Drivers and mechanisms of ocean deoxygenation

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Direct observations indicate that the global ocean oxygen inventory is decreasing. Climate models consistently confirm this decline and predict continuing and accelerating ocean deoxygenation. However, current models (1) do not reproduce observed patterns for oxygen changes in the ocean's thermocline; (2) underestimate the temporal variability of oxygen concentrations and air-sea fluxes inferred from time-series observations; and (3) generally simulate only about half the oceanic oxygen loss inferred from observations. We here review current knowledge about the mechanisms and drivers of oxygen changes and their variation with region and depth over the world's oceans. Warming is considered a major driver: in part directly, via solubility effects, and in part indirectly, via changes in circulation, mixing and oxygen respiration. While solubility effects have been quantified and found to dominate deoxygenation near the surface, a quantitative understanding of contributions from other mechanisms is still lacking. Current models may underestimate deoxygenation because of unresolved transport processes, unaccounted for variations in respiratory oxygen demand, or missing biogeochemical feedbacks. Dedicated observational programmes are required to better constrain biological and physical processes and their representation in models to improve our understanding and predictions of patterns and intensity of future oxygen change.

he oxygen content of the ocean has been declining substantially during the past decades¹⁻³, and climate models predict a further acceleration of this deoxygenation under global warming^{4,5}. Geological evidence of large-scale marine anoxia under warm climate conditions in the distant past, regional low-oxygen events linked to abrupt warming during the last deglaciation⁶, and the existence of feedback processes that may amplify sustained anthropogenic perturbations, all point to the possibility of tipping the warming ocean into larger-scale anoxia on millennial timescales^{7,8}.

The existence of relatively small water volumes with low to no oxygen, also called oxygen minimum zones (OMZs), is a natural phenomenon in today's ocean9, most intense in subsurface waters of the Arabian Sea and in the areas of the eastern boundary upwelling regions in the tropical oceans off California, Peru and Namibia, where high biological production in the surface waters and associated high respiratory oxygen demand are met by low oxygen supply via a sluggish circulation^{10,11} (Fig. 1). In these oxygen-deficient zones, lower oxygen thresholds lethal to most marine organisms are crossed¹² and anaerobic remineralization processes consume fixed nitrogen¹³, while phosphate (and also iron¹⁴) release from sediments is enhanced, leading to an excess in phosphate relative to fixed nitrogen (Pexcess; Fig.1). Following upwelling into the light-lit surface waters, Pexcess might stimulate nitrogen fixation, exacerbate eutrophication and subsequent oxygen consumption and thereby constitute a positive deoxygenation feedback¹⁵. Feedbacks of deoxygenation on the climate system may arise from elevated fluxes of potent greenhouse gases, in particular nitrous oxide (N₂O; Fig. 1), from the ocean to the atmosphere that have been measured above oxygen-deficient regions16 and may counteract the predicted oceanwide decline in marine N₂O emissions under global warming^{17,18}. Expansions of low-oxygen ocean regions¹⁹ are therefore expected to have substantial biogeochemical, ecological, economic and eventual climatic consequences. However, deoxygenation is not restricted to low-oxygen environments. It occurs at all oxygen concentrations in all ocean basins^{1,2} and also affects a growing number of coastal regions²⁰. Yet, a quantitative mechanistic understanding of marine oxygen changes is lacking. Current models do not reproduce observed patterns of oxygen changes in the ocean's thermocline²¹

and, as discussed in more detail below, tend to underestimate oxygen variability and trends^{3,4,22-24}.

Gaps in our understanding and model-data discrepancies

The most recent and comprehensive analysis of observed oxygen changes shows a 2% decline of marine oxygen during the 50-year period since 1960 (ref. 1), that is, 96 Tmol yr⁻¹ for the entire ocean depth range and 26 Tmol yr⁻¹ for the 0 to 1,200 m layer. This amount is lower than earlier estimates of upper-ocean (100 to 1,000 m) deoxygenation between the 1970s and 1990s of about 55 Tmol yr⁻¹ (ref. ²), and similar to the 24 Tmol yr^{-1} O₂ loss estimated for 0 to 1,000 m for the period 1958 to 2015 (ref. 3). For the upper ocean, a tight relationship between decreasing O2 inventories and increasing ocean heat content was depicted³. In the 1960s and early 1970s, the global ocean heat content weakly decreased, associated with a nearly stagnant oxygen content. This period was followed by global deoxygenation related to ocean heat content increase from 1980 to 2015 (ref.³). For the past decades, current climate models reach, on average, about 70% of the observed rate of deoxygenation at 300 m depth²¹. However, integrated over the entire global ocean, the same models simulate an ocean-wide oxygen decline less than half of the observed rate^{4,25}. Interestingly, the solubility-driven decline of most models investigated in the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC AR5)²⁶ agrees within <10% with the observational estimate (13 Tmol yr⁻¹), hinting at model deficiencies in representing circulation and mixing or biogeochemical processes.

In addition to a systematic underestimation of deoxygenation rates inferred from observations, current models also display a reduced interannual-to-decadal variability in oxygen changes compared to observations at time-series sites in the subtropical and subpolar oceans²² and in the equatorial Pacific²³. Moreover, models generally do not reproduce observed regional patterns of recent oxygen changes^{21,24}, with particular deficiencies in the tropical thermocline where observations indicate a significant increase in the volume of oxygen-deficient waters during the past 50 years¹, but most models reveal little significant change or even a small oxygen increase^{4,21,27}. All biogeochemistry climate models investigated in

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Fig. 1 Thermocline ocean ventilation. Schematic view of thermocline ventilation patterns with, as an example, a focus on the eastern subtropical North Pacific OMZ. The wind-stress curl in the subtropics drives subduction of oxygenated waters that, via ocean interior circulation or western boundary currents, reaches biotically productive upwelling regions at the eastern boundary. High oxygen demand, together with weak oxygen supply due to sluggish circulation, results in the occurrence of an OMZ. The inset shows processes particularly relevant to OMZs connected to eastern boundary upwelling. Fixed nitrogen is lost via denitrification and anammox, producing nitrogen that can be lost from the ocean via gas exchange, and leaving behind excess phosphate, P_{excess}. Nitrogen fixation may eventually reduce the excess phosphate. A side product of denitrification (and nitrification) is the greenhouse gas nitrous oxide, N₂O. Under low-oxygen conditions, the sediments can release phosphate and iron into the water column, which could, following upwelling, further enhance the upper-ocean nutrient supply.

