Ocean deoxygenation: Everyone’s problem

Causes, impacts, consequences and solutions

Summary for Policy Makers

WCPA WORLD COMMISSION ON PROTECTED AREAS

Government Offices of Sweden
Ministry of the Environment and Energy

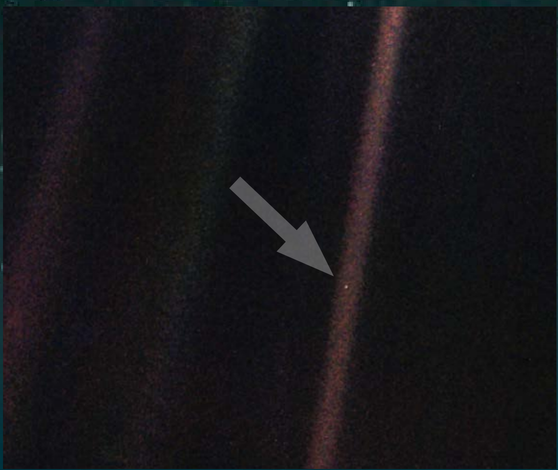
United Nations Educational, Scientific and Cultural Organization

Intergovernmental Oceanographic Commission

Sustainable Development Goals

INTRODUCTION

More people have stood on the surface of the moon than have ever visited the deepest part of the ocean. All 7.7 billion people who live on Earth are nevertheless dependent on a healthy functioning ocean, whether they know it or not. The ocean represents 97% of the physical habitable space on the planet and is central to sustaining all life on Earth. It was the late famed American astronomer Carl Sagan, looking at the Earth as the 'pale blue dot' in the most distant image ever taken of Earth from over 6 billion kilometres away by the 1970s space probe Voyager 1, who summed it up by saying



Earth - a pale blue dot © NASA/JPL-Caltech

'.....That's home. That's us. On it everyone you love, everyone you know, everyone you ever heard of, every human being who ever was, lived out their lives'.

It is therefore surprising that we have yet to even realize the full impact that our activities have had on the life-sustaining ocean that dominates and colours our world from afar. The 2019 Intergovernmental Panel on Climate Change (IPCC) Special Report on the Ocean and Cryosphere in a Changing Climate[1] sets out a stark warning of the changes we have brought about, and along with that publication, this new report on ocean deoxygenation is part of an urgent global awareness-raising exercise to drive far greater ambition and more rapid and decisive action.

Amazingly it has only been since 2000 that significant and dedicated effort has been directed at raising awareness and understanding of the consequences of greenhouse gas emissions on the ocean. We now know that the carbon dioxide emitted by human activities is driving the ocean towards more acidic conditions – the so-called phenomenon of ocean acidification. Only in the past decade has it started to become more widely recognized that the temperature of the global ocean is also being significantly affected as a result of the effect that the carbon dioxide and other potent greenhouse gases are having in the Earth's atmosphere. Some 93% of potential atmospheric heating caused by emissions since the mid-20th century has been absorbed by the ocean, creating the phenomenon of ocean warming – or what might now be more correctly described by the scale of the effect as ocean heating. The awareness of these two phenomena, on top of existing concerns such as overfishing, pollution and habitat destruction, has begun to trigger significant concern about the impacts on marine biodiversity and the functionality of the ocean as a whole, and how this may influence issues such as weather, crop success and water supplies, with implications for people everywhere.

This summary and the accompanying comprehensive technical report[2] show that the heating of sea water and progressive acidification are by no means the only major global consequences of greenhouse gases emissions in the marine realm. It has been known for some decades that nutrient run-off from agriculture causes oxygen-depleted zones to form in the sea, as life-giving oxygen is used up in the water column and on the sea floor. But the true scale of the causes and impacts of the phenomenon called 'ocean deoxygenation'

1 https://report.ipcc.ch/srocc/pdf/SROCC_FinalDraft_FullReport.pdf
2 www.iucn.org/deoxygenation

have remained elusive. Is there a link to climate change, and what consequences does this hold both now and in the future for people and the environment? Working with 67 scientific experts representing 51 institutes in 17 countries, what is presented here is the largest peer-reviewed study conducted so far on ocean deoxygenation. Expressed in the words of the world's leading scientists on this topic it shows the inescapable fact that human activities are now driving life-sustaining oxygen from the ocean. Society needs to wake up – and fast – to the sheer enormity of detrimental changes we are now causing to the Earth's regulatory systems, and the now near-monumental efforts that will be needed by governments and society to overcome and reverse such effects.

What is reported here and in the full technical report is probably an underestimation of what is happening now. Science is incomplete and broader awareness of ocean deoxygenation is just happening, but what is already known is very worrying. This work should be of interest and concern to everyone. It is intended to spur additional interest in the underlying research needed, especially as we are about to enter the United Nations Decade of Ocean Science for Sustainable Development (2021 – 2030). The focus of this decade is to support efforts to reverse the cycle of decline in ocean health, so increased awareness of ocean deoxygenation is very timely. The Decade of Ocean Science is also intended to align ocean stakeholders worldwide behind a common framework that will ensure ocean science can fully support countries in creating improved conditions for sustainable exploitation of the ocean.

This report on ocean deoxygenation is perhaps the ultimate wake-up call needed to dramatically raise our ambitions to tackle and immediately curb our emissions of carbon dioxide and other powerful greenhouse gases such as methane. This is needed before human actions irreparably impact and change the conditions favourable for life on earth, and that drive and underpin the natural values we all hold close in our daily lives.

Ocean deoxygenation facts at a glance

The bulk of excess heat retained by the Earth due to greenhouse gas warming is being absorbed by the ocean. Ocean deoxygenation is occurring at all depths due to lower solubility of oxygen in warmer waters, stronger vertical stratification (steeper temperature gradient) inhibiting diffusion of oxygen from surface to deep ocean, and more sluggish deep circulation reducing oxygen supply to deep waters. Alongside this, increased nutrient inputs to the ocean through river runoff and atmospheric deposition are promoting algal blooms, increasing oxygen demand and causing development of hundreds of coastal hypoxic (dead) zones as well as intensification of naturally formed low-oxygen zones.

- The global ocean oxygen inventory has decreased by ~2% over the period 1960 to 2010.
- Ocean model simulations project a further decline in the dissolved oxygen inventory of the global ocean of 1 to 7% by the year 2100, caused by a combination of a warming-induced decline in oxygen solubility and reduced ventilation of the deep ocean.
- Climate change related longer-term oxygen trends are masked by oxygen variability on a range of different spatial and temporal scales.
- The decline in the oceanic oxygen content can affect ocean nutrient cycles and the marine habitat, with potentially detrimental consequences for ecosystems, dependent people and coastal economies.
- Ocean oxygen loss is closely related to ocean warming and acidification caused by increasing carbon dioxide driven by anthropogenic emissions, as well as biogeochemical consequences related to anthropogenic fertilization of the ocean; hence a combined effort investigating the different stressors will be most beneficial to understand future ocean changes.

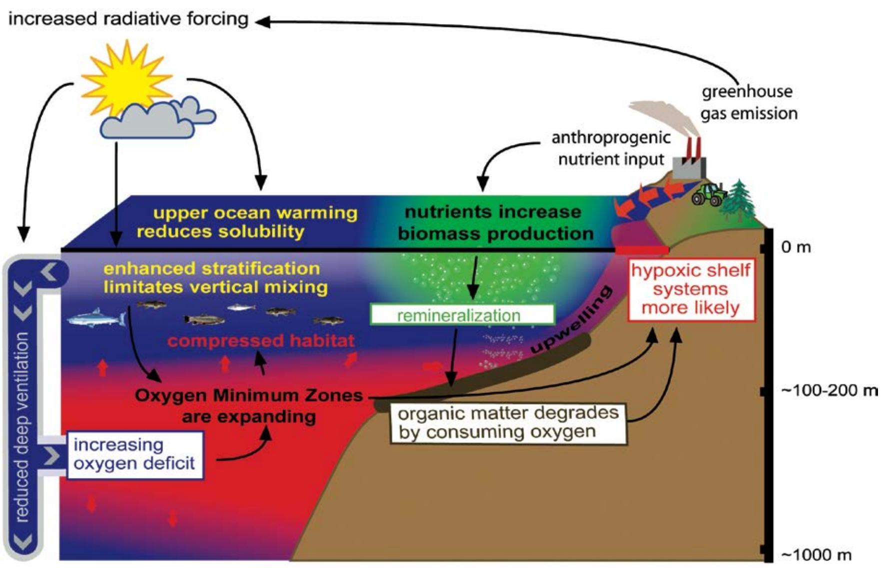
WHAT IS OCEAN DEOXYGENATION?

Whilst the actions on trying to clean-up the ocean have generally focused on the impacts from pressures such as fishing, pollution, habitat destruction, invasive species and plastic, there is no environmental variable of such ecological importance to marine ecosystems that has changed so drastically in such a short period of time as a result of human activities as dissolved oxygen. Present-day deoxygenation of the ocean is starting to progressively alter the balance of life, favouring hypoxia-tolerant species at the expense of hypoxia-sensitive ones. The loss of oxygen in the ocean can broadly be put down to two overlying causes – eutrophication as a result of nutrient run-off from land and deposition of nitrogen from the burning of fossil fuels, and the heating of ocean waters due to climate change, primarily causing a change in ventilation with the overlying atmosphere and a reduced ability to hold soluble oxygen.

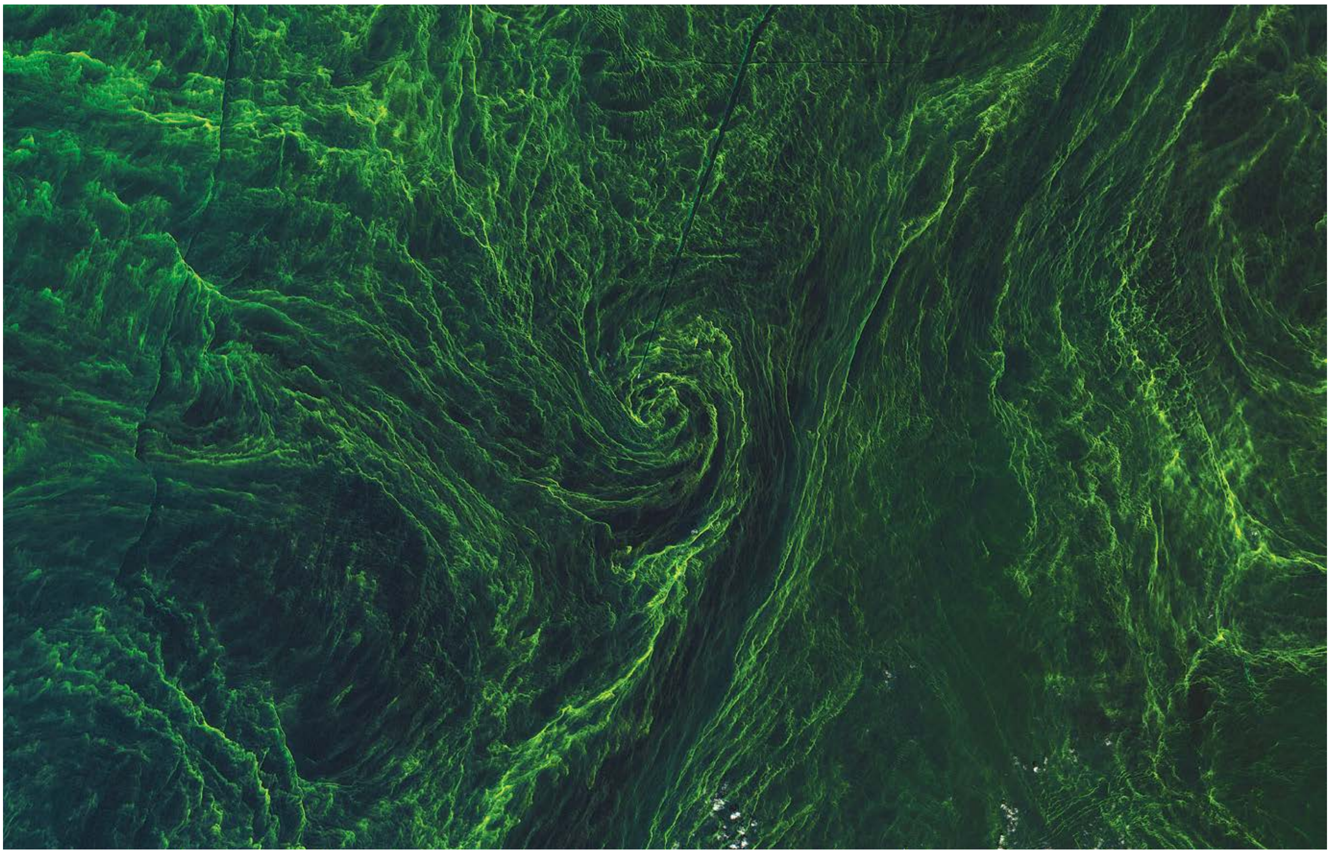
Since the middle of the 20th century we have come to realize that over-enrichment of waters with nutrients or organic matter (eutrophication) is a problem that threatens and degrades coastal ecosystems, alters fisheries, and impacts human health in many areas around the world. Over 900 areas of the coastal ocean and semi-enclosed seas around the world have already been identified as experiencing the effects of eutrophication. Of these, over 700 have problems with hypoxia, but through nutrient and organic loading management on adjacent land about 70 (10%) of them are now classified as recovering. The global extent of eutrophication-driven hypoxia and its threats to ecosystem services are well documented, but much remains unknown as to the long-term human health, social, and economic consequences, and its effects in combination with other ocean stressors.

