**Ocean Ventilation & Deoxygenation in a Warming World: Introduction and Overview**

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**Abstract**

Changes of ocean ventilation rates and deoxygenation are two of the less obvious but important indirect impacts expected as a result of climate change on the oceans. They are expected to occur because of (a) the effects of increased stratification on ocean circulation and hence its ventilation, due to reduced upwelling, deep water formation and turbulent mixing, (b) reduced oxygenation through decreased oxygen solubility at higher surface temperature, and (c) the effects of warming on biological production, respiration and remineralisation. The potential socio-economic consequences of reduced oxygen levels on fisheries and ecosystems may be far-reaching and significant.

At a Royal Society Discussion Meeting convened to discuss these matters, 12 oral presentations and 23 posters were presented, covering a wide range of the physical, chemical, and biological aspects of the issue. Overall, it appears that there are still considerable discrepancies between the observations and model simulations of these processes. Our current understanding of both the causes and consequences of reduced oxygen in the ocean, and our ability to represent them in models are therefore inadequate, and the reasons for this remain unclear. It is too early to say whether or not the socio-economic consequences are likely to be serious. However, the consequences are ecologically and climatically potentially very significant, and further research on these indirect impacts of climate change via reduced ventilation and oxygenation of the oceans should be accorded a high priority.

**1) Introduction**

The most obvious impacts of climate change on the ocean are the warming of the surface mixed layer, causing thermal expansion and hence sea-level rise, and the bio-geographical consequences for ecosystems (due to shifts of species ranges and abundances). These, together with ocean acidification and possible modification of the large-scale overturning circulation, are widely recognised and have been thoroughly reviewed by the IPCC in AR5 (see especially Chapter 30 of the report of Working Group 2, [1]). The evidence for, and possible consequences of, less obvious indirect effects such as those due to an increase of the ocean’s stable stratification (caused by the faster warming of its surface layers relative to deeper water [2]) have however only begun to emerge clearly in the past few years. The scientific and socio-economic consequences of such effects are nevertheless potentially far-reaching, as they are likely to affect many physical, biogeochemical and biological systems. These less obvious (indirect) impacts of climate change on the oceans due to the effects of increased stratification include changes of upwelling, deep-water formation and ventilation, biological production and remineralisation rates, and especially de-oxygenation. Observations have demonstrated steadily declining ocean oxygen concentrations at depths far shallower than the long studied classical oxygen minimum zones [1, 4]. These losses were not predicted by theory, although in retrospect they could have been [5, 6]. They suggest disturbing impacts for marine ecosystems and for changes in the rain of chemical energy in the form of particulate organic carbon – the food supply – to the deep sea floor. Much of the ocean is already geochemically quite close to the “edge of anoxia” [3] and de-oxygenation is likely to lead to the growth of hypoxic and anoxic “dead zones”, with probable effects on ecosystems, and the production of biogenic and radiatively active gases (like N2O). The IPCC [1] notes that: “Regarding the ocean loss of dissolved oxygen (deoxygenation) ocean carbon and oxygen models suggest that it is likely that large decreases in oceanic dissolved oxygen will occur during the 21st century, predominantly in the sub-surface mid-latitude oceans, due to enhanced stratification and warming. There is however no consensus on the future development of the volume of hypoxic and sub-oxic waters because of large uncertainties in potential biogeochemical effects and in the evolution of tropical ocean dynamics.” By far the most widely cited mechanism to account for the observed losses is increased stratification [2] – but ventilation of the interior ocean is achieved by a complex of processes, and there is a dearth of both observations and theory to evaluate the impact of increased stratification on these. The biogeochemical consequences are also complex: reductions in ocean vertical mixing could also deplete nutrient transport to the sunlit upper ocean resulting in lower primary production. Warmer waters tend to increase the microbial decomposition rate of organic matter, increasing the return of nutrients at shallower depths [7]. None of these processes are well enough captured in either current experiments, regular observations or models.

