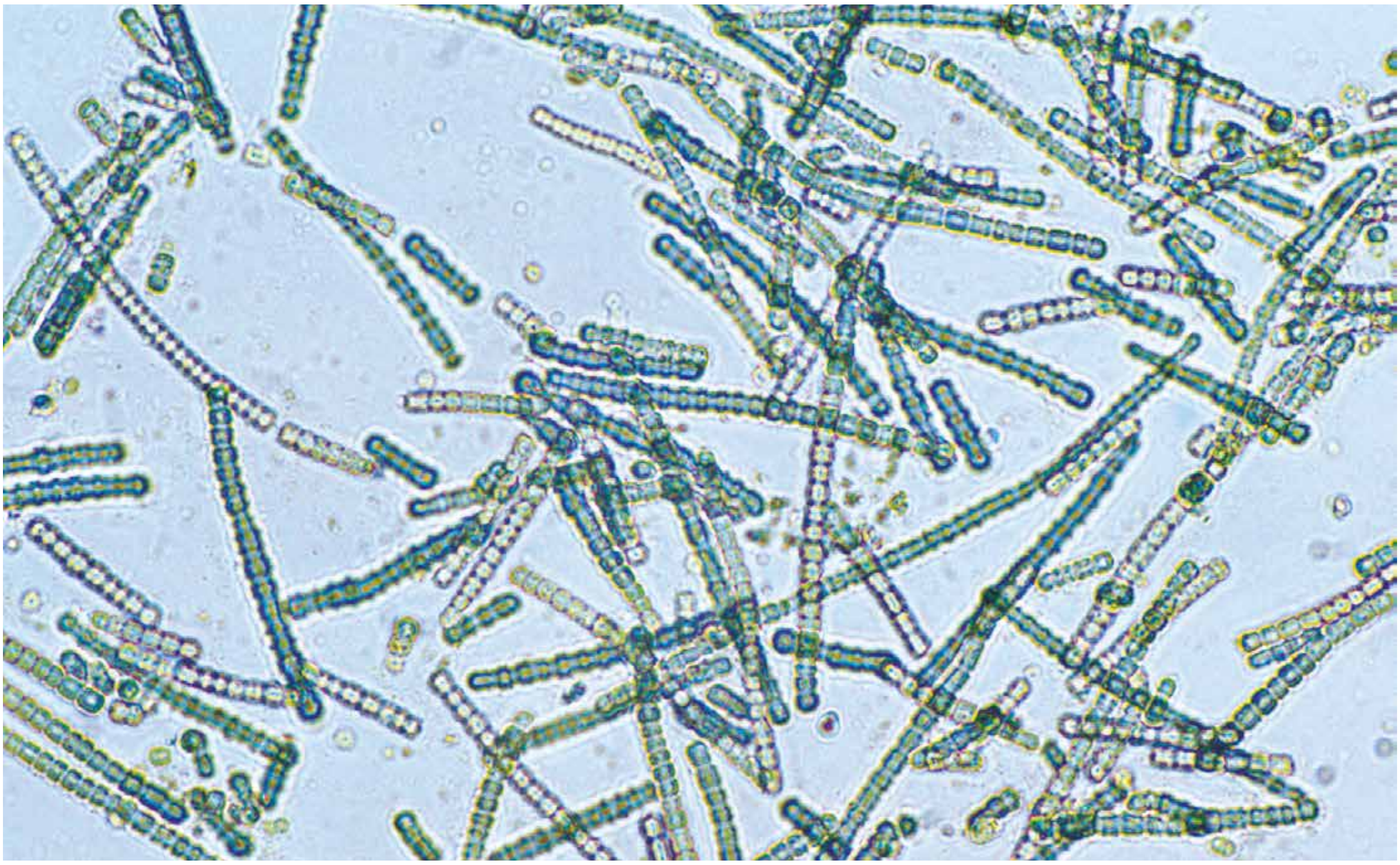
Three out of the five mass extinctions that have occurred throughout Earth's history have so far been linked to expanded Ocean anoxia. These mass extinctions all happened during the current Phanerozoic Eon, in the Ordovician, Devonian and Permian periods (periods are smaller geological time units than eons typically lasting many millions of years, and one eon can contain several periods) (Figure 2.2). The Ordovician mass extinction (85% death rate, ca. 443-445 million years ago) occurred during a period of rapid cooling, which probably changed Ocean circulation and expanded anoxia (Bartlett *et al.,* 2018). The Devonian mass extinction (70% death rate, ca. 375 million years ago) is similarly associated with expanded Ocean anoxia. This was probably related to the development of rooted land vegetation, which increased weathering on land, thereby delivering more phosphorus to the Ocean and increasing productivity. This, in turn, would have increased the organic matter reaching the deep sea, which upon decomposition would have decreased oxygen in the deep-sea (Zhang *et al.,* 2020). The Permian mass extinction (95% death rate, ca. 252 million years ago) is the largest known in Earth's history. This extinction is associated with expanded Ocean anoxia and was most likely caused by high levels of CO_2 released from volcanoes and the resulting global warming. The global warming led to slower Ocean circulation and Ocean deoxygenation (Kiehl & Shields, 2005). Overall, while the mechanisms may vary, enhanced Ocean anoxia, sometimes associated with climate change, was likely responsible for some of the major mass extinctions in Earth's history.

A dinosaur skeleton of the species *Edmontosaurus annectens* at the Royal Ontario Museum in Canada. All dinosaurs went extinct about 65 million years ago, during the Cretaceous mass extinctions.



Credit: Lucas Devisscher, Emma Losfeld and Anouk Hofman; Artevelde University of Applied Sciences

Figure 2.2 Geological times, mass extinctions (where 70-95% of life on Earth died) and increase of oxygen in the atmosphere since the formation of Earth. The four eons (Hadean, Archean, Proterozoic and Phanerozoic) are highlighted in brown, dark green, light green and blue, respectively. The periods of the Phanerozoic Eon are shown in different shades of blue. The skulls symbolise the occurrence of a mass extinction. The organisms shown represent their evolution (except for the modern human symbol, which indicates that we are currently in the Holocene). Note that the Phanerozoic Eon is not to scale (indicated by the break in the graphic). Oxygen levels are shown as a percentage of the current atmospheric oxygen level.



A cyanobacteria (blue-green algae) Cylindrospermum species under magnification. The evolution of oxygen producing cyanobacteria was associated with the first marked increase of oxygen in our atmosphere.

Encrusting sponge in the Mediterranean Sea. Sponges were among the first animals to evolve around 600 million years ago.

2.2 Oxygen in the atmosphere

2.2.1 Sources and sinks of atmospheric oxygen

The concentration of oxygen in the atmosphere is a balance between the processes releasing oxygen to the atmosphere (sources) and the processes consuming it (sinks) (Figure 2.3). Oxygen comes from primary production by cyanobacteria, plants and algae, but most of this oxygen is consumed again when these organisms respire and as their remains are decomposed by other organisms (Box 2.1). Therefore, if all the organic matter produced by photosynthesis was respired, all the oxygen produced during photosynthesis would be used and no oxygen would accumulate in the atmosphere. However, some organic matter escapes respiration and instead becomes buried in sediments, therefore some oxygen is not used. This unused oxygen represents a surplus, and is a net source of oxygen to the Ocean and ultimately to the atmosphere. In other words, the burial of organic matter creates a small imbalance between oxygen production and consumption through which oxygen slowly accumulates in the atmosphere. Therefore, the oxygen we breathe today has slowly accumulated in the atmosphere over very long time-scales as a result of organic matter burial.

Perhaps less obvious, the burial of pyrite (FeS_2, a naturally occurring mineral that is commonly found in a variety of rocks and geological formations) also represents a source of oxygen to the atmosphere[1]. Pyrite is a common mineral in marine sediments and its burial has the same impact on oxygen accumulation in the atmosphere as the burial of organic matter. In marine sediments, both organic matter and pyrite are buried, while on land, organic matter is buried as coal with very little accompanying pyrite. Thus, in the Ocean, both organic matter and pyrite contribute to the oxygen release to the atmosphere, while on land it is mainly organic matter burial (Figure 2.4). During the last 12,000 years (throughout the Holocene) the burial of organic matter and pyrite in the Ocean has contributed 86% of the oxygen that has accumulated in the atmosphere, while the burial of coal on land has contributed the remaining 14% of oxygen (see Section 2.2.2).

Oxygen is consumed by reacting with organic matter and pyrite in sedimentary rocks (i.e. rocks that are formed on or near the Earth's surface from the compression of pre-existing rocks or remains of dead organisms), and by reactions with volcanic gases (Figure 2.2). The reaction of oxygen with volcanic gases occurs very rapidly and does not depend on oxygen concentration. This process is thought to have declined in importance throughout time as the Earth's interior has cooled and the release of gases from the Earth's mantle to the surface has declined (Holland, 2009). In one hypothesis, the Great Oxygenation Event (GOE) resulted when the flux of gases from the Earth's interior (mostly hydrogen) decreased so much that the reactions to consume atmospheric oxygen could not happen anymore (Holland, 2009), resulting in increase of oxygen concentration in the atmosphere.

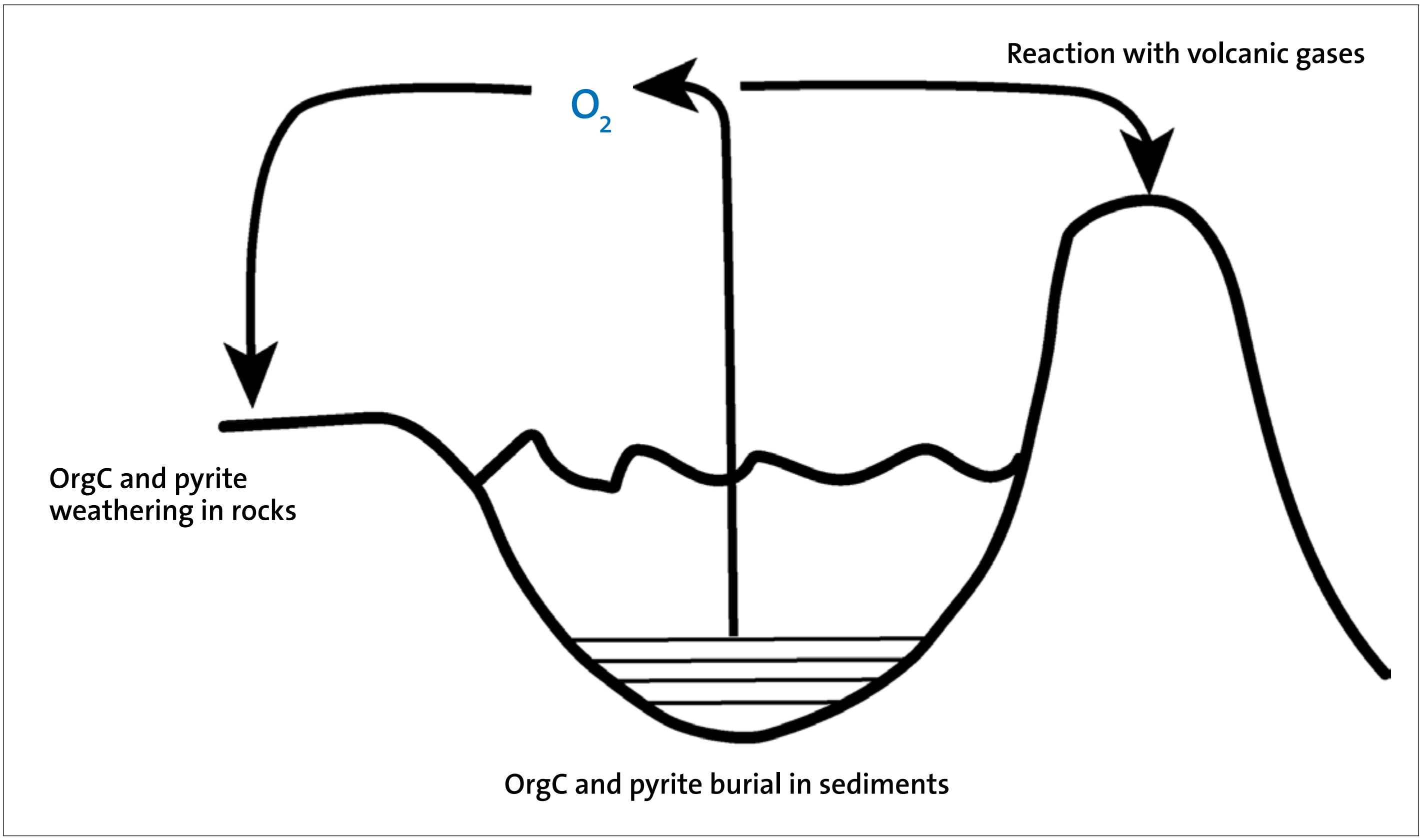


Figure 2.3 The major processes controlling the concentration of atmospheric oxygen. Oxygen accumulates in the atmosphere as a result of organic matter (OrgC) and pyrite being buried into sediments, and it is consumed by reacting with organic matter and pyrite in sedimentary rocks during weathering and through reactions with volcanic gases.

[1] The burial of pyrite also represents an oxygen source to the atmosphere through the oxidation of organic matter by sulphate reduction and the fixation of the sulphide product as pyrite in sediments. The net reaction is: $16H^+ + 8SO_4^{2-} + Fe_2O_3 \rightarrow 8H_2O + 4FeS_2 + 15O_2$

2.2.2 Contribution of the land and Ocean to the oxygen in the atmosphere

The rate at which oxygen is currently produced is about the same on land as in the Ocean (see Chapter 3), leading to the notion that every second breath we take comes from the Ocean (Box 2.2 and Figure 2.5). However, almost all this oxygen is rapidly respired again: the oxygen produced on land is respired by terrestrial organisms, while the oxygen produced in the Ocean is respired by marine organisms (Figure 2.5).

Oxygen has accumulated in the atmosphere over geological time scales (millions of years) due to the burial of small amounts of organic matter and pyrite in sediments (Section 2.2.1). In broad terms, the Ocean has been responsible for nearly all the oxygen in the atmosphere from the time of cyanobacterial evolution (around 2.4 billion years ago). Data are available to estimate a more precise contribution of the land and Ocean to the oxygen in the atmosphere for the last 12,000 years. However, it has to be remembered that oxygen in the atmosphere has accumulated over millions of years (not just over the last 12,000 years) and that the processes of oxygen liberation were not constant over geologic time.

Throughout the Holocene (the last 12,000 years), organic matter has been buried in Ocean sediments at a rate of 0.016 Petamol (1 Pmol = 10^{15} mol) per year (Wallmann, 2010). In contrast, on land, organic matter burial in peat is roughly four times slower (0.0033 Pmol per year) (Canfield *et al.,* 2020). The oxygen released to the atmosphere from the Ocean and land is approximately equal to the organic matter burial rate (i.e. four times lower on land than in the Ocean). Pyrite burial in Ocean sediments contributed another ca. 0.005Pmol of oxygen to the atmosphere (Figure 2.4) per year during the Holocene (approximately 1.5 times more than all carbon burial on land) (Canfield, 2005). If we sum these sources of oxygen to the atmosphere, organic matter and pyrite burial in the Ocean have released a total of 0.021Pmol of oxygen per year and organic matter burial on land has released 0.003Pmol of oxygen per year to the atmosphere during the Holocene. The combined oxygen release to the atmosphere from the Ocean and land was thus 0.0243Pmol per year, of which 86% of this oxygen came from the Ocean. Therefore, if we consider the sum of the processes that ultimately control the oxygen content of the atmosphere, the Ocean is responsible for more than six out of seven breaths humans breathe! As noted above, on short times scales, the organisms in the Ocean and land produce similar amounts of oxygen (Figure 2.5 and Chapter 3). It is not known what the oxygen release rates from carbon and pyrite burial are today, because they are measured over time scales of thousands of years.

2.2.3 Controls on atmospheric oxygen

As explained in Section 2.2.1, the reactions of oxygen with pyrite and organic matter represent oxygen removal mechanisms (i.e. oxygen sinks) from the atmosphere (Figure 2.3). There are, however, natural control mechanisms that ensure that oxygen levels do not drop below levels which would impact life on Earth. The rate of oxygen removal depends on the oxygen concentration in the atmosphere (Chang & Berner, 1999), where the rates of oxygen removal through reaction with organic matter and pyrite become slower as oxygen concentration decreases. This creates a negative feedback that helps to keep oxygen concentration from becoming too low. Pyrite oxidation (i.e. the reaction of pyrite with oxygen) happens very fast and may only control oxygen at very low levels of oxygen (0.001% of present oxygen levels), but organic matter oxidation is slower and could control oxygen levels even at current oxygen concentrations (Daines *et al.,* 2017).

There are other biogeochemical feedbacks that could help regulate oxygen concentrations. One potentially important feedback is related to controls on the concentrations of phosphorus in the Ocean (Colman *et al.,* 1997). Phosphorus is an essential element for life that is primarily delivered to the Ocean via continental weathering. It is a key limiting nutrient in primary production, and it is generally considered the most important limiting nutrient over long geological times. Phosphorus is buried at higher rates in marine sediments when the Ocean is oxygenated, because its burial efficiency depends on the availability of oxygen at the seabed. The increase in phosphorus burial results in lower phosphorus concentration in the Ocean, in turn reducing the rates of primary production. As primary production decreases, so does the burial of organic matter and the amount of oxygen that is released to the atmosphere. Similarly, when oxygen decreases, anoxia expands, resulting in lower rates of phosphorus burial, thereby increasing phosphorus concentrations in the Ocean. This in turn enhances the rates of primary production and organic matter burial, therefore increasing the amount of oxygen release. The expansion of Ocean anoxia should therefore lead to an increase in oxygen concentrations in the Ocean and atmosphere, due to the biogeochemistry of phosphorus, which acts as a negative feedback and keeps oxygen concentrations from becoming too low. Phosphorus is also delivered to and buried in lake sediments. However, lakes have relatively short lives, and are not viewed as long-term repositories for phosphorus and are, therefore, not important in oxygen control.

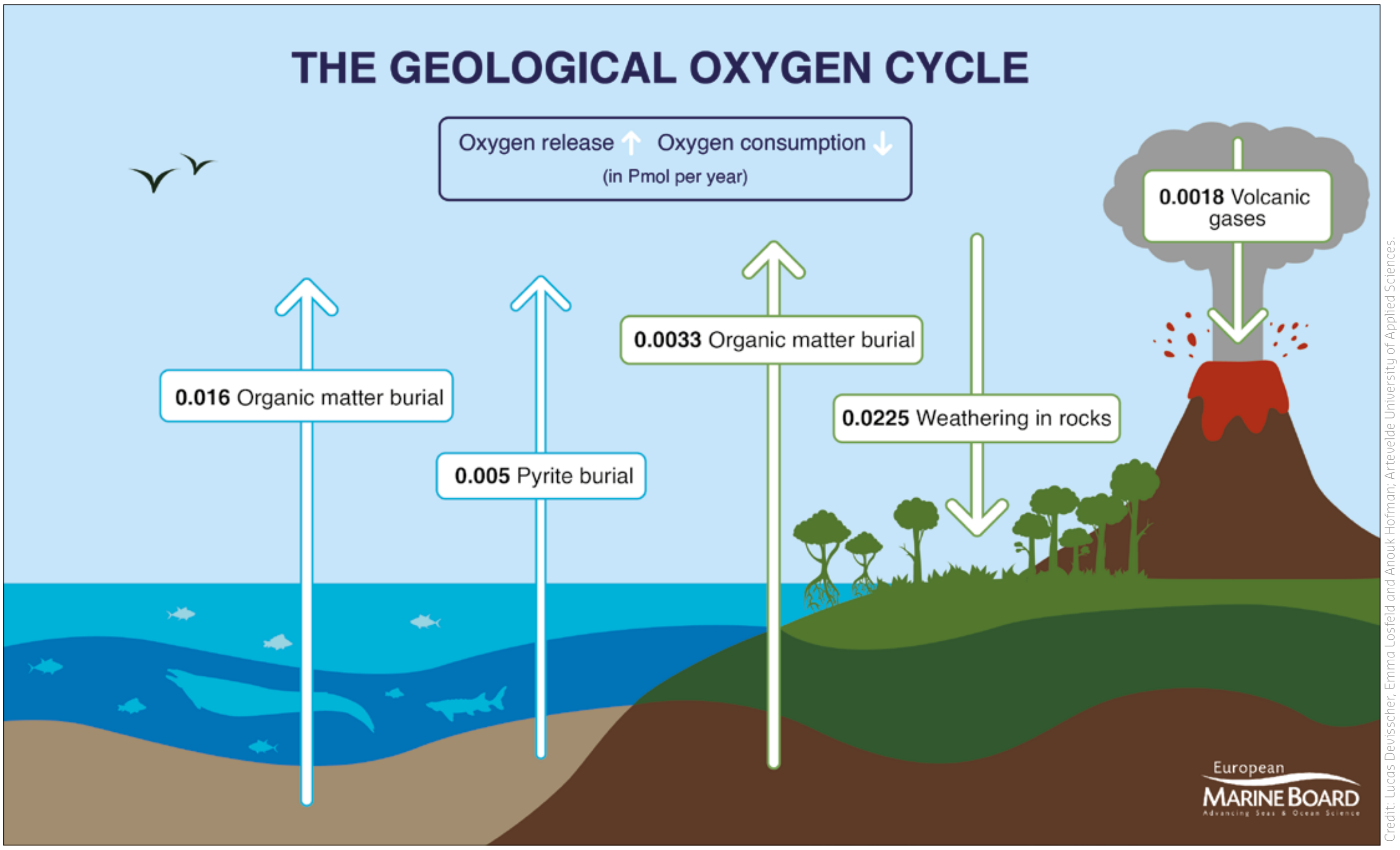


Figure 2.4 The geological oxygen cycle. Oxygen fluxes are given in Pmol per year.

Box 2.2 Does every second breath we take come from the Ocean?

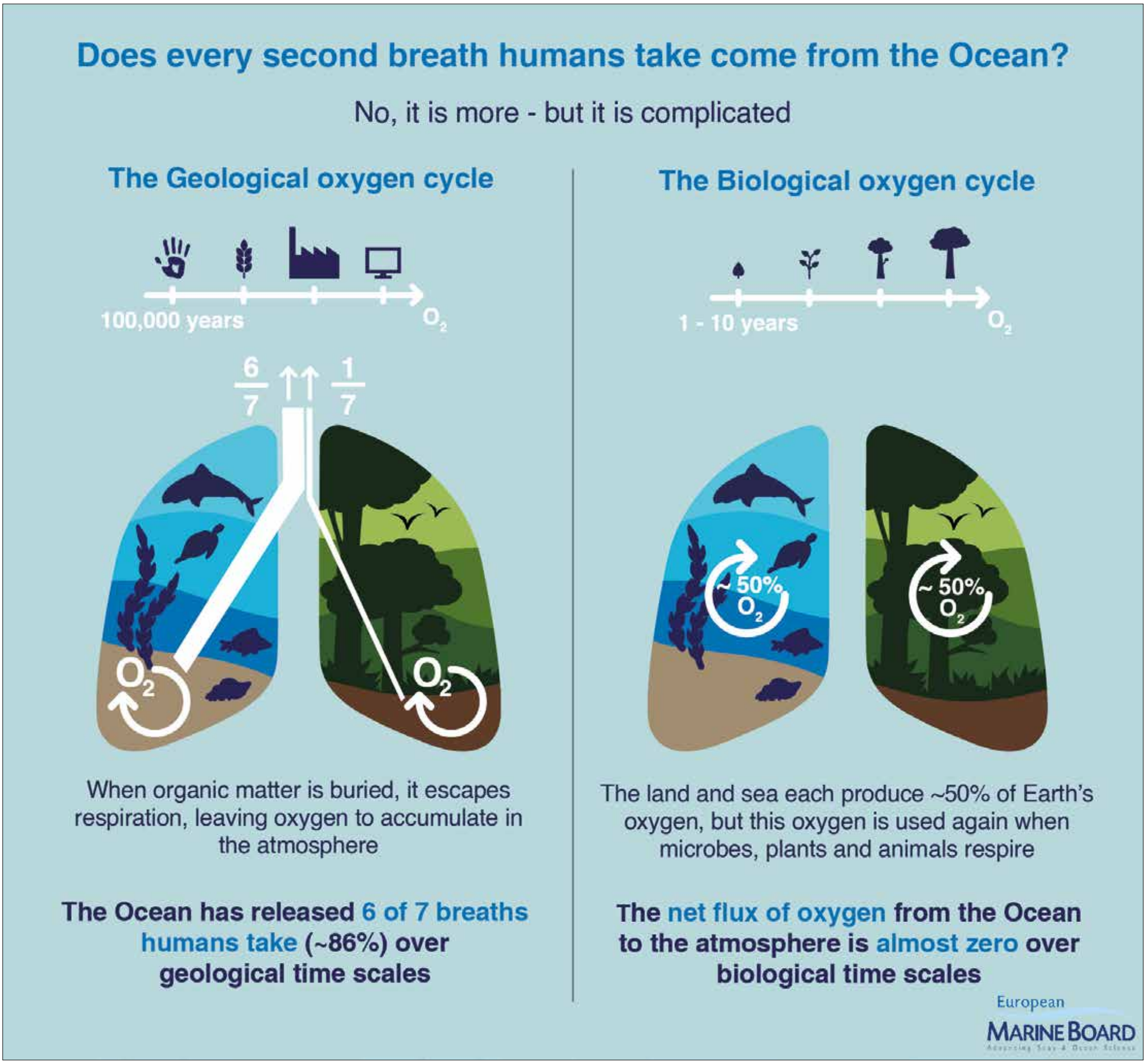
The land and Ocean each produce ~50% of Earth's oxygen, leading to the notion that every second breath we take comes from the Ocean. But is this statement correct?