What is particularly new with this report is the additional focus on the more recently recognized effect of lowered oxygen resulting from ocean warming, which is now affecting enormous areas of the ocean. The atmospheric warming resulting from greenhouse gas emissions being taken up in ocean water is now driving vast changes in the physical and biological make-up of the sea. The two causes also interact, with warming-induced oxygen loss tipping coastal areas into eutrophication-driven hypoxia and may contribute to the dramatic increase in regards of coastal hypoxia. The combination of eutrophication-driven hypoxia, which can be relatively easily and quickly reversed if the necessary measures are put in place, and hypoxia due to climate driven warming, that can't easily be reversed – if at all – is driving the emergence of ocean deoxygenation as a new issue of global significance.

Human activities have altered not only the oxygen content of the coastal and open ocean, but also a variety of other physical, chemical and biological conditions that can have negative effects on physiological and ecological processes. Ocean deoxygenation is but the latest consequence of our activities to be recognized. Ocean warming, ocean deoxygenation, and ocean acidification are major 'stressors' on marine systems and typically co-occur because they share a common cause. Increasing carbon dioxide emissions into



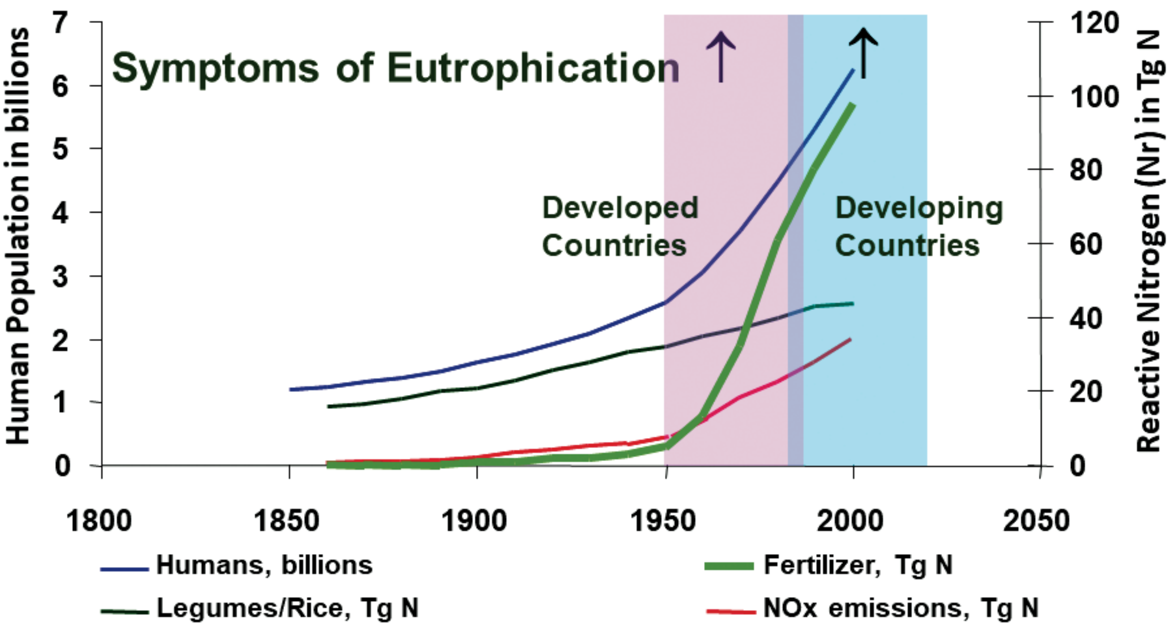
Schematic of interactions of open ocean oxygen minimum zone (OMZ, red) with hypoxic shelf system and dead zones on continental shelves of eastern ocean boundaries (modified after Stramma et al., 2010).



Cyanobacteria bloom in Baltic Sea © lavizzara / Shutterstock.com.

the atmosphere simultaneously results in warming, deoxygenation, and acidification of marine systems, whilst nutrient pollution also contributes to increases in the severity of deoxygenation and acidification. As a result, marine systems are currently under intense and increasing pressure from the cumulative effects of these multiple stressors, and with current expected sustained trajectories for greenhouse gas emissions the changes in the ocean will only continue and intensify. The combined effects of these 'stressors' can be either greater than, less than, or the sum of each stressor alone; there remains large uncertainties surrounding their combined effects.

Naturally hypoxic areas do exist, supporting species with special physiological and behavioural features, but all organisms have limits, and for many even small declines in oxygen have physiological and ecological costs. The importance of maintaining adequate levels of oxygen in the ocean is perhaps best summarized by the former motto of the American Lung Association: "if you can't breathe nothing else matters".



Period in which the symptoms of eutrophication and hypoxia/anoxia began in developed countries and how the onset of symptoms has shifted in more recent years to developing countries (Rabalais et al. (2014), modified from Galloway and Cowling (2002) and Boesch (2002)).

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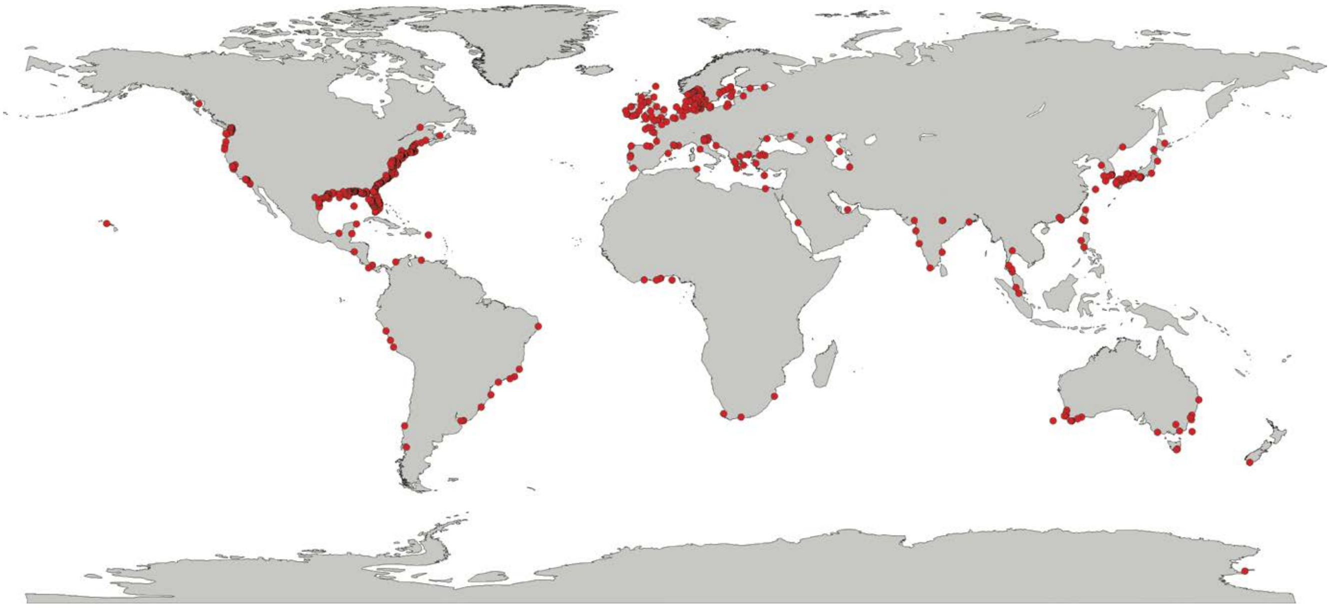
WHAT IS HAPPENING ALREADY?

‘Breathing water’ is hard work as a given volume of water holds far less oxygen than the equivalent volume of air. This makes the physiological performance and behavioural repertoire of marine organisms heavily dependent on their ability and capacity to extract oxygen from the ambient sea water. Any departure from normal levels of ocean oxygen can be a challenge to species that have evolved and adapted to certain levels of available oxygen for their day-to-day lives.

Since the middle of the 20th century, the increased river export of nitrogen and phosphorus, and atmospheric deposition of nitrogen from burning of fossil fuels, has resulted in eutrophication in coastal areas (including semi-enclosed seas) world-wide. High anthropogenic nutrient loads fertilize coastal waters, increasing the biomass of phytoplankton and other organisms. As these organisms die and defecate, the organic matter sinks and decays. This decay process, caused especially by microbes dependent on aerobic (oxygen-utilizing) respiration, depletes oxygen in the surrounding water. How this plays out at regional and local scales is shaped by the physical structuring and layering of the water column and how long water is retained before reaching the ocean. Saline (salt) or thermal (heat) stratification, or both, dictate the presence of a pycnocline (strong density difference in the water column) across which dissolved oxygen diffusion is hindered. Increased water



Coastal waters that have reported oxygen concentrations <2 mg L^{-1} (63 µmol L^{-1} or 61 µmol kg^{-1}) (red dots) (Diaz & Rosenberg, 2008; Isensee et al., 2016). Most systems shown in this figure reported their first incidence of low oxygen after 1960.