IPCC AR5 show a decline of the global ocean oxygen content during the twentieth century and predict a continued and accelerating deoxygenation during the twenty-first century for all greenhousegas emission scenarios considered⁴.

Drivers of deoxygenation

Deoxygenation in the ocean interior results from an imbalance of oxygen consumption and physical supply from the ocean surface²⁸. Due to rapid air-sea gas exchange, surface waters continuously approach oxygen saturation. Surface-water oxygen concentrations depend predominantly on the mixed-layer temperature, and oxygen solubility decreases with increasing temperatures. The warming-induced decline in solubility explains, until now, about half of the deoxygenation in the upper 1,000 m (refs ^{1,2}). Other processes, such as changes in the downward transport of oxygen-rich surface waters and upward transport of oxygen-poor waters affecting

the local distribution of oxygen, as well as changes in oxygen consumption via biotic respiration, also have substantial impacts. Transport changes can result from changes in the large-scale overturning circulation, in particular the wind-driven subtropical-tropical exchange within the shallow overturning associated with the subtropical cells (STCs)²⁹⁻³¹ and the global, deep meridional overturning circulation. While the strength of the shallow and deep overturning is known to vary on interannual-to-multidecadal timescales due to the variability in wind and buoyancy forcing associated with different climate modes (in particular, the Pacific Decadal Oscillation (PDO), El Niño-Southern Oscillation (ENSO), North Atlantic Oscillation (NAO), Atlantic Multidecadal Oscillation (AMO) and Atlantic Meridional Mode (AMM)), systematic changes in the circulation may also occur as a result of anthropogenic warming. Near-surface warming of the subtropical and tropical oceans was found to be associated with enhanced



Fig. 2 | Warming-induced changes in thermocline ventilation. Zonally averaged schematic view of the thermocline ventilation for the historical situation (blue) and under ocean warming (red). Ocean warming reduces surface densities: $\rho_{i, historical} > \rho_{i, warmingr}$ ventilated layers tend to shoal and thin. Equatorial upwelling under ocean warming is thus associated with reduced O₂ undersaturation in the equatorial mixed layer. It results in reduced O₂ uptake or anomalous O₂ outgassing, which is superimposed on the ubiquitous O₂ outgassing due to the warming of the ocean surface. Reduced mixing due to enhanced thermocline stratification under ocean warming might additionally contribute to reduce the O₂ supply to the ocean interior. For schematic simplicity, the wind field and associated Ekman transport and Ekman pumping are assumed to be identical in both periods.

stratification and poleward migration of isopycnal outcrops^{32,33} that results in a shift of isopycnal layers ventilated by subduction in the subtropics and is associated with an anomalous ocean oxygen loss in equatorial upwelling regions as shallower overturning tends to upwell waters with higher oxygen concentrations (Fig. 2). Enhanced stratification might impact the downward mixing of oxygen via reduced mixed-layer depths and/or reduced diapycnal mixing in the more strongly stratified layer below (Fig. 2). Model results indicate that in the subtropics, the vertical pumping induced by the wind-stress curl contributes to a shallower ventilation in a more stratified environment under global warming, and a reduced lateral induction across the sloping base of the shoaling winter mixed layers³² (Fig. 2). These effects may be counteracted by increased subduction rates due to a strengthening of the wind forcing, as was found for the Pacific trade-wind regions³⁴ and the Southern Ocean³⁵. Enhanced freshwater discharge due to warming-induced glacial melting at high latitudes is associated with a reduction in the deep meridional overturning circulation in most state-of-the-art global climate models³⁶. Wind and buoyancy flux-induced changes in oxygen transport processes in the ocean interior will impact the residence times and redistribution of oxygen, which might, for example, affect the volume of lowoxygen waters27,29.

Changes in oxygen consumption can also have many causes, including direct temperature effects on metabolic rates³⁷, CO_2 effects on organisms, ecosystems and the quality of sinking particles^{38,39}, and changes in nutrient supply from the ocean interior, from land or the atmosphere⁴⁰. A recent model-based sensitivity analysis of possible effects of these drivers on oxygen levels during the past 50 years revealed the potential of each of these individual processes to generate oxygen losses of about 0.01–0.02 µmol kg⁻¹ yr⁻¹

in the tropical thermocline²¹, that is, about 10% of the total local rate of change observed. It is noteworthy that changes in respiration rates or sinking speeds of freshly produced organic matter predominantly affect the vertical profile of oxygen consumption rather than the integrated oceanic oxygen loss. Accelerated remineralization at higher temperatures is expected to move oxygen consumption to shallower depths, leaving less substrate available for respiratory oxygen consumption in deep waters⁴¹. As a result of lowered oxygen concentrations in near-surface waters, accelerated remineralization may even result in enhanced air–sea fluxes of oxygen and thus a net oceanic oxygen gain. Reduced export to greater depth, on the other hand, may reduce burial of organic matter. A complete cessation of present-day burial would generate an additional oxygen demand of 0.002 Pmol O₂ yr⁻¹ (ref. ⁴²), that is, 50 times smaller than the currently estimated oceanic oxygen loss¹.

