Climate Change Impacts on Dissolved Oxygen Concentration in Marine and Coastal Waters around the UK and Ireland

Mahaffey, C.[1], Artioli, Y.[2], Hoogakker, B.[3], Hull, T.[4], Hunter, W.[5], Greenwood, N.[4,6], Palmer, M.[2] Sharples, J.[1], Wakelin, S.[7] and Williams, C.[7]

1. Department of Earth, Ocean and Ecological Sciences, School of Environmental Sciences, 4 Brownlow Street, University of Liverpool, L69 3GP, UK
2. Plymouth Marine Laboratory, Prospect Place, Plymouth, Devon PL1 3DH
3. The Lyell Centre, Heriot Watt University, EH14 4BA, Edinburgh, UK
4. Centre for Environment, Fisheries and Aquaculture, Pakefield Road, Lowestoft, NR33 0HT, U K
5. Agri-Food and Biosciences Institute, 18a Newforge Lane, Belfast, BT9 5BX
6. Centre for Ocean and Atmospheric Sciences, School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK
7. National Oceanography Centre, Joseph Proudman Building, 6 Brownlow Street, Liverpool, L3 5DA, UK

Citation: Mahaffey, C., Artioli, Y., Hoogakker, B., Hull, T., Hunter, W., Greenwood, N., Palmer, M., Sharples, J., Wakelin, S. and Williams, C. Climate change impacts on dissolved oxygen concentration in marine and coastal waters around the UK and Ireland. MCCIP Science Review 2025, 33pp.

doi: 10.14465/2025.reu07.oxy

Submitted: 03 2025

Published online: 07 2025

KEY FACTS

What is already happening

- Since the 1960s, the global oceanic oxygen content has declined by more than 2%.
- Oxygen deficiency has been detected in the North Sea and Celtic Sea. Observations are more frequent in the North Sea and have detected more frequent and intense seasonal oxygen depletion but the extent of oxygen depletion elsewhere in UK shelf seas is unknown.
- Ocean warming alongside increased vertical stratification are driving increased oxygen depletion, with seasonally stratified regions more prone to oxygen deficiency than permanently mixed regions.

What could happen in the future

- Average annual mean dissolved oxygen concentration in the global ocean is projected to decline by 1.5 to 4% by 2090 for all RCPs., equivalent to a warming of 1 to 4 ºC. This decline will be most acute below the thermocline away from the surface.
- For UK shelf waters, models project that oxygen depletion will intensify and last longer in the central North Sea and Celtic Sea, regions currently experiencing oxygen depletion. The mean oxygen concentration is projected to decline mostly strongly (3 to 4% by 2100) in the North Sea and Western English Channel. Deeper

regions exposed to exchange with the open ocean (the Irish shelf and Shetland shelf) are expected to be less affected, decreasing by ~ 2 %.

- The predicted increase in temperature over this century for UK shelf seas will lead to a decrease in dissolved oxygen through the whole water column because of reduced solubility.
- The risk of oxygen deficiency in summer will increase because of lower oxygen levels experienced during the preceding winter and spring, as well as transport of low oxygen waters from estuaries and potentially adjacent seas.
- Increase in the frequency and intensity of marine heatwaves may exacerbate oxygen loss, driving both thermal stress to marine life alongside low oxygen availability
- Increased rainfall and runoff would increase the risk of eutrophication and cause oxygen concentrations to locally decrease.
- Continued warming and reduced oxygen availability will affect the metabolism, health, and reproduction of many marine organisms, which could have major impacts on ecosystems and commercial fisheries.

SUPPORTING EVIDENCE

Introduction

Oxygen is essential for breathing or 'respiration' by almost all life on Earth, including marine life. Dissolved oxygen concentrations in the global ocean have declined by 2% since the 1960s (Rhein *et al.*, 2013; Oschilies et al., 2018, Schmidtko et al., 2017). While excessive nutrient loading or 'eutrophication' may be the driver for the decline in dissolved oxygen concentrations in estuaries and near coastal regions (Diaz and Rosenberg, 2008), the observed global decline in dissolved oxygen has been attributed to ocean warming (Schmidtko et al., 2017). Climate models predict future rates of oxygen decline will increase globally in response to warming (Keeling *et al.*, 2010; Bopp *et al.*, 2013; van der Molen *et al.*, 2013: Gulev et al., 2021) . Depletion of dissolved oxygen can lead to a region being defined as either *oxygen deficient*, when dissolved oxygen concentrations are less than 6 mg/litre (equivalent to ~192 µmol/kg), *hypoxic* when oxygen concentrations are less than 2 mg/litre (equivalent to ~64 µmol/kg) or *anoxic* when oxygen concentrations are less than 0.5 mg/litre (equivalent to ~30 µmol/kg).