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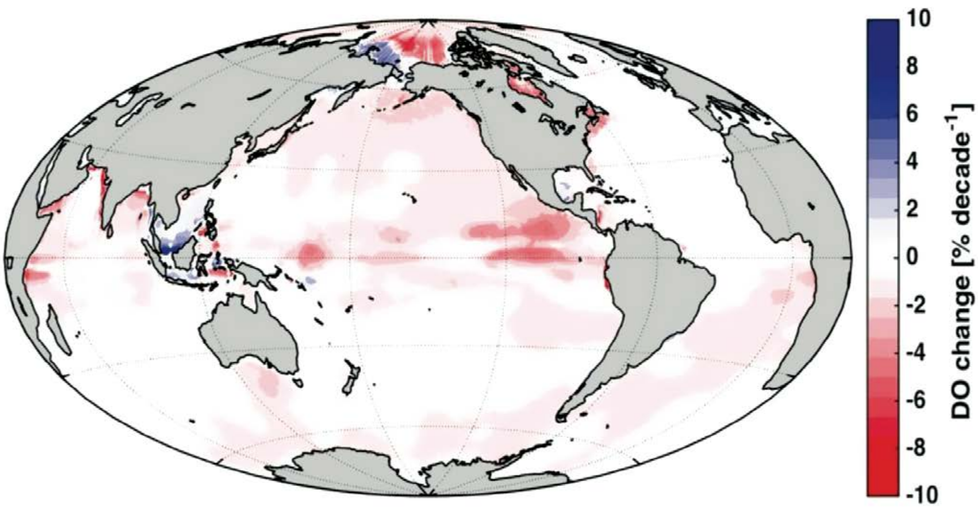
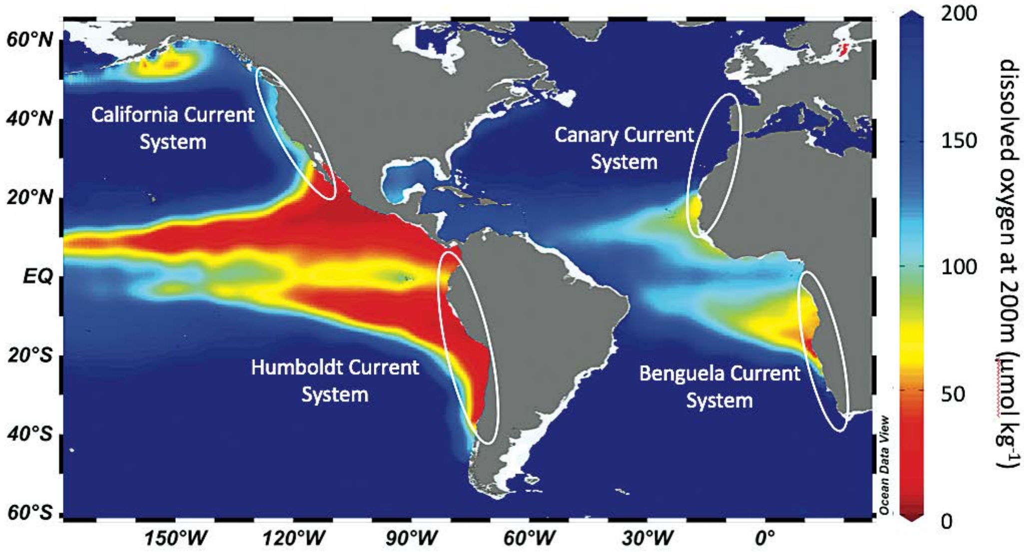
residence time also enhances the probability of oxygen depletion occurring in a coastal area. Physical barriers such as sills at depth and advection of offshore waters can also affect the level of deoxygenation, positively or negatively.

The overall consequence of perturbations to the equilibrium state of the ocean-atmosphere system over the past few decades is that the ocean has now become a source of oxygen for the atmosphere even though its oxygen inventory is only about 0.6% of that of the atmosphere. Over extended periods of time, enhanced respiration due to warming will tend to generate oxygen deficits close to the sea surface. The increased near-surface vertical oxygen gradient may even increase ocean uptake of oxygen from the atmosphere.

The global ocean oxygen content has decreased by an estimated 1 - 2% since the middle of the 20th century. From a climate change perspective one aspect of increasing seawater temperatures is to reduce the solubility of oxygen (and other gases) in the water – simple physics is that a colder liquid holds more dissolved gas – but this is only partly to blame for the overall losses of ocean oxygen now being observed. There is good evidence that such temperature increases explain about 50% of oxygen loss in the upper 1000 m of the ocean, which corresponds to a solubility-driven oxygen loss



Estimated change driven by climatic warming in oxygen content of the global ocean in percentage decade^{-1} since 1960 (Schmidtko et al., 2017). Red tones denote oxygen declines, and blue tones increases.



Location of the four major eastern boundary upwelling systems and dissolved oxygen values at 200m depth illustrating the location of each system relative to oceanic oxygen minimum zones. Data from World Ocean Atlas 2013.

of about 0.013 Pmol O_2 yr^{-1}. Until now the solubility-driven contribution to oxygen loss below 1000 m depth amounts to about 2% (about 0.001 Pmol O_2 yr^{-1}), and according to the most recent estimate of global deoxygenation (0.096 ± 0.042 Pmol O_2 yr^{-1}), solubility changes account for 15% (range 10 - 30%) of the total oxygen loss during 1960 – 2010.

Most of the oxygen loss has been caused by changes in ocean circulation and associated ventilation – gas exchange – which brings oxygen from the atmosphere and surface waters to depth. This is being compounded by reduced ocean mixing and changes in currents and wind patterns. There is less confidence in the magnitude of the knock-on effect on respiration – another factor to explain lowered oxygen. Less than 15% of the oxygen decline can be attributed to warming-induced changes in respiration of particulate and dissolved organic matter.

While the biogeochemical and physical changes associated with ocean warming, deoxygenation and acidification occur all over the world's ocean, the imprint of these global stressors has a strong regional and local nature. Perhaps among the best known areas subject to low oxygen are the Baltic Sea and Black Sea. These are the world's largest semi-enclosed low oxygen marine ecosystems. While the deep basin of the Black Sea is naturally anoxic, oxygen depletion in the north-western portion of the Black Sea has been attributed to high nutrient loads. The extensive low oxygen conditions currently observed in the Baltic Sea are the result of enhanced nutrient inputs from runoff from land, exacerbated by global warming.

The impacts of deoxygenation are not though limited to enclosed seas. Eastern boundary upwelling systems (EBUS) are one of the ocean's most productive biomes, supporting one fifth of the world's wild marine fish harvest.

Mass die-off of lobsters in St Helena Bay, South Africa © G.C. Pitcher.

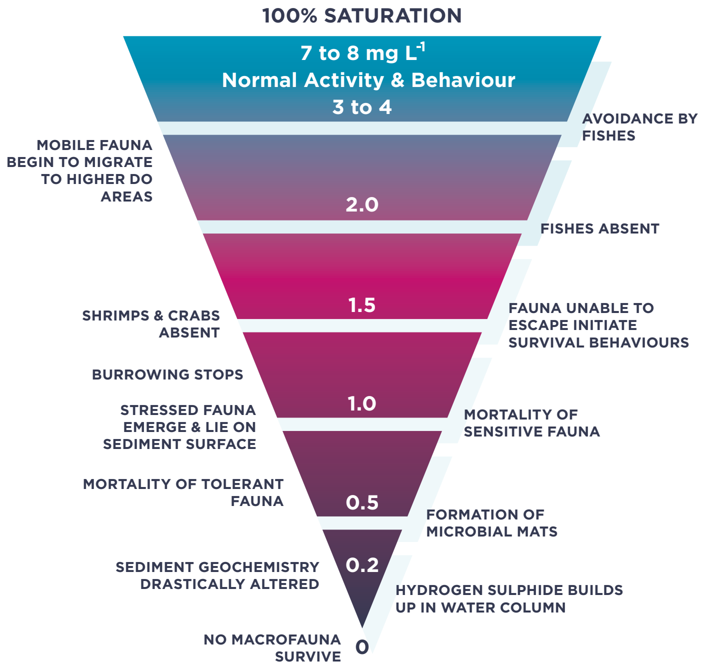
These ecosystems are defined by ocean currents that bring nutrient rich but oxygen-poor water to the eastern edges of the world's ocean basins. As naturally oxygen-poor systems, EBUS are especially vulnerable to further changes in global ocean deoxygenation and so what happens to the oxygen content of EBUS will ultimately ripple out and affect many hundreds of millions of people.

The dynamics of EBUS are intimately linked to global alterations in ocean chemistry and circulation from climate change. Upwelling currents connect the vast region of the subsurface open ocean, that is experiencing declines in dissolved oxygen, with the productive coastal waters of EBUS. The strength and location of upwelling currents depend on wind fields that are also affected by climate change. For some systems, this combination of changes will result in an intensification and expansion of coastal low oxygen zones (LOZ).

In comparison to the open ocean, long-term changes in dissolved oxygen availability in dynamic EBUS are much more challenging to understand. Nonetheless, important trends have started to emerge. In a number of these systems, dissolved oxygen has declined by approximately 10 µmol kg^{-1} per decade. This is of great concern because many EBUS locales already sit near to if not past what some consider as the key threshold for hypoxia of 60 µmol O_2 kg^{-1}. Observations of climate change-driven strengthening in winds that drive the upwelling delivery of low-oxygen and nutrient-rich waters in some systems carries heightened risks of ecosystem changes that outpace those expected from ocean deoxygenation alone. EBUS are key regions for the climate system due to the complex of oceanic and atmospheric processes that connect the open ocean, troposphere and land, and the fact that they host Oxygen Minimum Zones (OMZs), responsible for the world's largest fraction of water column denitrification and for the largest estimated emission (0.2 - 4 Tg of N yr^{-1}) of the greenhouse gas nitrous oxide.

Because many EBUS are already exposed to low-oxygen conditions, the risk of crossing important biological thresholds that regulate the distribution and productivity of fishery-dependent stocks, and ecosystem functioning are heightened. Shallow water anoxia has already resulted in mass die-offs of fish and shellfish in some systems. Expansion of low oxygen zones have led to rapid, transient invasion of hypoxia-tolerant jumbo squid in others. Movement of fish away from low oxygen zones have also affected the accuracy of fishery independent surveys even as the need for tools for managing in the face of climate change grows.

EBUS are also prone to high-biomass harmful algal blooms (HABs) and provide some of the earliest accounts of events of anoxia linked to red tides. The expansion of algal blooms is more readily apparent in Asia than in any other part of the world's ocean and it is here that relationships between



Range of behaviour and ecological impacts as dissolved oxygen levels drop from saturation to anoxia.

the increasing prevalence of HABs and aquaculture operations are increasingly reported. Several model predictions show the likelihood for increased nutrient pollution and, correspondingly, for continued regional and global expansion of coastal hypoxia and anoxia linked to harmful algal blooms.

From available data it is obvious that oxygen-limited areas (including anoxic waters, OMZs and less severely hypoxic areas) have expanded dramatically throughout most of the Atlantic during the last 50 to 100 years and this is clearly related to human activities. Oxygen limited waters, hypoxic and even anoxic conditions are now found in many coastal areas in the Atlantic Ocean including in connected seas like the Mediterranean, the Gulf of Mexico, and the Black Sea and Baltic Sea. Alongside this, large ocean basins such as the equatorial and southern Atlantic are being affected by decreasing oxygen levels, although such conditions were present in deep waters long before anthropogenic activities started to have an influence on the marine environment. In addition to many coastal waters, oxygen limited waters are also found at mid-water depths in most of the Atlantic Ocean basins, usually at 300 to 1000 m depths. The oxygen concentrations in these areas have decreased during the last 60 years, partly due to ocean warming, partly as a result of decreased mixing and ventilation.

Elsewhere the low-oxygen zones of the Indian Ocean are expected to continue to expand and intensify. The northern Indian Ocean contains about two thirds of the global continental margin area in contact with very low oxygen (< 0.2 ml O_2 L^{-1}) waters, and also houses the world's largest naturally formed shallow low-oxygen zone (off western India). With countries surrounding its semi-enclosed basins, accounting for about a quarter of the global human population, its environment, biodiversity and living resources, are most vulnerable to human-induced changes, especially deoxygenation.

Such expansions in the volume of OMZs have many deleterious effects on marine life including loss of habitat, changes in food webs, reduced growth and reproduction, physiological stress, migration, vulnerability to predation, disruption of life cycles, and, in extreme cases, death. When dissolved oxygen is depleted below detection levels, as happens within a large volume of water at mid-depths within the OMZ of the Arabian Sea, the microbial community respires anaerobically, predominantly utilizing nitrate, an essential nutrient, converting it to inert molecular nitrogen (N_2) and nitrous oxide (N_2O), a potent greenhouse gas. While molecular nitrogen produced through this process (denitrification) modulates the reactive nitrogen balance and marine biological productivity, oceanic nitrous oxide emissions play an important role in Earth's radiation balance.

The OMZ of the Bay of Bengal retains some oxygen in minute traces, but still enough to inhibit large-scale denitrification. The volume of water containing traces of oxygen (< 0.2 ml O_2 L^{-1}) in the northern Indian Ocean is much larger than the volume of functionally-anoxic OMZ of the Arabian Sea, this in conjunction with the extreme sensitivity of denitrification to vanishingly low oxygen levels underlines the non-linear response of molecular nitrogen and nitrous oxide production to ocean deoxygenation. Thus, expansion and intensification of oceanic OMZs are expected to have large impacts on productivity as a result of reactive nitrogen loss, and on climate through enhanced production of nitrous oxide.