Somewhat larger oxygen losses may occur via the accelerated respiration of dissolved organic matter (DOC) at elevated temperatures⁴³. A data-guided model study for coastal waters suggests a warming-induced DOC respiration of 0.4-0.5 nmol O2 J-1 (ref. 44), which could, if representative for the world ocean, explain up to 10% of the observed deoxygenation. Another contribution to enhanced oxygen loss arises from increased delivery of new nutrients, which has been identified as a major cause of coastal deoxygenation²⁰. Regarding open-ocean deoxygenation, estimates of the impact of atmospheric nutrient supply differ in magnitude among different model studies that employ different assumptions about biological feedbacks, such as the response of nitrogen fixation to changes in ambient nutrient levels, but are generally viewed small compared to circulation effects on oxygen^{21,40}. While current evidence suggests that biogeochemical processes can explain a relatively small part of the oceanic oxygen loss, large uncertainties remain and a

comprehensive quantitative understanding of the different physical and biological contributions to observed oxygen changes in different regions of the world ocean is lacking.

The fact that models tend to underestimate observed rates of the multidecadal oxygen decline^{1,4}, as well as of interannual-to-decadal variability^{22,23}, indicates that current state-of-the-art models still misrepresent or neglect relevant processes. Misrepresentation of transport processes might in particular result from a generally too coarse vertical and horizontal resolution and too diffuse thermocline in models, questioning the accuracy to which the balance of advective versus diffusive transport processes or effects linked to the warming-induced increase in stratification can be simulated. Biogeochemical feedbacks, such as elevated release of phosphorus and iron from anoxic sediments⁴⁵, can present positive feedbacks on oxygen decline⁴⁶, but have, until very recently¹⁵, not been included in global biogeochemical models. Other processes not generally considered in current models include the role of vertically migrating zooplankton in biogeochemical cycling47,48 or possible top-down effects from the expansion of fisheries⁴⁹, which may have regional impacts on oxygen distributions²¹, but are unlikely to explain a significant portion of net oceanic oxygen loss⁵⁰. Impacts of redoxsensitive changes in nutrient stoichiometry on changes in plankton composition and nitrogen fixation^{51,52}, export and respiratory oxygen demand are poorly understood⁵³, as are their sensitivities to environmental change and their potential contributions to ongoing marine deoxygenation. Another possible explanation for the limited success of current models in reproducing observed oxygen changes are uncertainties in historic wind forcing that have a major impact on simulated rates and patterns of oxygen changes²¹. On millennial timescales, but not of immediate concern on decadal-to-centennial scales considered here, global warming could destabilize submarine methane hydrates and subsequent oxidation of methane released from the sea floor could lead to regional oxygen depletion⁵⁴.

Thermocline oxygen changes

The oceanic thermocline covers the stratified region between the oceanic mixed layer and the more homogeneous intermediate and deep waters below about 1,000 m. In the current climate, it accommodates extended OMZs, in particular along the eastern subtropical margins where high oxygen demand associated with productive upwelling systems is met by relatively weak oxygen supply. Atlantic and Pacific OMZs are located in the shadow zones of the ventilated thermocline, that is, regions not reached by the equatorward flow of oxygenated waters from the subtropics⁵⁵. The resulting sluggish flow regimes in the eastern tropics and subtropics are mainly ventilated by mesoscale eddies, weak zonal jets extending over the entire widths of the oceans, though they are particularly energetic near the equator, and diapycnal mixing from above and below²⁹. Model studies reveal a close correlation between declining oxygen levels and increases in water age on isopycnal surfaces in the thermocline, with a large portion of the oxygen variance explained by changes in water age, suggesting that reduced ventilation is the dominant driver of thermocline deoxygenation²².

Circulation in the thermocline is predominantly wind-driven and, as such, particularly sensitive to changes in wind patterns, for example, those associated with major climate modes (PDO, ENSO, NAO, AMO, AMM). Circulation dynamics are further affected by warming-induced increases in stratification, changes in the depth of the winter mixed layer and a poleward displacement of isopycnal outcrop regions^{32,56} (Fig. 2). Variations in the eddy-driven circulation might as well have the potential to generate long-term oxygen changes^{29,57}. Substantial changes in thermocline properties, including oxygen concentrations, have been observed^{24,58–60}, but attribution to different forcing agents such as anthropogenic warming, internal climate variability or a combination of both (that is, changing internal variability in a warming world) is challenging⁶¹.

Observations and model simulations indicate differences in recent changes in thermocline properties in the Atlantic and Pacific Oceans^{60,62}, some of which may be linked to characteristic climate modes. Recent investigations in the North Pacific found that a dominant fraction of decadal variability is explained by the North Pacific Gyre Oscillation (NPGO) and the PDO^{56,63}. NPGO dynamics are driven by atmospheric variability in the North Pacific and capture the decadal expression of Central Pacific El Niño events in the extratropics, much as the PDO captures the low-frequency expression of eastern Pacific El Niño events60. PDO and NPGO jointly control modulations in the subduction of oxygenated mode waters⁵⁶, low-frequency upwelling and alongshore transport dynamics in the North Pacific sector, while the eastern Pacific El Niño dominates in the South Pacific⁶³. A model analysis of changes in tropical Pacific air-sea oxygen fluxes found a tight ENSO modulation, with oxygen flux anomalies leading sea surface temperature anomalies by about 4 months, indicating that flux anomalies were dominated by local changes in upwelling and downwelling rather than heating or biological processes²³. That study also identified a substantial (>50%) underestimation of simulated ENSO-associated oxygen flux variations, which might be related to deficits in the simulated stratification changes and/or an inadequate representation of equatorial intermediate currents in current models⁶⁴. Further poleward, in the California Current System, a combination of observations and ocean reanalysis products between 1950 and 2010 found oxygen changes that were not significantly correlated with the dominant Pacific climate modes, but instead were primarily controlled by ocean circulation dynamics⁶⁵. Subsurface oxygen anomalies originating in the North Pacific gyre were shown to propagate with the mean gyre circulation via the North Pacific Current into the coastal upwelling system off California on a timescale of about 10 years.