These controversial issues are now being considered seriously among specialists, and they were felt by the authors to be ripe for wider consideration and more extensive debate, especially as it is unlikely that all the possible mechanisms or consequences have yet been conceived. The effects of altered upwelling systems and reduced oxygenation could have very serious adverse effects on some of the most productive ecosystems in the world, and the fisheries that they support, with far-reaching impacts on human societies especially in the developing world. The impact on globally important sources of protein could be very serious indeed. “Dead zones” are already a significant source of environmental concern (e.g. in the Gulf of Mexico) and they can already lead to fish kill events (e.g. in the Benguela system off southern Africa): these would very likely be made worse. The biogeochemical systems of the oceans play a significant role in regulating atmospheric oxygen levels: and the consequences of major changes to these in the long term are incalculable.

The subject matter is highly inter-disciplinary, and needs exposure to a large and diverse scientific community, so that the possible ramifications can be properly explored. This therefore formed the rationale for a Royal Society Discussion Meeting on “Ocean Ventilation & Deoxygenation in a Warming World” that was held in London on 12-13 September 2016, and the papers presented at that meeting form the content of this special issue.

The meeting aimed to cover all relevant aspects of oceanography, including its physics (the circulation and mixing of stratified fluids, and interaction with the atmosphere), geo-chemistry (the controls on macro and micro-nutrient and oxygen levels, including interactions with sediments) and marine biology at all trophic levels (from primary producers through to fisheries and top predators), including especially controls on primary production and the heterotrophic microbial processes leading to remineralisation of organic matter and oxygen consumption).

Its objectives were to stimulate

1. Wider and fuller appreciation of the potential for subtle but far-reaching impacts of climate change on oceanic ecosystems
2. Lively interdisciplinary debate on the interaction of ocean physical & biogeochemical systems, and the mechanisms of possible changes on the fundamental controls on oceanic biological production
3. Faster progress on understanding the potential consequences, and the crucial problems that should form part of the future research agenda.
4. Increased trans-disciplinary interaction and collaboration on a problem of high potential societal importance

It followed on from an earlier (and much smaller) “brainstorming” meeting held at the Royal Society Kavli International Centre in 2011. Other relevant previous meetings on the subject are the

EurOcean conference on Ocean Deoxygenation held in Toulouse (October 2011) <http://www.eur-oceans.eu/conf-oxygen> and the International Liege Colloquium on “Low oxygen environments in marine, estuarine and fresh waters” (Liege, May 2014) <http://modb.oce.ulg.ac.be/colloquium/2014/>

**2) Overview**

Twelve papers were presented at the meeting, and the final versions of ten of these are included in this volume ([9] to [18]).

Ralph Keeling (paper not included in this volume) reviewed what we know about recent oxygen trends based on results from oceanic and atmospheric O2 measurements. Human activities are causing systematic decreases in the O2 content of both the atmosphere and the oceans. The atmospheric loss is driven primarily by the burning of fossil fuels, while the oceanic loss is driven primarily by warming-induced reductions in O2 solubility and slowing of ocean circulation, i.e. reduced ventilation. Oceanic deoxygenation could have potentially large environmental consequences, particularly if continued warming leads to an expansion of hypoxic or suboxic waters, as suggested by some models. Measurements of O2 in both the ocean and atmosphere are recognized as having considerable diagnostic value, and this has fueled an expansion of measurements and measurement capabilities in recent years. The oceanic O2 measurements have helped to establish the magnitude and mechanisms of recent O2 changes. The atmospheric O2 measurements have helped to quantify global carbon sinks and to provide a window into sources of oceanic O2 variability via the tracer atmospheric potential oxygen (APO ~ O2+CO2). APO measurements show strong signals related to ocean ventilation which vary from year to year, and the well-measured global APO trend can potentially be used to quantify the global oceanic deoxygenation rate.