There does, however, remain a critical lack of information from potential hotspots for deoxygenation, including the mouths of the Indus, Ganges-Brahmaputra, and Irrawaddy rivers. Thus, pictorial representations of the current extent of ocean deoxygenation almost certainly underplay the effects being experienced in the world ocean. Capacity building and networking are needed to expand/improve monitoring of deoxygenation and other impacts of global change in the ocean.

Ocean deoxygenation impacts at a glance

Loss of biomass

- Direct mortality of fisheries species
- Direct mortality of prey species
- Reduced growth and production
- Reduced recruitment

Loss of biodiversity

- Mortality of sensitive species
- Reduced diversity
- Increased susceptibility to disease and other stressors
- Lower food web complexity

Loss of habitat

- Crowding of organisms into suboptimal habitats
- Increased mortality risks from both natural predation and fishing pressure
- Forced departure from preferred habitat
- Altered or blocked migration routes

Altered energy and biogeochemical cycling

- Increased energy flow through microbes
- Production of toxic hydrogen sulphide
- Release of phosphorus and other nutrients from sediments that fuels algal blooms
- Loss of denitrification

WHAT MAY HAPPEN IN THE FUTURE?

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The current climate change model simulations for the end of this century project a decrease of ocean oxygen in both the high and low emission scenarios, while the projections of river exports to the coastal ocean indicate that eutrophication will likely continue or worsen in many regions of the world. Warming is expected to further amplify the deoxygenation issue in coastal areas influenced by eutrophication by strengthening and extending the stratification of the sea water.

As the ocean warms from the surface, stratification is expected to increase, with a tendency for a slowing down of the ocean circulation in the open ocean. A slowed down circulation is expected to account for up to 50% of the observed deoxygenation in the upper 1000 m, and for up to 98% in the deep ocean (> 1000 m depth). Spatial patterns and individual mechanisms are not yet well understood and further improvements are needed in models to improve projections. Respiration rates of dissolved organic matter (DOM) are also expected to increase with temperature. Estimates of respiration are difficult because of the poorly known composition and biological accessibility of dead organic matter. Incubation experiments indicate some warming-induced acceleration of respiration, which might explain up to 10% or 0.01 Pmol O_2 yr^{-1} of the observed oxygen loss. A corresponding decline of the ocean's dead organic matter inventory has not yet been observed.

Further climate-driven warming of bottom waters may also result in enhanced destabilization of methane gas hydrates, leading to enhanced release of methane from sediments, and subsequent aerobic respiration of methane to carbon dioxide. There is, however, little observational evidence for a warming-induced acceleration of methane release taking place already. As the ocean continues to warm, it will lose yet more oxygen due to the direct effect of temperature on gas solubility. Additionally, reductions in vertical mixing associated with enhanced upper-ocean buoyancy stratification will also occur leading to respiration-driven oxygen depletion at depth. The ocean as a whole is expected to lose about 3 – 4% of its oxygen inventory by the year 2100 under a "business-as-usual" scenario (RCP8.5) with most of this loss concentrated in the upper 1000 m of the water column where species richness and abundance is highest.

The future intensification and expansion of low oxygen zones can have further ecosystem consequences as oxygen dependent cycling of elements by microbes alter the supply of nutrients or in extreme cases, lead to increased production of toxic hydrogen sulphide gas (H_2S). Low oxygen EBUS are also regions of carbon dioxide enrichment as the loss of dissolved oxygen is coupled to the production of carbon dioxide. In combination with ocean uptake of human carbon dioxide emissions, carbon dioxide levels in some EBUS have already reached levels where the calcium carbonate shells of marine organisms are now being readily dissolved. Eastern boundary upwelling systems thus represent hotspots for both hypoxia and ocean acidification where development of mitigation and adaptation solutions are urgently warranted.

It is predicted that there will be distinct regional differences in the intensity of oxygen loss as well as variations in ecological and biogeochemical impacts. There is consensus across models that oxygen loss at mid and high latitudes will be strong and driven by both solubility reductions and increased respiration effects. Projections are more ambiguous in the tropics, where

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models suggest that there will be compensation between oxygen decline due to reduced solubility and oxygen increase caused by reductions in cumulative respiration. Thus, oxygen concentrations in the core of present-day oxygen minimum zones may increase; however, the total volume of waters classified as “suboxic” and “hypoxic” is still likely to grow substantially.

Low oxygen conditions and increased temperature jointly limit the viable habitat for marine macro-organisms. Continued ocean warming accompanied by deoxygenation will drive habitat contraction and fragmentation in regions where oxygen levels decline below metabolic requirements. Expansion of suboxic zones will likely disrupt the cycling of nitrogen in the ocean; denitrification may increase, yielding greater rates of fixed nitrogen loss from the ocean. Perturbations to the nitrogen cycle may include substantial changes to nitrous oxide production, though this is highly uncertain.

In the short term, marine organisms respond to ocean deoxygenation through changes in their physiology and behaviour. Alteration in feeding behaviour and distribution pattern are classically observed, potentially leading to reduced growth and to more difficulties completing their life cycle. Vertical habitat compression is also predicted for organisms in the upper ocean and coastal waters. In the medium term, epigenetic processes (non-genetic influences on gene expression) may provide marine populations with a rapid way to acclimate to the rapidly changing oxygenation condition state. However, this developing field of biological sciences is too recent to fully evaluate the contribution of epigenetic responses to marine organisms’ adaptation to ocean deoxygenation. Changes in the phenology (timing of life stage-specific events) of marine species, in relation with ocean deoxygenation have not yet been observed. However, deoxygenation generally co-occurs with other environmental disturbances (ocean warming and acidification) which are also liable to affect marine species’ life cycles. The lack of understanding of their interactions and synergies currently restricts our ability to assess marine populations’ capacity to phenologically respond to ocean deoxygenation.

It is currently difficult to predict whether or which marine species will be able to adapt successfully to the changes now being observed in dissolved ocean oxygen. In the long term, adaptation through natural selection may occur but is most likely in species with very short generation times. Such evolutionary adaptation is, however, far more difficult to envisage in most commercial fish species which are characterized by long generation time. Between now and 2100, approximately 80 generations of sardine (*Sardina pilchardus*; age at first maturity: 1 year) but only 10-15 generations of Atlantic cod (*Gadus morhua*; age at first maturity: 5 to 8 years) will follow one another. The numbers of generations in either scenario is modest, and cast doubts on the capacity of commercial fish species in particular, to adapt to the fast-changing ocean conditions.

Large inter-individual and inter-specific variation in tolerance to reduced oxygen availability exists in nature. This diversity in marine species’ responses makes them challenging to comprehend. Moreover, synergies with other environmental stressors, whether natural or anthropogenic such as, ocean warming and ocean acidification, add to this difficulty. Over the last 30 years, marine biologists and physiologists have made tremendous efforts to gain understanding of how marine animals respond to environmental conditions and to reduced oxygen availability. Despite all these efforts there is still a long way to go and intensifying collaboration between physiologists, ecologists, modellers and managers is key to providing policy makers and marine resources’ managers with fully operational, science-based information.

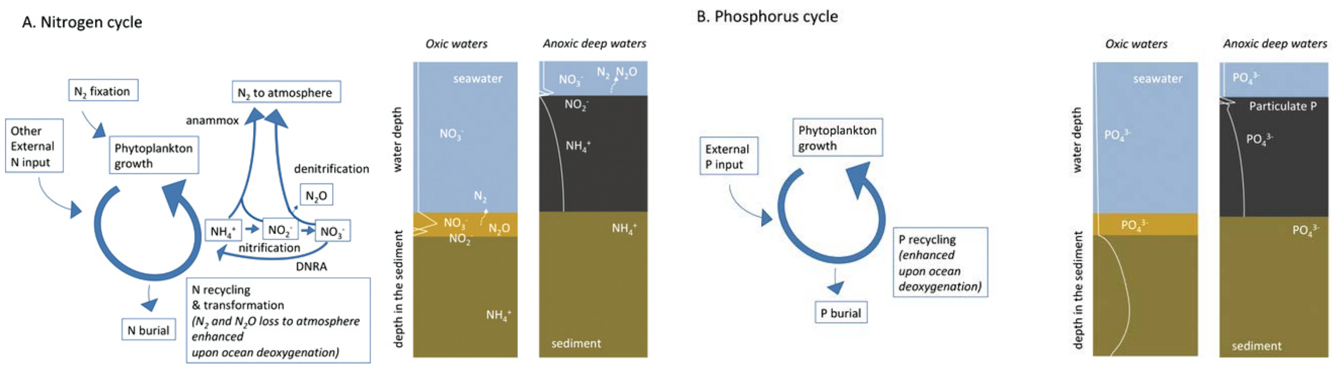
WHY IS IT IMPORTANT?

The consequences of increasing ocean deoxygenation will play out at different scales in the Earth/Ocean system. Within individual estuaries, worsening low oxygen reduces critical habitat for fisheries species and favours oxygen-tolerant species (like many jellyfishes) within food webs. In wind-driven coastal upwelling regions, physical mechanisms occur where cold, nutrient-rich and low oxygen waters upwell supporting a high abundance of ocean plants (i.e. primary productivity). Under future scenarios global warming could modify the oxygenation of such waters that would affect other services, such as fisheries. At broader scales, ocean deoxygenation may influence the ocean-atmosphere interaction of gases. This is because when OMZ waters upwell and impinge on the euphotic zone, there is the potential release to the atmosphere of greenhouse gases such as nitrous oxide, carbon dioxide and methane, which will further exacerbate global warming with subsequent feedbacks to stratification, biological productivity and the oxygen inventory.

Oxygen minimum zones play an essential role in the global nitrogen cycle, in which various chemical species such as ammonium, nitrite, nitrate, nitrous oxide, and nitrogen gas participate, and different bacterial processes are involved in transformations from one chemical species to another. Substantial nitrogen losses are observed in OMZs and they account for approximately 10% of global denitrification; the process by which nitrate is reduced to nitrogen gas by microbes when oxygen is not present. On land this process is vital to the recycling of nitrogen in the Earth's system for soil health, microbial and plant growth, and animal health. Denitrification, however, can also worsen global warming through the production of nitrous oxide. With global warming, OMZs are projected to significantly expand, leading to alterations in the oceanic nitrogen balance and enhanced oceanic nitrous oxide production, further exacerbating warming of the atmosphere and the ocean.

Alongside influences of the nitrogen cycle, the recycling of phosphorus (P) in marine systems is enhanced when oxygen levels in sea water are extremely low or absent. The resulting increased availability of phosphorous can further enhance productivity and thus oxygen demand in deeper waters. This positive feedback-loop between productivity, oxygen loss and increased phosphorus availability can contribute to further deoxygenation in both the open ocean and coastal systems. The sediments of areas of the ocean closest to land - the continental margins - can act as a source of the trace nutrient iron (Fe) to waters in adjacent open ocean areas. This sediment release of iron responds non-linearly to ocean deoxygenation and is at a maximum when oxygen concentrations near the sea floor are low and sulphide is not present. This implies that ocean deoxygenation may initially enhance iron availability for primary producers, followed by a decline in iron availability when waters become sulphidic. Building a better understanding of the coupled element cycles and their links to ocean oxygen will strengthen our ability to predict the impacts of climate change. Global warming will alter ventilation and source water properties, oceanic stratification, near-surface wind, mesoscale activity, upwelling rates, low cloud cover, and air-sea exchange of gases and particles. Understanding these changes and their compensating/synergistic influences on the future trajectory of ocean deoxygenation is important but challenging due to the scarcity of available biogeochemical data and global model biases.

