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Ocean Oxygen Loss:
If Fish Could Talk

Summary

Almost all life on Earth depends on oxygen. The global oceans are currently losing oxygen due to global warming, and oxygen-starved dead zones are expanding. The loss of oxygen is known as deoxygenation. This major threat to marine ecosystems, biodiversity, fisheries, and human societies has not gained much public awareness yet, despite posing as much of a risk as ocean warming and acidification. Ocean oxygen loss can also lead to emissions of toxic gases, such as hydrogen sulphide, and greenhouse gases, such as nitrous oxide, methane, and carbon dioxide, potentially worsening global warming. Ocean deoxygenation can only be mitigated if greenhouse gas emissions are rapidly reduced to zero.

- Dissolved oxygen in the global ocean has decreased by over 2% since 1960 due to global warming, with localised declines of up to 50%.
- Ocean oxygen loss is already driving mass mortality events and causing significant habitat shrinkage for economically critical species. Lack of oxygen harms fish and fisheries by reducing fish size and increasing the risk of disease, blindness, and respiratory failure.
- Ocean oxygen loss leads to the release of greenhouse gases, such as nitrous oxide (N_2O) and methane (CH_4), and the release of the toxic gas hydrogen sulphide (H_2S).
- Although ocean deoxygenation due to global warming will persist for centuries, rapid reductions in greenhouse gas emissions will limit the negative consequences for marine ecosystems and fisheries.

Introduction

Today's atmospheric oxygen levels are more than sufficient to sustain life on land, but this is not the case for the ocean, where many regions are starved of oxygen. Contrary to the well-mixed atmosphere, oxygen concentrations in the ocean vary spatially, and there are large zones at intermediate depths (100-600 metres) that are very depleted in oxygen.

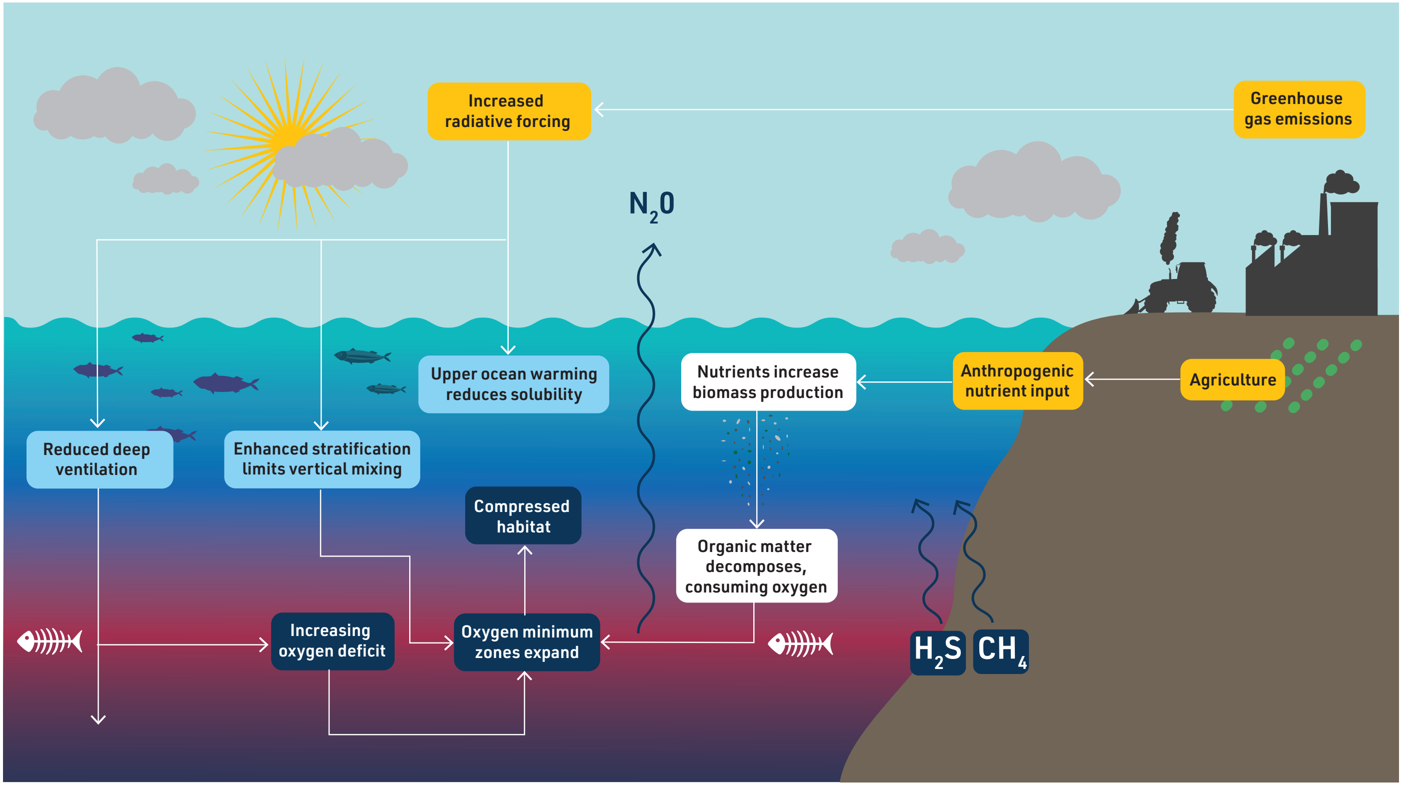
Ocean oxygen levels are decreasing due to human-induced climate change and nutrient run-off from land. Oxygen loss (also called deoxygenation) is already causing mass mortality events and changes to fisheries. This is a concern, as ocean oxygen loss has been associated with mass extinctions in the past (Meyer and Kump, 2008, Penn et al., 2018, Mancini et al., 2024). Low oxygen conditions are also associated with outgassing of greenhouse gases and toxic gases.