There are two ways to look at this statement:

1. **If "we" refers to humans:** While the land and Ocean each produce about half of Earth's oxygen, almost all of this oxygen is rapidly used again when organisms respire: terrestrial organisms use the oxygen produced on land, while marine organisms use the oxygen produced in the Ocean. This means that on short time scales (~1-10 years), the net release of oxygen from the Ocean is close to zero. Oxygen in the atmosphere has accumulated over millions of years (geologic time). Therefore, if "we" refers to humans, we have to calculate the contribution of the Ocean and land to the oxygen in the atmosphere: The Ocean has released ~86% of the oxygen in the atmosphere. **Therefore, six out of seven breaths humans take come from the Ocean.**

2. **If ''we" refers to all life on Earth:** If every second breath "we" take refers to all living organisms on Earth – both on land and in the Ocean – **then the sentence is correct**. We can say that every second breath taken by all life on Earth comes from the Ocean – recognising that phytoplankton in the Ocean produce the same amount of oxygen as land plants.

In both cases, the importance of oxygen produced in the Ocean – both for humans and all life on Earth – is clear.



Credit: Lucas Devisscher, Emma Losfeld and Anouk Hofman; Arteveld University of Applied Sciences.

Figure 2.5 Does every second breath humans take come from the Ocean? Illustrating the contribution of the land and Ocean to the oxygen in the atmosphere.

3 The modern oxygen cycle

Today, over 99% of all freely available oxygen is in the atmosphere, and only a very small fraction (<0.1%) is dissolved in the Ocean. Nevertheless, oxygen plays a critical role for life in the Ocean, just like it does for life on land. This chapter covers the modern oxygen cycle (i.e. from around the 19th century on, when we started to make oxygen measurements), and explains how, in contrast to the atmosphere, there are very sharp gradients in oxygen distribution in the Ocean. The chapter further describes the physical and biological processes influencing oxygen concentrations, and how global warming might affect the balance between oxygen production and consumption in the Ocean. Finally, natural variability of atmospheric and oceanic oxygen is discussed, in order to assess whether changes in current oxygen levels might also be affected by natural variability.

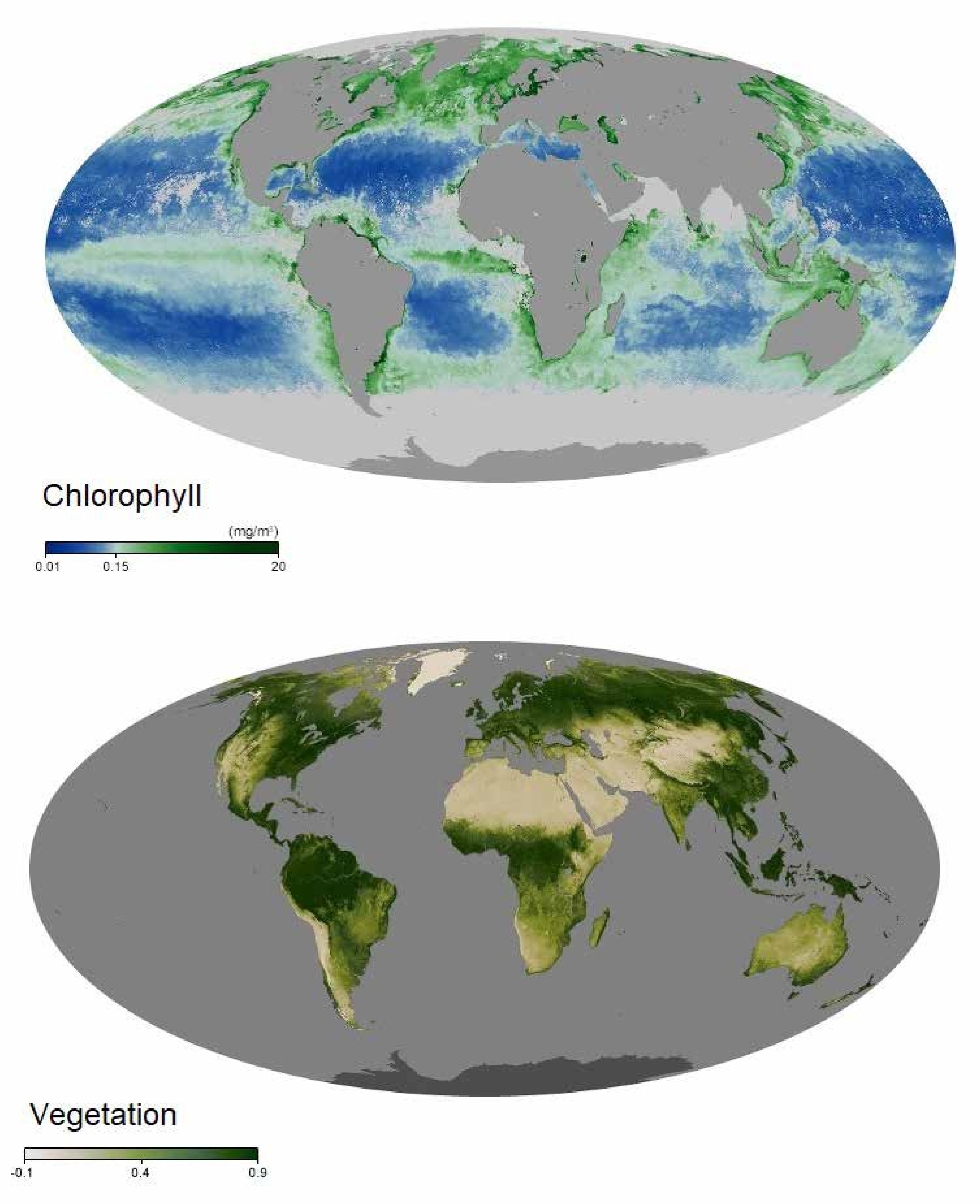
The key messages from this chapter are:

- The land and Ocean each produce about 50% of Earth's oxygen, yet almost all this oxygen is respired again by terrestrial and marine organisms, respectively - resulting in a virtually zero net change on atmospheric or Ocean oxygen;
- The burning of fossil fuels has only a very minor impact on atmospheric oxygen levels; however, it has a major impact on oceanic oxygen, which is decreasing due to global warming (see Chapter 4);
- While there are no substantial variations in oxygen in the atmosphere, there are very large differences in oxygen concentration in the Ocean, both geographical (high versus low latitudes) and throughout the water column. These differences result from both physical and biological processes; and
- The current trend of expanding and intensifying ODZs are a continuation of the millennial trends that were detected since the mid-Holocene, most likely amplified by anthropogenic climate change.

3.1 Oxygen in the atmosphere

3.1.1 Atmospheric oxygen dynamics

Today, the air in our atmosphere is made up of 20.95% oxygen. Our atmosphere contains more than 99% of the freely available oxygen on the planet, and this oxygen is essentially in equilibrium with the oxygen in the surface mixed layer of the Ocean. Due to the large amount of oxygen in the atmosphere the impact of seasonal variations in oceanic oxygen on the release of oxygen to the atmosphere due to temperature and primary productivity is very small (about 0.002%, Keeling & Shertz, 1992). In addition, almost all organic matter produced by photosynthesis (both on land and in the Ocean, Figure 3.1) is respired within months to years, resulting in virtually no net accumulation of oxygen in the atmosphere. Photosynthetic primary production on land and in the Ocean is about the same: around 5Pmol of oxygen per year (Field *et al.*, 1998; Keeling & Shertz, 1992) (Figure 3.2). Because photosynthesis and respiration are closely balanced, biological productivity has almost no impact on atmospheric oxygen concentrations over short time scales (Figure 2.5).



Credit: NASA

Figure 3.1 Global distribution of marine chlorophyll (in July 2022) and spatial extent of land vegetation (in July 2000), as proxies for the spatial distribution of photosynthetic oxygen and organic matter production[2].

[2] Animations of how marine chlorophyll changes over the year 2022 and how terrestrial vegetation cover changes over the year 2000 can be found here: https://earthobservatory.nasa.gov/global-maps

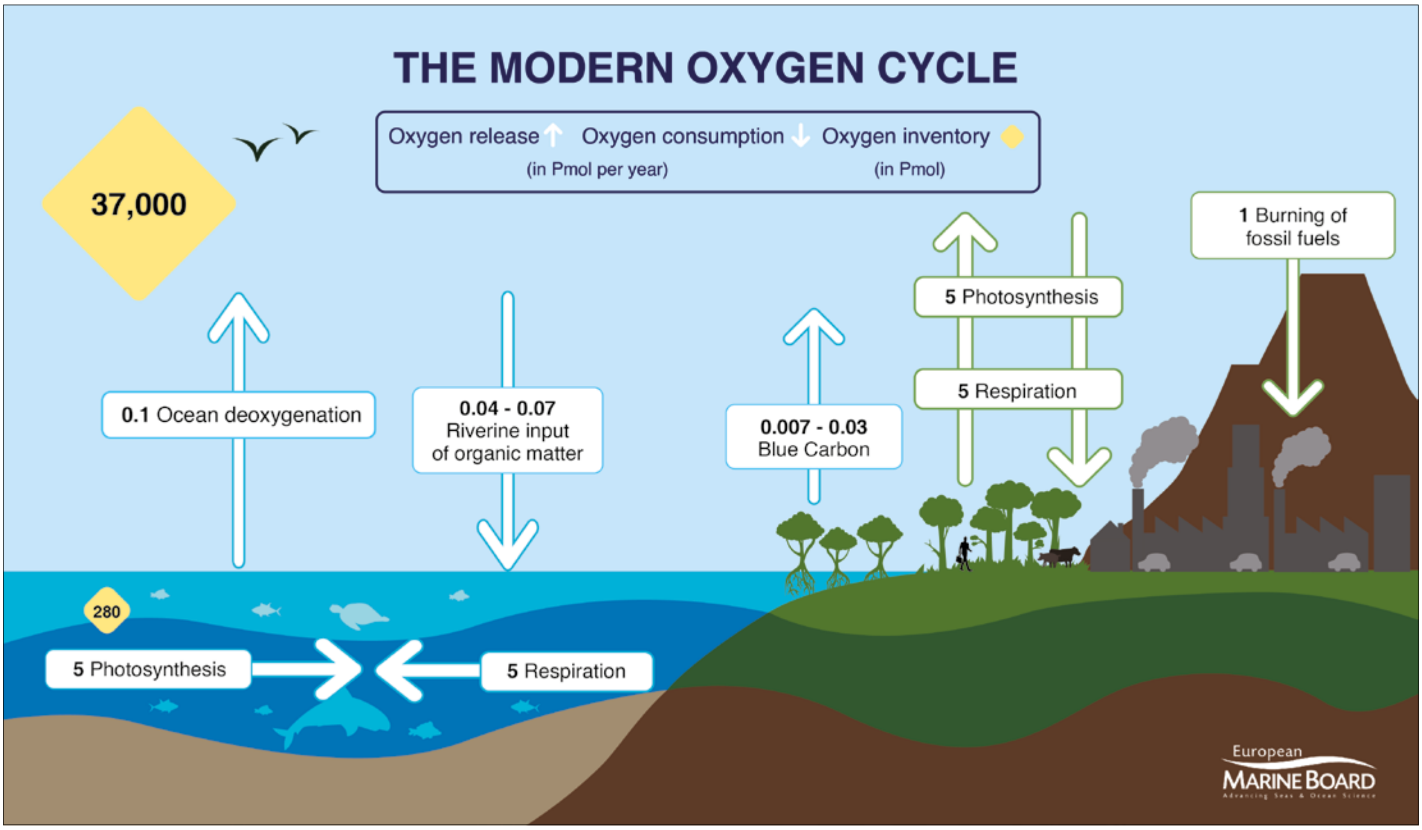
As described in Chapter 2, there have been two tipping points in the history of atmospheric oxygen: (1) The Great Oxygenation Event (GOE) where oxygen concentration rose dramatically in association with the evolution of cyanobacteria; and (2) the Paleozoic Oxygenation Event (POE), where an increase in oxygen was associated with the evolution of land plants and their impact on organic matter burial on land. To have a sustained increase in atmospheric oxygen, organic matter produced during photosynthesis must be removed from contact with the atmosphere (e.g. burial in soils or oceanic sediments) before it is respired (see Section 2.2.1). On the other hand, if organic matter that was previously locked away comes into contact with the atmosphere (e.g. through the extraction and burning of fossil fuels), there could be a sustained decrease in oxygen in the atmosphere. Below we explore below whether the burning of fossil fuels will lead to a significant decrease in atmospheric oxygen, resulting in a third tipping point.

3.1.2 Fossil fuels - the largest atmospheric oxygen sink

The burning fossil fuels is currently the largest single global oxygen sink, consuming about 1Pmol of oxygen per year since the early 21st century (Keeling & Manning, 2014, Figure 3.2). This is about 50 times larger than oxygen released due to burial of organic matter and pyrite (see Section 2.2.2 and Figure 2.4). From 1991 to 2014, the oxygen in the atmosphere decreased by about 76 parts per million (ppm) (i.e. 0.0076%) while the CO_2 increased by 35 ppm (i.e. 0.0035%) (Keeling & Manning, 2014). The proportionally smaller increase of CO_2 compared to the decrease of oxygen is because a large portion of the CO_2 released from the burning of fossil fuels is taken up and dissolved in the Ocean with no accompanying oxygen consumption/production. Therefore, CO_2 accumulates proportionally less in the atmosphere, although oxygen and CO_2 are consumed/produced at roughly equal quantities.

Different future fossil fuel burning scenarios will have differing impacts on the oxygen in the atmosphere. Work by Keeling *et al.,* (2021) shows that if we followed the 'business as usual' high-emission scenario, CO_2 will peak at 1,200 ppm in 2100, and oxygen will decrease by 1,700 ppm, a drop of 0.8% to a level of 207,700 ppm. If we assume that all of the known fossil fuel reservoirs (ca. 5,000Pg of carbon) are burnt, atmospheric oxygen will drop by 1.6% to 205,700 ppm. This means that the high emission scenario would take the oxygen inventory in our atmosphere down to 20.77% (from the current 20.95%) and burning all known fossil fuels will take it down to 20.57%. These are small changes. Therefore, while future climate change scenarios will lead to many threats to the climate, ecosystems and human well-being, the burning of fossil fuels will not have a significant impact on the oxygen available in the atmosphere and will not cause a new tipping point.

In conclusion, although there are seasonal cycles in oxygen production (e.g. more oxygen production in the summer) and small long-term trends (such as the decrease of oxygen due to burning of fossil fuels), on millennial time scales it is virtually impossible to significantly change atmospheric oxygen concentrations. Humans and other terrestrial species will therefore always have oxygen to breathe, but this might not be true for Ocean life (see Chapter 4).



Credit: Lucas Devisscher, Emma Losfeld and Anouk Hofman; Artevelde University of Applied Sciences.

Figure 3.2 The modern oxygen cycle. Oxygen reservoirs are given in Petamol (Pmol) and fluxes in Pmol per year.

3.2 Oxygen in the Ocean

Compared to the atmosphere, there is about 132 times less oxygen in the Ocean (< 0.1% of the freely available oxygen, Figure 3.2). While the atmosphere is well mixed on time scales shorter than a year, it takes about 1,000 times longer for the water in the Ocean to mix. This creates significant gradients in dissolved oxygen in the Ocean because the exchange of oxygen between the Ocean and the air, and photosynthesis and respiration of the organisms in the Ocean vary in time and space. Ocean oxygen concentrations therefore vary both geographically and throughout the water column.

3.2.1 Physical processes influencing oxygen concentrations in the Ocean

In surface waters, oxygen concentrations are highest in polar regions because cold water can hold more oxygen than warm water (i.e. oxygen has higher solubility in cold waters). When surface waters moving towards the poles cool, oxygen is taken up from the atmosphere resulting in high oxygen concentrations in the water. At low and mid latitudes, higher temperatures result in warm waters that can hold less oxygen. Surface waters warming on their way towards the tropical Ocean therefore tend to release oxygen to the atmosphere. As a result, surface waters at mid and low latitudes have lower oxygen concentrations (Figure 3.3a). Globally, the Ocean takes up nearly the same amount of oxygen as it releases.

Oxygen in surface waters is typically very homogenous, because surface waters are well mixed by the wind. Heat loss at night or in the winter can also enhance mixing because the water becomes denser. As noted before, this so-called surface mixed layer typically covers the first tens of metres of surface waters, although its depth changes seasonally. Within this layer, air-sea gas exchange typically homogenises oxygen levels within days (Kihm & Körtzinger, 2010). Temperature and salinity (and therefore the density of the water) are also fairly uniform in surface waters due to mixing. However, below this layer water properties change rapidly with depth creating sharp changes in temperature, salinity and density (called thermocline, halocline and pycnocline, respectively). The resulting sharp density changes inhibit mixing. Therefore, below the surface mixed layer oxygen concentrations can vary considerably within the water column (Figure 3.3b).

Polar regions are the main entry point for oxygen from the atmosphere into the Ocean due to the higher solubility of oxygen. This cold, oxygen-rich water sinks into deep waters, where the oxygen is transported by currents (blue arrows in Figure 3.3b; Figure 3.4). Between the deep, relatively well-oxygenated waters originating from the polar regions and the surface mixed layer, there is a body of water in the upper few hundred metres of the Ocean that is stratified and oxygenated by mostly wind-driven circulation that moves water towards the equator (red arrows in Figure 3.3b). This water is deflected to the west due to the rotation of the Earth (red arrows in Figure 3.3c), resulting in so-called ‘shadow zones’ along the eastern margins of the tropical Ocean. These regions are marked by low oxygen levels (Figure 3.3c) because they are out of reach from the westward turning flow and thus lack oxygenation by waters from higher latitudes. Most of the equatorward flow cycles back to high latitudes in narrow boundary currents (i.e. shaped by the presence of a coastline) along the western margin of each Ocean basin, such as the Gulf Stream in the North Atlantic.

3.2.2 Ocean oxygen dynamics: the interplay between biological and physical processes

Ocean oxygen dynamics are governed by physical and biological processes (Figure 3.4). The physical processes influencing oxygen concentration are described in Section 3.2.1. The two major biological processes influencing oxygen concentrations in the Ocean are: photosynthesis and respiration. In the sunlit Ocean surface waters (covering a maximum depth of around 200m), primary producers (mainly phytoplankton) produce oxygen through photosynthesis – and this oxygen constitutes about 50% of the oxygen produced on Earth (Box 3.1). Below the depth where light penetrates, no significant oxygen can be produced through photosynthesis, and oxygen is only supplied via physical transport. Conversely, the Ocean loses oxygen throughout the water column when microbes and multicellular organisms use oxygen during respiration. Primary producers that are not consumed, as well as other dead organisms, sink through the water column to the deep Ocean where they provide food and energy to deep-sea organisms that, in turn, consume oxygen. As this sinking matter is consumed, the amount of organic matter and the associated respiration decreases with depth (Figure 3.4). Most oxygen produced by photosynthesis in the sunlit surface layer is consumed by respiration throughout the water column. The total amount of respiration is controlled by the availability of organic matter, which ultimately depends on primary production in the surface Ocean. Although in coastal waters, some of this organic matter can be terrestrial, transported to the Ocean through rivers and groundwater.

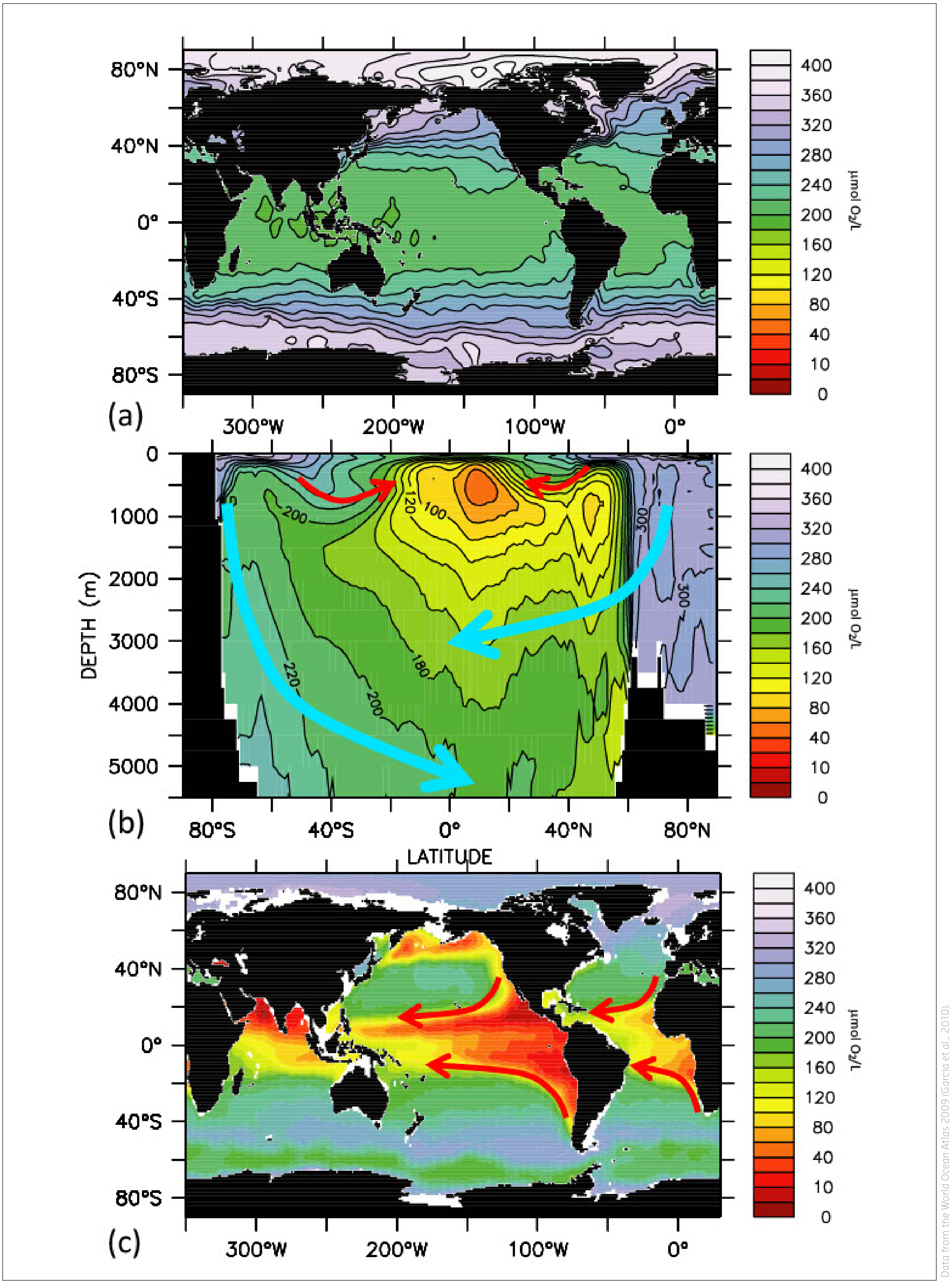
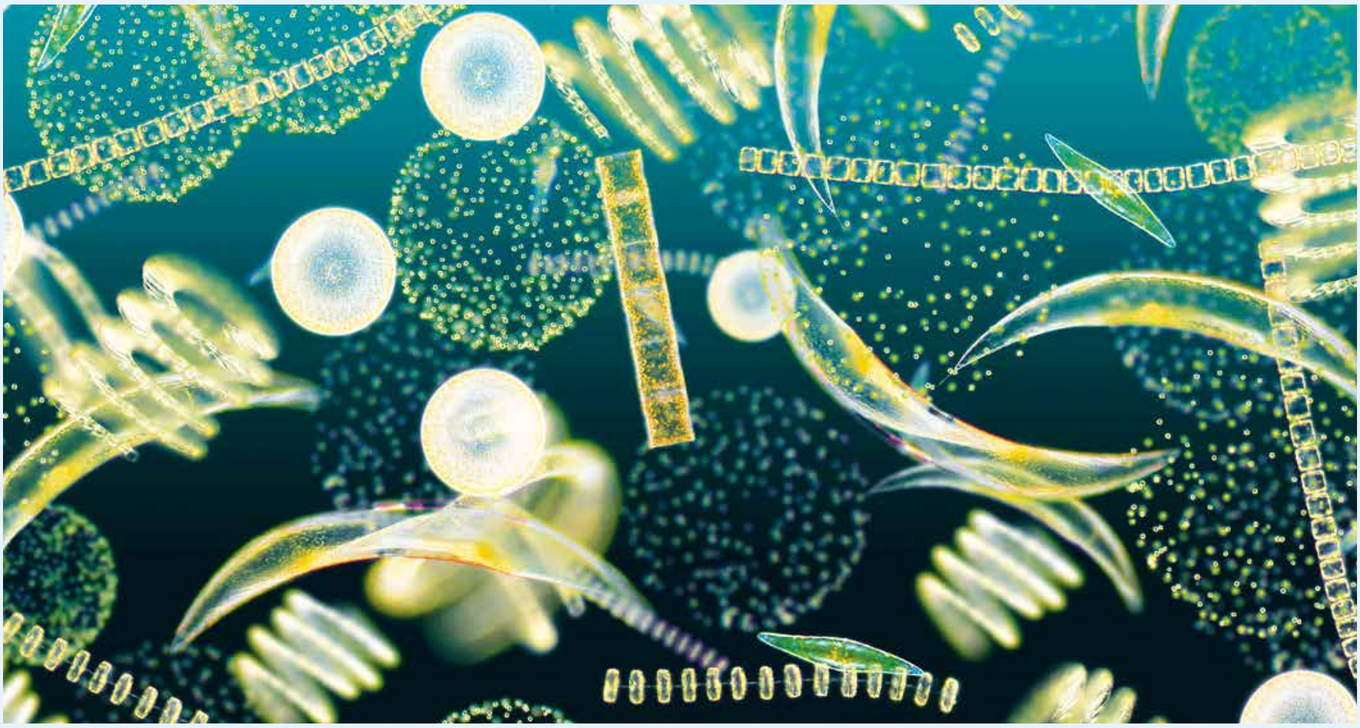


Figure 3.3 a) Annual mean concentrations of dissolved oxygen in surface waters globally. **b)** Annual mean concentrations of dissolved oxygen through the water column. Thick blue arrows illustrate how oxygen flows into the interior of the Ocean with cold and oxygen-rich waters flowing from the polar regions to the equator; thin red arrows illustrate the predominantly wind-driven circulation in the upper few hundred metres of the low- and mid-latitude Ocean. **c)** Annual mean dissolved oxygen at 300m depth globally, with the wind-driven lateral flow illustrated by the red arrows.