Alongside the influence of lowered oxygen on geochemical cycles, deoxygenation also has significant consequences for species and the services they provide. At the level of an individual organism there is a range of consequences that lowered oxygen in sea water can cause. The most obvious is reduced available oxygen in the water ventilated over the respiratory surfaces (gills, skin). This leads to reduced diffusion of oxygen across



Conceptual figure of nutrient pathways for (A) the nitrogen cycle and (B) the phosphorous cycle. Differences in the cycles of nitrogen and phosphorous are depicted between oxic waters and in anoxic deep waters. For the nitrogen pathways N_2 and N_2O loss to the atmosphere are enhanced upon ocean deoxygenation. For phosphorous, enhanced recycling occurs upon ocean deoxygenation.

the epithelium of the respiratory organs and accordingly less oxygen transported to the cells by the internal circulatory fluid (blood, extracellular fluid). A reduction in oxygenation of the circulatory fluid leads in turn to reduced oxygen availability to the cellular power houses (mitochondria). This then results in reduced energy production that in turn reduces capacity for activities such as growth and reproduction. Such impacts can lead to an increase in the risk of predation, affect recruitment, and alter population production (biomass) and demography.

Deoxygenation also reduces suitable habitats for many bottom-associated marine organisms, squeezes midwater species towards the better oxygenated surface waters, and disrupts biogeochemical cycles. These phenomena are already illustrated by impacts on species and shifts in the species composition of marine communities as described later in this summary.

The oxygen content in the world ocean has been reduced in the past and this has been associated with biodiversity changes and losses, similar to what we are starting to see today. From such records it is apparent that the current substantial degradation of marine ecosystems, including the loss of diversity, decreases in abundance, and changes in faunal composition often with increased dominance of opportunistic species, is matched by palaeo-indicators of past conditions. A combination of multiple indicators, influenced by low oxygen concentrations along with other environmental parameters, points to development of oxygen-deficient overlying waters. This evidence is even more striking when compared with long-term water quality data that indicate an increase in nitrogen or organic carbon loads. Faunal shifts in larger infauna (molluscs) occurred in the past with eutrophication and oxygen decline.

The scientific community is already concerned about and taking action on ocean deoxygenation. The Intergovernmental Oceanographic Commission of UNESCO (IOC-UNESCO) established the Global Ocean Oxygen Network (GO_2NE), which is committed to providing a global and multidisciplinary view of deoxygenation, with a focus on understanding its multiple aspects and impacts. It is this network which has largely contributed to the production of this report. At a recent Ocean Deoxygenation Conference held in in Kiel, Germany, in 2018, to discuss the decline of oxygen, its causes and consequences, the 300 attending scientists from 33 counties published the ‘Kiel Declaration’. This Declaration, with the subtitle ‘the ocean is losing its breath’, calls on all nations, societal actors, scientists and the United Nations to raise global awareness about ocean deoxygenation, take immediate and decisive action to limit pollution and in particular excessive nutrient input to the ocean, and to limit global warming by decisive climate change mitigation actions. This Declaration now needs to be heard loud and clear by policy advisers, decisions makers and the general public.

THE CONSEQUENCES OF OCEAN DEOXYGENATION FOR INDIVIDUAL COASTAL AND MARINE SPECIES, HABITATS AND ECOSYSTEMS

Estuarine and coastal benthos

There are a range of consequences for estuarine and coastal benthic species. Mobile benthic invertebrates will migrate away from water masses with low dissolved oxygen. Studies have shown that this results in diversity in benthic assemblages decreasing 13-fold; abundance of benthic infauna, 25-fold; and biomass, 10-fold as dissolved oxygen approached levels of 0.05 mg L^{-1} in a seasonally severe coastal low oxygen zone. As much as 343,000 to 734,000 MT carbon in the form of secondary production is lost from ecosystems annually over 245,000 km^2 when bottom waters are severely deoxygenated. The recovery of benthic communities under improved oxygen conditions may take years to decades and may not approach pre-impact conditions.

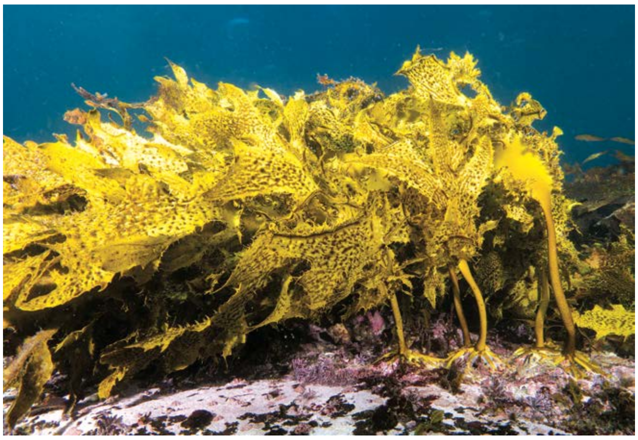
Severe deoxygenation on a seasonal basis in coastal waters alters benthic community composition. Deeper-burrowing infauna are replaced by mostly small, opportunist, surface deposit feeders that live in the upper 2 cm of the sediment. Diversity, number of taxonomic groups, abundance, and biomass decrease as the dissolved oxygen concentration decreases. The resultant sediments do not become azoic; multi-cellular organisms are mostly depleted except a few acclimated to severe hypoxia or anoxia but microbial communities thrive. Levels of severity of deoxygenation affect benthos differently with developmental life stages typically being more sensitive to deoxygenation than adults are. Taxa also differ in their sensitivity to low oxygen. Pericaridean crustaceans will be exterminated before many polychaete worms and sipunculans, whilst in terms of meiofauna, harpacticoid copepods are more sensitive than nematodes

This loss of infauna from deoxygenation affects ecosystem functioning. The loss of benthos that are bioturbators allows the redox potential discontinuity of the sediment to move closer to the sediment water interface. The loss of benthic organisms and secondary production decreases food availability to higher consumers, whilst at severely low oxygen levels, there are effluxes of ammonium and ortho-phosphates from the sediments that generate a negative feedback to further deoxygenation.

In estuarine and coastal environments areas of deoxygenation reduce suitable habitat for commercially important species. This in turn can cause reduced growth and affect market prices.

Kelp and macroalgae

Because kelps and other macroalgae are primary producers and absorb carbon dioxide and produce oxygen, it might be expected that the effects of hypoxia would be modest. However, kelps and other macroalgae also respire, which requires oxygen. Therefore, hypoxia may have detrimental effects on processes like net primary production (NPP), which supplies organic matter to support kelp food webs and ecosystems. However, the effects of hypoxia are expected to vary widely depending on the species of macroalgae and their habitat, since this group of organisms is diverse in their morphology and distribution.



Ecklonia radiata © John Turnbull.

Kelps and other macroalgae occur in nearshore systems across the world, which are dynamic and experience large fluctuations in oxygen, pH, and temperature. In dynamic coastal upwelling zones, low-oxygen events are often more episodic. Unlike respiration-driven hypoxia in bays and estuaries, these upwelling-driven exposures to hypoxia tend to be acute, with rapid onsets and recoveries, and typically lasting less than 24 hours each. It remains to be seen whether it is less likely for organisms in these systems to experience direct mortality due to adaptions to high degrees of natural variability in dissolved oxygen or whether they are close to their physiological limits.

Very little is known about the direct impacts of deoxygenation on macroalgae. On one hand, hypoxia may detrimentally affect metabolic processes, leading to lower net primary production. These processes are also expected to be affected during various stages in the macroalgal life cycle. However, many marine algae photorespire (using oxygen instead of carbon dioxide), reducing their photosynthetic efficiency, so decreasing oxygen concentrations may actually increase photosynthetic rates in some marine macroalgae. These predictions become complicated when considering the effects of oxygen in combination with co-occurring stressors like ocean acidification and ocean warming. Depending on factors like calcification, proximity to the benthos, growth rate, and carbon concentration mechanisms, these three stressors are predicted to differentially affect groups of macroalgae.

In addition to direct impacts on macroalgae, low oxygen (and upwelling-associated fluctuations in pH and temperature) could have profound effects on the grazers, decomposers, and predators that drive the structure and function of kelp ecosystems. There is a dearth of published studies on the responses of kelp forest organisms to low oxygen, but those that do exist suggest changes in foraging, feeding, and movement. Sedentary benthic invertebrates such as abalone may be detrimentally affected because depressions in the rocky bottom may retain pools of cold, acidic, low-oxygen water for hours after internal waves pass, much like a tide pool retains water from a retreating tide. Additionally, deoxygenation effects on organisms will likely alter trophic interactions and energy flow. Differences in vulnerability between grazers and predators may strengthen or weaken trophic cascades and top-down control on kelp populations.

Tropical ecosystems – corals, seagrass and mangroves

Deoxygenation affects tropical coastal ecosystems but is relatively understudied and poorly understood. The number of hypoxic ecosystems may be underestimated by an order of magnitude in the tropics due to lack of research capacity. Corals and seagrasses, for example, provide habitat to diverse communities of organisms that are vulnerable to low concentrations of oxygen. They themselves are vulnerable to hypoxia, and also have the ability to influence oxygen concentrations in the surrounding water, leading to feedbacks that can influence deoxygenation rates. The warmer temperatures typical of tropical ecosystems, combined with the dependence of coral reefs on calcification, suggests that a multiple-stressor perspective is needed for predicting the effects of deoxygenation in this region.

Evidence already demonstrates some of the scale and nature of impacts of deoxygenation in the tropics:

- 75%: percentage decline in coral diversity in a Panamanian hypoxic dead zone.
- 1,000,000: the number of dead coral reef fish following a single hypoxic event in Australia.
- 13%: percentage of coral ecosystems worldwide at elevated risk for deoxygenation.
- 8.66 mg L^{-1}: swing in dissolved oxygen concentration recorded in a mangrove pond over a 24-hour period from a low of 0.46 to a high of 9.12 mg L^{-1}.

Where hypoxia establishes along gradients of connectivity to terrestrial inputs and oceanic flushing, species may segregate or become restricted to a portion of a former range and fisheries catches may decline or be displaced. Low oxygen can also trigger biogeochemical changes that exacerbate hypoxia in feedback loops – where low oxygen can foster production of toxic sulphides, leading to further death of benthic plants and algae. The differential tolerances and abilities to acclimate in foundation species of corals, seagrasses, and mangroves can lead to decreases is overall diversity of foundation species, as seen in reef building corals, while communities may shift to dominance by stress tolerant species that have lower habitat complexity. That hypoxia mediates species interactions because of different stress tolerances of interactors means that pathogens may gain an advantage over stressed hosts, as in black band disease on corals, that increased stress

(A) Coral reef © blue-sea.cz; (B) Seagrass bed © Ethan Daniels/Shutterstock.com; (C) Mangroves © happystock/Shutterstock.com.

may increase dependence on mutualisms, as in sleep-swimming fish that flush hypoxic coral crevices with oxygenated water, and that algae may increase on reefs because they are more tolerant than corals to extremely low oxygen conditions.

Black band disease © Rogers et al. (2008).

Low-oxygen events can also cause mass mortality of habitat-forming seagrass and corals, such that ecosystem services including nursery function are lost, and structural complexity of habitats becomes simplified with a loss of structures such as coral reefs and seagrass beds that are built and maintained by aerobic organisms. Hypoxia in tropical ecosystems may interact with other global change stressors including ocean acidification and warming though the health and survivorship of corals and seagrasses may respond nonlinearly to changes in dissolved oxygen concentrations. Photosynthetic consumption of carbon dioxide and production of oxygen by corals and seagrasses may alleviate stresses associated with ocean deoxygenation and acidification, whilst on the other hand, increased respiration by photosynthetic organisms, particularly with warming, can have the opposite effect.

Mesopelagic communities

Mesopelagic communities include fish and other organisms inhabiting the intermediate depths of the sea, between about 200 and 1,000 m (approximately 650 and 3,300 ft) down. Mesopelagic community structure is directly dependent on the availability of oxygen for aerobic metabolism.

Diversity, abundance, distribution and composition of mesopelagic species are all influenced by variations in oxygen at both large and small scales. Ocean deoxygenation will decrease the minimum oxygen content in the mesopelagic zone and cause oxyclines to shift vertically (i.e. expansion of the OMZ core) in the water column. Within this ocean realm a species' ability to extract oxygen from sea water has evolved to meet specific oxygen demand. As a result, species do not have excess capacity, nor do they live in environments with excess oxygen relative to their evolved capacity; thus, they are susceptible to reductions in oxygen partial pressure and increasing temperature (which elevates metabolic demand).