Monika Rhein & co-authors [9] reviewed the ventilation variability of Labrador Sea water and its impact on oxygen and anthropogenic carbon. The ocean is a main player in the climate system. Owing to lack of historic observations, reliable estimates of, for instance, oceanic heat budgets were only possible after 1970. Since that time, ocean warming accounted for more than 90% of the increase in the Earth’s energy inventory, while only a small fraction heated the atmosphere, the continents, and was used for melting of sea ice, glaciers and ice sheets. The ocean also plays a major role in the long-term variability of the atmospheric temperature, and could for several years obscure the mean global temperature increase, mainly caused by anthropogenic emissions of CO2. The ocean warming also has consequences for the uptake of anthropogenic carbon by enhancing the vertical density stratification in the ocean and thus potentially reducing the ventilation of intermediate, deep, and bottom water. Changes in the intermediate water ventilation in the subpolar North Atlantic have occurred from the 1990s to today, a period well covered with oceanic observations. Although caused by natural variability of atmospheric modes on multiannual time scales (i.e. the NAO), this region provides a test bed to study the processes and mechanisms involved to improve our understanding of the changes expected under global warming. Ventilation of Labrador Sea Water (LSW) receives ample attention because of its potential relation to the strength of the Atlantic Meridional Overturning Circulation (AMOC). The authors provide an overview of the changes of LSW from observations in the Labrador Sea and from the southern boundary of the subpolar gyre at 47°N. A strong winter-time atmospheric cooling over the Labrador Sea led to intense and deep convection producing a thick and dense LSW layer as for instance in the early to mid-1990s. The weaker convection in the following years mostly ventilated less dense LSW vintages and also reduced the supply of oxygen. As a further consequence, the rate of uptake of anthropogenic carbon by LSW decreased between the two time periods 1996-1999 and 2007-2010 in the western subpolar North Atlantic. In the eastern basins, the rate of increase of anthropogenic carbon became greater due to the delayed advection of LSW that was ventilated in previous years. Starting in winter 2013/2014 and prevailing at least into the winter 2015/2016, production of denser and more voluminous LSW resumed. Increasing oxygen signals have already been found in the western boundary current at 47°N. On decadal and shorter time scales anomalous cold atmospheric conditions over the Labrador Sea lead to an intensification of convection. On multidecadal time scales, the “cold blob” in the subpolar North Atlantic projected by climate models in the next 100 years is linked to a

weaker AMOC and weaker convection (and thus deoxygenation) in the Labrador Sea.

Lisa Levin [10] reported some Physiological and Ecological Implications of Ocean Deoxygenation for Vision in Marine Organisms: Continental margins play fundamental roles in ocean biogeochemical cycling and are increasingly valued as a source of fisheries, energy, biodiversity and potentially mineral resources. Margin settings are highly sensitive to climate-induced changes in winds, upwelling, stratification, circulation, nutrient supply and freshwater input, all of which can affect oxygenation. Observations over the last half-century show major declines in ocean dissolved oxygen concentrations at intermediate depths, particularly on margins of the NE Pacific. Climate change has induced ocean deoxygenation and exacerbated eutrophication-driven hypoxia in recent decades, affecting the physiology, behavior, and ecology of marine organisms. The high oxygen demand of visual tissues and the known inhibitory effects of hypoxia on human vision raise the questions if and how ocean deoxygenation alters vision in marine organisms.This is particularly important given the rapid loss of oxygen and strong vertical gradients in oxygen concentration in many areas of the ocean. This review evaluates the potential effects of low oxygen (hypoxia) on visual function in marine animals and their implications for marine biota under current and future ocean deoxygenation based on evidence from terrestrial and a few marine organisms. Evolutionary history shows radiation of eye designs during a period of increasing ocean oxygenation. Physiological effects of hypoxia on photoreceptor function and light sensitivity, in combination with morphological changes that may occur throughout ontogeny, have the potential to alter visual behavior and subsequently, the ecology of marine organisms, particularly for fish, cephalopods and arthropods with “fast” vision. Visual responses to hypoxia, including greater light requirements, offer an alternate hypothesis for observed habitat compression and shoaling vertical distributions in visual marine species subject to ocean deoxygenation, that merits further investigation.