Box 3.1 Approximately 50% of Earth's oxygen is produced in the Ocean

Marine algae and plants produce about 50% of Earth's oxygen – and most of this oxygen is produced by phytoplankton. But what are phytoplankton?

Phytoplankton are microscopic marine algae that, similar to terrestrial plants, require sunlight in order to live and grow because they obtain their energy through photosynthesis. They are the foundation of marine food webs, supporting most life in the Ocean. The distribution of phytoplankton can vary considerably both geographically (e.g. Figure 3.1) and seasonally, and is influenced by sunlight, nutrient availability, water temperature, salinity, and Ocean currents. Phytoplankton are mainly found floating in sunlight surface waters. They also require nutrients like nitrogen, phosphorus, and iron to grow and reproduce, therefore areas with high nutrient availability often have high phytoplankton concentrations. Water temperature and salinity can also influence the distribution of phytoplankton because different types of phytoplankton have different temperature and salinity preferences or tolerances. Finally, Ocean currents can transport phytoplankton over large distances, which affects their distribution patterns.



Credit: Richard Kirby

Phytoplankton, magnified with a microscope. The citizen science Secchi Disk study[3] is mapping the global phytoplankton distribution with the help of seafarer participation.

Marine algae (such as kelp and seaweed) and seagrasses are also important oxygen producers in the Ocean. They are most abundant in coastal waters and play an important role in supplying oxygen to coastal marine areas.

Credit: Stefan Andrews (Ocean Image Bank)

Credit: Ben Jones (Ocean Image Bank)

Marine macro-organisms, such as kelp and seagrass, also play an important role in producing oxygen in the Ocean.

[3] http://www.secchidisk.org/

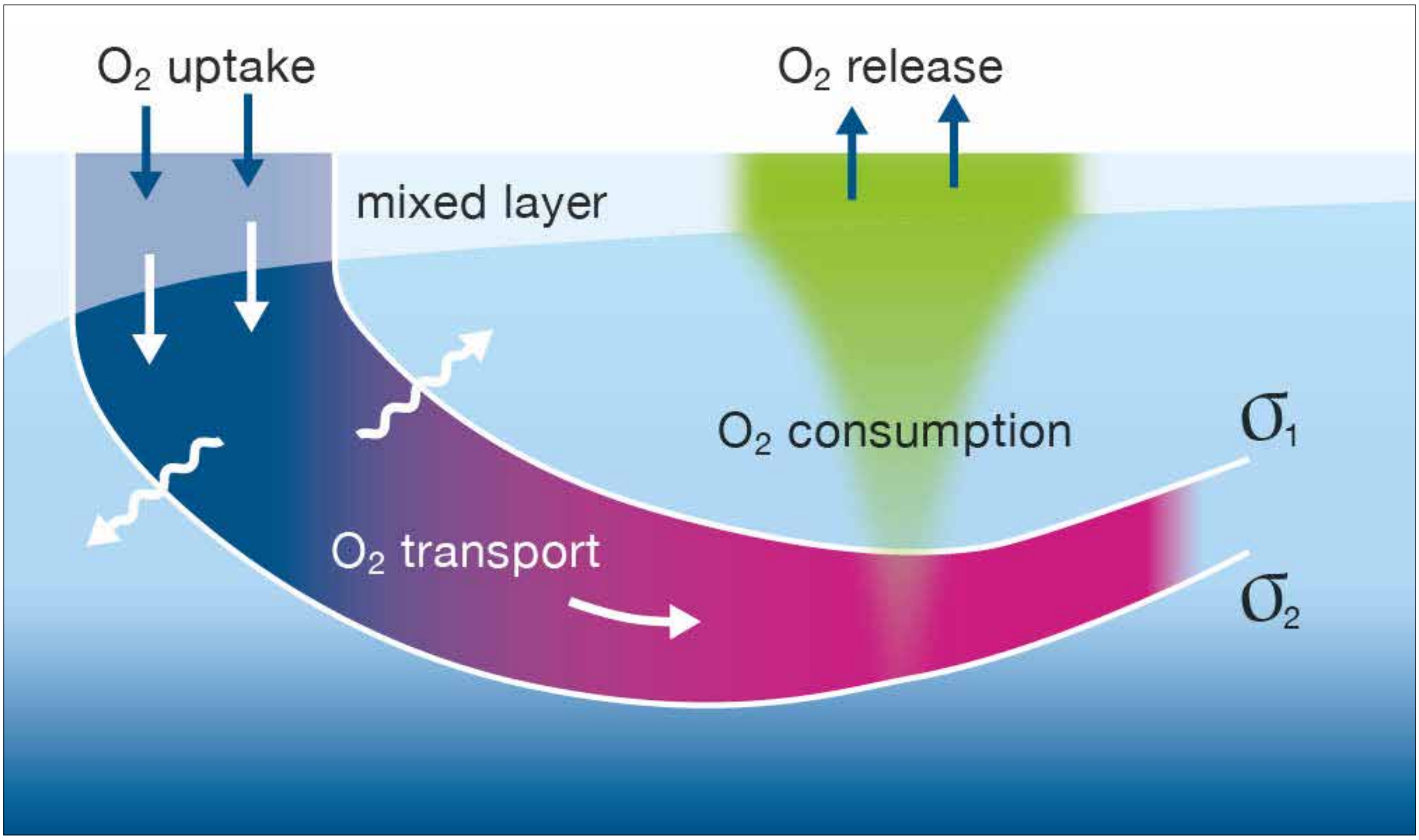


Figure 3.4 Schematic representation of oxygen uptake and release, physical transport, and biological production and consumption in the Ocean. Oxygen is mostly taken up into the Ocean in the cold waters of the high latitudes, in which oxygen is most soluble. When this water sinks into deeper waters, it oxygenates deeper parts of the Ocean. Transport of oxygen in the interior of the Ocean happens along density layers (isopycnals marked as σ1 and σ2). Some organic matter (green) produced by photosynthesis in the surface Ocean sinks and oxygen is consumed through its respiration throughout the water column, leading to a decline in oxygen as water flows from the poles to the equator in the Ocean's interior (the colour change from blue to pink illustrates the decreasing oxygen concentration from oxygen-rich waters originating in the poles).

The increased amount of respiration in waters with more organic matter results in extended low-oxygen regions, Oxygen Deficient Zones (ODZs), at tens to a few hundred metres below the surface in the western coasts of Peru/Chile, Namibia, California and Mauritania/Senegal, also called the Eastern Boundary Upwelling Systems (EBUS) (Figure 3.5). This is because these regions are extremely productive (i.e. produce a lot of organic matter) due to high nutrient inputs. The large amounts of nutrients are due to strong wind-circulation patterns, which push surface waters away from the coast, causing deeper, nutrient-rich waters to rise and replace the surface waters (called upwelling). These nutrients enhance primary and secondary production in these upwelling zones, which support the largest fisheries in the world. The high primary production implies very high oxygen consumption rates. Just below the surface mixed layer, this leads to the most intense and thickest ODZs found in the Ocean. Naturally occurring ODZs are thus the result of an interplay of physical and biological processes.

3.2.3 Modern oceanic oxygen sources and sinks

As explained in previous sections, photosynthesis generates oxygen that is again consumed once the organic matter is respired. However, the organic matter that is not respired and instead is buried in Ocean sediment creates a net oxygen source of about 0.021Pmol per year globally (see Section 2.2.2 and Figure 2.4). This oxygen source is counteracted by the oxygen that is consumed when riverine input of organic matter is respired (presently consuming about 0.04-0.07Pmol of oxygen per year, Resplandy *et al.,* 2018; Figure 3.2). If we add the oxygen that is not used due to the burial of organic matter and the oxygen that is consumed when the riverine organic matter is respired, today's Ocean appears to use more oxygen than it releases (i.e. it is a net oxygen sink, where overall more oxygen goes into the Ocean than out of it; Smith & Mackenzie, 1987). However, we still do not have good enough estimates for these individual oxygen fluxes. In addition, global warming leads to reduced oxygen uptake and enhanced oxygen outgassing (Chapter 4). This deoxygenation, represents a new source of oxygen from the Ocean to the atmosphere of about 0.1Pmol of oxygen per year (Schmidtko *et al.,* 2017). This could shift the balance to a net flux of oxygen from the Ocean to the atmosphere. Thus, Ocean deoxygenation represents a source of oxygen from the Ocean to the atmosphere, at the cost of a shrinking oceanic oxygen inventory.

Another way that the Ocean could become a source of oxygen to the atmosphere – without the cost of shrinking oxygen concentrations in the Ocean – is through blue carbon approaches, such as expanding seagrass, salt marsh and mangrove ecosystems. These approaches are aimed at managing carbon, but, if they are well-managed, they can also be a source of oxygen to the

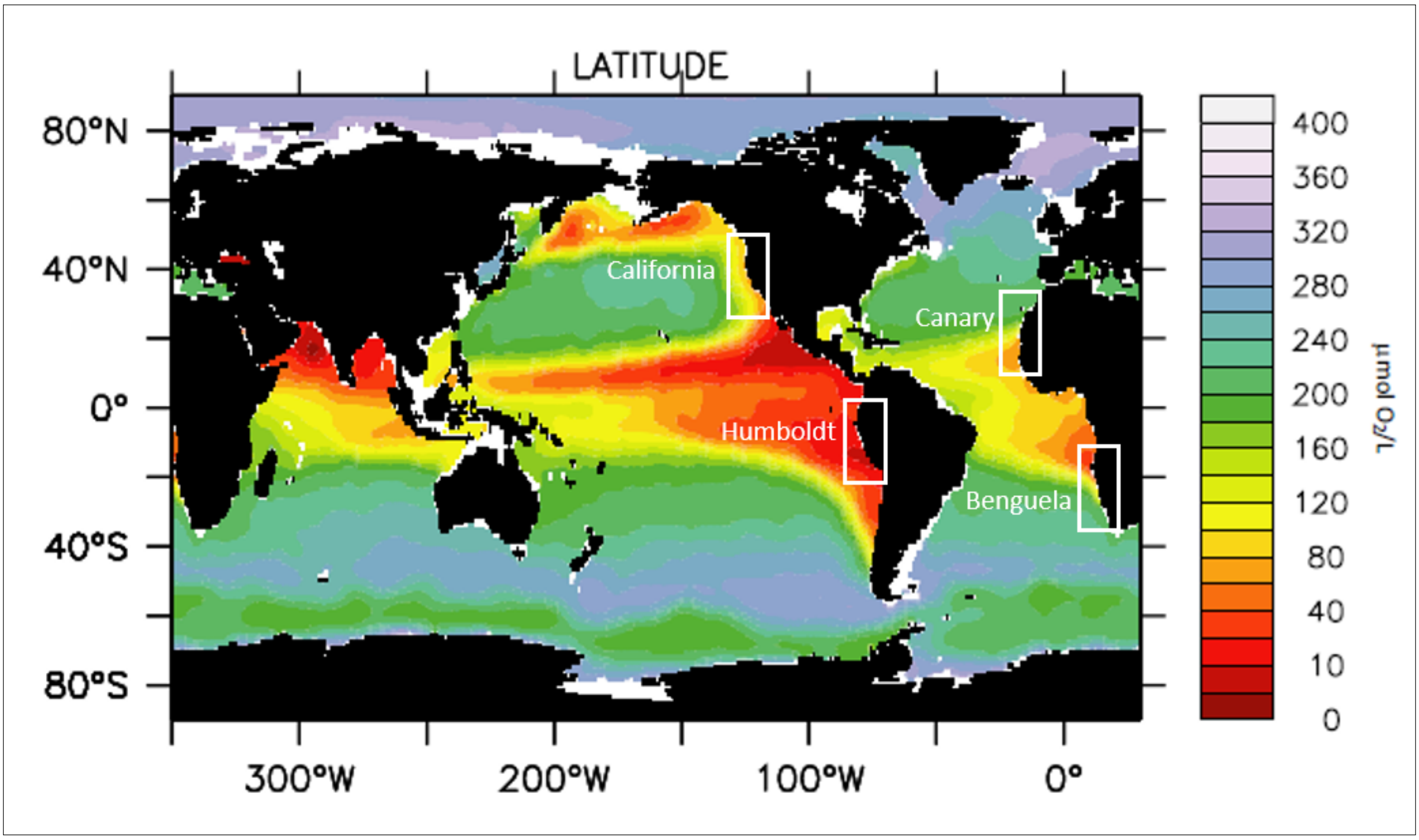


Figure adapted from the World Ocean Atlas 2009 (Garcia *et al.*, 2010).

Figure 3.5 The four major Eastern Boundary Upwelling Systems (EBUS) drawn against the annual mean dissolved oxygen concentrations at 300m depth globally. The four EBUS are: the Humboldt Current System (west coast of Peru/Chile), the Benguela Current System (west coast of Namibia and South Africa), the California Current System (California west coast) and the Canary Current System (west coasts of Mauritania/Senegal).

atmosphere through the continued burial of organic matter. Well-managed means that, among others, coastal erosion is counteracted, dredge and fill operations do not affect these systems, and coastal development and pollution are minimised. All organic carbon that these systems accumulate in biomass (predominantly in mangroves) or bury in sediments (seagrasses and salt marshes) leaves behind the oxygen generated during its photosynthetic production. Estimates of the potential oxygen source to the Ocean and ultimately the atmosphere via global blue carbon organic matter removal are between 0.007-0.03Pmol oxygen per year, if macroalgae are included (e.g. Bertram *et al.*, 2021; Krause-Jensen & Duarte, 2016; Figure 3.2), but these numbers are still largely hypothetical. Blue carbon could provide as much oxygen to the atmosphere as is currently created through the natural burial of oceanic organic matter. However, uncertainties in these estimates are large and it has been argued that they are biased towards high values (Williamson & Gattuso, 2022). The European Marine Board is currently working on a Policy Brief on Blue Carbon[4] that will be available in the summer of 2023 and will provide a state-of-the art overview of the topic as well as science and policy recommendations.

3.2.4 The balance between primary production and respiration in a warming climate

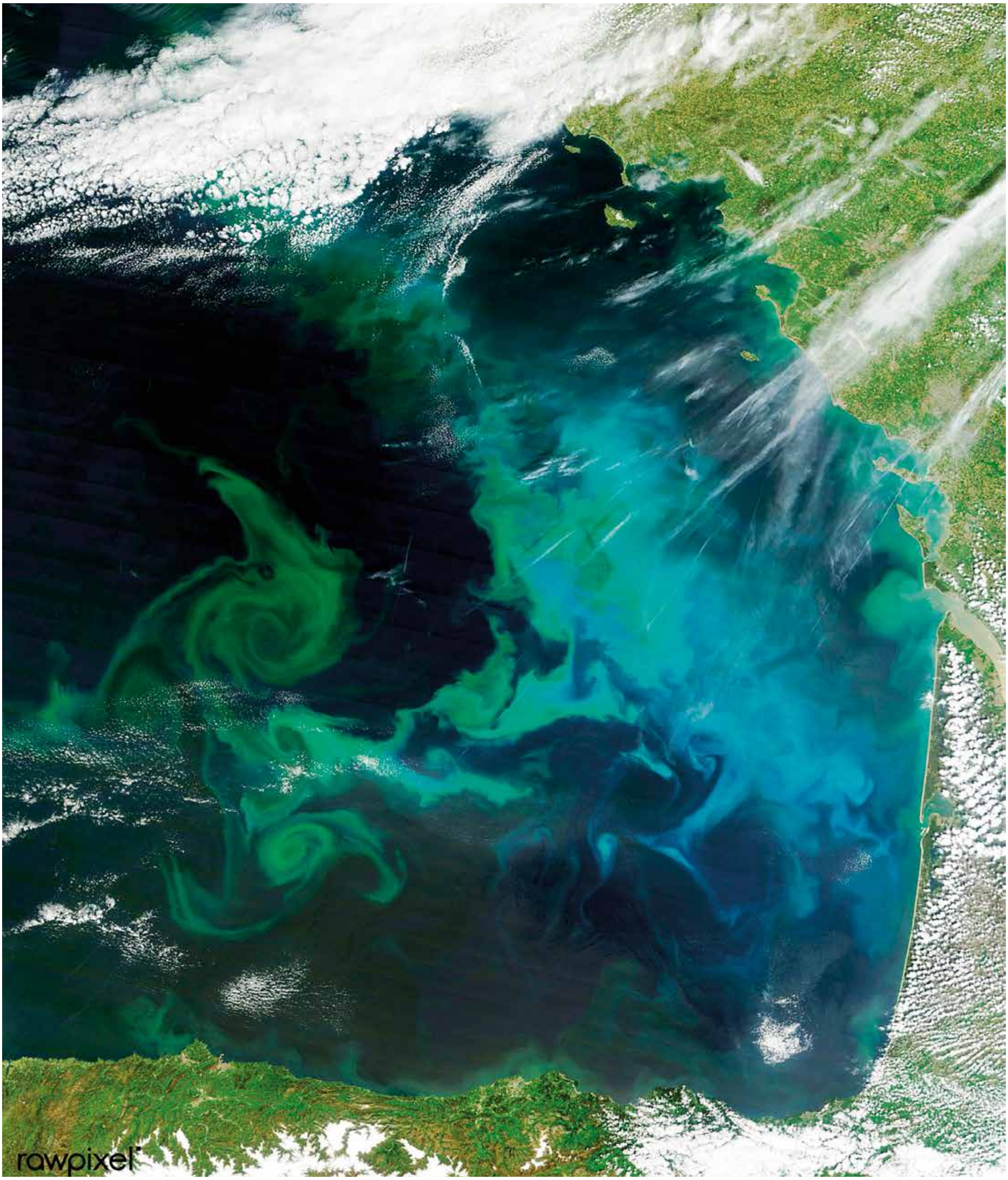
Human induced global warming and nutrient run-off from agriculture will cause changes in phytoplankton distribution and activity. For instance, climate-changed induced alterations in oceanic circulation and wind patterns, will alter the availability of nutrients regionally. Increased nutrient run-off from rivers into the Ocean from agriculture is also already altering primary production and respiration rates (Chapter 4) and nutrient enrichment is foreseen to worsen in the future, unless effective management measures are put in place (Malone & Newton, 2020). Moreover, warming surface waters due to climate change will increase the metabolic rates. This complex interplay of climate change induced changes in the Ocean means that organisms will have to adapt and this will result in new community structures of plankton communities.

Because of the complex combination of changes that will take place, there are large uncertainties in primary production projections for the future (Tagliabue *et al.*, 2021). Nonetheless, most models predict a decrease in Ocean primary production and its associated oxygen production over the next decades (Bindoff *et al.*, 2019; Kwiatkowski *et al.*, 2020), although with large regional variations. In low- to mid-latitudes, oxygen production is expected to decrease in some regions of the Ocean, because increased stratification will reduce the amount of nutrients reaching the surface waters (D'Alelio *et al.*, 2020). In light-limited, high-latitude areas, increased upper-Ocean stratification and reduced ice cover are expected to enhance primary production, at least temporarily (Pinkerton *et al.*, 2021).

Respiration consumes oxygen and its rate is expected to increase with higher temperatures (Gillooly *et al.*, 2001). However, we still have a poor knowledge of the biogeochemical processes that

[4] https://www.marineboard.eu/blue-carbon

interact with temperature to determine respiration rates and their variation with climate change. The poor understanding of organic matter respiration rates and locations reduces the quality of model projections of Ocean respiration and its balance with photosynthesis in a warming climate. Hence, we do not have enough knowledge yet to accurately predict how global warming will affect oxygen production and consumption, and their spatial patterns in the future Ocean.



Phytoplankton bloom in the Bay of Biscay.

3.3 Natural variability of atmospheric and Ocean oxygen

Air bubbles trapped in Antarctic ice cores have shown that the amount of oxygen in the atmosphere has declined by 0.7% (from about 21.09% to the current 20.95%, Stolper *et al.,* 2016) over the last 800,000 years. Although the reason is not entirely clear, this decline is consistent with a small reduction in the burial of organic matter due to a long-term global cooling trend. Global cooling leads to a reduction in the burial of organic matter, because organic matter is degraded faster and more efficiently under oxygenated conditions. Therefore, in a colder and better oxygenated Ocean, enhanced organic matter degradation leads to a reduction in burial.

In contrast to the slow change in the concentration of oxygen in the atmosphere, marine oxygen conditions can change much faster. Geological records have shown this for ODZs that have expanded and contracted on glacial-interglacial, millennial, centennial and decadal time scales. These changes were caused by a combination of changes in temperature-driven oxygen solubility, the redistribution of nutrients related to changes in biological productivity and Ocean circulation in response to the global climate fluctuations (Jaccard & Galbraith, 2012).

In order to assess the magnitude, cause and importance of current Ocean deoxygenation (see Chapter 4) it is important to quantify the natural variability of oceanic oxygen and understand how this is linked to climate. Natural oxygen variability occurs on a wide range of temporal scales from seasonal to multi-millennial.

3.3.1 Glacial-interglacial variability of oceanic oxygen and Oxygen Deficient Zones (ODZs)

At the Last Glacial Maximum (about 21,000 years ago, a time period during the last ice age where the ice sheets where at their largest extent) the upper Ocean (i.e. the top 1,500m) was generally better and the deep-sea less well oxygenated than today, because reduced deep-sea circulation led to oxygen depletion in the deep-sea while the colder surface waters could hold more oxygen (Jaccard & Galbraith, 2012). When the glaciers were largely melted (deglaciation, ca. 21,000-11,700 years ago), this pattern reversed. The warmer and saltier surface waters in high latitudes stimulated deep-water formation and thus oxygenation of the deep-sea. The subsurface Ocean experienced most of the warming and regional deoxygenation, resulting in a progressive intensification and general expansion of the ODZs. These examples illustrate the well-established general pattern for strong climate variations like glacial-interglacial cycles, in which warm climates correspond to less oxygenated surface and subsurface waters, as well as strong ODZs. The paragraphs below explore the millennial variability of ODZs, which occurred under more moderate climate variation.

3.3.2 Millennial variability of oceanic oxygen and ODZs

During the last glacial period (115,000-14,000 years ago) 25 rapid climate fluctuations of quick warming and more gradual cooling in the North Atlantic were associated with the occurrence of oxygen-poor conditions during the respective warm episodes. This effect was shown for the modern ODZs regions in the Atlantic, the Eastern Tropical North Pacific and the Arabian Sea (west of India) (red areas in Figure 3.5) (Altabet *et al.,* 2002).

Two major deoxygenation events also occurred after the Last Glacial Maximum (ca. 21,000 years ago) in the Mediterranean. The first was in the Alboran Sea in the Western Mediterranean (ca. 15,000 years ago) and lasted for a couple of millennia (Pérez-Asensio *et al.,* 2020). The second affected the entire Eastern Mediterranean deeper than 500m roughly 9,500 to 5,500 years ago, and occurred during the Holocene Climate Optimum (a warmer than average period during the Holocene) (Tesi *et al.,* 2017). Both events were driven by a combination of warming and freshening of the seawater following the melting of ice sheets or Monsoon-driven precipitation changes. These sudden changes led to lighter surface waters, which did not sink as readily, thereby reducing oxygenation in the deep Mediterranean Sea. In addition, the nutrient-rich freshwater input further enhanced primary production, increasing oxygen demand at depth.

During the last 12,000 years (in the Holocene) ODZs in the global Ocean also varied substantially, although this period is characterised by rather stable and warm global climate conditions. For instance, the Eastern Tropical South Pacific ODZ was better oxygenated during the warm mid-Holocene Climate Optimum (which occurred roughly 9,500 to 5,500 years ago) than during the current late Holocene. According to model simulations these changes were caused by changes in Ocean circulation rather than regional biology (Segschneider *et al.,* 2018). Similarly, over the last 6,000 years, there has been a gradual decrease in oxygen supply to the Arabian Sea ODZ via currents from the Indian Ocean, which has led to a gradual intensification of the Arabian Sea ODZ (Rixen *et al.,* 2020). Thus, both the Eastern Tropical Pacific and the Arabian Sea ODZs are currently receiving less oxygen via Ocean circulation than during the mid-Holocene.

Taken together, over millennial time scales, warm climates are also often associated with less oxygenated surface and subsurface waters, and intensified ODZs (as during the glacial-interglacial cycles). However, when climate fluctuations are moderate, the development of ODZs can differ regionally, because of the specific regional dynamics.

3.3.3 Decadal variability of ODZs

ODZs also vary at decadal and interannual time scales. These ODZ variations are related to phenomena which impact sea surface temperature, such as the Pacific Decadal Oscillation (PDO)[5] and the El Niño-Southern Oscillation (ENSO)[6], which are patterns of recurring warm (El Niño) and cool (La Niña) phases across the tropical Pacific (Figure 3.6). The Eastern Tropical North Pacific ODZ shows decadal fluctuations with more oxygenated conditions during cold phases of the PDO and the opposite during warm PDO phases (Stramma *et al.,* 2020). These effects can last from years to decades. Similar effects are seen on shorter time scales such as the interannual sea

[5] https://psl.noaa.gov/pdo/
[6] https://psl.noaa.gov/enso/

surface warming and cooling patterns of ENSO variability (El Niño and La Niña respectively), or simply seasonality.

On decadal time scales, the variability of the oxygen conditions in the ODZs of the Eastern Boundary Upwelling Systems (EBUS) (Section 3.2.2 and Figure 3.5) depends on the intricate interplay between local conditions (such as local wind mixing versus stratification) and remote forcing (e.g. the equatorial current system, the eastern boundary currents and ENSO like events). These in turn affect the current circulation patterns, the productivity of the region and the intensity of the upwelling (e.g. Bachèlery *et al.,* 2016; Bettencourt *et al.,* 2015).