For mesopelagic species changes in temperature and oxygen profiles within the water column may therefore decouple or enhance competition among different mesopelagic zooplankton species and the larger predators that forage on them at depth by changing zooplankton abundances, distributions, and the depth of layers, and altering species composition and diversity. The biogeochemical cycles (i.e. the biological pump and microbial assemblages) that rely on the mesopelagic zooplankton community will be substantially altered.

Decreasing oxygen partial pressure (PO_2) in any habitat will reduce aerobic metabolic performance of all species living there (but PO_2 will not decrease in surface waters that are in equilibrium with the atmosphere). For the mesopelagic species decreased oxygen will reduce capacity for prey capture and predator evasion, and, depending on the extent of deoxygenation and interacting effects of rising temperature, may lead to species-specific reductions in survival, growth and reproduction.

Shallower upper oxycline and hypoxic layers may result in species-specific suppression of vertical movements and compression of aerobic vertical habitat towards the surface. This may alter the ecological relationships between species living in different depth strata, and it may reduce abundance of species as they are forced into shallower, well-lit waters with higher predation pressure. In addition, it may reduce diversity in the OMZ core and alter the species composition of the ecosystem and biogeochemical cycles and the efficiency of the biological carbon pump. Future expansion of OMZs will force the lower oxycline community into deeper waters. This may alter life histories (diapause and reproduction) of seasonal inhabitants, predator-prey interactions with deeper bathypelagic species and may further alter biogeochemical cycles and efficiency of the biological pump.

Continental margin mesopelagic communities

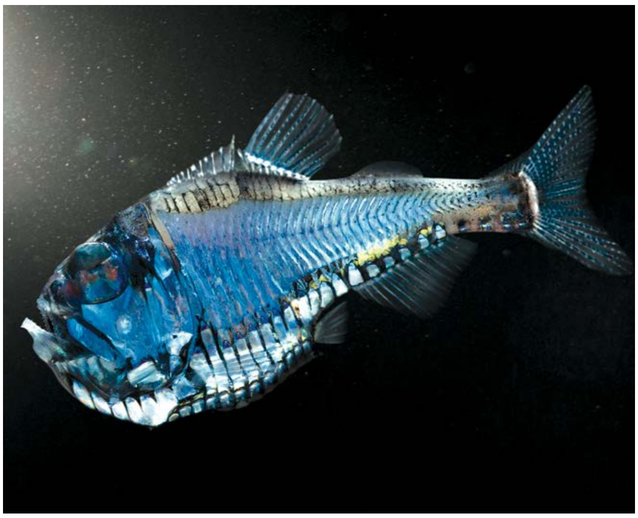
Global climate models predict global warming will lead to declines in midwater oxygen concentrations, with greatest impact in regions of OMZs along continental margins. Time series from these regions indicate there have been significant changes in oxygen concentration, with evidence of both decadal variability and a secular declining trend in recent decades. The areal extent and volume of hypoxic and suboxic waters have increased substantially in recent decades with significant shoaling of hypoxic boundary layers along continental margins.

The mesopelagic communities in continental OMZ regions are unique, with the fauna noted for their adaptations to hypoxic and suboxic environments. However, mesopelagic faunas differ considerably, such that deoxygenation and warming could lead to the increased dominance of subtropical and tropical faunas most highly adapted to OMZ conditions.

Denitrifying bacteria within the suboxic zones of the ocean's OMZs account for about a third of the ocean's loss of fixed nitrogen. Denitrification in the eastern tropical Pacific has varied by about a factor of 4 over the past 50 years, about half due to variation in the volume of suboxic waters in the Pacific. Continued long-term deoxygenation could lead to decreased nutrient content and hence decreased ocean productivity and decreased ocean uptake of carbon dioxide. Deoxygenation could also lead to increased oceanic release of nitrous oxide, a powerful greenhouse gas that is microbially produced in suboxic conditions.

There are few time series to evaluate the impact of declining oxygen on the mesopelagic fauna of continental margins. However, in the California Current a broad suite of mesopelagic fishes has declined ~77%, highly correlated with a 22% decline in midwater oxygen concentrations. Several tropical-subtropical taxa noted for their adaptations to hypoxic conditions have increased in dominance. The Humboldt squid, adapted to preying on mesopelagic fishes in the hypoxic boundary layer, has dramatically increased its range and apparent abundance.

Mesopelagic micronekton is a key trophic link between the zooplankton and a variety of predators: squids, tunas, sharks and other fishes, and a number of marine mammals and seabirds of special conservation interest, so a widespread decline in mesopelagic fishes could have profound consequences for global marine ecosystems and fisheries. Continental margins in upwelling areas are exposed to naturally occurring hypoxia over an area of 1.1 million km^2; the resulting oxygen gradients provide excellent natural laboratories for understanding adaptations, tolerances, thresholds and ecosystem responses to ocean deoxygenation.



Hatchetfish *Agyropelecus affinis* © Paulo Oliviera / Alamy stock photo.

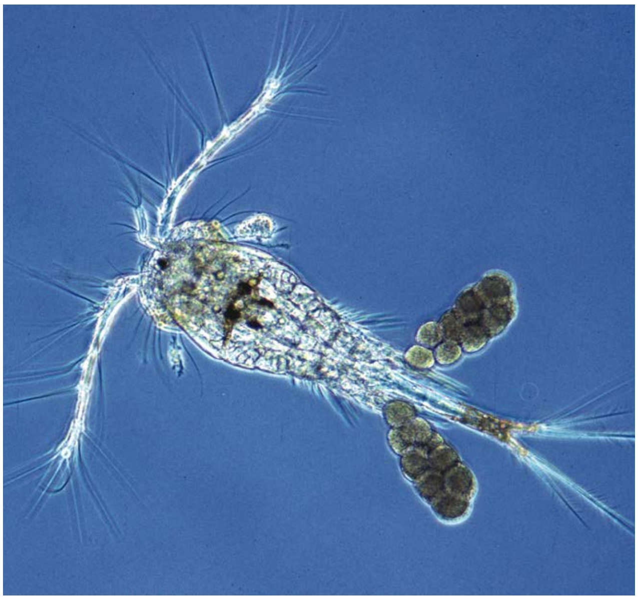
Expanding oxygen minimum zones will change the structure and function of benthic communities on continental margins through alteration of the taxonomic composition, body size, food-web structure, bioturbation and carbon cycling. Community diversity is especially sensitive to hypoxia, with decreases in diversity consistently observed under hypoxic conditions across all size classes of animals (from meiofauna to demersal fish). Loss of diversity can lead to reduced adaptive capacity and less resilience to various perturbations. Deoxygenation on continental margins is already causing habitat compression for hypoxia-intolerant demersal and benthic species, and habitat expansion for hypoxia-tolerant species, leading to altered species interactions, including those with humans.

Estuarine and coastal plankton

Seasonal deoxygenation of estuarine and coastal ecosystems leads to a variety of impacts on estuarine and coastal plankton. For zooplankton this includes lower overall abundance; altered community structure with smaller, egg carrying taxa and gelatinous zooplankton increasing with decreasing dissolved oxygen; shallower vertical distributions and reduced vertical migration extent; sub-lethal impacts including reduced size at adulthood; and reduced growth rates. Pelagic predator-prey interactions can be altered if zooplankton prey utilize hypoxic waters as a refuge from fish predation. Conversely, avoidance of low oxygen bottom waters can result in zooplankton aggregations at the interface of hypoxic waters which can be sought out by zooplankton predators.

In coastal ecosystems with shears and differential flow between surface and deep layers, avoidance of low oxygen bottom waters can influence spatial dynamics of zooplankton populations by altering emigration and immigration patterns, and residence times. There is a need for ecosystem models of estuarine and coastal seas to incorporate seasonal hypoxic bottom waters to better understand the impacts of current and future deoxygenation on pelagic food webs.

Low oxygen bottom waters may result in lower overall zooplankton abundances, with lower grazing pressure on phytoplankton. This may result in limiting food levels for zooplankton-feeding fish. Low oxygen waters may also result in zooplankton species changes with a shift



Copepod *Oithona davisae* © Albert Calbet.

to smaller sized individuals. Thus, different zooplankton species may be less nutritious to their fish predators, and the presence of smaller zooplankton prey may require that more zooplankton be consumed by fish to meet their nutritional needs

Zooplankton using mild hypoxic bottom water as a refuge from predation may have a number of consequences. Zooplankton-feeding fish may avoid the low oxygen bottom waters and thus have reduced consumption of zooplankton. Zooplankton-feeding jellyfish by contrast can tolerate low oxygen waters more than fish and thus may replace fish as the dominant consumers of zooplankton.

Zooplankton may avoid severe hypoxic bottom waters and aggregate at the depth interface of rapidly decreasing oxygen which may result in enhanced feeding zones for zooplankton predators.

The differences between environmental supply of oxygen and the organism's demand for oxygen drive the response of plankton to deoxygenation. The definition of hypoxia as a concentration does not account for the decreasing solubility of oxygen and increasing metabolic rate of organisms with increasing temperature. At high temperatures organisms may be in stressful or lethal conditions even when the concentration of dissolved oxygen is above levels defined as hypoxic ($<2mg\ L^{-1}$). The actual effect of hypoxia is very likely species and temperature specific, related to each zooplankton species oxygen demand.

Elasmobranchs

All of the more than 1000 species of sharks, skates and rays are obligate water-breathers with comparatively high absolute oxygen demands being relatively large-bodied, active predators. With broad distributions across aquatic habitats exhibiting large variations in physico-chemical variables including oxygen concentration indicates elasmobranch physiology, behaviour and ecology to be strongly influenced by oxygen depletion.

Many elasmobranchs show rapid behavioural responses to hypoxic water by increased activity associated with avoidance. Nonetheless, elasmobranchs also appear capable of withstanding mild hypoxia with circulatory and/or ventilatory responses, perhaps even for extended periods. However, such strategies may be insufficient to endure moderate, progressive or prolonged hypoxia or anoxia. As water temperatures rise with climate warming most elasmobranchs (as ectotherms) will exhibit elevated metabolic rates and will be increasingly less able to tolerate the effects of even mild hypoxia associated with ocean deoxygenation. Thus, sustained hypoxia in warmer coastal waters is likely to lead to shifts in elasmobranch distributions.

Expansion of OMZs in the open ocean in particular are predicted to have significant population-level implications for pelagic elasmobranchs as they become habitat compressed into surface layers by shoaling hypoxic water and, thus, potentially at greater risk of capture from surface fisheries.. Surface layers overlying OMZs appear to be space-use hotspots of pelagic sharks that may be increasingly likely to undergo significant 'habitat compression' (reduced habitat volumes) with expanding OMZs. Such waters above OMZs are known to be hotspots of commercial fishing for pelagic sharks, and expanding OMZs may lead to further risks of overexploitation of threatened species, such as the already overfished shortfin mako, *Isurus oxyrinchus*. A priority is therefore to mitigate ocean deoxygenation effects on elasmobranchs, such that future catch rates are controlled in the light of climate change rather than for exploitation to be exacerbated by ocean oxygen losses.

Shortfin mako *Isurus oxyrinchus* © Richard Robinson / Alamy stock photo.

Tunas and billfish

Tunas and billfishes should be especially sensitive to low ambient oxygen conditions given their high metabolic rates as well as the large differences between their resting and maximum metabolic rates. Although there are many behavioural similarities among the different species, there are also clear and demonstrable differences in growth rates, maximum adult size, physiological abilities, low-oxygen tolerances, and preferred environmental conditions.

Atlantic blue fin tuna *Thunnus thynnus* © Paulo Oliviera / Alamy stock photo.

Climate change is projected to alter oxygen concentrations throughout the open ocean, with most regions undergoing decreases due to a slowdown in ocean ventilation and a decline in surface oxygen solubility. Between 200 and 700 m depth (a vertical range including depths to which tunas and billfishes commonly descend to forage), the greatest and most certain decreases in oxygen concentrations are projected to occur in the North Pacific and much of the Southern Ocean, while the smallest and least certain changes are projected to occur within the tropical Pacific Ocean. Along a north-south line through the middle of the Pacific Ocean (160°W longitude), projected oxygen concentration decreases are most pronounced from 15°N to 50°N between 250 and 750 m depth and south of 50°S between 50 and 300 m depth.