Laurent Bopp [11] considered ocean (de)oxygenation from the Last Glacial Maximum to the 21st century: insights from Earth System Models. In response to anthropogenic climate change, coupled climate-marine biogeochemical models used over the past 15 years all project a long-term decrease in the ocean O2 inventory, referred to as ocean deoxygenation. This general trend is confirmed by the latest projections from the CMIP5 Earth System Models, with reductions in the ocean O2 inventory from 1.5 to 4% in 2090s relative to 1990s for all future scenarios. Largest declines are concentrated at mid-depths in the North Atlantic, North Pacific and Southern Ocean. The processes at play are linked to surface ocean warming, which reduces both O2 solubility and the rate at which the surface waters are transported downward. However large uncertainties for future projections of ocean deoxygenation remain for the subsurface tropical oceans where the major Oxygen Minimum Zones are located. Here, Bopp and co-authors combine global warming projections, model-based estimates of natural short-term variability, as well as data and model estimates of the Last Glacial Maximum ocean oxygenation to gain some insights into the major mechanisms of oxygenation changes across these different time-scales. They show that the primary uncertainty on future ocean deoxygenation in the subsurface tropical oceans is in fact controlled by a robust compensation between decreasing oxygen saturation due to warming and decreasing apparent oxygen utilization (AOU) due to increased ventilation of the corresponding water masses. Modeled short-term natural variability in subsurface oxygen levels also reveals a compensation between oxygen saturation and AOU, controlled by the latter. Finally, using a model simulation of the Last Glacial Maximum, reproducing data-based reconstructions of past ocean (de)oxygenation, they show that the deoxygenation trend of the sub-surface ocean during the deglaciation was controlled by a combination of warming-induced decreasing oxygen saturation and increasing AOU driven by a reduced ventilation of tropical sub-surface waters.

The basic need for improved understanding of ventilation processes was addressed by Alberto Naveira-Garrabato and colleagues [12] who drew attention to the very different mechanisms of water mass ventilation in southern versus northern oceans. The vast area of the southern ocean contributes hugely to global scale water mass ventilation and formation. The processes regulating ocean ventilation at high latitudes are re-examined based on a range of observations spanning all scales of ocean circulation – from the basin scales of gyres to the centimetre scales of turbulence. It is shown that ocean ventilation is controlled by mechanisms that are different in important ways from those that set the ocean's overturning circulation, contrary to the common assumption of broad equivalence between the two when interpreting the role of ventilation in Earth's major climate transitions. Illustrations of how recognizing this distinction may change our view of how ventilation changes shape climate transitions were offered.

Andreas Oschlies [13] considered spatial patterns of deoxygenation and their sensitivity to natural and anthropogenic drivers. Observational estimates and numerical models both indicate a significant decline in marine oxygen levels over the past decades. Spatial patterns, however, differ considerably between observed and modelled estimates, particularly in the tropical thermocline that hosts open-ocean oxygen minimum zones, where observations indicate a general oxygen decline, whereas most current models simulate increasing oxygen levels. Possible reasons for the apparent model-data discrepancies are examined. In order to attribute observed historical variations in oxygen levels, mechanisms of change in oxygen supply are studied with sensitivity model simulations. Specifically, the role of equatorial jets, of lateral and diapycnal mixing processes, and of changes in the wind-driven circulation are investigated. Predominantly wind-driven changes in the low-latitude ventilation are identified as major factor contributing to oxygen changes in the low-latitude thermocline during the past decades. Possible implications for likely future climate change on the evolution of oxygen minimum zones are discussed.

Peter Brewer [14] dealt with the chemical physics of ocean oxygen losses under climate change, and specifically with the need to report ocean biogeochemical rates as functions of temperature, not depth. For over 50 years ocean scientists have oddly represented ocean oxygen consumption rates as a function of depth but not temperature. This unique tradition or tactic now extends across such a wide range of oceanic biogeochemical processes that it inhibits useful discussion of climate change impacts where specific and fundamental temperature dependent terms are required. Depth, but not temperature, dependent functions, as of now, form the basis for the most widely used climate-biogeochemical models. Tracer based determinations of oxygen consumption rates, and thus CO2, PO4 etc production rates, in the deep sea are near universally reported as a function of depth in spite of their well-known microbial basis. Recent work has shown that a carefully determined profile of oxygen consumption rates in the Sargasso Sea can be well represented by a classical Arrhenius function with an activation energy of 86.5 kJ mol-1 leading to a Q10 of 3.63. This indicates that for 2°C warming there will be a 29% increase in ocean oxygen consumption rates, and for 3°C warming a 50% increase, leading to large scale ocean hypoxia. Here it is shown that the same principles apply to a world-wide collation of tracer based oxygen consumption rate data and that some 95% of ocean oxygen consumption is driven by temperature, not depth, and thus has a strong climate dependence. The Arrhenius/Eyring equations are no simple panacea and they require a non-equilibrium steady state to exist. Where transient events are in progress this stricture is not obeyed and one such example will be shown. This rapid injection of fresh organic material and its associated microbial population is still clearly in non-steady state and revealed as such in the observed oxygen consumption rate data.