Overall, ODZs have intensified and/or expanded in recent decades. For instance, an expansion and intensification of the Tropical Pacific and Arabian Sea ODZs has been observed since 1960. These trends are heading in the same direction as the millennial-scale development since the mid-Holocene, where oxygen in the ODZs of the Eastern Tropical Pacific and the Arabian Sea has decreased due to changes in Ocean circulation. In the tropical Pacific, a 1975 regime shift from PDO cold to PDO warm has probably also contributed to the observed oxygen decline. However, during the last two decades, the PDO has shifted again to a colder phase, so that an additional effect of human induced climate warming and associated reduced oxygen solubility is likely (see Chapter 4). The observed oxygen decline in the last decades is thus both linked to natural climate fluctuations and anthropogenic activities. It is not yet clear to which degree each of these factors has contributed to the observed oxygen loss, but they all drive oxygen trends in the same negative direction (see Chapter 4 for more information on human-induced oxygen loss).

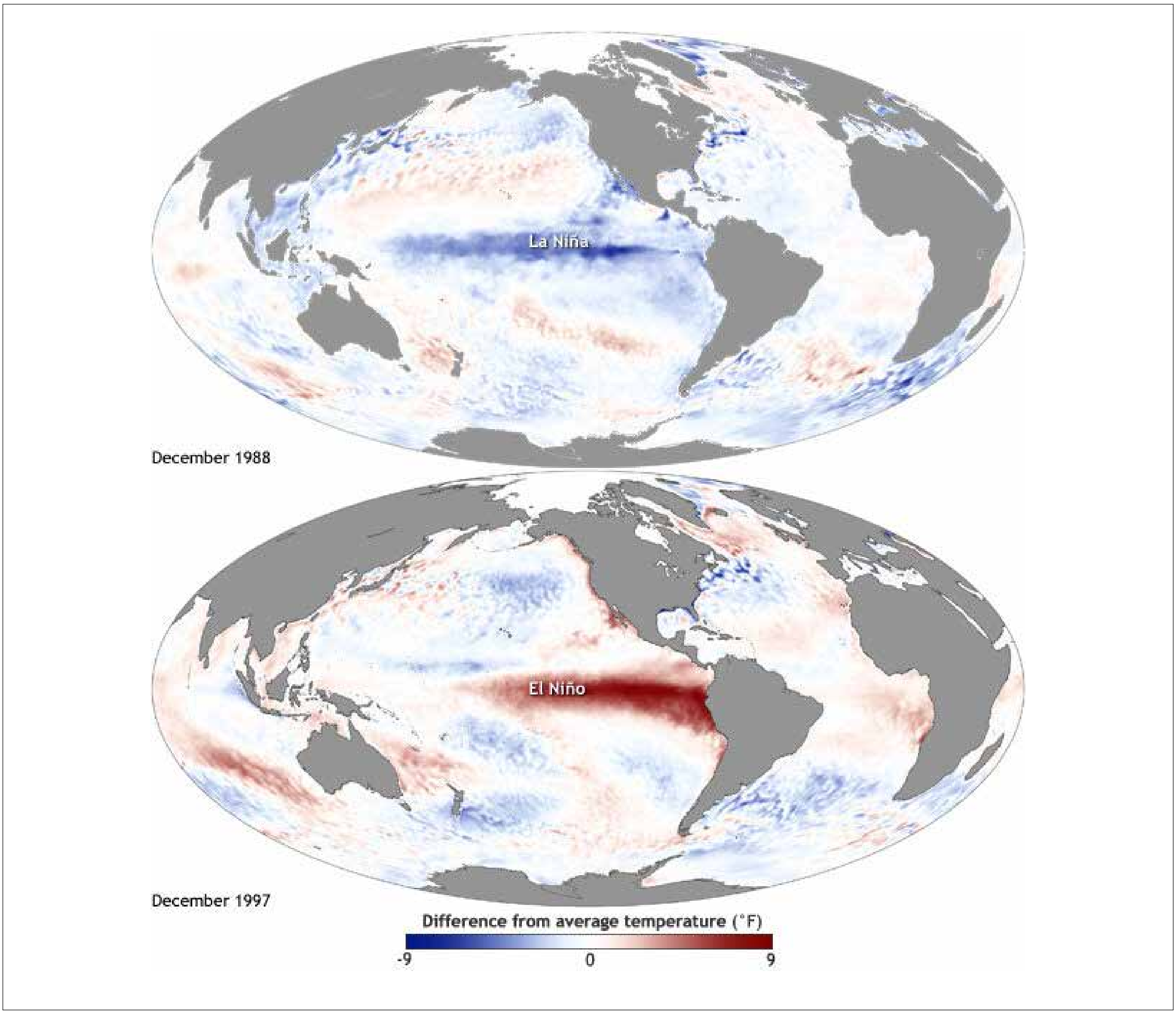


Figure 3.6 Maps showing the El Niño Southern Oscillation (ENSO) sea surface temperature anomaly in the Eastern Tropical North Pacific Ocean. Temperatures are shown as difference (on a scale from 0 to 9) from the average temperature (in Fahrenheit). Top: A strong La Niña with colder than average sea surface temperatures in 1998. Bottom: A strong El Niño with warmer than average sea surface temperatures in 1997.

[7] https://www.climate.gov/news-features/blogs/enso/what-el-ni%C3%B1o%E2%80%93southern-oscillation-enso-nutshell

4 Current Ocean deoxygenation

Since the middle of the 20th century, the Ocean has been losing oxygen, termed Ocean deoxygenation. These changes are taking place on such a large scale that they might have long lasting implications for for Ocean ecosystem functioning, life in the Ocean, and ultimately humans, who depend on the Ocean. This chapter explains the mechanisms that lead to oxygen loss in the Ocean, describes how much oxygen has already been lost since the mid-20th century, and how much more the Ocean might still lose by the end of this century. The chapter also outlines deoxygenation events in the four major European marginal and (semi-) enclosed seas, namely the Mediterranean, the Baltic, the Black Sea, and the North-Western European coastal seas. Finally, the impacts of deoxygenation on biogeochemical cycles, marine life and ecosystems, as well as on marine ecosystem services, are explained.

The key messages from this chapter are:

- The Ocean has been losing oxygen since the 1950s, mainly due to human induced global warming and anthropogenic nutrient input;
- In the open Ocean, oxygen loss is primarily driven by physical changes due to climate change: increasing temperatures reduce the amount of oxygen seawater can hold, and the combined changes in wind and precipitation patterns, as well as higher temperatures increase stratification, thereby hindering oxygen transport to deeper waters;
- In coastal waters, eutrophication (excessive nutrient input) is the main cause of increased oxygen loss; yet, warming, increased precipitation and delivery of freshwater will worsen the situation;
- Low oxygen levels alter the cycling of many elements in the marine environment that are important for life. It also promotes the production of nitrous oxide and methane in the Ocean, both of which are greenhouse gases that may be released to the atmosphere;
- Biogeochemical feedbacks enhance oxygen loss in marine systems;
- Deoxygenation strongly impacts life in the Ocean: it can lead to habitat loss, major changes in diversity, food-web interactions and ecosystem structure. Acute or chronic low oxygen levels can result in mass mortality; and
- Deoxygenation negatively affects marine ecosystem services (e.g. decreasing and displacing fisheries, and reducing the aesthetic and cultural value), and it can hinder the transition to a sustainable blue economy and to healthy open Ocean and coastal waters.

4.1 Deoxygenation in the coastal and open Ocean

4.1.1 Mechanisms of Ocean deoxygenation

Human induced global warming and anthropogenic nutrient input have been causing Ocean deoxygenation since the mid-1900s (Figure 4.1). Global warming leads to oxygen loss, both directly, by reducing the solubility of oxygen in seawater, and indirectly, through changes in biogeochemical and physical dynamics, such as intensifying stratification, which reduces the transport of oxygen into the Ocean interior and slows down Ocean circulation (Figure 4.1). This reduced transport of oxygen into the Ocean interior will reduce the oxygenation of the deep-sea over a time scale of decades to hundreds of years to come - even if anthropogenic greenhouse gas emissions would stop today (see Chapter 6). The timeline of recovery for the deep-sea to re-oxygenate depends on water depth and location (Oschlies, 2021). Increased stratification also leads to increased oxygen release from the surface Ocean to the atmosphere. This is because the surface waters, which are over-saturated with oxygen, and the subsurface waters, which are under-saturated with oxygen (from photosynthesis and respiration, respectively), cannot mix.

While the importance of the different mechanisms driving oxygen loss as a result of global warming is uncertain, the direct thermal effect explains only ~15% of the oxygen decrease observed globally. Hence, indirect effects dominate the current oxygen loss in the Ocean (Schmidtko *et al.*, 2017). Importantly, the mechanisms of deoxygenation in the Ocean differ with water depth. In the top 1,000m of the water column, ~50% of the oxygen loss is attributed to changes in oxygen solubility, and the remaining ~50% is due intensified stratification (which hinders mixing of water) and a slowed down circulation. Below 1,000m depth, changes in Ocean circulation and deep water formation explain up to 98% the observed oxygen loss (Breitburg *et al.*, 2018).

Eutrophication as a result of nutrient run-off is another major source of oxygen loss in the Ocean (Figure 4.1). Since the 1950s, synthetic fixation of nitrogen to form ammonia (NH_3) has been applied at an industrial scale for the mass production of nitrogen fertiliser. Mining of phosphorus for use in phosphorus-fertiliser has also accelerated. The increased application of these fertilisers in agriculture has led to a doubling of riverine inputs of nitrogen and phosphorus into global coastal waters over the 20th century (Beusen *et al.*, 2016). This influx of nutrients has led to eutrophication (over-enrichment in nutrients) of coastal waters in many regions (Figure 4.2).

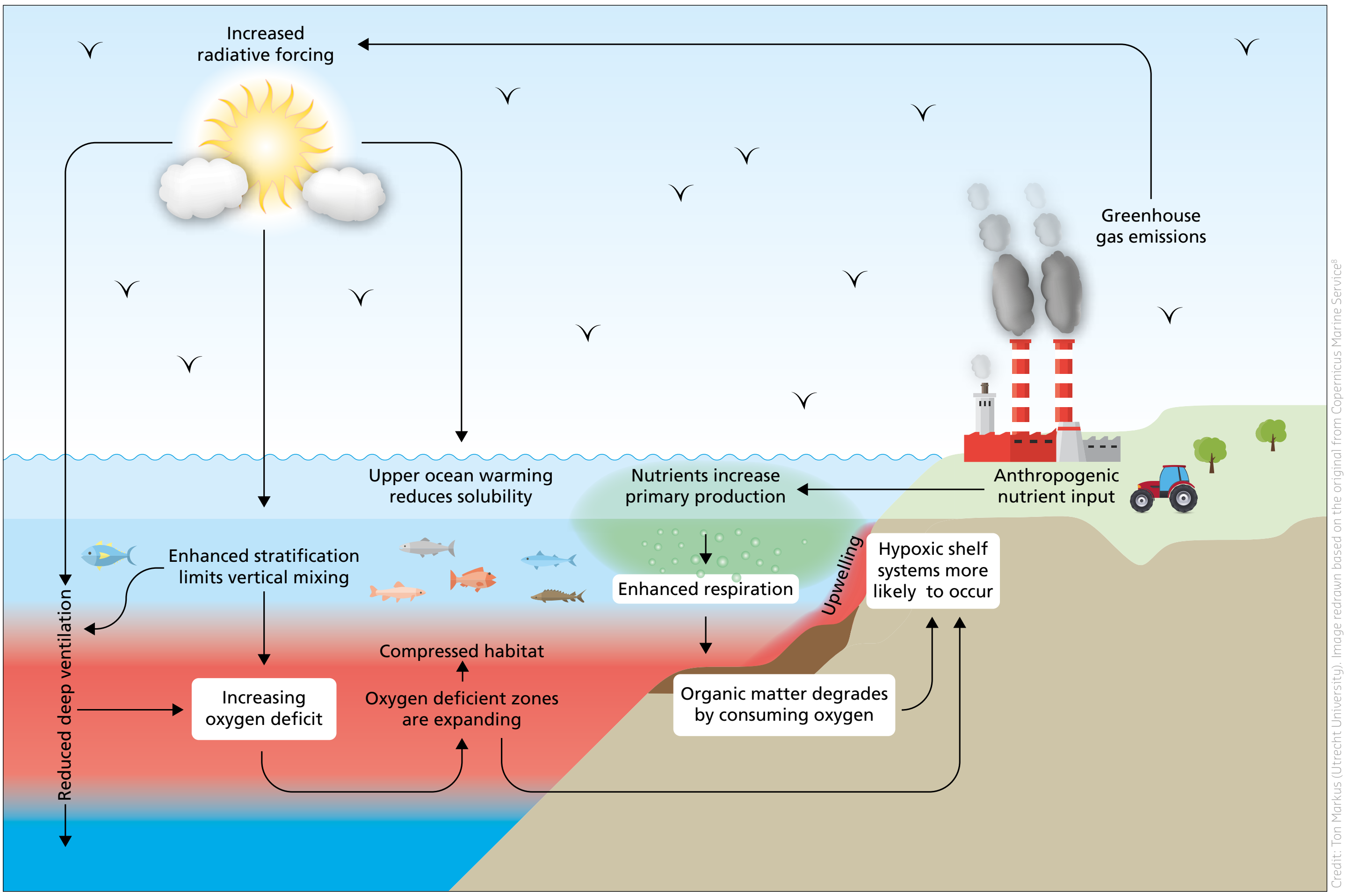


Figure 4.1 Mechanisms of oxygen loss in the Ocean: global warming and anthropogenic nutrient input are causing deoxygenation in the Ocean.

[8] https://marine.copernicus.eu/explainers/phenomena-threats/deoxygenation

Credit: Marilaure Grégoire

Figure 4.2 Coastal eutrophication is a worldwide phenomenon. This picture depicts the coast of Brittany in France, where the green substance is an algal bloom caused by excess nutrients (eutrophication).

Eutrophication stimulates primary production and may lead to large algal blooms that can sink to the seabed. When bottom waters cannot mix with surface waters due to stratification, the oxygen consumed cannot be replaced, and hypoxia (defined as an oxygen concentration of less than 62 µmol/kg) or anoxia develops. Low oxygen in coastal waters is often an intermittent feature (e.g. seasonal) but can also be near-permanent as, for example, in the Baltic Sea, where nutrient input from agricultural fertilisers has caused one of the biggest Oxygen Depleted Zones (ODZs) in the world.

Projections of riverine nutrient inputs to coastal areas indicate that eutrophication will likely continue in many regions globally and will be further amplified by warming that will reduce oxygen solubility and ventilation of bottom waters (i.e. the transport of oxygen rich surface waters to deeper waters). However, temporal changes (from years to seasons) in coastal hypoxia in the global coastal Ocean are currently not well-quantified.

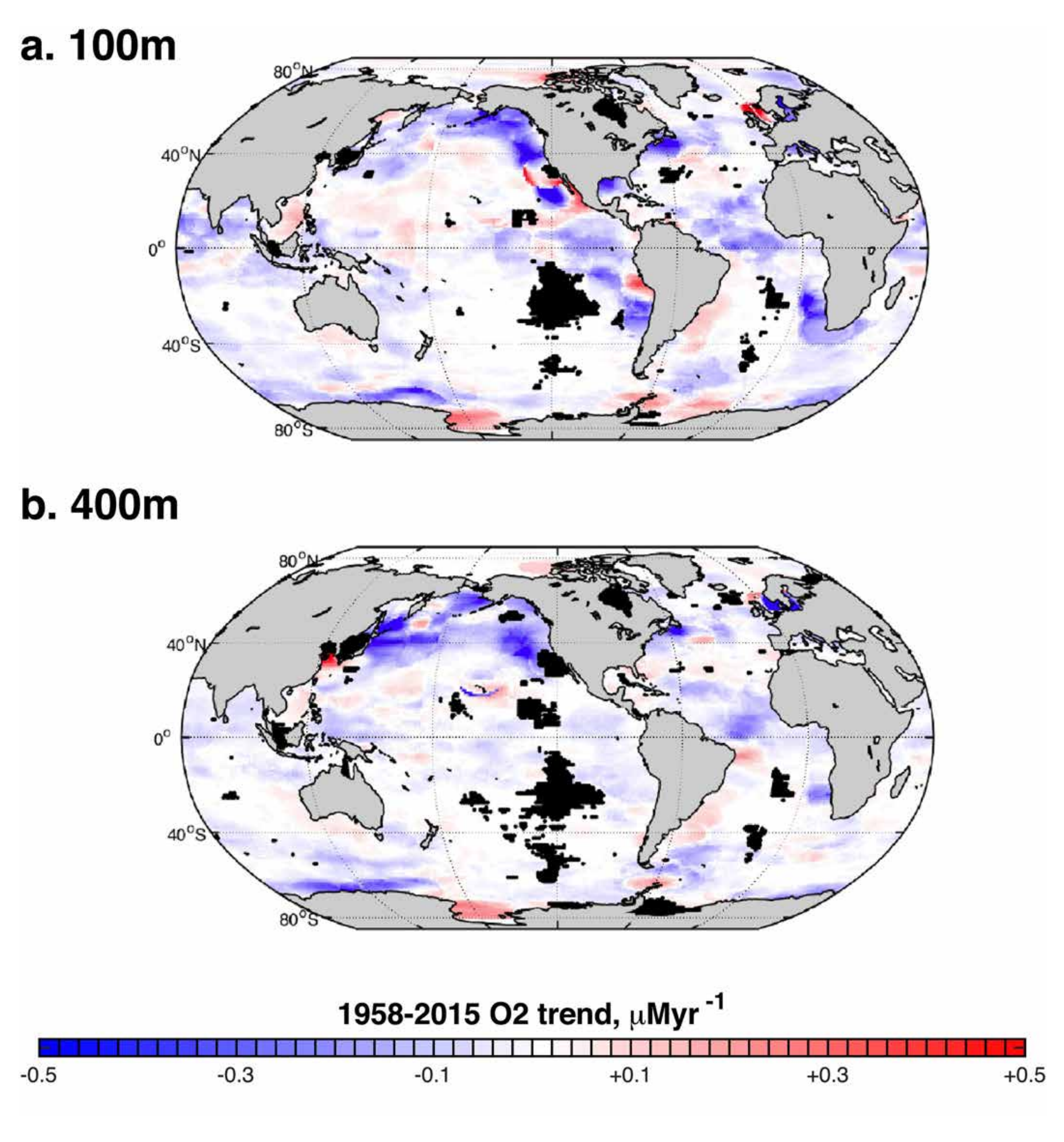
4.1.2 Quantifying the amount of oxygen loss in the Ocean

The oxygen concentration in the Ocean has decreased by 0.5-3% (1.1-6.8Pmol) over the past five decades (e.g. Bopp *et al.,* 2013; Schmidtko *et al.,* 2017). Model projections for the end of this century show a further decrease of several percent (~2-3%) under both the “business-as-usual” and the “high mitigation” IPCC greenhouse gas emission scenarios (Bopp *et al.,* 2013). Global models are able to reproduce the observed decline in the global oceanic oxygen inventory since 1960. However, they appear to systematically underestimate observed rates of deoxygenation, and are not able to recreate spatial (region-specific) patterns of decrease, in particular the observed decline in the depth of the tropical thermocline, the transition layer between warm surface waters and colder deeper waters (e.g. Oschlies *et al.,* 2018).

The human-induced climate change effects on the Ocean to date have disturbed the equilibrium in oxygen between the Ocean and the atmosphere, reducing the amount of oxygen that enters the Ocean from the atmosphere and increasing the amount of oxygen released from the Ocean. Hence, the Ocean is becoming a source of oxygen to the atmosphere (Bopp *et al.,* 2002) at the expense of a decrease in oceanic oxygen concentrations (see Section 3.1.5).

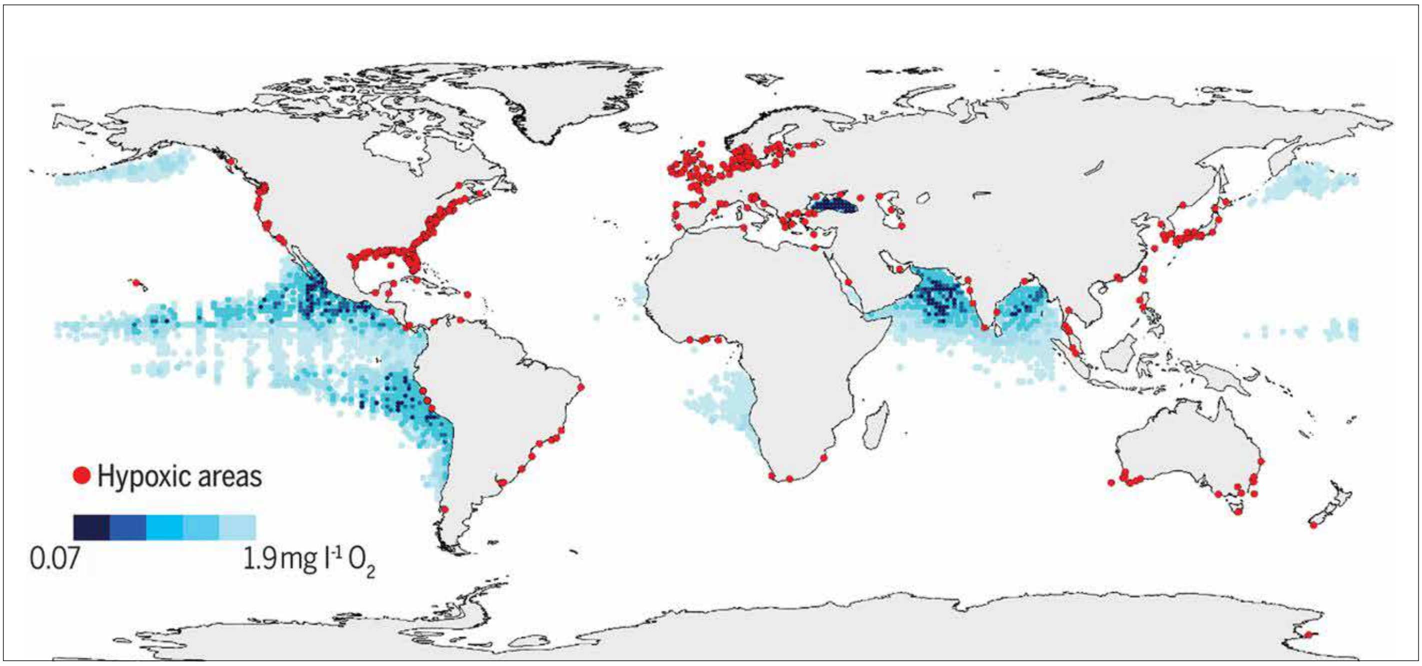
Regions with historically very low oxygen concentrations are expanding and new low oxygen regions are forming. Naturally occurring ODZs (at 100-1000m water depth), such as the Tropical Pacific and Arabian Sea ODZs (red areas in the respective seas of Figure 3.3c), have thickened and expanded by an area about the size of the European Union (4.5 million km^2) since the middle of the 20^{th} century. The volume of anoxic coastal areas, which are completely oxygen depleted, has also quadrupled over the same time period (Schmidtko *et al.,* 2017; Stramma *et al.,* 2010). The degree of oxygen decline is not uniform but varies across Ocean basins and depths (Ito *et al.,* 2017, Figure 4.3). The largest loss is observed at the main thermocline, between 100-300m deep in the Tropical and North Pacific Ocean, the Southern and Arctic Ocean and the South Atlantic Ocean (Schmidtko *et al.,* 2017). Moreover, rates of oxygen decline seem to be faster in the coastal Ocean (<30 km from the coast) than in the open Ocean (>100 km from the coast) (Gilbert *et al.,* 2010).

Globally, in the coastal Ocean, hypoxic and anoxic areas are mostly intermittent features that recurrently appear in the summer near the benthic boundary layer (i.e. the water directly above the seabed where processes are influenced by the seabed), or in wider volumes of the water column, when the oxygen consumption through respiration outpaces the oxygen supply by ventilation and bottom photosynthesis (e.g. Pitcher *et al.,* 2021). The number of coastal hypoxic sites has increased in response to worldwide eutrophication (Breitburg *et al.,* 2018; Diaz & Rosenberg, 2008, Figure 4.4), however the exact scale of this oxygen trend in coastal areas is still debated. This is because there are not enough oxygen observations in international databases to make a comprehensive quantitative assessment of the severity of low-oxygen conditions at seasonal and interannual scales. This is particularly critical in regions with limited institutional infrastructure to measure and share oxygen data, and where the connection with National Oceanographic Data Centres (NODCs) and international oceanographic databases is not always well established, or where NODCs do not exist (Grégoire *et al.,* 2021).



Credit: Ito *et al.,* 2017 (Reprinted with permission from Geophysical Research Letters)

Figure 4.3 Global map of oxygen decrease (blue) and increase (red) between 1958-2015 at a depth of (a) 100m and (b) 400m. Black areas represent incomplete data.



Credit: Breitburg et al. (2018), including data from Diaz & Rosenberg (2008). Reprinted with permission from AAAS

Figure 4.4 Global distribution of hypoxic areas (i.e. O_2 < 62 µmol/kg) in the coastal and open Ocean. In coastal areas, more than 500 sites have developed low oxygen conditions over the past half century (red dots), while in the open Ocean the extent of low oxygen waters amounts to several million km_3 (blue dots refer to conditions at 300m).

Credit: Chris LeBoutillier, Pexels

Anthropogenic greenhouse gas emission is driving Ocean deoxygenation.

4.2 Deoxygenation in European regional seas

With a coastline of 185,000km[9], the European continent is bordered by a number of marginal (shelf-) and (semi-) enclosed seas. The oxygen dynamics of coastal zones and adjacent Ocean basins differ from the ones in the open Ocean due to the close connection between surface waters, the seabed, tides and influences from land, including rivers, land use, and runoff. There is also growing human pressure from heavy and overlapping use of these marginal and enclosed seas (e.g. from transport, fisheries, energy production and recreation). Changes in oxygen-related water quality will therefore have a large impact on coastal ecosystems and strong socio-economic effects. This section describes the historical and current deoxygenation events of the four major European marginal and (semi-) enclosed seas. The historical events are provided as a reference to understand the current oxygen changes.