Even though the impacts of ocean oxygen loss are already significant and have profound implications for humanity, the subject has not yet gained much public awareness. This is slowly changing, with, for example, the establishment of the Global Ocean Oxygen Decade (GOOD) programme which is endorsed by the United Nations Decade of Ocean Science for Sustainable Development (2021-2030).

Ocean oxygen dynamics

Oxygen concentrations in the ocean are driven by physical and biological processes. In the sunlit zone near the surface, phytoplankton produce oxygen through photosynthesis. This source of oxygen, in combination with physical gas exchange between the atmosphere and ocean, ensures that most ocean surface waters are saturated in oxygen. The saturation concentration depends predominantly on water temperature, with cold surface waters being better oxygenated than warm surface waters.

As organic matter sinks through the water column it is consumed by microbes, which use up oxygen in the process. Ocean zones that are located below surface regions with high biological productivity can become severely oxygen depleted, especially if the physical transport of oxygen-rich waters into these zones is weak. These Oxygen Minimum Zones often occur near nutrient-rich zones along the eastern margins of the tropical oceans and can stretch from 10's to 100's of metres below the surface. In coastal regions with extensive agriculture or other sources of nutrient run-off, excessive nutrient enrichment (eutrophication) can occur, triggering algal blooms that deplete oxygen in the water, with detrimental impacts on marine life.