Carol Robinson (paper not included in this volume) covered deoxygenation impacts on biogeochemical cycles, climatic gases, microbial activity and ecosystems. Dissolved oxygen concentration is a major determinant of the microbially mediated processes responsible for the production and turnover of climatically relevant gases in the ocean. Ocean models predict declines of 1 to 7% in the global ocean O2 inventory over the next century due to lower solubility of oxygen at warmer temperatures, and increased stratification preventing equilibration of the ocean interior with the atmosphere. Additionally, eutrophication continues to lead to hypoxic or anoxic conditions in the coastal zone. Due to microbial respiration, water separated from equilibration with the atmosphere by increased stratification will contain both low O2 and high CO2 concentrations. Low oxygen environments enable the production of nitrous oxide as a by-product of nitrification and denitrification and methane through anaerobic methanogenesis, with most O2 deficient systems acting as net sources of CO2, N2O and CH4 to the atmosphere. The presentation provided an overview of the effect of ocean deoxygenation on microbial community structure and the cycling of climatically important gases including CO2, N2O and CH4.

Andrew Watson [15] considered the biogeochemical regulation of oxygen, and anoxia in the past, present and future. The major biogeochemical cycles which keep the present-day Earth habitable are linked by a network of feedbacks which has led to a broadly stable chemical composition of the oceans and atmosphere over hundreds of millions of years. This includes the processes which control both the atmospheric and oceanic concentrations of oxygen. However, one notable exception to the generally well-behaved dynamics of this system is the propensity for episodes of ocean anoxia to occur and to persist for 105 – 106 years, these OAEs (Ocean Anoxic Events) being particularly associated with warm “greenhouse” climates.  OAEs are, it is believed, amplified by positive feedbacks on the nutrient content of the ocean: low oxygen promotes the release of phosphorus from ocean sediments, which increases ocean productivity and drives more anoxia in the subsurface water, leading to a potentially self-sustaining condition of deoxygenation. In the paper included here, with co-authors Tim Lenton and Benjamin Mills, the authors examine with a model the extent to which the increase in phosphorus supply to the oceans caused by human activities could lead to extensive deoxygenation. Both runoff of phosphorus obtained from mining, and increased phosphorus fluxes due to enhanced weathering under a warmer climate, could substantially increase the extent of deoxygenation on millennial timescales, but only under extreme scenarios would a global scale OAE result.

Andy Bakun [16] considered dynamic deoxygenation within intensified coastal upwelling circulations. Major deoxygenation commonly takes place in ocean regions that feature particularly intense coastal upwelling circulations. Prominent examples discussed herein include the seasonal Somali Current upwelling, which during the southwest monsoon becomes the most intense coastal upwelling cell existing in the world’s oceans, and the upwelling that occurs on a more continuous basis in the ocean off Lüderitz, Namibia, constitutes the most intense of the world’s “classical” eastern ocean boundary upwelling systems. Concerns about enhanced ocean deoxygenation arise in view of the arguable likelihood that coastal upwelling systems around the world may further intensify as anthropogenic climate change proceeds. In the opinion article published here, Bakun describes similarities and differences of these systems, proposing also a mechanism for the recent appearance of a seasonal oxygen deficient dead zone off the coast of Oregon. He proposes that the ecosystems in upwelling systems can be subject to non-linear regime shifts as a result of intensification of upwelling under climate change, potentially interacting with commercial fishing pressure, that may cause substantial increases in water column hypoxia.

Oliver Andrews and colleagues [17] presented results from a ocean biogeochemical modelling study into the possible causes of observed ocean deoxygenation. Earth System Model (ESM) projections indicate that a reduction in the oxygen inventory of the global ocean, termed ocean deoxygenation, is a likely consequence of on-going anthropogenic warming. Current models are, however, unable to consistently reproduce the observed trends and variability of recent decades, particularly within the established tropical OMZs. Their hindcast simulations using a state-of-the-art global ocean biogeochemistry model suggest that increasing carbon-to-nutrient ratios in carbon fixation driven by rising pCO2 in the euphotic zone may drive oxygen depletion within the ocean interior due to increased organic carbon export and subsequent remineralisation. Atmospheric forcing is shown to influence simulated interannual variability in ocean oxygen, particularly due to differences in imposed variability of wind stress and heat fluxes.