In the Atlantic, the ventilation associated with the wind-driven STCs is strongly asymmetric due to the current state of the Atlantic meridional overturning circulation (AMOC) favouring the southern cell and weakening the northern cell. Large parts of the central and intermediate water layers of the tropical North Atlantic are thus currently ventilated from the South Atlantic⁶⁶. A reduction of the AMOC, which is suggested to occur under global warming, will thus reduce the ventilation of the North Atlantic thermocline from the Southern Hemisphere. Such ventilation changes are found in model simulations with prescribed AMOC weakening accompanied by a subsurface warming of the equatorial and South Atlantic and a weakening of the thermocline stratification67. AMOC variations may undergo multidecadal variations associated with AMO forcing, thus impacting the ventilation of the tropical thermocline by the STCs on these timescales. STC variations on similar time scales can be directly forced by variations in the trade winds of the Atlantic and Pacific Oceans^{30,31,68}.

The superposition of different forcings and mechanisms makes attribution of causes and effects on oxygen distributions challenging. For example, a recent study using observations from the tropical North Atlantic showed diverging oxygen trends in the upper and lower part of the OMZ during the last decade that were superimposed on the multidecadal oxygen decrease⁵⁸: a strong oxygen decrease near the deep oxycline at about 300 m resulting in a shoaling of the OMZ was suggested to be the result of a weakening and shoaling wind-driven circulation. The oxygen increase below was instead attributed to a strengthening of zonal jets that supply oxygen from the western tropical Atlantic to the east, which followed a phase of weakening zonal jets since the 1970s (ref. 57). The available timeseries of oxygen in the tropical North Atlantic reveals substantial variability on timescales shorter than the expected anthropogenic changes²⁹. Still, from observations that cover only a few decades, it remains difficult to differentiate oxygen changes that result from global warming from those related to natural internal climate variability. Until now, oxygen changes in the tropical thermocline and in



Fig. 3 | Oxygen change in the ocean. a,b, Observational estimate of the 50-year (1960 to 2010) oxygen change in the upper (**a**: 0–1,200 m) and deep (**b**: 1,200 m-sea floor) ocean in µmol kg⁻¹ per decade. Data are taken from ref. ¹. Lines indicate boundaries of OMZs with less than 80 µmol kg⁻¹ oxygen anywhere within the water column (dashed/dotted), less than 40 µmol kg⁻¹ (dashed) and less than 20 µmol kg⁻¹ (solid). DO, dissolved oxygen.

the North Atlantic could not be attributed to anthropogenic forcing, whereas an anthropogenic deoxygenation signal emerges poleward of 30° – 40° in both hemispheres⁶¹.

Deep-ocean oxygen changes

There have been few studies of oxygen changes in the deep ocean⁶⁹. While concentration changes are relatively small, the large volume and long timescales may well make this part of the world ocean a major reservoir for absorbing and processing oxygen changes. Recent investigations of changes in oceanic heat uptake motivated by the need to better understand the so-called hiatus in the rise of atmospheric temperatures showed an increased importance of the deep ocean in the planetary heat budget since the 1990s (ref. ⁷⁰). While increased deep-ocean temperatures point toward a small role of oxygen solubility, it is the weakening of the deep meridional over-turning circulations that would have the largest potential to reduce the deep oxygen concentrations¹.

Historic oxygen measurements indicate a global oxygen loss of 70 Tmol yr⁻¹ below 1,200 m depth, with decreasing oxygen in almost all deep-ocean basins over the last 50 years. The strongest loss happened in the equatorial and North Pacific, the Arctic and the Southern Ocean¹. The only exception was the North Atlantic (15° N– 60° N), with oxygen loss in the upper ocean and a slight oxygen gain in the deep ocean below 1,200 m (Fig. 3). This is in good agreement with an earlier detailed regional analysis of observations that showed a significant increase in heat content and decrease of oxygen in the upper, mode and intermediate waters over the last five decades, while heat content decreased and oxygen increased in the

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deep water masses, the Lower Intermediate Water and the Labrador Sea Water throughout the North Atlantic⁷¹. Following the southward path of North Atlantic deep water masses across the equator, an oxygen increase was also observed on isopycnal surfaces in the deep western boundary current off northern Brazil since the year 2000 (ref. ⁷²).

In the North Pacific, temperature increased and oxygen decreased at depths and density layers down to 4,000 m between 1956 and 2006 (ref. 73). In the Japan Sea, a deep ocean warming below 2,000 m was associated with oxygen changes of -0.47μ mol kg⁻¹ yr⁻¹ in the eastern Japan Sea Basin and -0.46 µmol kg⁻¹ yr⁻¹ in the Yamato Basin in the period 1960 to 2000, probably related to a reduction of Japan Sea Deep Water formation rates⁷⁴. This long-term trend was superimposed on a bidecadal oscillation of the North Pacific Index, the anomaly of the wintertime sea surface pressure of the North Pacific, possibly linked to the 18.6-year modulation of the diurnal tide⁷⁵. Temperature profiles in the Japan Sea show a warming by as much as 0.1-0.5 °C in the upper 1,000 m and by 0.01 °C below 2,000 m for a 30-year period associated with the oxygen decrease in the deep layer⁷⁵. The eastern Japan Sea shows the behaviour of a closed basin with a limited exchange with the North Pacific and may serve as a natural laboratory for global deep-ocean change in the future⁷⁶. In the South Pacific, a comparison of sections off Chile in 1967 and 1995 at 28° S revealed an oxygen decrease between about 1,800 and 2,900 m, which may indicate enhanced southward boundary current flow⁷⁷. To our knowledge, the only indication for a primarily biotically induced deep-ocean oxygen change comes from the Arabian Sea, where a deepening and intensification of the oxygen minimum was described to be related to an increase in Indian monsoon wind intensity and the OMZ expansion driven at depth by increased respiratory oxygen consumption, whereas the OMZ's near-surface contraction was induced by increased ventilation78.