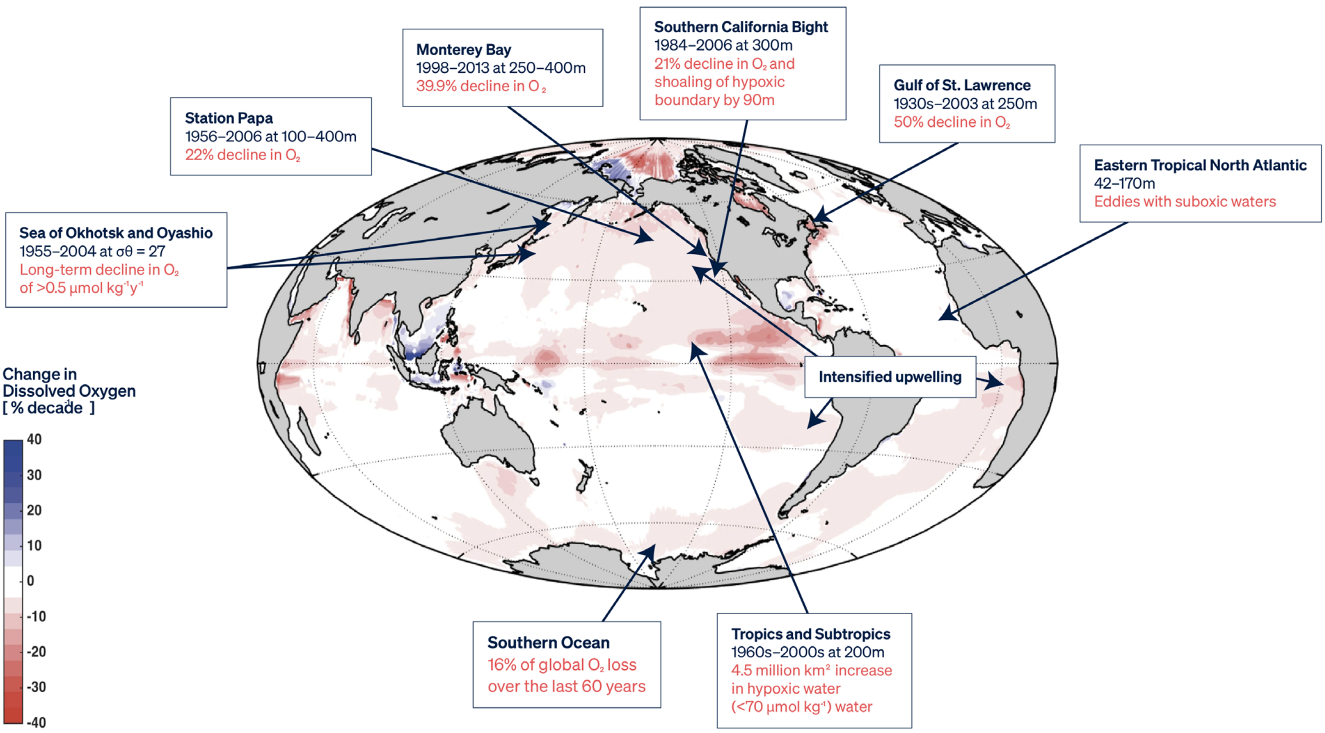
Mechanisms of oxygen loss in the ocean
(redrawn from https://marine.copernicus.eu/explainers/phenomena-threats/deoxygenation)

Current ocean deoxygenation

The total ocean oxygen content has decreased by 1.1-6.8 10^{15} mol (more than 2%) and the volume of anoxic waters in the Pacific Ocean has quadrupled since 1960 (Schmidtko et al., 2017). Oxygen Minimum Zones at 200 m depths have expanded by 4.5 million km^2, corresponding to ~60% of the size of Australia (Stramma et al., 2010), and new low oxygen regions are appearing. Rates of oxygen loss seem to be faster in coastal oceans than in the open ocean (Gilbert et al., 2010). The largest declines are observed in the tropical and north Pacific Ocean, the Arctic, the Southern Ocean, and the South Atlantic Ocean (Schmidtko et al., 2017). On coral reefs, hypoxia is already widespread, with 84% of reefs globally experiencing weak to moderate hypoxia and 13% experiencing severe hypoxia (≤ 61μmol O_2/kg, Pezner et al., 2023).

Changes in oxygenation in the open ocean are mainly caused by global warming. A warmer surface ocean holds less oxygen because the solubility of gases depends on temperature. Warmer surface waters are also less dense and therefore lead to stronger vertical stratification of the ocean, which results in less exchange with deeper ocean layers. Oxygen transport into the ocean's interior is reduced and oxygen levels below the surface decline. The direct effect of warming on solubility is responsible for over 50% of the observed oxygen loss in the upper 1,000 meters of the ocean, and for ~15% of the total oxygen loss across all depths (Breitburg et al., 2018). The remaining 85% is caused by the indirect effects of warming, including changes in stratification and large-scale circulation (Breitburg et al., 2018).

In coastal waters, changes in oxygenation have to date primarily been caused by nutrient run-off from rivers. Nitrogen and phosphorus-based fertilizers have doubled riverine inputs of nutrients into coastal waters over the 20th century (Beusen et al., 2016). Many coastal regions experience seasonal eutrophication as a consequence, and this phenomenon is exacerbated by the increased warming of shallow coastal waters due to climate change in recent decades.