4.2.1 Mediterranean Sea

The Mediterranean is a semi-enclosed sea, which is currently well ventilated due to active deep circulation. However, for several millions of years, recurring deoxygenation has affected the Mediterranean, leading to the formation of organic-rich, nearly black marine sediments, known as sapropels (Rohling *et al.,* 2015) (Figure 4.5). Mediterranean sapropel formation is correlated with the cyclical intensification of African monsoons that occur approximately every 36,000 years. Intense monsoons increase freshwater and nutrient input to the Eastern Mediterranean that, in turn, change the general circulation and increase biological productivity, which is followed by increased oxygen consumption due to the respiration of this organic matter. The most recent deoxygenation event occurred in the Mediterranean about 10,000 years ago during the Holocene. The event lasted 3,000 years, due to a combination of warming and freshening of the seawater (see Section 3.3.2).

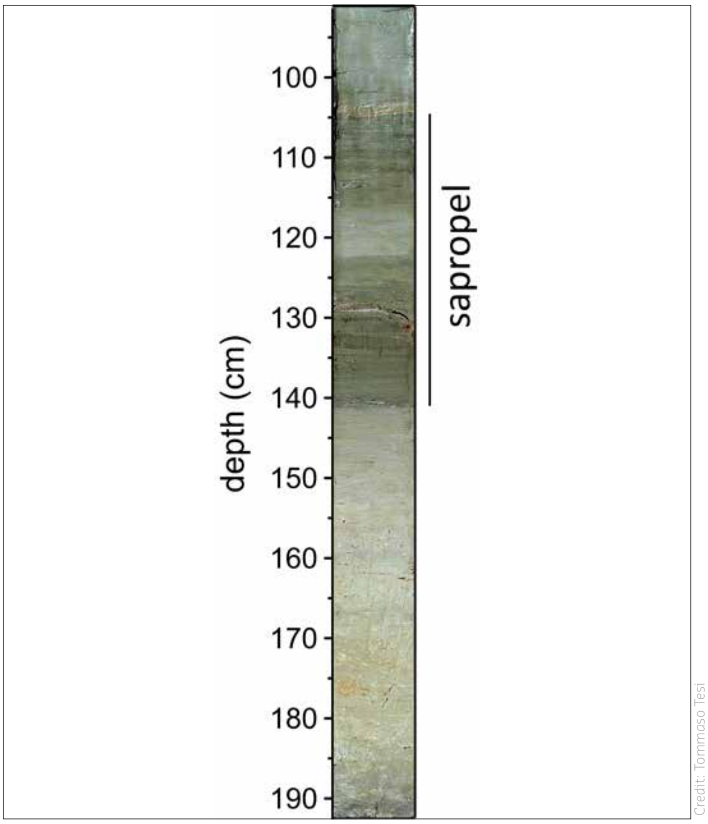


Figure 4.5 Sediment core collected in the Southern Adriatic Sea. The dark sediment shows the sapropel deposited about 10,000 years ago.

Although the modern Mediterranean is well mixed and largely oligotrophic (nutrient poor), oxygen depletion has been observed in summer in the shallow northern Adriatic Sea, which fluctuates between hypoxic and anoxic conditions. The frequency of these events varies as a function of the nutrient supply by the Po River and how stagnant the water becomes in summer. Since the 1990s, EU regulations have reduced the anthropogenic input of nutrients and, consequently, the frequency of these deoxygenation events.

In the western Mediterranean basin, the intensity of deep-water formation in the Gulf of Lion is decreasing (although there are strong inter-annual variabilities) and this, in turn, is decreasing the oxygen supply in intermediate waters (Fourrier *et al.,* 2022). Projections show that the ventilation of the deep-sea will strongly decrease in the Mediterranean in the future. This will impact oxygen levels at depth across the Mediterranean (Somot *et al.,* 2018).

4.2.2 Baltic Sea

The Baltic Sea was formed ca. 8,000 years ago when a freshwater lake became connected to the North Sea due to rising sea levels. Because of its low salinity compared to the open Ocean, it is prone to deoxygenation as a result of strong salinity stratification, which inhibits vertical mixing. Since its formation, the Baltic Sea has been subject to three distinct intervals of low oxygen. The first occurred when it was formed and lasted until 4,000 years ago. The low oxygen concentrations were a result of increased stratification linked to climatic warming and elevated salinity, because oceanic water entered into the Baltic Sea. The second event, also caused by increased stratification, occurred between 1,700-700 years ago during a period of relative warming in the Medieval age (called the Medieval Climate Anomaly) (Jilbert & Slomp, 2013). The third, modern deoxygenation event began ca. 1950 and is the direct consequence of human induced eutrophication (nutrient enrichment), with global warming exacerbating the situation (Kuliński *et al.,* 2022).

4.2.3 Black Sea

Around 8,000 years ago, with rising sea levels, high salinity Mediterranean seawater also entered the Black Sea, filling the bottom basin of what had previously been a fully enclosed freshwater lake. This created a permanent salinity stratification, which inhibited vertical mixing and oxygenation of subsurface waters, so that a permanent deep, anoxic and sulphidic marine basin developed.

[9] https://www.eea.europa.eu/themes/water/europes-seas-and-coasts

Credit: Mirko Fabian, Pexels

Agricultural nutrient-run off from fertilisers is causing deoxygenation in European coastal seas.

Currently only the top 100-150m of the >2,000m deep Black Sea are well-oxygenated so that approximately 87% of its total volume is oxygen poor. The top layers of the Black Sea are well oxygenated because of winter cooling and surface water mixing. However, below this depth, stratification acts as barrier for the vertical mixing and exchange of oxygen. Only at times, when seawater enters from the Mediterranean through the (only 36m deep) Bosporus Strait (which connects the Black Sea to the Sea of Marmara), the deeper oxygen poor water layers of the Black Sea are oxygenated. With its massive amount of toxic hydrogen sulphide, formed by the lack of oxygen, the Black Sea is the largest sulphidic basin in the world.

In the last decades, warming and further deoxygenation of the Black Sea have occurred. From 1955 to 2015, the inventory of oxygen in the Black Sea has decreased by 44% and the average oxygen penetration depth has decreased from 140m in 1955 to 90m in 2015. Because of fewer persistent and extreme cold events, the volume of cold water forming annually has reduced, and together with intense eutrophication during the 1980s, the well oxygenated top layer has become shallower (Capet *et al.,* 2016). On the north-western shelf, eutrophication in the 1980's has led to bottom hypoxia with deleterious consequences for benthic species like mussels (Mee, 2006). The reduction of fertilizer use in the 2000's has improved the situation, but bottom hypoxia is still present along the coast, where warming reduces oxygen solubility and extends the stratification period.

4.2.4 North-Western European coastal seas

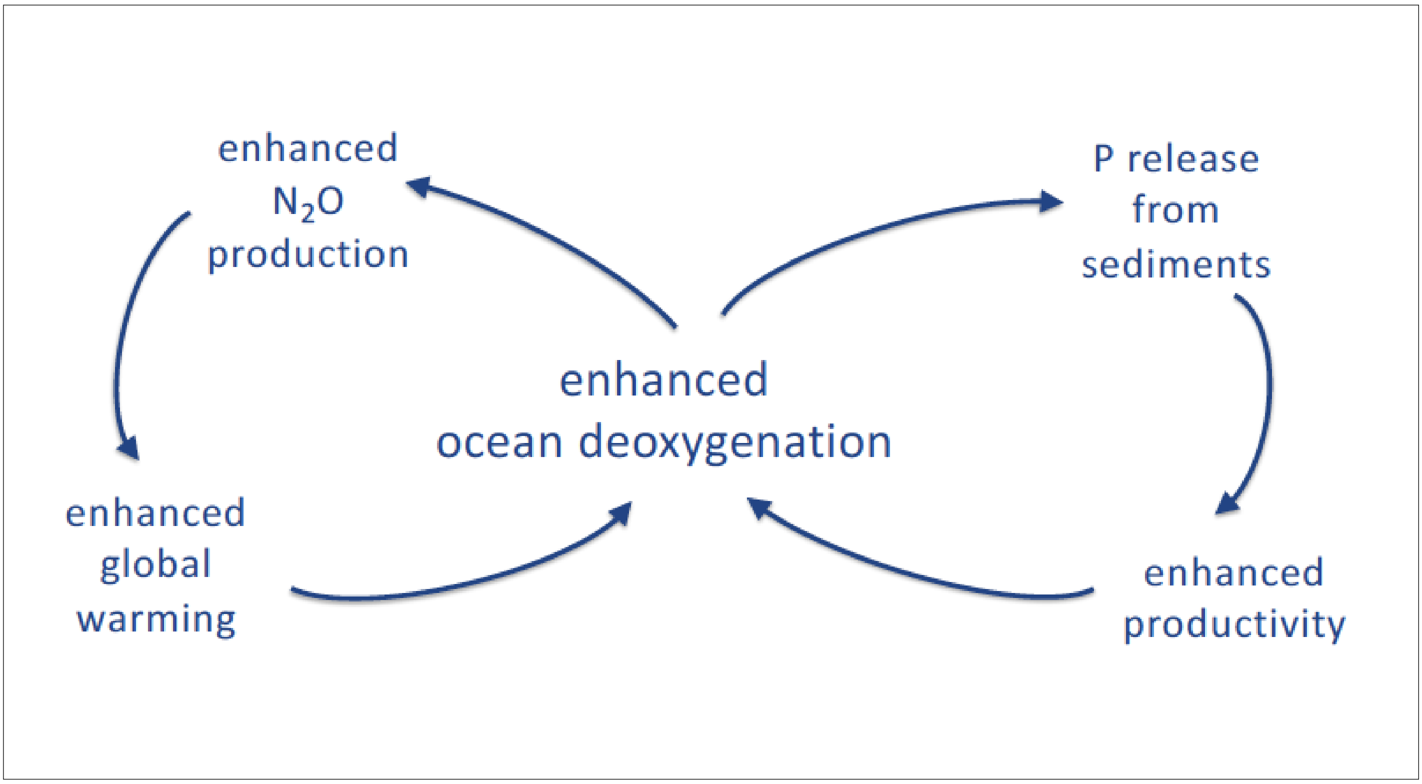
The coastline of the North-Western European shelf was very different at the end of the last ice age (18,000 years ago), with the North Sea and Irish Sea forming around 10-12,000 years ago as sea levels rose due to the ice melt. This shelf region has likely been well oxygenated since formation, though in the 1980s, low oxygen levels in the bottom waters of some regions of the North Sea have been reported during late summer (Topcu & Brockmann, 2015). These low oxygen levels are possibly caused by summer stratification in waters on the continental shelf, fuelled by increased nitrogen inputs from rivers, although the extent of the observed oxygen decline appears to be more strongly regulated by biological processes (Große *et al.,* 2016). Seasonal hypoxia, likely driven by eutrophication, has been found to occur in some estuarine waters in France (Dubosq *et al.,* 2022), including the Rhone Delta (southern France), and Spain (Iriarte *et al.,* 2010) along the Bay of Biscay. Along the British Isles coast and shelf, including the Irish Sea, there is no evidence to date for anoxic or hypoxic conditions occurring (O'Boyle *et al.,* 2009). Continued reductions in riverine inputs of nitrogen and phosphate to this region, in response to the Nitrates Directive (Directive 91/676/EEC, 1991), the Water Framework Directive (Directive 2000/60/EC, 2000) and the EU Marine Strategy Framework Directive (Directive 2008/56/EC, 2008), are acting to decrease the risk of localised eutrophication and subsequent hypoxia. In general, however, over the wider North West European Shelf, the near-bottom oxygen concentrations in summer are expected to continue to decline due to global warming (Wakelin *et al.,* 2020).

4.3 Impact of deoxygenation on biogeochemical processes

Deoxygenation of marine ecosystems dramatically changes the cycling of elements which interact with living organisms (i.e. bio-active elements), such as carbon, nitrogen, phosphorus, sulphur and trace metals (i.e. metals that are present in very small quantities in seawater, such as iron). Where oxygen is low or absent, animals can no longer thrive and the energy produced at the surface by phytoplankton is instead transferred to microbes, which consume the sinking organic matter (Diaz & Rosenberg, 2008). With a lack of oxygen, aerobic respiration of organic matter (i.e. using oxygen) is constrained, but anaerobic degradation (i.e. without oxygen) takes place through microbially-driven processes. Especially in coastal regions, this anaerobic degradation can lead to the release of ammonium (NH_4^+), toxic hydrogen sulphide (H_2S), the potent greenhouse gas methane (CH_4) from the seafloor. The reaction of oxygen with these compounds can then contribute to further oxygen loss (Testa & Kemp, 2011). In eutrophic coastal systems, methane may even be released to the atmosphere (Rosentreter et al., 2021).

Low oxygen enhances nitrogen (N) loss in marine ecosystems, because the forms of nitrogen that can be easily used by living organisms (i.e. bioavailable nitrogen), such as nitrate (NO_3^-), nitrite (NO_2^-) and/or ammonium (NH_4^+), are transformed to dinitrogen gas (N_2), which only a few organisms can use. This transformation occurs through microbial processes called denitrification and anaerobic ammonium oxidation, and occurs in sediments and the water column of ODZs of both the open and coastal Ocean. The resulting nitrogen loss may lead to lower primary productivity if nitrogen fixation – the compensating microbial process – does not balance nitrogen loss. In coastal systems, ammonium may also accumulate and support further productivity. The relevant feedbacks and timeline for these processes remain uncertain. Both nitrification (i.e. the conversion of NH_4^+ to NO_2^- and NO_3^- in a process using oxygen) and denitrification (the processes in which NO_3^- is converted to the low-bioavailable N_2) may also produce nitrous oxide (N_2O), another potent greenhouse gas (Breitburg *et al.,* 2018; Lam & Kuypers, 2011), which can contribute to further global warming and deoxygenation (Figure 4.6). Low oxygen zones currently account for a large proportion of marine nitrous oxide emissions to the atmosphere (Breitburg *et al.,* 2018).

Recycling of the essential nutrient phosphate is enhanced in low oxygen zones because of enhanced regeneration of phosphate from organic matter (linked to a lower retention of phosphorus by anaerobic bacteria) and release of phosphate bound to iron (Fe)-oxides (Figure 4.6). This enhanced recycling accelerates in coastal systems where oxygen is so low that hydrogen sulphide (H_2S) reacts with iron oxides liberating phosphate. This can lead to efficient reuse of phosphate by phytoplankton, which may ultimately further increase Ocean deoxygenation through increased primary productivity (Figure 4.6). In the Baltic Sea, such recycling results in excess phosphate relative to nitrogen in surface waters, thereby stimulating growth of N_2-fixing cyanobacteria, and the production and degradation of organic matter, promoting further deoxygenation (Conley & Slomp, 2019).



Credit: Caroline Slomp

Figure 4.6 Examples of feedbacks involving nitrogen (N) and phosphorus (P) in the Ocean that enhances deoxygenation.

Ocean deoxygenation leads to major changes in the cycling of bio-essential metals (i.e. metals that are essential for the functioning of living organisms), such as iron, manganese, cobalt, nickel, copper and zinc (Lam & Anderson, 2018). The release of metals from marine sediments may increase when there is low oxygen, for example due to changes in mineral solubility, potentially increasing primary productivity. However, ongoing deoxygenation may also lead to enhanced sequestration of metals in organic matter and sulphide minerals in sediments, making them potential indicators of bottom water oxygen and/or hydrogen sulphide concentrations (called redox proxies). Examples of metals that can be used as redox proxies are iron, which is sequestered in sulphide minerals in the presence of hydrogen sulphide (Conley & Slomp, 2019), and molybdenum (Mo), which increases in sediments in low oxygen water. Knowledge of the marine cycling of (trace) metals and their isotopes in low oxygen zones is still incomplete because of a lack of observations and/or difficulty of the analyses. This incomplete knowledge applies to both the cycling of bio-essential metals and that of (trace) metals used solely as redox proxies (Bennett & Canfield, 2020).

Biogeochemical cycles of elements in low oxygen zones are intimately connected (Ulloa *et al.,* 2012). For example, microbial removal of methane in the water column, can be linked to removal of oxygen, nitrate and/or nitrite. This happens through oxidation-reduction (i.e. redox) reactions, in which methane is oxidised (i.e. it loses electrons) and oxygen, nitrate and/or nitrite are reduced (i.e. they gain electrons), which transforms them into other compounds. Our knowledge of such coupled biogeochemical processes and their microbial drivers is still incomplete, which hinders model projections of the biogeochemistry of the future Ocean. Many questions also remain on how coupled biogeochemical cycles in low oxygen zones will change, due to seasonal and episodic changes in the input of organic matter and water circulation. A key example is the periodic release of hydrogen sulphide to the water column during “sulphidic events” in low oxygen zones, driven by the enhanced organic matter input, which not only impact biogeochemical cycling but can also kill fish (Callbeck *et al.,* 2021).

Multiple biogeochemical feedbacks in low oxygen marine systems can act to sustain a low oxygen state. As mentioned above, a more efficient recycling of phosphate and ammonium from sediments in low oxygen zones may fuel further algal blooms, thereby decreasing oxygen concentrations upon respiration of this organic matter. Another feedback is related to the accumulation of organic matter in anoxic sediments. Part of this organic matter is degraded anaerobically (without oxygen) which enhances the release of methane, ammonium and hydrogen sulphide to the waters above. Because microbes use these compounds to obtain energy with oxygen (i.e. they oxidise the compounds), the oxygen demand increases. The continued release of these compounds, even after re-oxygenation, means that the area might not recover because oxygen will continue to be used to oxidise the compounds. The strength of these feedbacks (“legacy of hypoxia”), which are particularly relevant in coastal systems, depends on how much organic matter accumulates at the seabed and the residence time of the overlying water (i.e. the time it takes for the overlying water to be “renewed”, which means that it is exchanged, or mixed with new water). The Baltic Sea is a key example of a coastal system suffering from strong legacy effects (Conley & Slomp, 2019). By contrast, the Louisiana shelf in the Gulf of Mexico, is barely affected because of a much shorter residence time of the overlying water. This emphasises the need to consider system-specific and multi-disciplinary characteristics of low oxygen areas (Fennel & Testa, 2019).

4.4 Effect of deoxygenation on marine life and ecosystem structure

Oxygen supports life in the Ocean, which is the largest ecosystem on the planet. Deoxygenation has a strong impact on marine life, which require oxygen concentrations above certain thresholds to function normally, and the impact increases with the degree of oxygen deficiency (Table 4.1). Low oxygen leads to migration and mortality of fish, crustaceans and other animals. The threshold of 62 µmol/kg, used in this report to define hypoxia, is frequently seen as the boundary below which metabolic stress occurs (Rabalais *et al.,* 2010), but species, taxa and trophic groups vary greatly in their tolerance and behavioural response and can already be affected at concentrations above this threshold (e.g. Vaquer-Sunyer & Duarte, 2008). In the absence of sufficient oxygen, animals will reduce their respiration rate and will no longer continue energetically expensive processes such as reproduction, digestion and movement. In some species, vision can be affected. At oxygen levels much lower than the species-specific threshold, survival depends on the ability of an animal to activate oxygen-independent pathways of energy production, although most marine species have a very poor ability to respire in the absence of oxygen. While some coastal and benthic fauna are adapted to acute or chronically low oxygen levels, the most common consequences at the ecosystem level are changes in community structure and mass mortality (Figure 4.7; Breitburg *et al.,* 2018).

Many species of marine animals require different habitats throughout their growth and development; hence, an individual will face very different degrees of oxygen depletion over its lifetime. For example, European sea bass (Dicentrarchus labrax) is a species that inhabits coastal and estuarine areas during the first three years of its life, and is therefore exposed to acute hypoxic events during juvenile growth (Dufour *et al.,* 2009). Just before reaching maturity, juvenile sea bass migrate offshore to feed and subsequently join spawning areas in the open Ocean. In contrast, marine intertidal molluscs experience much more frequent and extreme fluctuations in oxygen concentrations. Intertidal rhythms result in lack of oxygen during low tide, when intertidal animals, such as molluscs, close their shells to prevent water loss.

Oxygen availability is a key determinant of the vertical and horizontal distribution of organisms in the Ocean. Expanding low oxygen zones in the open Ocean reduce the vertical habitat of, for instance, fish and their prey, because the vertical extent of the well-oxygenated surface waters decreases, while that of the subsurface hypoxic waters expands, encroaching into shallower waters. This is known as habitat compression, which can lead to major changes

OXYGEN CONCENTRATION AND TERMINOLOGY	IMPACT ON ORGANISMS
≤ 62 µmol/kg (hypoxia)	
Hypoxic zones are areas where oxygen concentrations are too low for organisms to function normally. Although ~62 µmol/kg is the conventional threshold for hypoxia, thresholds can vary strongly between different groups of organisms and with temperature. Crustaceans and fish, which are both important for the fishing industry, seem to be the most sensitive.	Organisms show reduced fitness and aberrant behaviour. Depending on the dynamics in oxygen changes and mobility of the organisms, further decrease in oxygen concentration would lead to migration and increased mortality of the different species.
~ 5-10 µmol/kg (suboxia)	
Suboxic zones are the transition layers between oxic water (with oxygen) and anoxic water. The oxygen concentration in these zones is very low.	Disappearance of practically all multi-cellular life.
<1 µmol/kg (anoxia)	
Anoxic zones have no oxygen. Technically, this means 0 µmol/kg O_2, but because of measurement uncertainty a small positive threshold value of around 1 µmol/kg is used.	Only anaerobic microorganisms (i.e. not requiring oxygen for energy production) are present.

Table 4.1 Effects of low oxygen concentrations on marine organisms. Adapted from the CLAMER factsheet prepared for the Marine Board Special Report *Synthesis of European Research on the Effects of Climate Change on Marine Environments* (Heip *et al.*, 2011)

Credit: Grant Pitcher

Figure 4.7 Mass mortality of lobsters due to low oxygen along the coast of South Africa in March 2022.

in food-web interactions and ecosystem structure in surface waters. Habitat compression can increase the vulnerability of fish to predation as they have less space into which they can escape. Only some hypoxia-tolerant species of fish and invertebrates can hide in the expanding hypoxic areas, where their predators cannot find them and their competitors are excluded (Breitburg *et al.,* 2018). Extreme and short-term habitat compression events can also occur on sub-seasonal and seasonal time scales through natural variability. These events have the potential for major impacts on ecosystem functioning and require further study (Köhn *et al.,* 2022).

Predators, such as sharks, skates and rays have comparatively high oxygen demands because they are large-bodied, active predators. They are therefore less able to tolerate hypoxia, and their behaviour and distribution will be strongly influenced by oxygen depletion. Moreover, as seawater temperatures rise with climate change, the metabolic rates of these animals will also increase. This means that they will need even more oxygen to sustain their metabolism, while there will be less oxygen in the water. Sharks, skates and rays are therefore very vulnerable to deoxygenation and will be increasingly less able to tolerate the effects of even mild hypoxia (Sims, 2019).

Deoxygenation also leads to major changes in the faunal diversity and food web structure of coastal ecosystems. A key example is the Baltic Sea where hypoxic events have led to the loss of benthic fauna, such as fish, crustaceans, worms, echinoderms and molluscs (Vaquer-Sunyer & Duarte, 2008). In tropical regions, coral reefs are also impacted by hypoxic events (Altieri *et al.,* 2017). Importantly, the recovery of an ecosystem from severe hypoxia differs because of the different needs for populations to recover, including species-specific food and habitat requirements. As a result, a system can only fully recover when the different components of the ecosystem have recovered. This generally lengthens the timeline of ecosystem recovery following severe hypoxia (Diaz & Rosenberg, 2008). When hypoxia persists, there are often long-lasting changes in ecosystem composition, with a shift to much lower species diversity and abundance (Rabalais & Baustian, 2020).

Very limited research to date has focused on the evolutionary implications of the differences within a given species (i.e. intra-specific variation) in low oxygen tolerance thresholds. However, marked intra-specific variation in responses to changes in oxygen and other environmental conditions appear across populations and life stages, even when standardising for age and environmental conditions (Joyce *et al.,* 2016). Natural selection acts on individuals within a population, so it is of specific interest to study individual differences in oxygen thresholds to understand how populations, and, in turn, species will respond to deoxygenation.

Credit: Kimberly Jeffries (Ocean Image Bank)

Predators, such as sharks, skates and rays have comparatively high oxygen demands and are therefore especially vulnerable to deoxygenation.

4.4.1 Multiple stressors

Deoxygenation is one of the most challenging environmental stressors for marine animals, but many other stressors may exacerbate its impact. Ocean acidification and warming, which frequently co-occur with deoxygenation, are prime examples. This "triple threat" to Ocean ecosystems has a common cause: the rise of anthropogenic CO_2 in the atmosphere driving climate change. Climate change may also change precipitation on land and hence freshwater inputs, which may impact stratification and consequently oxygen supply (Fennel & Testa, 2019). Warming seawaters also increase the respiratory and metabolic rate of marine organisms, which enhances their oxygen demand, while at the same time there is less oxygen in warmer seawater. This worsens the physiological impact of deoxygenation. Currently, we cannot accurately predict the impact of these combined processes within the expanding low oxygen areas of the Ocean and impacts on the physiology of marine organisms (Breitburg *et al.,* 2018).

Various indices have been developed to quantify the effects of warming and deoxygenation on marine organisms. These include, for example, the "metabolic index", which represents the relationship between oxygen supply and demand (Deutsch *et al.,* 2020) and the "aerobic growth index", which calculates a theoretical oxygen supply-to-demand ratio (Clarke *et al.,* 2021). These indices have been used to assess potential spatial patterns in habitat loss for fish and other species under continued global warming and deoxygenation (Clarke *et al.,* 2021). While the combined effects of warming and low oxygen are frequently studied, limited empirical data are available on the effects of additional stressors (i.e. three or more stressors). One solution may be to conduct experiments in the field that incorporate environmental variations on multiple time scales and provide a truly biologically relevant multiple-stressor perspective.