The meridional overturning circulation associated with the formation of Antarctic Bottom Water is globally of similar strength compared to the overturning circulation of North Atlantic Weep Water. During recent decades, a general warming of these bottom water masses spreading northward into the Pacific, Atlantic and Indian Oceans, together with a general reduction in overturning strength, was observed^{79,80}. This is mirrored by an oxygen decrease by more than 12 Tmol yr⁻¹ in the Southern Ocean below 1,200 m (Fig. 3b, ref. ¹). However, this signal is not apparent in an analysis of oxygen concentrations of retreating Antarctic Bottom Water^{81,82}, limiting the decrease to the deep water masses above the newly formed bottom water. Both the replacement of well-oxygenated bottom waters by older water masses and the oxygen decrease in these older water masses lead to the significant Southern Ocean oxygen decrease.

Outlook

Ocean oxygen time-series have been key for identifying ongoing ocean deoxygenation. They provide vital information for detecting temporal trends and variability⁸³ and for ground-truthing of numerical models that are required to extrapolate to past and likely future changes in the ocean's storage of oxygen and related biogeochemical tracers. While repeat shipboard hydrography is essential for studying long-term oxygen trends, moored observations and time-series stations are particularly important with respect to intraseasonal, seasonal and interannual oxygen variability. The current oxygenobserving system progresses by collecting more oxygen data using Argo profiles and by deploying oxygen sensors within the global tropical moored buoy array. A specific challenge remains the deep ocean, where improved observational coverage is needed to better quantify and mechanistically understand oxygen changes.

So far, observational estimates allowed to identify tight negative correlations between air–sea fluxes of O_2 and heat, even though the ratio of global oxygen loss to heat uptake is several times larger than would be expected solely from the effect of heating on oxygen

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solubility⁸⁴. While changes in ventilation and respiration associated with warming must explain most of the observed oxygen change, a quantitative attribution and mechanistic understanding is still lack-ing. This impedes attribution of the main drivers, although the close relation to ocean warming is suggestive of its leading role not only for ocean heat but also oxygen content³.

Improving our capacity to predict basin-scale and regional patterns of ocean deoxygenation, and thus their possible biogeochemical, ecological, societal, economic and eventual climatic impacts, requires: (1) continuous high-quality oxygen measurements resolving spatial and temporal scales of oxygen changes⁸⁵; (2) resolving the considerable discrepancies, many of them systematic, between observations and current models in patterns and amplitudes of recent oxygen variations^{3,21,23}; (3) developing a better quantitative process understanding of biological and physical oxygen sinks and sources via dedicated observational programmes^{24,29}; and (4) improving the representation of oxygen supply and consumption processes in numerical models by improved process parameterizations and increased resolution⁸⁶. Analysis of abiotic transient tracers, such as suggested by the protocol for the forthcoming Ocean Model Intercomparison Project⁸⁷, will help to better constrain changes in ocean circulation and to improve physically driven variations in oxygen levels. Uncertainties to be addressed include those in the atmospheric forcing fields applied to historical ocean simulations.

A better understanding of biogeochemical processes, such as the response of biological production, export, respiration, nitrogen fixation and benthic fluxes to environmental changes is required to narrow down uncertainties in estimates of biogeochemical contributions to ocean deoxygenation. Special attention should be given to possible feedback loops associated with redox-sensitive changes in individual nutrient fluxes. Promising tools for progress are dedicated process studies with multi-disciplinary observational programmes that include collection of physical parameters and oxygen, measurements of biogeochemical processes associated with nutrient and carbon cycles, and observations of the biological system that address changes in stoichiometry, species composition and ecological functioning (for example, ref. 88). An important contribution for developing a comprehensive system can arise from closely associated modelling studies that allow putting the various datasets into a coherent context (for example, ref. 89). Denser coverage of oxygen observations in space and time, jointly with dedicated biogeochemical-physical process studies and hypothesis testing by numerical modelling, will help to better understand the drivers and mechanisms of ongoing ocean deoxygenation.

Future projections of potential ocean ecosystem stressors, such as deoxygenation, warming and acidification, and changes in ocean productivity, are uncertain due to incomplete understanding of fundamental processes, the interplay of combined stressors⁹⁰, internal climate variability, and divergent carbon emission scenarios²⁵. An improved ability to quantitatively understand and predict deoxygenation will not only provide information about risks to marine ecosystems and the ocean's biogeochemical state, but will, because of tight physical and biogeochemical linkages, also directly advance our understanding of the changing heat and carbon cycles of our planet.

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References

- Schmidtko, S., Stramma, L. & Visbeck, M. Decline in global oceanic oxygen content during the past five decades. *Nature* 542, 335–339 (2017).
- Helm, K. P., Bindoff, N. L. & Church, J. A. Observed decreases in oxygen content of the global ocean. *Geophys. Res. Lett.* 38, L23602 (2011).
- Ito, T., Minobe, A., Long, M. C. & Deutsch, C. Upper ocean O₂ trends: 1958–2015. Geophys. Res. Lett. 44, 4214–4223 (2017).
- Bopp, L. et al. Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences* 10, 6225–6245 (2013).