Percentage change in dissolved oxygen per decade since 1960.σϴ stands for density surface and RCP stands for representative concentration pathway (redrawn from Levin, 2018; base map adapted from Schmidtko et al., 2017).

Future projections

Current ocean deoxygenation due to global warming is not easily reversible and will persist for centuries, even if greenhouse gas emissions were to cease today (Oschlies, 2021). Until atmospheric CO_2 concentrations, which continue to rise, finally plateau, surface oceans will continue to warm, and the oceans will continue to lose oxygen.

The simulation of ocean oxygen concentrations is challenging, as oxygen levels depend on complex physical and biogeochemical processes (see Section "Ocean Oxygen Dynamics"). These processes must be represented correctly in a climate model to simulate oxygen realistically. State-of-the-art Earth System Climate Models systematically underestimate the observed rates of oxygen loss and are also not very skilful in reproducing the observed patterns of deoxygenation (Oschlies et al., 2017; Oschlies et al., 2018). An important challenge here is the representation of biogeochemistry in models, as our knowledge of coupled biogeochemical processes is still incomplete. Bearing these caveats in mind, model projections for the end of this century predict a further decrease of several percent even for "high mitigation" greenhouse gas emission scenarios (Bopp et al., 2013). For the "business as usual" scenario, more than 94% and 31% of coral reefs, respectively, are projected to experience weak to moderate and severe hypoxia by the end of the century (Pezner et al., 2023).

Oxygen thresholds and their impact on marine organisms

The ability to adapt to low oxygen concentrations varies between species. When metabolic stress occurs due to insufficient oxygen availability, organisms will reduce their respiration rate and no longer continue energetically expensive behaviour such as reproduction or movement. At even lower concentrations, changes in community structure and mass mortality can occur (Breitburg et al., 2018).

- Regions with oxygen concentrations below 61µmol/kg of seawater are defined as hypoxic and most organisms exposed to such low O_2 concentrations show reduced fitness and aberrant behaviour.
- If O_2 levels fall to 5-10 µmol/kg, the conditions are called suboxic and multicellular life cannot survive anymore.
- Below 1 µmol/kg of O_2, conditions are anoxic and only anaerobic microorganisms can survive.

Physiological and morphological impacts

Deoxygenation has been linked to reduced growth in a vast range of taxonomic groups (Sampaio et al., 2021) and a shift away from large-bodied fish to smaller, less palatable species (Salvatteci et al., 2022, Lefort et al., 2015). Reductions in length of up to 89% have been observed in the laboratory in temperate fish species when exposed to low oxygen concentrations (Bejda et al., 1992, McNatt et al., 2004).

Exposure to low oxygen conditions can delay when fish produce eggs, reduce how many eggs they produce and even cause blindness by impacting the shape and function of the light detecting cells in eyes (Landry et al., 2007, McCormick and Levin, 2017), with damage to these cells potentially occurring within minutes (Wong-Riley, 2010, Erecińska and Silver, 2001).

Warming water, combined with deoxygenation, reduces oxygen availability at the same time as increasing metabolic demand for oxygen. This can lead to respiratory distress, followed by respiratory failure and death (Clarke et al., 2021). The consequences of deoxygenation for fisheries and the world's future food supply could thus be tremendous (Oschlies et al., 2018, Rose et al., 2019).

Impacts on fisheries

In response to deoxygenation, many marine species are already shifting to new habitats (Humphries et al., 2024, Breitburg et al., 2018, Kim et al., 2023, Wannamaker and Rice, 2000). Tuna, sharks, and billfish, are shifting higher in the water column (Waller et al., 2024, Bograd et al., 2008, Vedor et al., 2021) while blue marlin in the eastern Atlantic have experienced an annual loss of vertical habitat of one metre per year, equating to a 15% loss of habitat between 1960 and 2010 (Stramma et al., 2012). In Peru and California, anchovies are forecast to lose half of their habitat by the end of the century due to oxygen loss (Howard et al., 2020). Habitat "compression" increases the risk of overfishing at the surface and the likelihood that at-risk species are falsely considered to be rebounding (Humphries et al., 2024). Declining oxygen can also drive major declines in biodiversity (Laffoley and Baxter, 2019).