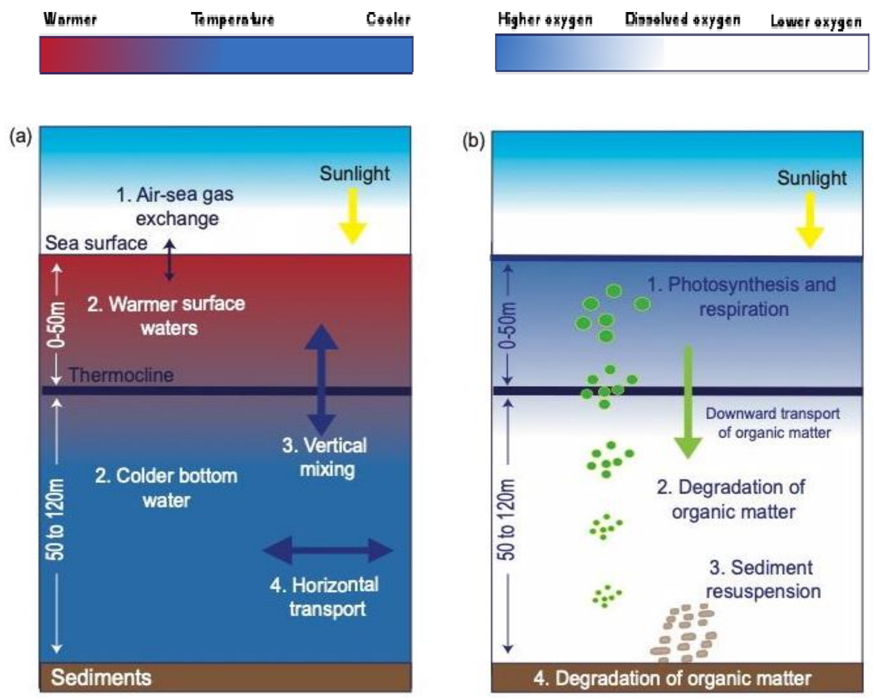
The development of oxygen deficiency can have deleterious effects on the marine ecosystem (Vaquer-Sunyer and Duarte, 2008; Breitburg *et al.*, 2018) with the onset of hypoxia or anoxia increasing the severity on the ecosystem response. While the decline in dissolved oxygen in the deep ocean is a global problem, the intensity and impact of dissolved oxygen depletion or 'deoxygenation' is also apparent in the coastal and shelf seas (Diaz and Rossenberg, 2008; Breitburg *et al.*, 2009; Gilbert *et al.*, 2010; Townhill *et al.*, 2017a; Breitburg *et al.*, 2018). The challenge is to better understand the multiple processes that currently control dissolved oxygen to accurately assess the future risk of oxygen deficiency, hypoxia or anoxia in response to climate change (Oschlies *et al*., 2017). Here, we focus on the processes controlling oxygen concentrations in the North-west European shelf seas, which encompasses UK coastal and shelf seas.

What controls oxygen in the marine environment?

Oxygen constitutes 20.95% of our atmosphere and its behaviour is strongly linked to the processes that cycle carbon in the atmosphere and ocean. Over the past 20 years, there has been a small but measurable decrease in the levels of oxygen in the atmosphere due to the burning of fossil fuels (Keeling and Shertz, 1992; Manning and Keeling, 2006, Martin et al 2017). Loss of atmospheric oxygen poses no risk to ecosystems or humans for the foreseeable future. Dissolved oxygen concentrations in the ocean are controlled by a combination of physical and biological processes (Figure 1a and b). Oxygen in the atmosphere readily exchanges with the surface ocean, termed air-sea gas exchange (Figure 1a). Temperature affects the solubility of dissolved oxygen in seawater, with oxygen being more soluble in colder water and less soluble in warmer water (Figure 1a). For example, a 1°C increase in ocean temperature will cause dissolved oxygen concentrations to decrease by approximately 5 µmol/kg or 0.16 mg/litre over typical ranges of salinity (30 to 35) and temperature (10 to 20°C) observed in UK marine waters. *Oxygen saturation* is a common parameter used to describe the ratio of dissolved oxygen in seawater relative to the maximum amount of oxygen that will dissolve in seawater at a given temperature, salinity, and pressure if it were in equilibrium with the atmosphere. Biological activity produces dissolved oxygen via photosynthesis and tends to cause oxygen saturation to be greater than 100%, termed *oversaturation* (Figure 1b).