- 5. Keeling, R. F., Körtzinger, A. & Gruber, N. Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci* 2, 199–229 (2010).
- Praetorius, S. K. et al. North Pacific deglacial hypoxic events linked to abrupt ocean warming. *Nature* 527, 362–366 (2015).
- 7. Watson, A. J. Oceans on the edge of anoxia. Science 354, 1529-1530 (2016).
- 8. Watson, A., Lenton, T. & Mills, B. Ocean deoxygenation, the global phosphorus cycle, and the possibility of human-caused large-scale ocean anoxia. *Phil. Trans. R. Soc. A* **375**, 20160318 (2017).
- Paulmier, A. & Ruiz-Pino, D. Oxygen minimum zones (OMZs) in the modern ocean. *Progr. Oceanogr.* 80, 113–128 (2009).
- Wyrtki, K. The oxygen minima in relation to ocean circulation. *Deep Sea Res.* 9, 11–23 (1962).
- Karstensen, J., Stramma, L. & Visbeck, M. Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans. *Prog. Oceanogr.* 77, 331–350 (2008).
- Diaz, R. J. & Rosenberg, R. Spreading dead zones and consequences for marine ecosystems. *Science* 321, 926–929 (2008).
- Kalvelage, T. et al. Nitrogen cycling driven by organic matter export in the South Pacific oxygen minimum zone. *Nat. Geosci.* 6, 228–234 (2013).
- Scholz, F., McManus, J., Mix, A. C., Hensen, C. & Schneider, R. R. The impact of ocean deoxygenation on iron release from continental margin sediments. *Nat. Geosci.* 7, 433–437 (2014).
- Niemeyer, D., Kemena, T. P., Meissner, K. J. & Oschlies, A. A model study of warming-induced phosphorus–oxygen feedbacks in open-ocean oxygen minimum zones on millennial timescales. *Earth Syst. Dynam.* 8, 357–367 (2017).
- Arevalo-Martinez, D. A., Kock, A., Löscher, C. R., Schmitz, R. A. & Bange, H. W. Massive nitrous oxide emissions from the tropical South Pacific Ocean. *Nat. Geosci.* 8, 530–533 (2015).
- Martinez-Rey, J., Bopp, L., Gehlen, M., Tagliabue, A. & Gruber, N. Projections of oceanic N₂O emissions in the 21st century using the IPSL Earth system model. *Biogeosciences* 12, 4133–4148 (2015).
- Landolfi, A., Somes, C. J., Koeve, W., Zamora, L. M. & Oschlies, A. Oceanic nitrogen cycling and N₂O flux perturbations in the Anthropocene. *Global Biogeochem. Cycles* 31, 1236–1255 (2017).
- Stramma, L., Johnson, G. C., Sprintall, J. & Mohrholz, V. Expanding oxygen-minimum zones in the tropical oceans. Science 320, 655–658 (2008).
- 20. Breitburg, D. et al. Declining oxygen in the global ocean and coastal waters. *Science* **359**, eaam7240 (2018).
- Oschlies, A. et al. Patterns of deoxygenation sensitivity to natural and anthropogenic drivers. *Phil. Trans. Roy. Soc. A* 375, 20160325 (2017).
- Long, M. C., Deutsch, C. & Ito, T. Finding forced trends in oceanic oxygen. Global Biogeochem. Cycles 30, 381–397 (2016).
- Eddebbar, Y. A. et al. Impacts of ENSO on air-sea oxygen exchange: observations and mechanisms. *Global Biogeochem. Cycles* 31, 901–921 (2017).
- Stramma, L., Oschlies, A. & Schmidtko, S. Mismatch between observed and modeled trends in dissolved upper-ocean oxygen over the last 50 yr. *Biogeosciences* 9, 4045–4057 (2012).
- Frölicher, T. L., Rodgers, K. B., Stock, C. A. & Cheung, W. W. L. Sources of uncertainties in 21st century projections of potential ocean ecosystem stressors. *Global Biogeochem. Cycles* **30**, 1224–1243 (2016).
- IPCC Climate Change 2013: The Physical Science Basis (eds Stocker, T. F. et al.) (Cambridge Univ. Press, 2013).
- Cabré, A., Marinov, I., Bernardello, R. & Bianchi, D. Oxygen minimum zones in the tropical Pacific across CMIP5 models: mean state differences and climate change trends. *Biogeosciences* 12, 5429–5454 (2015).
- Levin, L. A. Manifestation, drivers, and emergence of open ocean deoxygenation. Annu. Rev. Mar. Sci 10, 229–260 (2018).
- Brandt, P. et al. On the role of circulation and mixing in the ventilation of oxygen minimum zones with a focus on the eastern tropical North Atlantic. *Biogeosciences* 12, 489–512 (2015).
- Duteil, O., Schwarzkopf, F. U., Böning, C. W. & Oschlies, A. Major role of the equatorial current system in setting oxygen levels in the eastern tropical Atlantic Ocean: a high-resolution model study. *Geophys. Res. Lett.* **41**, 2033–2040 (2014).
- Ridder, N. N. & England, M. H. Sensitivity of ocean oxygenation to variations in tropical zonal wind stress magnitude. *Global Biogeochem. Cycles* 28, 909–926 (2014).
- 32. Liu, C. & Wang, Z. On the response of the global subduction rate to global warming in coupled climate models. *Adv. Atmos. Sci.* **31**, 211 (2014).
- Durack, P. J. & Wijffels, S. E. Fifty-year trends in global ocean salinities and their relationship to broad-scale warming. J. Clim. 23, 4342–4362 (2010).
- England, M. H. et al. Recent intensification of wind-driven circulation in the Pacific and the ongoing warming hiatus. *Nat. Clim. Change* 4, 222–227 (2014).
- Liu, L. L. & Huang, R. X. The global subduction/obduction rates: their interannual and decadal variability. J. Clim. 25, 1096–1115 (2012).
- Stouffer, R. J. et al. Investigating the causes of the thermohaline circulation to past and future climate changes. J. Clim. 19, 1365–1387 (2006).
- Brewer, P. G. & Peltzer, E. T. Depth perception: the need to report ocean biogeochemical rates as functions of temperature, not depth. *Phil. Trans. R. Soc. A* 375, 20160319 (2017).