Species loss from warming and oxygen depletion due to accelerating greenhouse gas emissions will become comparable, by the end of this century, to the amount of species lost due to all human activities (both on land and in the Ocean) since the industrial revolution, and may culminate in a mass extinction similar to those in Earth's past (Penn & Deutsch, 2022; see Figure 2.2). Projected species loss depends on the anthropogenic greenhouse gas emissions scenarios that we will end up following. Extinction risk is greatest when climate anomalies are strong (i.e. there is a large difference between the average climate over a period of several decades or more, and the climate during a particular month or season), or when species are living close to their physiological thresholds. The most vulnerable regions are the highly productive ecosystems with naturally low oxygen concentrations, such as the Eastern Boundary Upwelling Systems (Figure 3.5) (Penn & Deutsch, 2022). These regions also support some of the world's richest fisheries and species loss will have strong detrimental consequences for our economy and society.

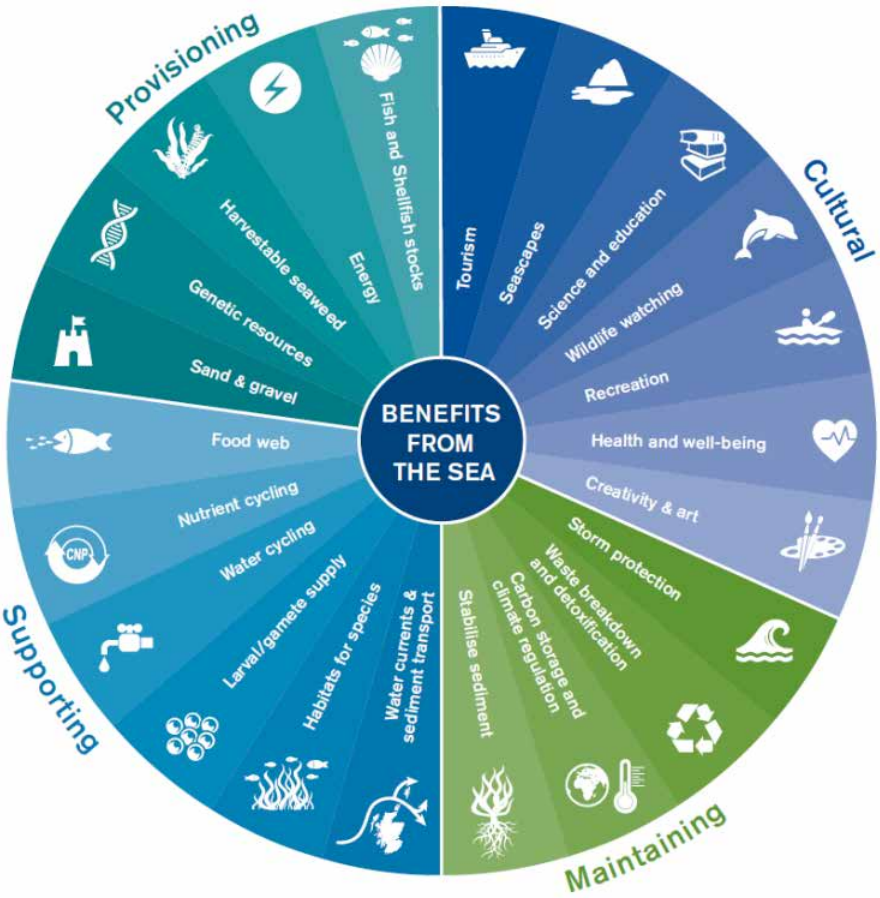
4.5 Deoxygenation and ecosystem services

The majority of marine ecosystem services (Figure 4.8) are dependent on oxygen dynamics. Both oxygen depletion below biologically vital thresholds and oxygen loss in well-oxygenated waters may impact ecosystem services via direct effects on animals, biogeochemical processes and ecosystem structure (see Sections 4.3 and 4.5).

It is difficult to quantify the influence of only oxygen depletion on ecosystem services, because it typically co-occurs with other stressors, such as warming and acidification. Other stressors such as eutrophication, overfishing (or resource overexploitation) and habitat degradation also co-occur in oxygen-depleted coastal locations and contribute to the impacts, which makes it even more difficult to quantify the impacts of oxygen depletion alone. Nonetheless, numerous effects on ecosystem services have been observed.

Direct consequences, such as the direct exposure of fish or benthic species to hypoxia, and eventual habitat loss in deoxygenated areas, can influence food provisioning. Both benthic commercial species (e.g. lobsters and shellfish) and commercial species living in the water column (e.g. fish) can be lost, with the loss of the former often preceding the loss of the latter. In addition to the somewhat gradual reduction in living resources, the relatively swift reversal to anoxic conditions in coastal regions can cause fish deaths (Figure 4.9), and thereby severely reduce the food availability for a given area (Limburg *et al.,* 2020). An example of a long-lasting effect of hypoxia is the mass mortality of Norway lobsters in the Kattegat sea (located between the North Sea and the Baltic Sea) in 1988. The lobsters did not recover even after re-oxygenation of the bottom waters, because of changes in benthic species that altered the food resources (Conley & Josefson, 2001). Less is known about the impact of oxygen loss on non-living material provisioning, although deoxygenation alters the biogeochemical landscape and can influence the type of raw materials (e.g. metals) deposited in a sea area. Moreover, altered water quality, such as the accumulation of toxic sulphidic deep waters, can negatively impact aquaculture through sulphide toxicity or oil and gas industries through corrosive effects on the infrastructure.

Process and modelling studies demonstrate the effects of deoxygenation on the regulating services provided by the Ocean, including climate regulation, nutrient recycling and habitat maintenance (Limburg *et al.,* 2020). Changes in the Ocean's carbon storage and uptake mechanisms – a key climate mitigation service - are closely tied to the Ocean's oxygen concentration, and consequently are impacted directly by deoxygenation (Hayes & Waldbauer, 2006). The production of greenhouse gases in oxygen deficient zones further diminishes the climate mitigation service provided by the Ocean (Levin & Le Bris, 2015). In addition, the loss of coral reefs (Altieri *et al.,* 2021) or fauna over seamounts (Ross *et al.,* 2020) has also been attributed to deoxygenation. The loss of these types of habitats signifies the loss of other regulatory services, such as habitat maintenance and biodiversity support, which indirectly ties to provisioning services and aesthetic services (in the case of coral reef loss).



Credit: NatureScot (Open Government License)

Figure 4.8 Marine ecosystem services and their influence on human well-being.

In a deoxygenating Ocean, cultural and aesthetic services are likely to diminish. A direct effect of oxygen depletion may be the replacement of once-healthy and aesthetically-pleasing coastlines with foul-smelling places (e.g. due to animal die-offs or the production of hydrogen sulphide, which has a strong sulphur smell that reduce the areas appeal (Limburg *et al.,* 2020). In addition, the degradation of coastal ecosystems does not end with the depletion of oxygen; rather, this is an intermediate step that is followed by more obvious and damaging effects, such as the production of toxic algal blooms and the creation of marine mucilage (or sea snot, a gelatinous component of marine organic matter that can aggregate into thick masses, float on the sea surface and can be dangerous for recreational users of the sea). Although more research is needed, deoxygenating areas may be more susceptible to such outbreaks. For instance, the most severe mucilage outbreaks to date have been documented in the northern Adriatic, intermittently between the years 2000-2020 (Precali *et al.,* 2005), and in the Marmara Seas, intermittently during the 2010s and 2020s, with the most intense event occurring in 2021 (Figure 4.10). This 2021 mucilage outbreak was both the longest in duration and the largest in areal extent recorded to date, and comparative analyses indicate that this event was of historical magnitude. Both the Marmara Sea and the Adriatic suffered from serious coastal hypoxia caused by anthropogenic nutrient run-off at the time of the outbreaks.

Figure 4.9 Dead fish following a low oxygen event in coastal waters in Ostend, Belgium in 2018.

Figure 4.10 Mucilage in the Marmara Sea, which is currently facing deoxygenation and rapid ecosystem decline.

5 Methods to study Ocean oxygen

Measuring and modelling Ocean oxygen is critical to accurately map deoxygenation, forecast oxygen loss and predict the effects of Ocean deoxygenation on the marine environment. This chapter describes methods and technologies that are available to study Ocean oxygen, including technological advances and limitations that still have to be overcome, such as the need for more observations and more accurate models of Oxygen Deficient Zones (ODZs).

The key messages from this chapter are:

- Technological advances (e.g. sensor development and autonomous platforms) have increased our capabilities to observe Ocean oxygen, enabling continuous measurements, increased spatial coverage and a better understanding of important processes affecting oxygen dynamics. Yet, more observations are needed and some areas remain under-sampled;
- Although the scientific and societal need to better understand ODZs and their variability is driving technological advances, observing and modelling very low oxygen concentrations remains challenging;
- Seabed sediments record the history of deoxygenation dating back millions of years. However, paleo oxygenation data sets from the geological past are still scarce and scattered;
- Earth System Models (ESMs) are powerful tools to assess how the land and Ocean will respond to different natural or anthropogenic scenarios. However, accurately representing oxygen variations in ESMs is challenging because low oxygen concentrations are the result of a balance between two large opposing processes: the ventilation of deeper waters with oxygen-rich surface waters and respiration; and
- Costal models can support the implementation of regional management strategies, such as managing excessive nutrient run-off through rivers leading to oxygen deficiency. To improve these models, data on atmospheric conditions and riverine inputs of nutrients and organic matter at higher spatial and temporal resolution are needed.

5.1 Measuring Ocean oxygen

Scientists have been interested in measuring oxygen in the Ocean since the inception of Oceanography (Dittmar, 1880). A critical step in the evolution of Ocean oxygen studies was the development by Winkler (1888) of an analytical wet chemistry method to measure oxygen in seawater, called the Winkler method. Modern variants of this method still underpin best practice in oceanographic oxygen measurements today (Langdon, 2010). The adaptation of the Winkler method for use onboard research vessels enabled the first basin-scale investigation of oxygen in the early 20th century (Wüst *et al.*, 1932). It has since been the main method used in international (repeated) hydrography studies, such as the Geochemical Ocean Section Study (GEOSECS)[10], the Joint Global Ocean Flux Study (JGOFS)[11], the World Ocean Circulation Experiment (WOCE)[12], the Climate Variability and Predictability Experiment (CLIVAR)[13] and the Global Ocean Ship-based Hydrographic Investigations Program (GO-Ship)[14]. Initially, discrete oxygen samples were collected using sampling bottles (e.g. Niskin bottles; Figure 5.1) which were deployed over the side of the ship using a hydrowire (i.e. a wire which is equipped to be lowered over the side of a ship into the water) and can be closed from the surface electronically or with a messenger (i.e. a dropping weight deployed on the wire).

[10] https://iridl.ldeo.columbia.edu/SOURCES/.GEOSECS/index.html?Set-Language=en
[11] http://usjgofs.whoi.edu/
[12] https://www.ewoce.org/
[13] https://www.clivar.org/
[14] https://www.go-ship.org/

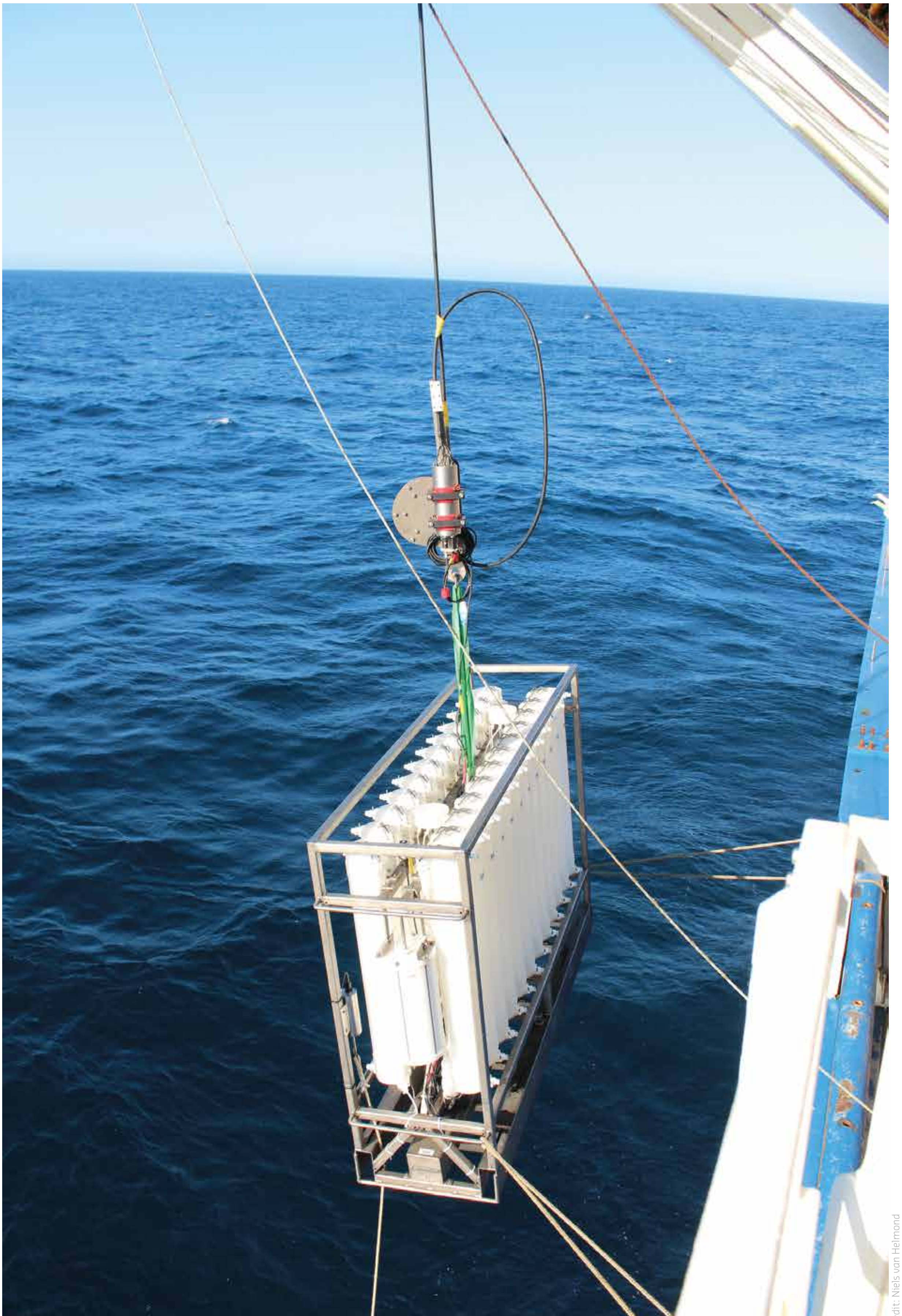


Figure 5.1 Niskin bottles used to collect discrete water samples. Niskin bottles are plastic cylinders with stoppers at each end to seal the bottle and ensure no accidental introduction of dissolved oxygen during the descent or ascent.

Credit: Niels van Helmond

Figure 5.2 A Conductivity-Temperature-Depth (CTD) device. The combination of CTDs with dissolved oxygen sensors and Niskin bottle collections facilitates the continuous measurement of oxygen in the water column.

The advent of electrochemical and optical fluorescence oxygen sensors (from around the 1970s and the early 2000s, respectively) has dramatically changed our capacity to measure oxygen. This has allowed continuous measurements of oxygen in the water column to be made, thanks to the inclusion of Clark oxygen electrodes - an electrode system that measures ambient dissolved oxygen concentrations in water (Clark *et al.,* 1953), in a standard Conductivity-Temperature-Depth (CTD) device (Figure 5.2). A CTD is an instrument cluster that measures seawater conductivity (a measure of the salinity of water), water temperature, and depth. While Clark oxygen electrodes have been a mainstay in oceanography for many decades, they have known issues with long-term reproducibility in deep-sea environments (Edwards *et al.,* 2010).

5.1.1 Step change in observing capacity by modern oxygen sensors

A long-standing challenge in the observation of Ocean oxygen has been to increase the spatial and temporal coverage of data in order to observe seasonal or long-term trends. Going to sea is expensive and the standard Winkler method (see above) is labour-intensive, and requires shipboard technicians and sampling equipment, making it expensive to use at large spatial scales. Repeat hydrography programs, such as the ones described above, do provide a valuable baseline for important Ocean regions, but some areas of the Ocean (e.g. Southern Ocean, Pacific and Indian Oceans) are still poorly studied due to logistics and cost.

Recently, low-power sensing optical sensors, called optodes, with good long-term accuracy and precision, have been developed, and can be applied to study oxygen (Bittig *et al.,* 2018). This new technology allows oxygen to be sampled at increased spatial and temporal ranges. Optodes are now routinely deployed on a range of Ocean-going platforms, including on the Argo network of autonomous floats[15] (Roemmich *et al.,* 2019; Figure 5.3). Argo is an international programme that collects information from the open Ocean using a fleet of robotic instruments that drift with the Ocean currents and move between the surface and deeper water, with standard Argo floats able to reach ~2,000m depth). Argo floats are deployed over the global Ocean and collect vertical profiles of temperature and salinity, along with other parameters, roughly every 10 days and relay their data back to shore via satellite links. The inclusion of oxygen optodes within the Argo program is the result of a major effort by the Argo community on sensor qualification (Bittig *et al.,* 2018) and data management (Virginie *et al.,* 2022) following foresight and effort by the Ocean biogeochemistry community (Gruber *et al.,* 2010) and Argo float manufacturers. Oxygen optodes form part of the Biogeochemical Argo program, along with sensors for nitrate and chlorophyll. There are now more than 500 Argo floats equipped with oxygen sensors, which represents 12-15% of the global array (generating >4,000 vertical oxygen profiles per year).

The data quality that can be obtained from optodes depends on their calibration method. A community-adopted calibration and calculation method has reduced uncertainty by a factor of two to three compared to the previous generation, resulting in an oxygen concentration precision of ~2 µmol/kg (e.g. Grégoire *et al.,* 2021). This compares to a precision of 0.15 µmol/kg for Winkler measurements (Langdon, 2010), which is therefore the reference method for measuring oxygen concentrations in the Ocean (except for very low oxygen environments such as ODZs) (Garcia- Robledo *et al.,* 2021), but this has limitations as highlighted above. The quality of measurement that oxygen sensors can make is improving continuously (Mignot *et al.,* 2019). Other Autonomous Underwater Vehicles (AUVs), such as Ocean gliders are now also routinely fitted with oxygen optodes (Barone *et al.,* 2019).

While the Argo programme provides good coverage for open Ocean oxygen data, Argo floats do not usually operate on the continental shelf. Only repeat hydrographic surveys or time series stations can make oxygen concentration measurements in these areas, and data resulting from these programs are scarce compared to Argo data. Therefore, many coastal areas, such as the southern continental shelf of the Mediterranean Sea, are not as well studied.

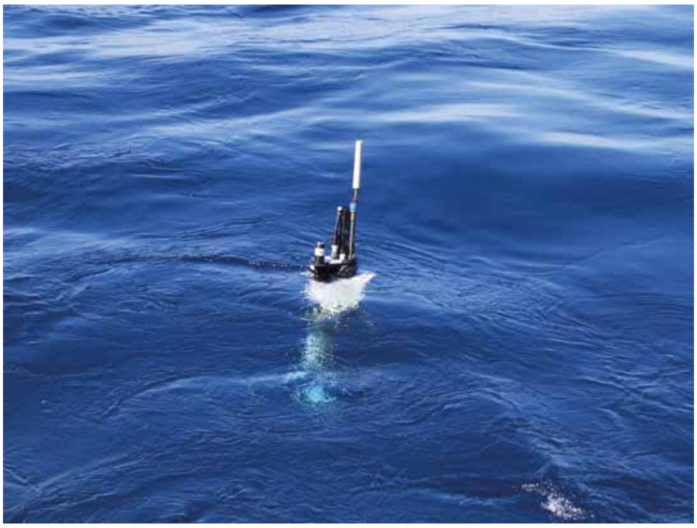


Figure 5.3 Left: An Argo float being deployed. **Right**: An Argo float with an oxygen sensor.

[15] https://www.argo.ucsd.edu

5.1.2 Measuring oxygen in ODZs

The value of data from repeat hydrographic surveys for oxygen is clear, in particular with regard to the expansion of ODZs (Stramma *et al.,* 2008). Interest in processes impacting oxygen cycling in ODZs has also driven improvements in observations, specifically the measurement of extremely low oxygen concentrations, typically below 1 µmol/L, which is at or below the detection limit of Winkler's method, Clark electrodes and oxygen optodes (Revsbech *et al.,* 2009). To measure such low concentrations of oxygen, the Switchable Trace Oxygen (STOX) electrode, a variant of the Clark electrode, was developed (Revsbech *et al.,* 2009, 2011). This electrode is very fragile and has a relatively slow response time, but it has enabled new insights into ODZs (Tiano *et al.,* 2014) revealing large zones of extremely low (nanomole -nM- level) or no oxygen.

5.1.3 Compiling and making Ocean oxygen data available

The recent initiative to establish a global database and atlas (GO2DAT) for Ocean oxygen measurements (Grégoire *et al.,* 2021) is a key step to making quality-controlled oxygen data openly available as a valuable resource to improve Ocean deoxygenation and Ocean health assessments. GO2DAT will gather oxygen data from both fixed and free-floating platforms, will adopt a community-agreed, fully documented meta-data format, and a consistent quality control procedure and quality flagging system. With the ever-increasing need to protect and sustainably manage the services the Ocean provides, GO2DAT will allow scientists to fully harness the increasing volumes of oxygen data delivered by the expanding global Ocean observing system and enable smooth incorporation of much higher quantities of data from autonomous platforms in the open Ocean and coastal areas into comprehensive data products in the years to come. This database will also link to existing international databases, such as the European Marine Observation and Data network (EMODnet)[16].

5.1.4 Determining the rates of biological processes impacting oxygen in the Ocean

Oxygen concentrations in the Ocean are affected by both physical and biological processes (Section 3.2.2), meaning that determining the exact causes of the observed oxygen changes can be challenging. A number of efforts are therefore trying to understand the individual effects of physical and biological processes on oxygen concentrations (Craig & Hayward, 1987).

The rates of biological processes impacting oxygen in the Ocean can be estimated thanks to analytical advances in mass spectrometry, a technique through which dissolved gases such as oxygen (O_2), Nitrogen (N_2) and Argon (Ar) can be measured in seawater (Emerson *et al.,* 1999). As Argon is not biologically active and is only impacted by physical mixing processes, the ratio of oxygen to Argon (O_2:Ar) in seawater can be used to make estimates of respiration (Barone *et al.,* 2019) and of net biological community production (the difference between gross photosynthesis, i.e. the overall photosynthesis before respiration, minus community respiration) (Teeter *et al.,* 2018). The advent of ship-based methods for the continuous monitoring of gases dissolved in water (Membrane Inlet Mass Spectrometry) has allowed the simultaneous measurement of CO_2 and O_2:Ar over basin scales (Guéguen & Tortell, 2008). Such basin scale measurements collect large amounts of data over wide areas, allowing to estimate the rate of these biological processes (particularly respiration and photosynthesis) at regional scale.

Credit: NOAA

Marine snow, such as depicted on this picture, is a shower of organic matter falling from the upper Ocean to the deep-sea. It serves as energy source for deep-sea animals, which consume oxygen upon its respiration.

[16] https://emodnet.ec.europa.eu/en

5.1.5 Measuring photosynthesis and respiration rates in the Ocean

Rate measurements (i.e. changes in concentration over time) of processes affecting oxygen concentration and distribution in the Ocean have been made as part of methods to measure primary production (Cullen, 2001). Community production is measured using either the Winkler method or oxygen optodes in a see-through bottle, while oxygen consumption (or respiration) is measured by the same methods in a dark bottle (Collins *et al.,* 2018).

Laboratory-based studies of the natural isotopic fractionation of oxygen (i.e. the partitioning of heavier and lighter oxygen isotopes) during marine photosynthesis (Luz & Barkan, 2000) have also advanced this field and provide information on gross oxygen production and respiration. The most reliable method for measuring gross oxygen production is the ^{18}O method, where water enriched with the oxygen-18 isotope ($H_2{}^{18}O$) is added to a sample and the subsequent photosynthetic production of ^{18}O-labeled O_2 is measured by a mass spectrometer (Ferrón *et al.,* 2016). This method is not affected by respiratory processes or incubation duration. Estimates of oxygen production can also be made from incubations using the differences in isotopic fractionation of carbon ^{14}C to estimate marine primary production, assuming a known ratio of oxygen produced to CO_2 consumed.

Large-scale measurements of oceanic respiration have proven more difficult due to the slower nature of this process in the intermediate and deep Ocean. Estimates of large-scale respiration in the Ocean have come from oxygen datasets collected as part of international repeat hydrography programs. These estimates, measured as oxygen consumed over time, and defined as Oxygen Utilization Rate (OUR), are obtained using transient abiotic tracers to infer the OUR from the Apparent Oxygen Utilization (AOU). AOU is a measure of oceanic respiration based on the assumption that the surface oxygen concentration is close to saturation with the overlying atmosphere and, therefore, that the difference in oxygen concentration is the amount taken up by respiration since the last contact of the respective water mass with the atmosphere. Transient abiotic tracers are chemical compounds that have been released to the atmosphere by humans as part of industrial activities (e.g. Chlorofluorocarbons, which were once used to keep fridges and freezers cold) and that upon entering the Ocean can be used to infer the time-scale since a particular water mass was in contact with the atmosphere (i.e. water age). Therefore, transient abiotic tracers can be used to estimate the water age of a particular water mass and, thus, represent a temporal component that allows to infer OUR from AOU. However, vertical mixing of different water masses and transient abiotic tracer means that the true respiration rate can differ substantially from the calculated OUR (Koeve & Kähler, 2016).