The depth at which oxygen concentrations drop below 3.5 ml L^{-1} (a threshold hypoxic concentration for several tuna and billfish species including yellowfin and skipjack tunas, marlins, and sailfish) is projected to shoal throughout the global oceans, which may lead to widespread vertical habitat compression and changes in vertical movement patterns. Projected shoaling of the 3.5 ml L^{-1} threshold depth is especially pronounced within subtropical and mid-latitude Pacific Ocean regions. Oxycline depth is also projected to shoal by over 150 m in these same Pacific Ocean regions and throughout much of the Southern Ocean. Species residing in the temperate North Pacific, such as swordfish and yellowfin, bigeye, Pacific bluefin, and albacore tunas, may therefore be impacted by future oxygen changes more greatly than other species, as projected decreases in oxygen concentrations are greatest within their present-day ranges.

Changes in temperature and oxygen content have the potential to alter the distribution and catchability of tunas and billfishes in three dimensions. Because they are highly mobile, tunas and billfishes can exhibit complex shifts in their distributions in response to changing environmental conditions. Where surface layer temperatures become too warm, they may spend more time at depth (assuming oxygen concentrations are sufficient); where low-oxygen layers shoal or expand, they may spend more time near the oxygenated surface (assuming temperatures are not too warm), increasing their vulnerability to surface fishing gears. If no vertical refuge from unsuitable conditions is available, they may shift their distributions horizontally. Because temperature and hypoxia tolerances of tunas and billfishes are species-specific, any changes in temperature and oxygen content within the water column may modify competition among different species as their vertical and horizontal habitats shift in different ways, potentially altering established food web dynamics, ecosystem structures, and bycatch rates. Differential responses of prey species to changes in environmental conditions could also affect food web structures, the ability of tunas and billfishes to find food, age at first reproduction, and mean body sizes.

Future changes in the distributions of tunas and billfishes are likely to complicate stock assessments and to have important socio-economic effects. As spatial habitats of targeted tuna and billfish species shift, the ability of fishery-dependent, catch per unit effort (CPUE)-based abundance indices to capture stock dynamics accurately will be compromised, unless CPUE-standardization methods can adapt. Where populations of targeted tuna and billfish species decrease in abundance or move away from traditional fishing grounds, fishers will have to spend more resources to locate and catch these species or reconfigure their gear to target new ones. Economic, political, and regulatory constraints can, however, hinder the ability of fishers to effectively adapt, particularly if species move across management boundaries. Smaller-scale fisheries in developing nations and fisheries relying on vessels with limited range and low technological capabilities are likely to be most vulnerable to shifts in range or migratory patterns.

Ocean megafauna

Marine mammal distribution is primarily driven by prey availability. Therefore, community-wide impacts on gilled species affect the behaviours of marine mammals. Coastal hypoxia is increasing in areas of critical marine

Ocean deoxygenation consequences at a glance

- Oxygen is required by marine organisms to turn food into energy that can be used to grow and reproduce, as well as escape from, adapt to, and repair damage caused by other stressors. When ocean oxygen levels are insufficient, an organism may not have the necessary energy to withstand other stressors. Increasing global temperature simultaneously worsens oxygen decline and increases oxygen requirements of organisms that rely on aerobic respiration.
- Deoxygenation and the presence of areas with little or no oxygen is occurring in ever larger areas of the continental shelves. The consequences of continuous loss of global oceanic dissolved oxygen content are predicted to result in changed ecosystems, compression of currently biologically available habitats, and large-scale changes in ecosystem services.
- Low oxygen alone and in combination with other stressors can reduce the ability of an animal to fight pathogens and parasites, which can lead to increased intensity and prevalence of a number of diseases of marine animals. The energy deficiency resulting from low oxygen can also increase morbidity and mortality from diseases.
- Avoidance of low oxygen by species can result in altered spatial and temporal distributions, where mobile species may experience higher fishing mortality if fishers target well-oxygenated areas that serve as a refuge for animals forced to avoid oxygen-depleted habitat. Well-oxygenated habitat may also not be suitable as a refuge for species from oxygen-depleted areas because of the presence of other stressors such as high temperatures and predators.
- Reduced fish catches with decreasing economic profit in coastal states are expected. Specific ecosystem services can be negatively affected by combined deoxygenation, pollution and ocean acidification. Negative impacts are expected on biological regulation, nutrient cycling and fertility, food, ornamental resources (like corals, pearls, shell material), tourism and recreation.
- Deoxygenation directly affects species, ecosystems and many aspects of the ecosystem services provided by the open ocean and coastal waters. Its effects are overlain by climate variability, such that interactions and understanding of impacts and intertactions is limited.
- Oxygen declines induce species range shifts, changes to vertical and across-shelf movement patterns, and losses in spawning habitats resulting in:
    - Altered ecological interaction rates among predators and prey, and species that compete for resources.
    - Altered ecological interactions as invasive hypoxia-tolerant species increase in abundance.
    - Reduced fishery productivity as population replenishment declines for benthic spawning species and those that have strong habitat dependence for growth.
    - Increased fishery conflicts as multiple targeted species are compressed into restricted oxygen refuges.
    - Increased management uncertainty as fishery independent surveys are compromised by reduced accessibility of fish to survey methodology.
- Spatial and /or temporal expansion of areas currently affected by suboxia or anoxia as well as novel development of habitats with little or no oxygen in regions where they have previously been absent will result in:
    - Increased loss of nitrogen nutrients as denitrification intensifies.
    - Increased risk of water column hydrogen sulphide accumulation effects as sulphate reduction intensifies.
    - Altered ratios of nutrient availability as the flux of iron and phosphorus from sediment increases.
- Intensification of ocean warming, acidification, and other ocean stressors in conjunction with coastal hypoxia will result in:
    - A wider array of taxa and processes affected.
    - More rapid shift to no-analogue state in the modern ocean where multiple aspects of coastal ocean environment move away from natural ranges of exposure.

Elephant seal *Mirounga angustirostris* © MZPHOTO.CZ / Shutterstock.com.

mammal habitat. There are approximately 47 species of marine mammal in the hypoxia-affected regions of the Northern California Current System, Black Sea, Baltic Sea, and Gulf of Mexico.

Coastal hypoxia events lead to shifts in distribution, mobility, predator avoidance, and mortality of gilled animals. Severe or prolonged hypoxia can lead to shifts in food web, with potential for impacting foraging success of marine mammals. Increased ocean warming, and the resultant decreases in oxygen retention ability of saltwater suggest an imminent pattern of worsening hypoxia worldwide. These patterns may lead to increased pressure for marine mammal species that are already threatened or endangered. Conversely, increased rates of predation on gilled species incapacitated or spatially compressed by hypoxia may benefit certain marine mammals. Direct links between coastal hypoxia and marine mammals may be difficult to quantify, but abundant nearshore marine mammals are likely excellent study species to begin unraveling this issue.

Ocean deoxygenation drives offshore OMZ expansion and shoaling. This expansion may positively affect the foraging efficiency of northern elephant seals, due to (1) their increased ability to feed on inactive prey, (2) decrease of diving costs in terms of both time and energy expenditure, and subsequent increased prey search time in the bottom phase of foraging dives (3) elevated prey density related to the vertical compression of prey distribution. Increased dependency on the prey in the OMZ (about 40% of total their prey) may lead to species composition changes within the mesopelagic community. Increase of foraging efficiency by elephant seals may lead to further population increases, potentially resulting in large disturbance and shifts in the functioning of the mesopelagic ecosystem through top-down and trophic cascade effects.

Sperm and beaked whales, typical deep divers in the mesopelagic zone, foraging on squids which forage in the upper mesopelagic zone and often rest in the OMZ. Although foraging and vertical migration of squids remain unclearly defined, it is suggested that future shoaling of OMZ will cause the vertical compression of this ‘resting zone’, consequently giving a foraging advantage to sperm whales and beaked whales feeding on squid. Increased foraging efficiency in habitats where the OMZ shoaling occurs will enhance the role of deep diving mammals in the nutrient cycling via pumping nutrients to the surface waters from the OMZ, leading to an increase of production and nutrient flux to depths. This increased flux could ultimately affect oxygen consumption as a result of microbial respiration and nitrification in the oxygen limited zone, leading to further expansion of the OMZ.

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CONSEQUENCES FOR ECOSYSTEM SERVICES

Effects of ocean deoxygenation on people remain understudied and inherently challenging to assess. Few studies address the topic and those that do generally include the more readily quantified economic losses associated with ocean deoxygenation, exclude non-use and existence value as well as cultural services, and focus on relatively small, bound systems in capitalized regions. Despite the lack of extensive research on the topic, current knowledge based in both the natural and social sciences can offer useful insights into what can be expected from continued ocean deoxygenation in terms of generalized impact pathways.

People receive benefits from the ocean ecosystem services in the form of well-being (assets, health, good social relations, security, agency). Ecosystem services are translated to human well-being via social mediation, such that differences in levels of power and vulnerability determine how different social groups will experience hazards created by continued ocean deoxygenation. Despite not knowing the precise mechanisms of ocean deoxygenation-driven biophysical change, established social mechanisms suggest that ocean deoxygenation will exacerbate existing social inequities and disturbances.

Reductions in dissolved oxygen are expected to disrupt functioning of ecosystems and lead to habitat degradation, which will place challenges and new costs on existing systems for using ocean resources. Coral reefs, wetlands and marshes, and fish and crustaceans are most susceptible to negative effects of ocean deoxygenation, so people reliant on these systems will be particularly at risk of negative impacts. Some hypoxia-tolerant species may see benefits from reduced dissolved oxygen levels due to altered, if temporarily, and these should be considered in adaptation strategies.

People in low latitudes, coastal urban and rural populations, poor households in developing countries, and marginalized groups (such as women, children, and indigenous populations) are most vulnerable to the impacts of ocean deoxygenation. Communities where these characteristics overlap are uniquely vulnerable, notably coastal communities in West Africa and low income developing countries (LIDCs). Improved understanding of nuanced impact pathways of ocean deoxygenation to human well-being outcomes will be of critical importance for effective planning in response to ocean deoxygenation going forward. Analyses of ecosystem services should consider the entire range of ecosystem service types, even where not quantifiable, in order to provide the depth and accuracy of information needed for proper planning. Transdisciplinary approaches to assess systems holistically present promising means for gaining policy-relevant knowledge of complex and dynamic social-ecological system dynamics.

Policies and actions aimed at adapting to and mitigating for ocean deoxygenation, should focus on reducing the vulnerability of groups and individuals by addressing ultimate and proximate causes of high sensitivity and exposure, mitigating problems such as eutrophication, and building adaptive capacity. Attention should be paid to the central role that social institutions play in mediating access to ecosystem services and the inherent inequities in the ways in which humans experience natural hazards.

The consequences of ocean deoxygenation on ecosystem services at a glance

The consequences of ocean deoxygenation can and will likely have an increasing number of impacts and challenges for dependent human communities, economies and society as a whole.

- The reduction of the habitat available for pelagic, mesopelagic, and benthic organisms may cause:
    - Shifts in distribution of species leading to reduced availability of ecosystem services in areas of lost habitat and, in some cases, increased availability of ecosystem services in well-oxygenated waters or by species that see a competitive advantage in hypoxic areas.
    - Fewer human well-being benefits supplied by sectors (such as fisheries and tourism) that are reliant on negatively affected organisms and the services they supply.
    - Changes and uncertainty in sectors and groups reliant on affected species leading to associated costs of adaptation to new or increasingly less well predicted conditions.
    - Greater reductions in well-being experienced by more vulnerable groups, and any benefits of increased ecosystem service availability accrued to groups with greater adaptive capacity. Groups lacking capacity to adapt will see more negative outcomes than those with greater adaptive capacity.