NATURE GEOSCIENCE

- Oschlies, A., Schulz, K. G., Riebesell, U. & Schmittner, A. Simulated 21st century's increase in oceanic suboxia by CO₂-enhanced biotic carbon export. *Global Biogeochem. Cycles* 22, GB4008 (2008).
- Hofmann, M. & Schellnhuber, H.-J. Oceanic acidification affects marine carbon pump and triggers extended marine oxygen holes. *Proc. Natl Acad. Sci. USA* 106, 3017–3022 (2009).
- Ito, T., Nenes, A., Johnson, M. S., Meskhidze, N. & Deutsch, C. Acceleration of oxygen decline in the tropical Pacific over the past decades by aerosol pollutants. *Nat. Geosci.* 9, 443–447 (2016).
- Segschneider, J. & Bendtsen, J. Temperature-dependent remineralization in a warming ocean increases surface pCO₂ through changes in marine ecosystem composition. *Global Biogeochem. Cycles* 27, 1214–1225 (2013).
- 42. Wallmann, K. Phosphorus imbalance in the global ocean? *Global Biogeochem. Cycles* **24**, GB4030 (2010).
- Bendtsen, J., Hilligsøe, K. M., Hansen, J. L. S. & Richardson, K. Analysis of remineralisation, lability, temperature sensitivity and structural composition of organic matter from the upper ocean. *Progr. Oceanogr.* 130, 125–145 (2015).
- 44. Bendtsen, J. & Hansen, J. L. S. Effects of global warming on hypoxia in the Baltic Sea–North Sea transition zone. *Ecol. Model.* **264**, 17–26 (2013).
- Ingall, E. & Jahnke, R. Evidence for enhanced phosphorus regeneration from marine sediments overlain by oxygen depleted waters. *Geochim. Cosmochim. Acta* 58, 2571–2575 (1994).
- Conley, D. J., Carstensen, J., Vaquer-Sunyer, R. & Duarte, C. M. Ecosystem thresholds with hypoxia. *Hydrobiologia* 629, 21–29 (2009).
- Steinberg, D. K., Goldthwait, S. A. & Hansell, D. A. Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea. *Deep Sea Res. I* 49, 1445–1461 (2002).
- Kiko, R. et al. Biological and physical influences on marine snowfall at the equator. *Nat. Geosci.* 10, 852–858 (2017).
- Getzlaff, J. & Oschlies, A. Pilot study on potential impacts of fisheriesinduced changes in zooplankton mortality on marine biogeochemistry. *Global Biogeochem. Cycles* 31, 1656–1673 (2017).
- Bianchi, D., Galbraith, E. D., Carozza, D. A., Mislan, K. A. S. & Stock, C. A. Intensification of open-ocean oxygen depletion by vertically migrating animals. *Nat. Geosci.* 6, 545–548 (2013).
- Deutsch, C., Sarmiento, J. L., Sigman, D. M., Gruber, N. & Dunne, J. P. Spatial coupling of nitrogen inputs and losses in the ocean. *Nature* 445, 163–167 (2007).
- Landolfi, A., Dietze, H., Koeve, W. & Oschlies, A. Overlooked runaway feedback in the marine nitrogen cycle: the vicious cycle. *Biogeosciences* 10, 1351–1363 (2013).
- Mills, M. M. & Arrigo, K. R. Magnitude of oceanic nitrogen fixation influenced by the nutrient uptake ratio of phytoplankton. *Nat. Geosci.* 3, 412–416 (2010).
- 54. Yamamoto, A., Yamanaka, Y., Oka, A. SpringerAmpamp; Abe-Ouchi, A. Ocean oxygen depletion due to decomposition of submarine methane hydrate. *Geophys. Res. Lett.* **41**, 5075–5083 (2014).
- 55. Luyten, J. R., Pedlosky, J. & Stommel, H. The ventilated thermocline. J. Phys. Oceanogr. 13, 292–309 (1983).
- Kwon, E. Y., Deutsch, C., Xie, S.-P., Schmidtko, S. & Cho, Y.-K. The North Pacific oxygen uptake rates over the past half century. J. Clim. 29, 61–76 (2016).
- 57. Brandt, P. et al. Changes in the ventilation of the oxygen minimum zone of the tropical North Atlantic. *J. Phys. Oceanogr.* **40**, 1784–1801 (2010).
- Hahn, J., Brandt, P., Schmidtko, S. & Krahmann, G. Decadal oxygen change in the eastern tropical North Atlantic. *Ocean Sci.* 13, 551–576 (2017).
- Deutsch, C. et al. Centennial changes in North Pacific anoxia linked to tropical trade winds. *Science* 345, 665–668 (2014).
- 60. Deutsch, C., Brix, H., Ito, T., Frenzel, H. & Thomson, L. Climate-forced variability of ocean hypoxia. *Science* **333**, 336–339 (2011).
- Andrews, O. D., Bindoff, N. L., Halloran, P. R., Ilyina, T. & Le Quéré, C. Detecting an external influence on recent changes in oceanic oxygen using an optimal fingerprinting method. *Biogeosciences* 10, 1799–1813 (2013).
- Montes, E. et al. Decadal variability in the oxygen inventory of North Atlantic subtropical underwater captured by sustained, long-term oceanographic time series observations. *Global Biogeochem. Cycles* 30, 460–478 (2016).
- 63. Di Lorenzo, E. et al. Synthesis of Pacific Ocean climate and ecosystem dynamics. *Oceanography* **26**, 68–81 (2013).
- Dietze, H. & Loeptien, U. Revisiting "nutrient trapping" in global coupled biogeochemical ocean circulation models. *Global Biogeochem. Cycles* 27, 265–284 (2013).
- Pozo Buil, M. & Di Lorenzo, E. Decadal dynamics and predictability of oxygen and subsurface tracers in the California Current System. *Geophys. Res. Lett.* 44, 4204–4213 (2017).
- Peña-Izquierdo, J. et al. Water mass pathways to the North Atlantic oxygen minimum zone. J. Geophys. Res. Oceans 120, 3350–3372 (2015).
- 67. Chang, P. et al. Oceanic link between abrupt changes in the North Atlantic Ocean and the African monsoon. *Nat. Geosci.* **1**, 444–448 (2008).
- Rabe, B., Schott, F. A. & Köhl, A. Mean circulation and variability of the tropical Atlantic during 1952–2001 in the GECCO assimilation fields. *J. Phys. Oceanogr.* 38, 177–192 (2008).