Oxygen optodes have been used to directly measure *in situ* respiration rates and the remineralisation rate of organic matter, trapped while sinking through the water column, and then deployed at depth at the actual *in situ* temperature and pressure (Boyd *et al.,* 2015). STOX electrodes are now also routinely deployed to measure respiration under low oxygen conditions (Holtappels *et al.,* 2014). However, much of the current research focuses on microbial respiration (Robinson, 2019) and the respiration of individual organisms (Vajedsamiei *et al.,* 2021), such as zooplankton (Hernández-León *et al.,* 2019) and mesopelagic fish (Belcher *et al.,* 2020). There are, therefore, not yet any direct measurements of all respiration taking place on the Ocean basin scale.

The increase in temporal and spatial data coverage provided by the Biogeochemical Argo program has provided insight into net community productivity and respiration over large Ocean areas (Gordon *et al.,* 2020), although measurement uncertainty remains very large (Hemming *et al.,* 2022).

5.1.6 Air-sea oxygen fluxes

One of the first reports on Ocean deoxygenation used changes in the concentration of oxygen in the atmosphere to identify an oxygen increase in the atmosphere that was attributed to a flux of oxygen from the Ocean (Keeling *et al.,* 2009). The loss of oxygen from the Ocean to the atmosphere due to global warming has been estimated using the Atmospheric Potential Oxygen (APO), a measure to study air-sea gas exchange (Keeling *et al.,* 2010). APO is calculated using high precision measurements of CO_2 and the ratio of O_2 to N_2 in the atmosphere ($APO = O_2 + 1.1CO_2$) (Stephens *et al.,* 1998). APO is primarily influenced by air-sea exchanges of CO_2, O_2 and N_2, insensitive to exchanges with the land biosphere and impacted by the exchange between O_2 and CO_2 due to fossil fuel burning. Seasonal changes in APO are a good indicator of seasonal variations in upper-Ocean biological production and ventilation (Nevison *et al.,* 2018). Thus, direct measurements of air-sea fluxes of oxygen could, at least theoretically, be used to quantify the loss of oxygen from the Ocean. Although this has been done in a few studies, a large amount of measurements are needed to accurately estimate the loss of oxygen from the Ocean to the atmosphere.

5.1.7 Oxygen fluxes at the seabed

Sediments are important sinks for oxygen in the Ocean. Processes occurring in sediments can have a significant oxygen demand (Rasmussen & Jørgensen, 1992), impacting oxygen fluxes across the benthic boundary layer (the sediment-water interface) (Jørgensen *et al.,* 2022). Efforts to measure oxygen concentrations in sediments have been facilitated by the development of micro-electrode oxygen sensors (Reimers, 2007). Initially, micro-electrode oxygen sensors were used onboard research vessels, were sediment cores were incubated to estimate water-sediment exchange. Later this technology was applied in situ by using benthic landers (Figure 5.4) and chambers (strong plastic cylinders with lid, Figure 5.5) (Spagnoli *et al.,* 2019). The incorporation of micro-electrodes into benthic landers, has allowed to create "benthic stations", which provide time series of oxygen concentration at the seabed for a period of several months (Toussaint *et al.,* 2014). In addition, mobile platforms (called crawlers or rovers) have also been deployed to provide data on the spatial and temporal oxygen variations at the seabed (Lemburg *et al.,* 2018). During the last decade, oxygen micro-electrodes and optodes have been combined with acoustic Doppler velocimeters (ADV) measurements (which record three-

Credit: Ines Bartl

Figure 5.4 A benthic lander being deployed from a ship. Benthic landers are observational platforms that sit on the seabed to record physical, chemical or biological activity.

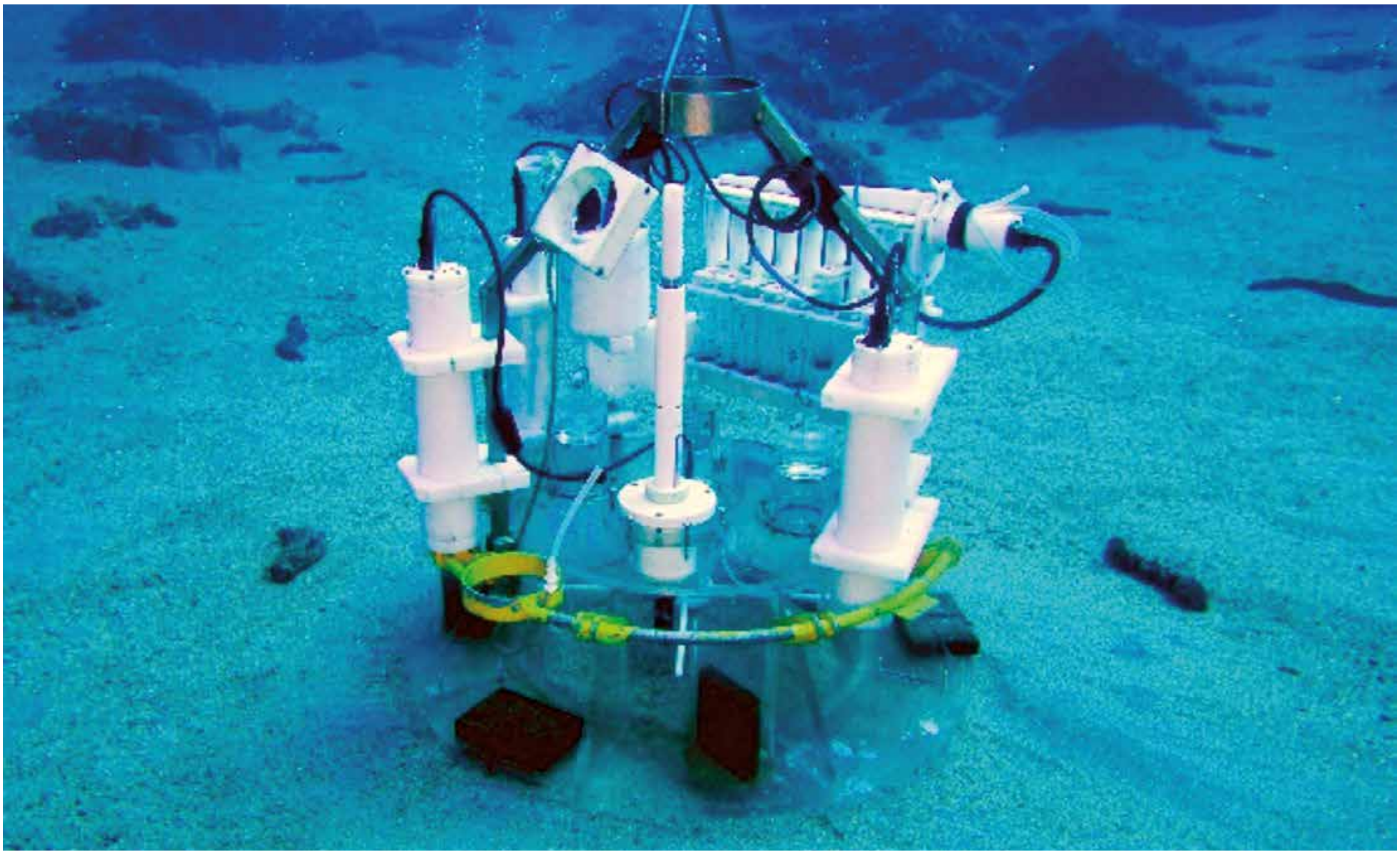


Figure 5.5 A benthic chamber operational on the seabed with various instruments.

dimensional current velocity field, temperature and depth) to measure oxygen fluxes at the sediment-water interface, without disturbing natural hydrodynamic and light conditions (e.g. Berg *et al.,* 2022). This is done through non-invasive Aquatic Eddy Covariance measurements, which measure vertical turbulent fluxes, such as the vertical oxygen fluxes at the sediment-water interface.

5.1.8 Reconstructing oxygen levels of the past

In the absence of observations, proxy data obtained from lake and marine sediments provide indirect evidence on past oxygen dynamics. Although this information is mostly non-quantitative, proxy data allow to reconstruct the degree of oxygenation at the seabed and in the water column over thousands to millions of years (see Chapter 2 and Section 3.3). Proxies encompass a wide range of different ecological and chemical parameters. For example, changes in benthic foraminifera (single-celled heterotrophic organisms with calcium carbonate shells) diversity are widely used to reconstruct bottom-water deoxygenation events because different foraminifera species can live at different oxygen levels (e.g. infaunal species living in the sediment versus epifaunal species living at the surface of the seabed can tolerate different levels of oxygen). Frequently these ecological data are combined with redox-sensitive elements, i.e. elements which can be used as semi-quantitative indicators for bottom-water oxygen concentrations because they are found more frequently in oxygen-poor sediments, such as Uranium (U), Vanadium (V), Molybdenum (Mo) and Antimony (Sb), and which are typically found in organic carbon-rich sediments. Their enrichment factor (i.e. the amount of substance relative to a standard), as well as their isotopic composition, varies as a function of the degree of oxygen deficiency (ranging from oxic to anoxic). Enrichment of sulphur, presence of pyrite and absence of biological mixing are also used as evidence of reduced oxygen conditions in bottom waters in the past. However, the oxygen concentrations inferred from redox-sensitive elements are semi-quantitative, because these elements only show clear signals when oxygen values are below certain (element-specific) thresholds. In addition to inorganic parameters, organic molecules provide information about past oxygen levels in the upper water column. For instance, specific pigments of green and purple sulphur bacteria are indicative of an anoxic euphotic zone (a zone with sufficient light to permit growth of plants) in which sunlight and reduced forms of sulphur provide the key ingredients for bacterial metabolism. Another proxy widely used in ODZs is the isotopic fingerprint of nitrogen ($\delta^{15}N$). In oxygen-poor conditions, denitrification (which converts bio-available NO_3^- to N_2) preferentially removes the light 14N and leaves a residual NO_3^- pool enriched in ^{15}N for phytoplankton to use. As a result, $\delta^{15}N$ values in sinking organic matter that accumulate in sediments increases with increasing oxygen deficiency.

Quantitative oxygen reconstructions have become a major new challenge. Promising results come from benthic foraminiferal assemblages and morphometric approaches, which analyse the size and shape of a species. In addition, since paleo oxygenation data sets are still scarce and scattered, future research would greatly benefit from the establishment of a large and systematic compilation and integration of semi-quantitative trace metal-based redox proxies, such as Cadmium (Cd), Rhodium (Rh) and Molybdenum (Mo), covering different modern environments to define standard thresholds for the objective classification of paleo oxygen levels (from oxic to anoxic). The combined use of several (semi-quantitative) trace metal-based redox proxies might allow to quantitatively reconstruct past oxygen conditions.

5.2 Modelling Ocean oxygen

5.2.1 Global oxygen simulations with Earth System Models

Mathematical Earth System Models (ESMs) are powerful tools to quantitatively assess the Earth System (which includes the land, water, biosphere and atmosphere) and its sensitivity to different natural or anthropogenic scenarios. ESMs consist of coupled atmosphere and Ocean general circulation models and include representations of processes relevant to Ocean biogeochemistry. When applied to the present-day climate, their main purpose is to understand and quantify climate-relevant processes and their interactions, ideally providing a good match with observational data. The application of climate conditions from the geologic past to the models (e.g. atmospheric CO_2, solar variations, ice sheets, distribution of continents) helps to better understand mechanisms of climate variability and climate change, interactions, feedbacks and tipping points (e.g. as done in the Paleoclimate Modelling Intercomparison Project[17]). The results from paleo simulations, in comparison with presently observed and modelled climate and biogeochemical changes, enable to quantify natural variability and potentially to distinguish it from anthropogenic change. In combination with data from paleo reconstructions, such as the oxygen proxies mentioned in Section 5.1.8, models can be assessed for their ability to simulate climate states different from today, which increases confidence in their results and applicability for future climate projections. These future projections are important to inform society and policymakers about the potential risks of anthropogenic climate change, for instance through the Intergovernmental Panel on Climate Change (IPCC)[18]. The results from these climate projections feed integrated assessment models (IAMs) and thereby guide decision-makers in the development of adaptation and mitigation strategies.

In current ESMs, the atmosphere is treated as an unlimited source/sink for oxygen, enabling unlimited exchange with the land and Ocean. This is justified since oxygen fluxes are very small compared to the respective reservoir sizes (Figure 3.2). Consequently, the surface Ocean oxygen concentration is always close to equilibrium with the atmosphere and is controlled by temperature-dependent oxygen solubility. As part of ESMs, Ocean biogeochemical models convert nutrients, carbon and oxygen in constant molar ratios during photosynthesis and respiration (Redfield, 1963). While this balance between photosynthesis and respiration is required for modelling a steady-state closed system, it may be an over-simplification.

[17] https://pmip.lsce.ipsl.fr/
[18] https://www.ipcc.ch/

Sufficiently accurate simulation of ODZs remains a major challenge for Ocean biogeochemical models, because these low oxygen concentrations are the result of a subtle balance between two large opposing processes: ventilation (i.e. the process that transports oxygen-rich water from the surface mixed layer into the Ocean interior) and respiration. The finite and often coarse spatial resolution of models creates circulation errors, which affect the transport of elements and impacts the estimates of photosynthesis, sinking organic particle fluxes and respiration. To validate the models with observational data, careful tuning of (often not very well-known) parameters, such as growth rates or respiration rates, in Ocean biogeochemical models is required (e.g. Kriest *et al.,* 2017). A further challenge is to apply these models to different future climate states.

Today, global Ocean biogeochemical models are able to simulate some aspects of marine oxygen distributions, including ODZs. For instance, they indicate that in the future average Ocean oxygen concentrations will decrease due to reduced solubility. However, they mostly fail to reproduce the observed trends of intensifying and expanding ODZs over the last decades (Oschlies *et al.,* 2017) and they also disagree on future ODZ development (Kwiatkowski *et al.,* 2020). Because ODZs can develop differently under small and large climate fluctuations (see Section 3.3), it is helpful to also consider paleoclimate simulations when assessing mechanisms driving ODZ change and in order to try to distinguish natural variability from human-induced changes.

5.2.2 Modelling the regional and coastal Ocean

Global models are not ideal for assessing oxygen deficiency in coastal regions, due to their coarse resolution and lack of coupling with land, river discharge and sediments. Therefore, regional models have been developed, which are based on the same physical and biogeochemical principles, but are applied at different spatial and temporal resolution. These models require inputs from the larger global models to describe their boundary conditions (i.e. the locations in the model that are affected by external factors, such as rivers and the atmosphere) and to set model scenarios (i.e. future projections based on different values that a driver, such as the amount of greenhouse gases that we will emit, could take). Regional models for the coastal Ocean follow a weather-based approach with medium- to short-term projection windows (<20 years) and can therefore support the implementation of regional management strategies, such as managing excessive nutrient run-off through rivers, which can lead to coastal oxygen deficiency.

For instance, the use of three-dimensional coupled biophysical models and eutrophication models have proven useful for understanding modern coastal hypoxia and can be applied to future global warming scenarios (Yu *et al.,* 2015).

Projecting oxygen levels in individual coastal water bodies requires modelling the variability of ventilation and the balance between primary production and respiration, from hours to weeks and in response to changing river discharge (e.g. fresh water, inorganic nutrients, suspended particles), local weather conditions (e.g. storms, flooding events, wind direction and speed, heat waves), interactions with offshore regions (e.g. advection, upwelling), oxygen consumption in the sediments, and possibly the influence of the tidal cycle. In this way, coastal and regional models have the ability to represent oxygen dynamics at weekly to monthly time scales but their performances can be hampered by the quality of the input to these models (or boundary conditions). The main inputs that hamper the model quality and need good quantification are river discharge and atmospheric forcing information, which often lack the required spatial and temporal resolution (Gregoire *et al.,* 2019).

Coastal models are progressively evolving towards a seamless coupling of the river-estuary-coastal Ocean continuum. This will improve our quantification of the export of nutrients and, in particular, of nitrogen and phosphorus from the river- to the Ocean. As a result, the eutrophication process can be better modelled and predictions of coastal hypoxia improved. Future work should include the application of regional models to create early warning systems, for example to forecast potentially hazardous situations such as sulphidic events and harmful algal blooms (e.g. Davidson et al. 2021). This requires the implementation of an operational framework to deliver near real-time early warning forecasts with high accuracy.

Credit: Jordan Heath, Unsplash

To improve the quality of coastal models, data on riverine inputs of nutrients and organic matter at higher spatial and temporal resolution are needed.

6 Addressing Ocean deoxygenation through mitigation and adaptation

Addressing Ocean deoxygenation is critical to achieving the aims of the UN Decade of Ocean Science for Sustainable Development (Ocean Decade) and the EU Mission: Restore our Oceans and Waters (Mission Ocean). Although reversing Ocean deoxygenation is not easy, action is urgently needed. This chapter describes mitigation and adaptation strategies that can help reduce the impacts, and in some cases, reverse oxygen loss in the Ocean.

The key messages from this chapter are:

- Limiting global warming will, according to current models, stop upper Ocean deoxygenation. For this, it is key to reach net-zero emissions of anthropogenic emissions of greenhouse gases;
- Coastal deoxygenation can in many regions be efficiently reduced by limiting terrestrial run-off of nutrients and organic waste;
- Recovery and possibly additional growth of blue carbon vegetative coastal ecosystems can help to add oxygen to coastal waters and thereby reduce the impacts of deoxygenation. Yet, this mitigation strategy is restricted to small near-shore habitats where blue-carbon species can grow, and these habitats are also impacted by human activities;
- Engineered addition of oxygen into Ocean regions that would otherwise experience critical oxygen loss has been proposed and may help to locally increase oxygen levels, but at the likely expense of non-local side-effects that may even accelerate global Ocean deoxygenation. Better knowledge is required before the implementation of such ideas can be seriously considered; and
- The deep-sea is already experiencing deoxygenation as a result of previously emitted greenhouse gases and will continue losing oxygen for centuries. Reducing other stressors on deep-sea ecosystems is important to increase their resilience.

Ocean oxygen supports the largest ecosystem on the planet. To minimise the impacts of ongoing deoxygenation on marine life and the provision of marine ecosystem services, management options need to be explored and implemented. Science can provide the appropriate knowledge for action and strategies for mitigation and/or adaptation should be co-designed with stakeholders.

Ocean deoxygenation is caused by global warming and pollution from nutrients and organic waste, which particularly affects coastal waters. Management strategies for its mitigation should therefore include reducing and eventually reaching net-zero anthropogenic greenhouse gas emissions, in particular CO_2, and preventing excess nutrients from reaching water bodies. This applies to wastewater from households and industry, nutrient run-off from agricultural areas and supply of nutrients via the atmosphere, in particular nitrous oxides from combustion engines, volatilisation of ammonium from fertilised fields and animal manure, and aerosols, e.g. from forest fires.

In coastal regions, restoration of blue carbon vegetative ecosystems such as seagrass meadows, mangrove forests, tidal marshes and kelp forests may help to enhance oxygen levels via photosynthesis in the upper layers of the water column (Veettil *et al.,* 2022). To increase the net amount of oxygen in these marine ecosystems, the photosynthetically produced plant material has to be either buried in the sediment, or harvested and removed from the water before respiration occurs. There have been some successful restoration initiatives for mangroves (e.g. Mekong Delta, Vietnam) and tidal marshes (e.g. the Scheldt estuary in the Netherlands) (Duarte *et al.,* 2020; Macreadie *et al.,* 2021). Although restoration of seagrass meadows is more complex, there are also some notable efforts, e.g. restoration of eelgrass meadows (Zostera marina) in Virginia (Orth *et al.,* 2020). Potential large-scale restoration of blue carbon ecosystems estimated in the range of 17.5–41.6 million hectares (=175,000-416,000km^2) (Macreadie *et al.,* 2021) could correspond to a net source of 0.007–0.03Pmol oxygen per year (e.g. Bertram *et al.,* 2021; Krause-Jensen & Duarte, 2016). However, any program to

A deep-sea crab on reef-forming cold-water corals at 800m depth in the Menez Gwen Hydrothermal Field southwest of the Azores. Deep-sea ecosystems will suffer the effects of deoxygenation for centuries.

enhance blue carbon vegetative ecosystems may be counteracted by human activities, such as dredging and coastal development, that can prevent their development. Appropriate governance schemes will be required for blue carbon to have the desired long-term effects on ecosystems and biogeochemistry.

There have also been some suggestions to enhance dissolved oxygen in the Ocean by actively pumping oxygen-rich waters into oxygen depleted regions. Such strategies have worked successfully in small lakes, and field experiments have been carried out with mixed success in semi-enclosed seas, e.g. in the By Fjord in western Sweden (Stigebrandt *et al.,* 2015). Theoretical considerations and numerical modelling suggest that such engineering approaches might locally enhance oxygen levels, but would globally lead to a further decline in oxygen levels due to pumping-induced changes in nutrients and temperature (Feng *et al.,* 2020). Therefore, pumping dissolved oxygen into oxygen-poor waters is unlikely to change the balance of un-oxygenated and oxygenated water. In addition, in many areas the volume of ODZs defies the logistical resources to generate and pump enough dissolved oxygen and the pumping itself could release further CO_2 emissions if they are not powered by renewable energy. These methods require further study and risk assessment analysis before they can be implemented, and they also require good governance schemes to be in place in order to responsibly deal with intended and unintended local and non-local effects.

Modelling studies have shown that reaching net-zero CO_2 emissions will largely stop further warming of global atmospheric air temperatures (MacDougall *et al.,* 2020), which in turn will stop deoxygenation in the upper layers (covering approximately the upper 300m) of the Ocean (Oschlies, 2021). Deeper layers of the Ocean, however, are expected to continue losing oxygen for centuries due to the reduced oxygen solubility in surface waters compared to pre-industrial waters. These pre-industrial waters still make up most of the water in the Ocean interior today, but they are slowly being replaced by the warmer industrial era water, which holds less oxygen. Deep-sea oxygen loss is further exacerbated by the expected decline in the general overturning circulation in a more stratified Ocean, which will be the result of the warming and freshening of surface waters due to melting continental ice sheets. This decline increases the time water spends in the deep Ocean during which respiration of sinking organic matter continues to consume oxygen. Models suggest that the deep-sea may lose up to 10% of its oxygen, and locally more, due to anthropogenic greenhouse gases that have already been emitted, which could have substantial impacts on deep-sea ecosystems (Oschlies, 2021). The only viable management option for adapting to the impacts of deep-sea deoxygenation is to reduce other stressors acting on deep-sea ecosystems and to increase their protection so they can be more resilient to stress from deoxygenation. Although this is particularly critical for deep-sea ecosystems, reducing stressors in other marine ecosystems and increasing their protection, will also help to enhance their resilience to Ocean deoxygenation.

All management options require a reliable oxygen observation and monitoring system in the Ocean to ensure that the initial state and side effects can be measured and reported. Understanding if observed changes can be attributed to specific management options and separated from natural variations will remain challenging.

7 Recommendations

A well-oxygenated Ocean is vital to sustain modern biogeochemical cycles, which regulate the global carbon cycle and keep the Earth system in balance. The ongoing loss of oxygen is a rapidly increasing threat to marine life, the Ocean ecosystem and ultimately humanity, which depends on a healthy Ocean. Ocean deoxygenation affects water quality and marine food webs, thereby impacting fisheries, the economy and the billion humans who depend on the ecosystem services provided by the Ocean. The actions needed to halt and reverse Ocean deoxygenation, including reaching net-zero greenhouse gas emissions, reducing pollution, and increasing ecosystem resilience through protection and restoration, closely match the aims of the European Green Deal (COM/2019/6 final, 2019). Although these objectives require marked changes in our society and lifestyle, the cost of inaction and the consequences of deoxygenation are far greater than the costs of action. The threat of Ocean deoxygenation therefore represents another wake-up call on how critical it is to achieve those objectives. We conclude with the following recommendations for policy, management and science.

7.1 Recommendations for policy and management

To address the threat of Ocean deoxygenation we recommend to:

- **Recognise Ocean deoxygenation as one of the major threats to marine ecosystems:** Ocean deoxygenation is a major threat to marine ecosystems and stakeholders and policymakers need to understand that the impacts will be at least as severe as Ocean warming, Ocean acidification and sea-level rise;
- **Reduce and eventually reach net-zero anthropogenic emissions of greenhouse gases to stop upper Ocean deoxygenation:** Global warming is a major contributor to the decrease of oxygen in the Ocean and limiting global warming will stop upper Ocean deoxygenation. Decisive actions are needed to reduce and stop anthropogenic emissions of greenhouse gases;
- **Limit run-off of nutrients and organic waste into the Ocean to reduce and reverse coastal deoxygenation and hypoxia:** Nutrient run-off and other organic waste increases the consumption of Ocean oxygen, leading to deoxygenation;
- **Promote resilience of marine life to Ocean deoxygenation by reducing stressors and increasing protection, especially in deep-sea ecosystems:** Ocean deoxygenation is expected to continue for centuries in the deep-sea, even after reaching net-zero anthropogenic greenhouse gas emissions, because of the slow replacement of deep-sea waters by surface waters and the expected decline in the general overturning circulation in a more stratified Ocean; and
- **Include Ocean oxygen in future projections by intergovernmental bodies and in high-level frameworks for planetary health:** To spur action and societal awareness, Ocean deoxygenation should be included in societal and political frameworks for planetary health, such as the United Nations Sustainable Development Goals (SDGs) and the nine Planetary Boundaries of the Stockholm Resilience Centre[19], as well as in future projections and assessments performed by intergovernmental bodies, such as the Intergovernmental Panel on Climate Change (IPCC) and the Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES).

[19] https://www.stockholmresilience.org/research/planetary-boundaries/the-nine-planetary-boundaries.html

- **To provide the most accurate information on the role of the Ocean in the oxygen we breathe, we recommend using the following statements:**
  - ✓ The Ocean produces ~50% of Earth's oxygen;
  - ✓ Every second breath taken by all life on Earth comes from the Ocean; and
  - ✓ Since the origin of life on Earth, the Ocean has provided most of the oxygen in the atmosphere, and is responsible for 6 of 7 breaths humans take.