Mass mortalities

Marine heatwaves and mass mortality events due to deoxygenation are increasing in intensity and frequency (Garrabou et al., 2022, Fey et al., 2015). In response to low oxygen, many species decrease activity and metabolic rate, limiting the escape response (Waller et al., 2024). To date, over 50 mass mortality events due to hypoxia have been recorded in the tropics, likely an underestimate (Altieri et al., 2017). Hypoxia-driven mass mortality events of sharks and rays have been recorded in Texas, Cocos Islands, South Africa and Chile in the past twenty years (Waller et al., 2024). The impacts of deoxygenation on coral reefs can be particularly severe and may even outweigh the impacts of mass bleaching events (Altieri et al., 2017). Hypoxia has been observed to cause mass mortality of coral reefs at depths of up to 15 metres (Altieri et al., 2017, Haas et al., 2014). Mass mortality events can also occur when deep, oxygen-poor water upwells, impacting shallow water ecosystems (Chan et al., 2008).

Changes in biogeochemistry and release of greenhouse gases

When oxygen levels are low, microbes start to use other chemical compounds to consume organic matter. This can cause the release of the toxic gas hydrogen sulphide (H_2S) from sediments into the water column. Some low oxygen zones periodically release H_2S in so-called "sulphidic events" today and cause fish mortality (Callbeck et al., 2021). Ocean deoxygenation, ocean warming, and potentially the release of H_2S, are considered potential drivers of one of the largest extinction events in history, which occurred 252 million years ago during the Permian-Triassic and led to the extinction of 90% of marine species (Benton, 2018, Mancini et al., 2024).

Consumption of organic matter in low oxygen conditions produces nitrous oxide (N_2O), and marine N_2O emissions are likely to increase in the future (Naqvi et al., 2010). N_2O is a long-lived potent greenhouse gas; it also causes stratospheric ozone depletion. Most low-oxygen zones in the ocean are strong emitters of N_2O today, with record emissions observed in recent years (Arévalo-Martínez et al., 2015). Finally, anoxic conditions can lead to the release of methane (CH_4) from sediments. Most CH_4 is oxidized into CO_2 in the water column (Naqvi et al., 2010) but some CH_4 may reach the atmosphere in eutrophic coastal regions today (Rosentreter et al., 2021).

The effect of oxygen loss on the carbon cycle is complex. When oxygen levels are low, bacteria use one of the two macronutrients essential for life, nitrate, to consume organic matter. Oxygen loss in the ocean could therefore lead to global nutrient loss and thus lower primary productivity, which then could entail a weakening of the biological pump that sequesters CO_2 into the deep ocean. However, anoxic sediments release two other nutrients, phosphate and iron. Cyanobacteria thrive in phosphate-rich waters, and they can convert atmospheric nitrogen (N_2), which is not directly usable by most organisms, into ammonia, a form that can be assimilated by organisms, resulting in an overall increase in all nutrients. This could lead to a global increase in primary production, a strengthening of the biological pump, an increase in CO_2 uptake by the oceans and an intensification of oxygen loss. Our knowledge of these coupled biogeochemical processes is still too incomplete to produce trustworthy future projections.

Conclusion

Ocean oxygen loss is already widespread - and accelerating - in both coastal waters and the open ocean due to climate change and nutrient runoff. Despite remaining gaps in our understanding, we know enough to be concerned about its profound consequences for ocean life and humanity. Its impacts could potentially surpass those of ocean acidification or marine heat waves.

While it is well publicised that the oceans face numerous stressors such as pollution, overfishing, acidification, and warming, the issue of global oxygen loss in the ocean has not yet received as much public attention. Beyond its impacts on marine life and fisheries, deoxygenation influences the planet's cycles of carbon, nitrogen and other essential elements, and could increasingly cause ocean outgassing of greenhouse gases, further accelerating climate change.

Coordinated research programs that increase our fundamental understanding of oxygen loss and expand observations of current trends, particularly in deeper waters, are urgently needed to improve the accuracy of projections. While coastal oxygen loss can to a certain extent be reduced by limiting nutrient runoff from land, oxygen loss throughout the global ocean can only be mitigated if greenhouse gas emissions are rapidly reduced to zero.

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