- 69. Sloyan, B. M. et al. Deep ocean changes near the western boundary of the South Pacific Ocean. J. Phys. Oceanogr. 43, 2132–2141 (2015).
- Cheng, L. et al. Improved estimates of ocean heat content from 1960 to 2015. *Sci. Adv.* 3, e1601545 (2017).
- Stendardo, I. & Gruber, N. Oxygen trends over five decades in the North Atlantic. J. Geophys. Res. 117, C11004 (2012).
- 72. Hummels, R. et al. Interannual circulation in the Atlantic at 11°S. *Geophys. Res. Lett.* **42**, 7615–7622 (2015).
- Whitney, F. A., Freeland, H. J. & Robert, M. Persistently declining oxygen levels in the interior waters of the eastern subarctic Pacific. *Prog. Oceanogr.* 75, 179–199 (2007).
- 74. Watanabe, Y. W., Wakita, M., Maeda, N., Ono, T. & Gamo, T. Synchronous bidecadal periodic changes of oxygen, phosphate and temperature between the Japan Sea deep water and the North Pacific intermediate water. *Geophys. Res. Lett.* **30**, 2273 (2003).
- 75. Yasuda, I., Osafune, S. & Tatebe, H. Possible explanation linking 18.6-year period nodal tidal cycle with bi-decadal variations of ocean and climate in the North Pacific. *Geophys. Res. Lett.* **33**, L08606 (2006).
- 76. Kim, K. et al. Warming and structural changes in the East (Japan) Sea: a clue to future changes in global oceans? *Geophys. Res. Lett.* 28, 3293–3296 (2001).
- Shaffer, G. et al. Warming and circulation change in the eastern South Pacific Ocean. *Geophys. Res. Lett.* 27, 1247–1250 (2000).
- Lachkar, Z., Levy, M. & Smith, S. Intensification and deepening of the Arabian Sea oxygen minimum zone in response to increase in Indian monsoon wind intensity. *Biogeosciences* 15, 159–186 (2018).
- Purkey, S. G. & Johnson, G. C. Warming of global abyssal and deep Southern Ocean waters between the 1990s and 2000s: contributions to global heat and sea level rise budgets. J. Clim. 23, 6336–6351 (2010).
- Johnson, G. C., Purkey, S. G. & Toole, J. M. Reduced Antarctic meridional overturning circulation reaches the North Atlantic Ocean. *Geophys. Res. Lett.* 35, L22601 (2008).
- Andrie, C. et al. Variability of AABW properties in the equatorial channel at 35°W. *Geophys. Res. Lett.* **30**, 8007 (2003).
- van Wijk, E. M. & Rintoul, S. R. Freshening drives contraction of Antarctic Bottom Water in the Australian Antarctic Basin. *Geophys. Res. Lett.* 41, 1657–1664 (2014).
- Church, M. J., Lomas, M. W. & Muller-Karger, F. Sea change: charting the course for biogeochemical ocean time-series research in a new millennium. *Deep Sea Res. II* 93, 2–15 (2013).
- Keeling, R. F. & Garcia, H. E. The change in oceanic O₂ inventory associated with recent global warming. *Proc. Natl Acad. Sci. USA* 99, 7848–7853 (2002).
- Henson, S. A. Slow science: the value of long biological records. *Phil. Trans.* R. Soc. A 372, 20130334 (2014).
- Duteil, O., Böning, C. W. & Oschlies, A. Variability in subtropical-tropical cells drives oxygen levels in the tropical Pacific Ocean. *Geophys. Res. Lett.* 41, 8926–8934 (2014).
- Orr, J. C. et al. Biogeochemical protocols and diagnostics for the CMIP6 Ocean Model Intercomparison Project (OMIP). *Geosci. Mod. Dev* 10, 2169–2199 (2017).
- Karstensen, J. et al. Upwelling and isolation in oxygen-depleted anticyclonic modewater eddies and implications for nitrate cycling. *Biogeosciences* 14, 2167–2181 (2017).
- Thomsen, S. et al. Do submesoscale processes ventilate the oxygen minimum zone off Peru? *Geophys. Res. Lett.* 43, 8133–8142 (2016).
- 90. Gruber, N. Warming up, turning sour, losing breath: ocean biogeochemistry under global change. *Phil. Trans. R. Soc. A* **369**, 1980–1996 (2011).

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Author contributions

All authors discussed the results and wrote the manuscript. A.O. led the writing of the manuscript, P.B. and L.S. led the sections on thermocline and deep-ocean oxygen changes and S.S. led the data analysis.

Competing interests

The authors declare no competing interests.

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