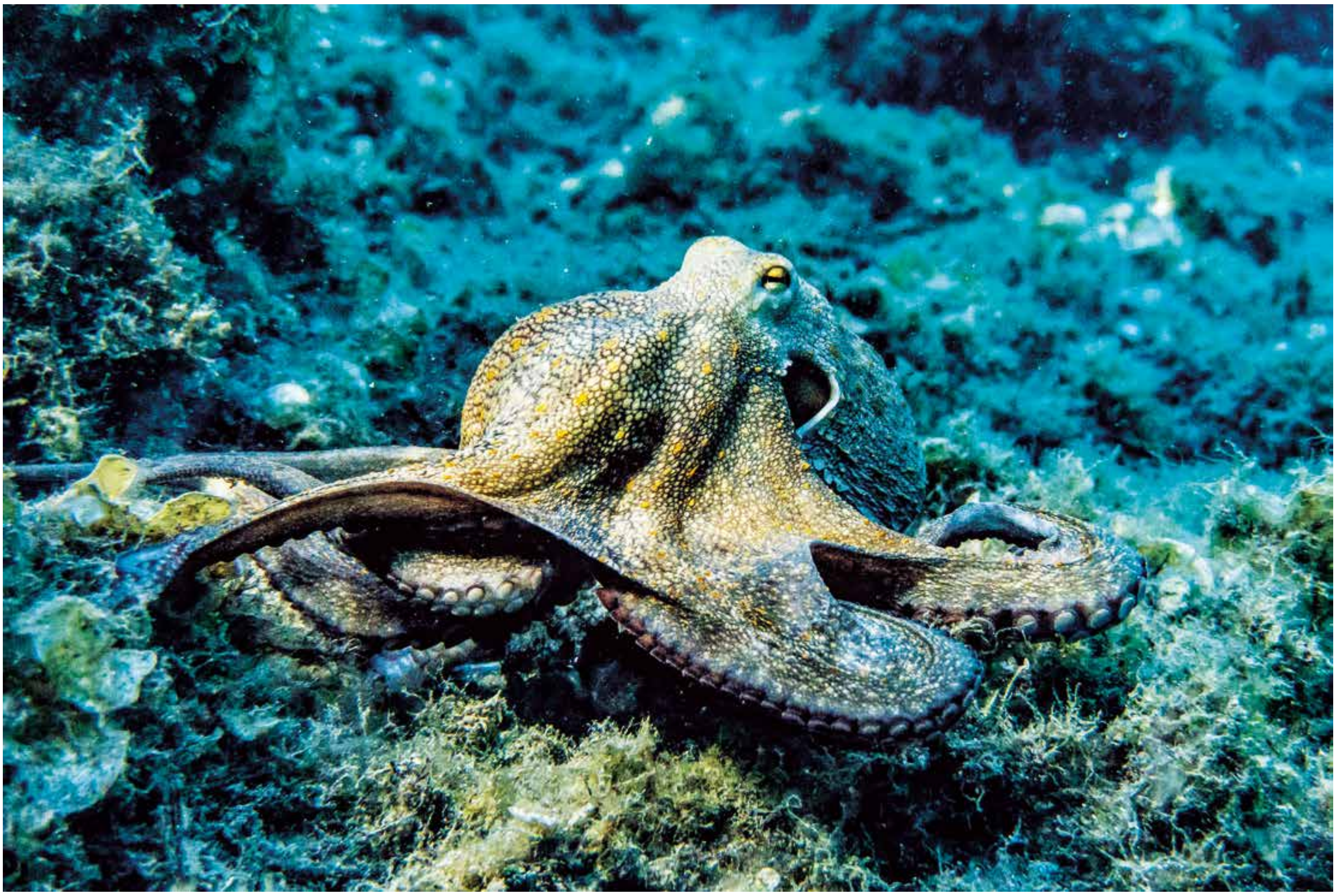
7.2 Recommendations for funders, research and monitoring

To advance our knowledge on Ocean oxygen dynamics, including deoxygenation, we recommend to:

- **Fund and perform coordinated research to better understand historical, current and future Ocean deoxygenation rates:** This includes research on feedbacks from biogeochemical cycles and their relation to historical mass extinction events. Moreover, oxygen should be included in climate simulations of the past;
- **Fund and perform targeted research to enhance understanding of the biological, chemical and physical processes controlling oxygen dynamics:** Key processes affecting oxygen dynamics such as carbon export and respiration, as well as the coupling of oxygen with biogeochemical cycles, sediments and the production of greenhouse gases are not well understood. Moreover, there is a need for better quantification of seawater residence times, mixing and ventilation rates to determine the individual effects of physical and biogeochemical processes on oxygen concentrations, which will require controlled experiments and field studies in the benthic and pelagic realm. Understanding and parameterisation of these key processes is essential for estimating consequences of different actions and for quantifying feedbacks to Ocean deoxygenation in the Earth system;
- **Fund and increase Ocean oxygen observations and modelling efforts to accurately document and predict Ocean oxygen changes:** Limited oxygen observations hinder the development of reliable parametrisations of processes and rates in models. More oxygen observations are needed to accurately estimate the total number of coastal hypoxic sites and to make a comprehensive assessment of the severity of low-oxygen conditions at seasonal and interannual scales. Oxygen concentration and variability in the Ocean should be monitored and studied at relevant spatial and temporal scales, and in a globally consistent manner, to accurately document and predict changes. Coordinated observing and modelling systems for both the open and coastal Ocean need to be developed to quantify oxygen changes and associated ecological and biogeochemical impacts, in particular in oxygen deficient zones where accurate measurement and modelling are challenging;
- **Develop new low-power and low-cost oxygen sensors and ensure that all oxygen data feeds into global databases:** New low-power and low-cost sensors need to be developed to increase the accuracy and range of Ocean observations, particularly for low oxygen concentrations. These sensors should be included in autonomous observing platforms and supported by best practices for data management, reporting and quality control. The data obtained from these sensors should feed into international and open-source databases, such as the Global Ocean Oxygen Database and Atlas (GO2DAT) and EMODnet[20]. In addition, all data should be shared and compiled into these open access databases to foster the generation of societally useful oxygen information products and indicators at the right resolution to users to support informed policy-making;
- **Include oxygen in multiple stressor studies of marine environments:** Deoxygenation is one of the most challenging environmental stressors for marine animals, but other stressors may exacerbate its impact. Ocean acidification and warming frequently co-occur with deoxygenation because they have a common cause: the rise of anthropogenic CO_2 in the atmosphere. It is therefore important to study this "triple threat" in combination. Moreover, other stressors, such as pollution and overexploitation can further exacerbate the impact of deoxygenation on marine life, ecosystems and ecosystem services;

[20] https://emodnet.ec.europa.eu/en

- **Fund and perform research to better understand how deoxygenation will impact marine life and ecosystems, from populations to ecosystems:** For instance, extreme habitat compression events can have major impacts on ecosystem functioning and require further study. It is also important to study the individual-specific differences in oxygen thresholds to understand how populations and, in turn, species will respond to deoxygenation; and
- **Fund and perform research to better understand the vulnerability of ecosystem services, our society and our economy to deoxygenation:** Qualitative and quantitative research are needed to better understand the ecosystem services supported by oceanic and coastal oxygen and to assess their vulnerability, as well as the vulnerability of our society and economy, to deoxygenation through appropriate socio-economic models coupled with ecosystem models. In particular, a better understanding is needed on how deoxygenation affects the climate regulation service of the Ocean (e.g. the cycling of carbon, nitrogen and oxygen; the production and absorption of greenhouse gases; and the areal extent of coastal vegetated ecosystems that contribute to carbon burial), provisioning services such as food (fisheries and mariculture) and water quality (e.g. in connection with harmful algal blooms); and habitat maintenance services, such as linking oxygen loss to biodiversity.



Credit: Pia B, Pexels

Most marine life relies on oxygen for its survival and Ocean deoxygenation is a rapid growing threat.

List of abbreviations and acronyms

AAAS	American Association for the Advancement of Science
ADV	Acoustic Doppler Velocimeter
AEC	Aquatic Eddy Covariance
AOU	Apparent Oxygen Utilization
APO	Atmospheric Potential Oxygen
AUV	Autonomous Underwater Vehicle
CLIVAR	Climate Variability and Predictability Experiment
CTD	Conductivity-Temperature-Depth device
EBUS	Eastern Boundary Upwelling Systems
ENSO	El Niño Southern Oscillation
ESM	Earth System Model
GEOMAR	Helmholtz-Zentrum für Ozeanforschung Kiel, Germany
GEOSECS	Geochemical Ocean Section Study
GO-SHIP	The Global Ocean Ship-based Hydrographic Investigations Program
GOE	Great Oxidation Event
GPP	Gross Primary Productivity
IAM	Integrated Assessment Model
IFREMER	Institut Francais de Recherche pour l'Exploitation de la Mer, France
IIM-CSIC	Instituto de Investigaciones Marinas, Spain
IPBES	Intergovernmental Panel on Biodiversity and Ecosystem Services
IPCC	Intergovernmental Panel on Climate Change
IRB	Institut Ruđer Bošković, Croatia
JGOFS	Joint Global Ocean Flux Study
NCP	Net Community Production
NOAA	National Oceanic and Atmospheric Administration, US
NODC	National Oceanographic Data Centre
NOE	Neoproterozoic Oxygenation Event

NPP	Net Primary Production
ODZ	Oxygen Deficient Zone
OMZ	Oxygen Minimum Zone
OrgC	Organic matter
OUR	Oxygen Utilization Rate
PDO	Pacific Decadal Oscillation
Pg	Peta gram
Pmol	Peta mol
POE	Paleozoic Oxygenation Event
ppm	Parts Per Million
psu	Practical Salinity Unit
SDGs	United Nations Sustainable Development Goals
WOCE	World Ocean Circulation Experiment

Glossary

Acoustic Doppler velocimeter (ADV) - An instrument used to measure the three-dimensional current velocity field, temperature and depth

Advection - The transport of a substance or of heat by the flow of a liquid. In the Ocean, advection takes place through currents

Aerobic - With oxygen, when referring to a process

Anaerobic - Without oxygen, when referring to a process

Anammox - A microbial process in which ammonium and nitrite are converted into nitrogen gas and water

Anoxic - Without oxygen, when referring to an environment

Apparent Oxygen Utilization - A measure of oceanic respiration based on the assumption that the surface oxygen concentration is close to saturation with the overlying atmosphere and, therefore, that the difference in oxygen concentration is the amount taken up by respiration since the last contact of the respective water mass with the atmosphere

Aquatic Eddy Covariance - Measures vertical turbulent fluxes, such as benthic oxygen fluxes

Argo - An international program that collects information on Ocean properties using a fleet of robotic instruments

Atmospheric Potential Oxygen - A measure to study oxygen air-sea gas exchange

Atom - A particle of matter that consists of a nucleus (formed of protons and neutrons) surrounded by electrons. The atom uniquely defines a chemical element, and the chemical elements are distinguished from each other by the number of protons that are in their atoms

Autotroph - An organism that can produce its own energy (i.e. food). Because autotrophs produce their own food, they are also called primary producers. The most well-known autotrophs are plants, which produce their own food through photosynthesis, using light, carbon dioxide and water, but there are also organisms (e.g. in the deep-sea) that can produce their food through other chemicals

Benthic boundary layer - The water directly overlying the seabed where processes are influenced by the presence of the bottom, i.e. the sediment-water interface

Benthic lander - Observational platforms that sit on the seabed or benthic zone to record physical, chemical or biological activity

Bio-active element - Elements that interact with living organisms

Bio-essential element - Elements that are essential for the functioning of most living organisms, such as carbon, oxygen, nitrogen, phosphorus and sulphur

Bioavailable - When referring to an element: the forms of the element, in which it is most easily used and taken up by living organisms. For instance, for nitrogen (N), the bioavailable forms are nitrate (NO3), nitrite (NO_2), ammonia (NH3) and ammonium (NH4)

Biogeochemical processes - The chemical, physical, geological and biological processes that occur in natural environments

Biosphere - The biosphere are all parts on Earth where life exists, or the sum of all ecosystems on Earth

Boundary conditions - The locations in a model, which are affected by external factors. For instance, where water flows in or out of the model due to external factors, such as rivers and the evapotranspiration in the atmosphere

Boundary currents - Ocean currents with dynamics determined by the presence of a coastline. Boundary currents can flow either along a western coastline (called western boundary currents) or along an eastern coastline (eastern boundary currents)

Chemosynthesis - The production of energy using chemicals instead of light, water and carbon dioxide, typically in the absence of sunlight (e.g. in the deep-sea)

Clark type oxygen electrodes - An electrode system that measures ambient dissolved oxygen concentrations in water

Climate anomaly - The difference between the average climate over a period of several decades or more, and the climate during a particular month or season

Conductivity - Temperature-Depth device - An instrument cluster that measures seawater conductivity (a measure of the salinity of Ocean water), water temperature, and depth

Deep-sea - The deep-sea are the waters below about 200m, the depth at which there is no longer enough sunlight for photosynthesis to occur

Deep water formation - The sinking of water masses from the surface to the deep-sea. Deep waters are formed where air temperatures are cold and where the salinity of the surface waters are relatively high. The combinations of salinity and cold temperatures make the water denser and cause it to sink to the bottom.

Denitrification - A microbial process in which nitrate and nitrite are reduced to nitrous oxide or nitrogen gas

Earth System - The four major subsystems of Earth (called spheres). These are the lithosphere (land), hydrosphere (water), biosphere (living things), and atmosphere (air)

Earth System Models - Mathematical models used to quantitatively assess the Earth System and its sensitivity to different natural or anthropogenic forcings. Earth System Models consist of coupled atmosphere and Ocean general circulation models and include representations of processes relevant to Ocean biogeochemistry

Eastern Boundary Upwelling Systems - Naturally oxygen-poor zones (along the western coasts of Peru/Chile, Namibia, California and Mauritania/Senegal) because they are highly productive due to an increased nutrient input from deeper waters, and poorly ventilated by circulation. The high productivity leads to high oxygen consumption rates

El Niño Southern Oscillation - A climate phenomenon resulting in warming or cooling of Ocean surface waters (to as deep as ~150m below the surface), with two opposite phases (el Niño/ la Niña). El Niño results in a warming of the Ocean surface, or above-average sea surface temperatures, in the central and eastern tropical Pacific Ocean. La Niña is a cooling of the Ocean surface, or below-average sea surface temperatures (SST), in the central and eastern tropical Pacific Ocean

Enrichment factor - The amount of substance of an element relative to a standard reference value

Eon - The largest unit of geological time. There have been four eons during Earth's history: Hadean, Archean, Proterozoic and Phanerozoic (the latter is the eon we are currently part of)

Epifauna - Animals living on the surface of the seabed

Eukaryotes - Organisms with organelles and a membrane-bound nucleus; animals and plants are eukaryotes

Euphotic zone - The region where light is sufficient for the growth of plants. It generally extends from the surface to a maximum of about 150m in the clearest oceanic water

Eutrophication - A process of enrichment of a natural system with nutrients and organic matter, which can lead to coastal oxygen deficiency

Euxinic - Without oxygen and sulphidic, when referring to an environment

Feedback - When referring to biogeochemistry, a process that either amplifies or diminishes the effect of a factor

Foraminifera - Single-celled heterotrophic organisms (i.e. which cannot produce their own energy through photosynthesis) with calcium carbonate shells

Global coastal Ocean/ coastal Ocean - The marine area from the shoreline to the edge of the continental margins

GO2DAT - A global database and Atlas for Ocean oxygen measurements

Great Oxidation Event - An event that occurred around 2.4 billion years ago, leading to a dramatic increase in the oxygen content of the atmosphere

Gross Primary Productivity - the amount of inorganic carbon fixed during photosynthesis in an ecosystem during a given period of time

Halocline - Stratification of two water layers due to a rapid change in salinity and therefore different water densities

Heterotroph - An organism that cannot produce its own energy from primary production (i.e. trough photosynthesis) and therefore consume organic matter, mainly plant or animal matter

Holocene - The current geological period, which started 11,700 years ago

Holocene Climate Optimum - The Holocene Climate Optimum was a warm period which occurred roughly 9,500 to 5,500 years ago, during the mid-Holocene. This warm period was followed by a gradual decline in temperature, of about 0.1 to 0.3°C per millennium, until about two centuries ago when this trend was rapidly reversed due to human-produced greenhouse gas emissions

Hydrowire - A wire which is equipped to be lowered over the side of a ship into the water

Hypoxia - Oxygen concentrations below 62 µmol/kg, when referring to an environment

Infauna - Animals living in the sediments of the seabed

Intra-specific variation - Differences occurring within individuals of a species

Ion - An atom that carries a positive or negative electric charge

Isopycnals - Layers within the Ocean that are stratified based on their densities and can be shown as a line connecting points of a specific density on a graph

Isotope - Variations of the same element that have the same number of protons but different numbers of neutrons in their nucleus

Last Glacial Maximum - A period of time during the last ice age, where the ice sheets were at their greatest extent (approximately 21,000 years ago)

Legacy of hypoxia - The delay in recovery of a system after a period of hypoxia because of biogeochemical feedbacks that increase the demand for oxygen

Mariculture - A branch of aquaculture in which marine organisms are cultivated, e.g. for food

Mass spectrometry - An analytical method that is used to measure dissolved gases such as oxygen (O_2), Nitrogen (N_2) and Argon (Ar) in seawater

Membrane Inlet Mass Spectrometry - A ship-based method for the continuous monitoring of gases dissolved in water

Model scenarios - Future projections of a model, based on different values that a driver, such as the amount of greenhouse gases that we will emit, might take

Mol - A unit denoting the amount of a substance, which is defined as 6.02214076×1023 elementary entities

Morphometry - The quantitative analysis of form (e.g. of a species), including size and shape

Multiple Stressors - More than one event, agent or environmental condition causing stress to individuals, populations or ecosystem

Neoproterozoic Oxygenation Event - A possible significant increase in oxygen levels in Earth's atmosphere and Ocean around 650-700 million years ago

Net Community Production - The difference between gross primary production and ecosystem respiration

Net Primary Production - The amount of carbon fixed during photosynthesis in an ecosystem during a given period of time minus respiration losses by the photosynthesisers

Nitrification - Microbial process in which ammonium is oxidised to nitrite and nitrate

Optodes - Low-power optical sensing device that optically measures a specific substance usually with the aid of a chemical transducer

Organic matter - All matter composed of carbon-based (i.e. organic) compounds. It is matter composed of organic compounds that have come from the faeces and remains of organisms such as plants and animals

Oxic - With oxygen, when referring to an environment

Oxidation - Reaction in which electrons are lost. This reaction often involves oxygen

Oxycline - A depth in the sea where there is a strong vertical gradient in oxygen concentrations

Oxygen Deficient Zones - Refers to regions in the Ocean where oxygen concentrations are below critical threshold values, thereby impacting marine life and/or biogeochemistry. ODZs can occur naturally in particularly intense Oxygen Minimum Zones

Oxygen Minimum Zones - Regions in the Ocean that display persistent, natural low oxygen concentrations in vertical profiles, often found to occur naturally in the tropical Ocean at a depth several tens to a few hundred metres .

Oxygen sink - A mechanism that consumes or removes oxygen

Oxygen solubility - The amount of dissolved oxygen seawater can hold (i.e. the concentration of oxygen in the water). This depends, among other factors, on water temperature

Oxygen source - A mechanism that produces or releases oxygen

Oxygen Utilization Rate - The oxygen consumption during a certain time period

Pacific Decadal Oscillation - A climatic oscillation which covers large areas of the Pacific Ocean over periods of several decades. Positive PDO phases are when sea surface temperatures are anomalously cool in the interior North Pacific and warm along the Equator and the Northeast Pacific Coast. Negative PDO phases are when this pattern is reversed

Paleozoic Oxygenation Event - A time in the geological past (~400 million years ago) when atmospheric oxygen first reached modern-like levels in association with the evolution and proliferation of land plants

Period - A unit of geological time smaller than an eon (e.g. one eon can comprise many periods). It typically lasts tens of millions of years

Peta - A unit which equals 1015

Photosynthesis - A process by which plants use sunlight, water and carbon dioxide to produce energy in the form of sugars and, as a by-product, oxygen

Photosynthetic primary production - The production of organic matter by organisms through photosynthesis, liberating oxygen in the process

Phytoplankton - Microscopic marine algae that similar to terrestrial plants require sunlight in order to live and grow, because they obtain their energy through photosynthesis

Plankton - Organisms in the Ocean that are carried by tides and currents, and cannot swim well enough to move against these forces (the word "plankton" comes from the Greek for "drifter" or "wanderer"). Plankton can be classified in several ways, including by size, type, and how long they spend drifting. But the most basic categories divide plankton into two groups: phytoplankton (plants) and zooplankton (animals)

Practical Salinity Unit - A unit to measure salinity in seawater based on the conductivity of seawater

Primary producers - Organism that can produce their own energy (i.e. food), also called autotrophs. The most well-known primary producers are plants, which produce their own energy through photosynthesis, using light, carbon dioxide and water. However, some organisms (e.g. in the deep-sea) can produce their own energy through other chemosynthesis (using other chemicals in the absence of sunlight)

Primary productivity - The amount of carbon fixed during photosynthesis in an ecosystem during a given period of time

Primary production - The creation of new organic matter by autotrophs (i.e. organisms that produce their own energy, such as plants and algae), when they do photosynthesis or chemosynthesis (the production of energy using chemicals - instead of light, water and carbon dioxide - typically in the absence of sunlight (this is by some bacteria and other organisms, for instance in the deep-sea)

Pycnocline - A depth in the sea where there is a strong vertical density gradient, acting as a barrier for vertical exchange/mixing

Pyrite - A naturally occurring mineral that is found in a variety of rocks and geological formations

Redox sensitive elements - Elements which can be used as indicators for bottom-water oxygen concentrations because they are found more frequently in oxygen-poor sediments, such as Uranium (U), Vanadium (V), Molybdenum (Mo) and Antimony (Sb)

Reduction - A reaction in which electrons are gained

Redox reaction - An oxidation–reduction or redox reaction is a reaction that involves the transfer of electrons between chemical species (i.e. atoms, ions, or molecules involved in the reaction). The chemical species that is oxidized loses electrons while the reduced one gains electrons

Residence time - When referring to seawater, the time it takes for a water mass to be "renewed", i.e. exchanged, or mixed with new water through currents, heat, rain, winds, etc.

Respiration - A process whereby living organisms breakdown sugars to carbon dioxide and water, generating energy and consuming oxygen. In humans and other animals this is called "breathing", but microbes also respire when they use oxygen to decompose organic matter thereby obtaining energy

Sapropels - Organic-rich, nearly black marine sediments

Saturation - The maximum possible amount of a gas (such as oxygen) dissolved in a volume of water at a given temperature

Secondary production - The formation of living mass (i.e. number and growth of individuals) of a population or group of populations of individuals, which depend on primary production, for their growth and survival (i.e. they are heterotrophs). It is the heterotrophic equivalent of primary production by autotrophs

Sedimentary rocks - Sedimentary rocks are types of rocks that are formed on or near the Earth's surface from the compression of pre-existing rocks or rests of once-living organisms

STOX electrode - The switchable trace oxygen (STOX) electrode is a variant of the Clark type electrode that is modified to have two sensing cathodes. This allows the measurement of extremely low oxygen concentrations

Suboxic zone - The transition layer between the oxic and anoxic waters (i.e. with and without oxygen), in which the concentration of oxygen is very low (~ 5-10 µmol/kg) and practically all multi-cellular life disappears

Sulphidic - An environment with hydrogen sulphide, also called "euxinic"

Sunlit Ocean surface waters - The sunlit waters extend from the surface to a maximum of about 200 meters

Surface mixed layer - The surface waters in the Ocean, which are typically well mixed by wind, and heat loss (e.g. at night or in the winter). This layer typically covers the first tens of metres of surface waters, although the depth of this layer changes seasonally

Thermocline - The transition layer between warm surface waters and colder deeper waters

Trace metal - Metals that are present in very small quantities, such as iron in seawater

Transient tracers - Chemical compounds that have been released to the atmosphere by humans through industrial activity (e.g. Chlorofluorocarbons, which were once used to keep fridges and freezers cold). Transient tracers act like a dye in Ocean currents that scientists can measure and track. Determining the age and the amount of these tracers in the water column can tell us about the rates and pathways of Ocean circulation and mixing patterns.

Ventilation - The process that transports water and important gases such as oxygen and carbon dioxide from the surface mixed layer into the Ocean interior

Water age - The time since a particular water mass was in contact with the atmosphere

Winkler method - An analytical wet chemistry method for measuring dissolved oxygen in water

Chemical compounds and formulas

Ammonia	NH_3
Ammonium	NH_4^{+}- -
Antimony	Sb
Argon	Ar
Cadmium	Cd
Carbon	C
Carbon-14 isotope	^{14}C
Carbon dioxide	CO_2
Ferric oxide	Fe_2O_3
Glucose	$C_6H_{12}O_6$
Hydrogen molecule (dihydrogen)	H_2
Hydrogen ion	H^+
Hydrogen sulphide	H_2S
Iron	Fe
Methane	CH_4
Molybdenum	Mo
Nitrate	NO_3^-
Nitrite	NO_2^-
Nitrogen	N
Nitrogen-14 isotope	^{14}N
Nitrogen-15 isotope	^{15}N
Nitrogen molecule (dinitrogen)	N_2
Nitrous oxide	N_2O
Oxygen (atom)	O
Oxygen-18 isotope	^{18}O
Oxygen molecule (dioxygen)	O_2
Phosphorus	P
Pyrite	FeS_2
Rhodium	Rh
Sulphate	SO_{42-}
Sulphide	S^{2-}-
Uranium	U
Vanadium	V
Water	H_2O
Water molecule enriched with oxygen-18 isotope	$H_2{}^{18}O$

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Annex 1

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