- The reduction in the abundance and recruitment of fish and other marine populations in regions of low oxygen levels may cause:
    - Reduced availability of food in areas experiencing low dissolved oxygen levels. Low latitude ocean systems and areas adjacent to high-density coastal populations will be most negatively affected.
    - Groups that are most reliant on affected ecosystem services and least able to adapt to changes will experience the most risk due to loss or reduction of ecosystem services.
    - Groups reliant on species and systems that are relatively more susceptible to low oxygen conditions, such as fish, coral reefs, and bivalves, will be more negatively affected.
    - Cascading effects and alteration of the foodweb structure may lead to increases in some ecosystem services, however, only groups with the capacity to take advantage of increased services will see benefits.

- The challenges in model development and observation quality, mean that:
    - Model development needs new observations and dedicated experiments placing demands on assets and social capacity.
    - Model uncertainty will lead to less complete knowledge and less effective management.
    - Increased costs of uncertainty and need for adaptation to new conditions.

Consequences of ocean deoxygenation on fisheries

Fisheries (commercial, artisan, recreational harvest) are an ecosystem service that provide employment and nutrition in the global food system. Worldwide production of capture fisheries has levelled off, while demand continues to increase. Over-harvesting and effects on habitat and the food web switches fisheries from an ecosystem service to a stressor. Deoxygenation is anticipated to expand over the next decades, and can affect fisheries through negative effects on growth, survival, and reproduction affecting biomass, and movement of fish affecting their availability to harvest. The extent of the deoxygenation effects on fisheries is anticipated to increase because the areas of the ocean that will show increasing deoxygenation overlap with the coastal and oceanic regions that support high fisheries production.

Quantifying the effects of deoxygenation on fisheries is complicated by the effects of co-varying environmental factors and other stressors also affecting the population dynamics of the species of interest, and because the dynamics of oxygen and fisheries (fishers and vessels) are highly site-dependent. Global climate change assessment involves simultaneous changes in temperature, acidity, and oxygen, as well as effects caused by other stressors such as sea-level rise. Isolating a direct hypoxia effect on fisheries landings using a correlation-based analysis of landings and nitrogen loadings across ecosystems is difficult, but trophic efficiency (landings per unit nitrogen loading) was lower in systems with extensive hypoxia.

Ocean deoxygenation affects fisheries in various ways. Examples include low oxygen effects on the target fish population itself through reduced recruitment and population abundance and examples of spatial distribution effects on the fish and crustaceans resulting in changes in the dynamics of fishing vessels. Analyses range from circumstantial evidence based on field data to extensive data and modelling. Modelling analyses demonstrate that in those situations when hypoxia alone may have small to moderate population-level effects, the effects can become large or amplified when hypoxia is combined with other stressors.

A prevalent effect of deoxygenation is changes in fishing locations in response to fine-scale distribution changes of the target species due to hypoxia that then affects the catchability and bio-economics of fishing. Catchabilities are relied upon for effective fisheries management and not including the effects of deoxygenation on catchability can result in ill-informed management analyses and incorrect harvesting advice.

Decreasing oxygen concentrations in habitats presently used by fish that support fisheries will result in species-specific reductions in growth, survival, and reproduction of individuals. When sufficient numbers are affected, there will be effects at the population level via reduced fishable biomass, as well as poor quality of fish (e.g. skinny) in the catch.

Increasing areas of the ocean will experience lower oxygen concentrations that will cause organisms to avoid lethal areas, and in some cases, cause individuals to aggregate around the hypoxia areas or shift their spatial distributions. This in turn will impact fisheries. Fishing activities will be affected economically (higher costs) by vessels requiring longer trips, spending less time fishing because they spend more time motoring to access the fishing grounds. In some situations, fish will become easier to catch (aggregation closer to shore) and more available to local fishers. In both cases, deoxygenation will affect management (likely being riskier than thought) that relies on relating catch to population abundance (catchability) because catches will no longer adhere to the underlying assumptions about catchability used in stock assessment.

Increasing deoxygenation is occurring worldwide, especially in coastal areas that also provide much of the world's commercial and subsistence fisheries catch. With the catch of wild fish approaching maximum sustainable levels, the need for accurate management advice is critical. Management needs to account for the effects of deoxygenation in its stock assessments and deliberations.

Further progress in the science of ocean deoxygenation is needed to better predict the patterns and consequences of ocean oxygen decline, and to inform policies and technological solutions to reduce further decline. Critical areas include:

- Expanding oxygen observations in the open ocean and coastal waters, including through integration with existing programmes and networks, targeting regions where more data will improve assessment of the current status and patterns of oxygen change.
- Experiments and observations to improve understanding of critical mechanisms that control the patterns and effects of oxygen declines.
- Numerical models with improved ability to predict current effects of low oxygen and other stressors, future changes in oxygen levels, and potential benefits of management options at global, regional and local scales.
- Assessments of effects on human economies and societies, especially where oxygen declines threaten fisheries, aquaculture and livelihoods.
- Development of a data management system, with rigorous quality control and leadership by a globally recognized oceanography data centre that provides open access for use in science and policy.
- Continued improvement of oxygen monitoring equipment, including sensors that accurately measure ultra-low oxygen concentrations and low-cost sensors that will make more extensive monitoring in undersampled coastal waters possible.
- Capacity building in coastal areas of the developing world for observations on core oceanographic parameters, especially oxygen, and on the impact of deoxygenation on fisheries and biodiversity, will have to be given high priority.

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WHAT CAN WE DO ABOUT IT?

The oxygen content of the open ocean and coastal waters has declined since the middle of the 20th century and is expected to decline further during the 21st century as a result of climate change and increased nutrient discharges. Consequences of this ocean oxygen decline include decreases in biodiversity, shifts in species distributions, displacement or reduction in fisheries resources, and changes in biogeochemical cycles.

Fossil fuel combustion and agriculture contribute to both global warming and over-enrichment of waters with nutrients. Sewage – biomass in untreated sewage and nitrogen and phosphorus in both treated and untreated sewage effluent – is also a major contributor to oxygen depletion in coastal waters. Nutrient reduction strategies that have been most effective have utilized legal requirements, set specific targets, and have employed monitoring to detect problems and responses to management strategies. A range of potential solutions to nutrient reduction exists and can be tailored to local needs and economies. Comparisons of models and observations suggests that models underestimate the true rate of ocean oxygen loss. Ocean deoxygenation may occur more rapidly and may be more severe than suggested by such models.

Reducing the rate of oxygen decline in the global ocean and minimizing the contribution of climate change to deoxygenation of coastal waters, requires a dramatic climate mitigation effort, primarily through urgent, radical and large global reductions in greenhouse gas emissions due to human activities. Restoring oxygen lost over the past century on less than millennial time scales will also require reducing atmospheric greenhouse gas concentrations to levels lower than the present through active greenhouse gas removal. Warming-driven deoxygenation cannot be easily reversed and so earlier action to limit carbon dioxide emissions and reduce warming will yield greater benefit.

Continued and enhanced efforts to quantify trends in deoxygenation and project future oxygen conditions, to understand deoxygenation effects on biological, biogeochemical and ecological processes, and to incorporate deoxygenation in development of fisheries and other management strategies are needed. Governance at scales ranging from local jurisdictions to international bodies such as the United Nations plays important roles in identifying the problem and solutions to deoxygenation, and in mitigation and adaptation efforts to reduce deoxygenation and its negative consequences.

Solutions to ocean deoxygenation, and development of adaptation strategies in its presence, depend on sound and sufficient science. The international scope of scientific collaboration on this issue is notable; scientific working and expert groups can help facilitate communication among different stakeholders, and support decision makers to take measures required to stem increasing deoxygenation at local, regional and global scales. Further progress is needed, however, in the science of ocean deoxygenation, especially to improve predictions of future conditions and impacts on human welfare.

Ocean deoxygenation is a progressive problem that needs immediate attention. Warming-driven deoxygenation cannot be easily reversed; indeed, the ocean oxygen inventory is likely to take centuries to recover from warming projected under "business-as-usual" emissions scenarios. Deoxygenation is intrinsically linked to climate warming; reduction of human-driven warming is the only means of preventing widespread ocean oxygen loss. Stabilization of climate-changing emissions, however, can enable ocean ventilation to recover to some degree, thereby mitigating oxygen loss. The longer the delay in dramatically raising ambitions and drastically cutting emissions, the greater are the consequences that will need to be faced in the future.

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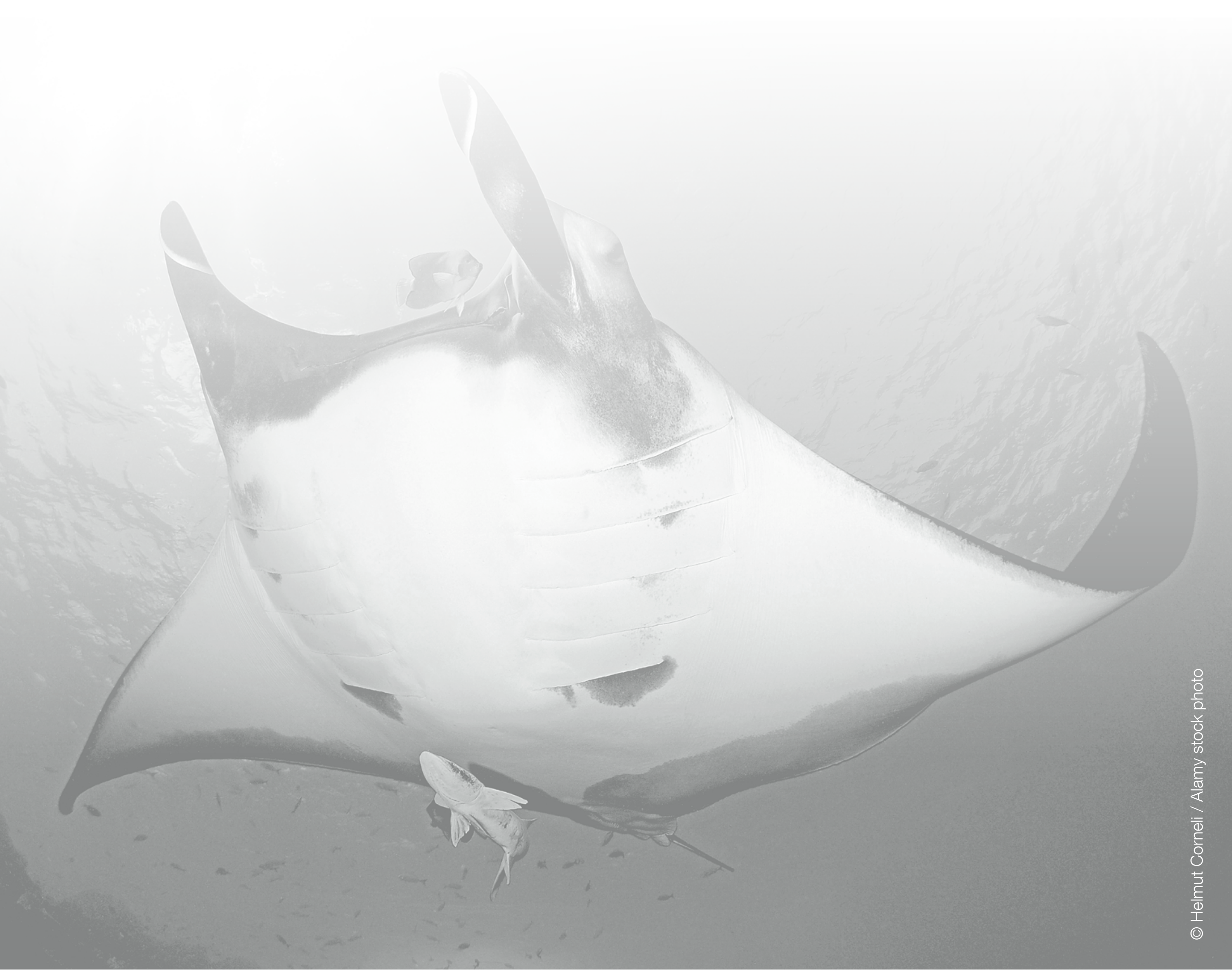

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INTERNATIONAL UNION
FOR CONSERVATION OF NATURE

WORLD HEADQUARTERS
Rue Mauverney 28
1196 Gland
Switzerland
Tel +41 22 999 0000
Fax +41 22 999 0002
www.iucn.org