Katherine Richardson (Bendtsen and Richardson [18]) reviewed the ocean’s changing role in the earth system in a warming world. From an Earth system (ES) perspective, ocean feedbacks on the global carbon cycle (and, thereby, climate system) are of particular interest. While the physical ocean feedbacks in the climate system are relatively well constrained, the biologically mediated feedbacks remain poorly understood. The authors study the dynamics of the ecosystem in the subtropical oceans where the water column is permanently stratified with phytoplankton generating net production, thus producing both oxygen and dissolved or particulate organic matter in a deep chlorophyll maximum below the surface mixed layer. They present data and a model to quantify how this system influences the oxygen content of the stratified water, and how this might change in the future. While warming of the near-surface ocean has relatively little direct effect on oxygen, plankton composition changes consequent on climate, in particular on the proportions of dissolved and particulate organic matter produced, could have a substantial influence on the oxygen content of the deeper waters.

In addition, 23 posters were presented: these are listed in an Annex at the end of the volume

**3) Discussion**

The evidence presented for declining oxygen levels in the subsurface ocean is now unequivocal, but the mechanisms for this decline are not yet clear. The effect of higher temperature in reducing oxygen solubility at the surface is straightforward, but models (Bopp [11]) suggest that the effects of reduced solubility and changes of apparent oxygen utilization should broadly compensate. The discrepancy between models and observations (Andrews [17] is particularly marked in the tropical thermocline (Oschlies [13]), but the cause has not been adequately established. It is possible that the effects of increased stratification on ventilation including the supply of oxygen by small-scale turbulent diffusion (Naveiro-Garabato, [12]) are poorly represented in existing models. However, the temperature dependence of respiration (and hence apparent oxygen utilization) is also not yet well established and is likely also poorly represented (Brewer, [14]). The biogeochemical and ecological consequences of reduced oxygen in compressing habitats are already significant in some areas and are likely to become far-reaching (Bendtsen & Richardson [18] and Watson [15]). Some subtle, surprising and hitherto largely unexplored consequences on predator-prey relationships may even be expected due to impaired vision at low oxygen levels (Levin [10],). In addition, the production of biogenic greenhouse gases such as nitrous oxide (N2O) in oxygen minimum zones is inadequately represented in current (CMIP5) models (Andrews [17]) and may be climatically significant.

Overall, it appears that our current understanding of both the causes and consequences of reduced oxygen in the ocean, and our ability to represent them in models are inadequate, and the reasons for this remain unclear. It is too early to say whether or not the socio-economic consequences are likely to be serious. However, the consequences are ecologically and climatically potentially very significant, and further research on these indirect impacts of climate change via reduced ventilation and oxygenation of the oceans should be accorded a high priority.

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Note: the incomplete references that follow are all to papers in this volume

9. Rhein, M. “Ventilation variability of Labrador Sea water and its impact on oxygen and anthropogenic carbon: a review”

10. Levin, L. “Physiological and Ecological Implications of Ocean Deoxygenation for Vision in Marine Organisms”

11. Bopp, L. “Ocean (de)oxygenation from the Last Glacial Maximum to the 21st century: insights from Earth System Models”

12. Naveira-Garabato, A. “High-latitude ocean ventilation and its role in Earth’s climate transitions”

13. Oschlies, A. “Patterns of deoxygenation - sensitivity to natural and anthropogenic drivers”

14. Brewer P. & Pelzer, E. “Depth Perception: The Need to Report Ocean Biogeochemical Rates as Functions of Temperature, not Depth”

15. Watson, A. “Ocean deoxygenation, the global phosphorus cycle, and the possibility of human-caused large-scale ocean anoxia”

16. Bakun, A. “Climate change and ocean deoxygenation within intensified surface-driven upwelling circulations”

17. Andrews O. “Biogeochemical modelling of dissolved oxygen in a changing ocean”

18. Bendtsen J. & Richardson K. “Photosynthetic oxygen production in a warmer ocean: The Sargasso Sea as a case study”