Dissolved oxygen is removed from water via breathing or respiration by marine plants, animals and microorganisms, and by the decay of organic matter back to nutrients; the combination of removal processes is referred to collectively as *biological oxygen consumption* in the present document. These removal processes tend to cause oxygen saturation to be less than 100%, termed *undersaturation* (Figure 1b). Note that in the sunlit surface layer of the ocean, biological oxygen production is typically greater than oxygen consumption resulting in net biological oxygen production, increasing the oxygen concentration above the saturated state. Conversely, in the deeper, dark layers of the ocean, oxygen consumption is typically greater than oxygen production leading to net biological oxygen consumption, decreasing the oxygen concentration below the saturated state (Figure 1b).

There is an important link between nutrients and oxygen in the marine environment. An increase in nutrients will generally increase production of organic matter via photosynthesis, causing an increase in dissolved oxygen production in the surface ocean. However, decay of accumulated organic matter by microbial respiration leads to a decrease in dissolved oxygen. Enhanced nutrient inputs into coastal regions have been shown to cause eutrophication (Painting *et al.*, 2013; Malone and Newton, 2020), one important side effect being a decline in dissolved oxygen. Hence, dissolved oxygen has been used as an indicator of the status of ecosystem health within the legislation designed to protect the UK marine environment through the Water Environment Regulations 2017 and the Marine Strategy Regulations 2010 and the Programme of Measures 2015, which are the UK implementation of the EU Water Framework Directive (WFD; Best *et al.*, 2007) and the Marine Strategy Framework Directive (MSFD, Ferreira *et al.*, 2011) respectively. However, in assessments made under this legislation, dissolved oxygen concentrations are used only to identify undesirable disturbance from the indirect effect of nutrient enrichment (OSPAR Common Procedure; Foden *et al.*, 2010) as an indicator within the eutrophication quality descriptor (MSFD Descriptor 5) and an indirect effect of nutrient enrichment (MSFD Criterion 5.3; Ferreira *et al.*, 2011). There is no additional requirement to monitor dissolved oxygen concentration under the legislation despite factors other than eutrophication being responsible for development of oxygen deficiency in coastal and shelf sea waters. Although dissolved oxygen was proposed as an indicator for Seafloor Integrity within the MSFD (Rice *et al.*, 2012), it was not included in the final selection of indicators. As a critical component of several indicators of good environmental status (GES), it is important to develop a thorough understanding of the controls and consequences of oxygen dynamics in UK coastal and shelf water and the potential response of oxygen dynamics to climate change.



Processes in (a)	Effect on dissolved oxygen		Processes in (b)	Effect on dissolved oxygen
1	Equilibrates oxygen between the atmosphere and ocean		1	Net oxygen production as photosynthesis is greater than respiration in surface waters
2	Oxygen is less soluble in warm water and more soluble in cold water		2	Net oxygen consumption during degradation of organic matter in the water column
3	Mixes oxygenated surface water with less oxygenated bottom waters		3	Oxygen consumption as more organic matter is made available from sediment resuspension
4	Transports water with different oxygen properties		4	Net oxygen consumption during degradation of organic matter in the sediments

Figure 1: Schematic representation of the vertical structure of (a) temperature and the physical processes that control the distribution of dissolved oxygen and (b) dissolved oxygen and the biological processes that control the distribution of dissolved oxygen in coastal and shelf seas. The underlying tables highlight the principal processes and their effect on dissolved oxygen dynamics. Surface and bottom waters are separated by a thermocline and thus this schematic represents processes in a stratified water column.

Physical processes, including vertical mixing and horizontal transport, redistribute oxygen vertically and horizontally (Figure 1a). The strength of vertical mixing and the degree of density stratification are key factors controlling the oxygen distribution in coastal and shelf seas (Figure 2a). Stratification occurs when water becomes separated into layers of different density with less-dense water overlaying a layer of denser water. Layers close to the surface may be less dense due to the addition of lower salinity water, for example from freshwater run-off from rivers, or from warming, which typically occurs due to the seasonal solar heating cycle.

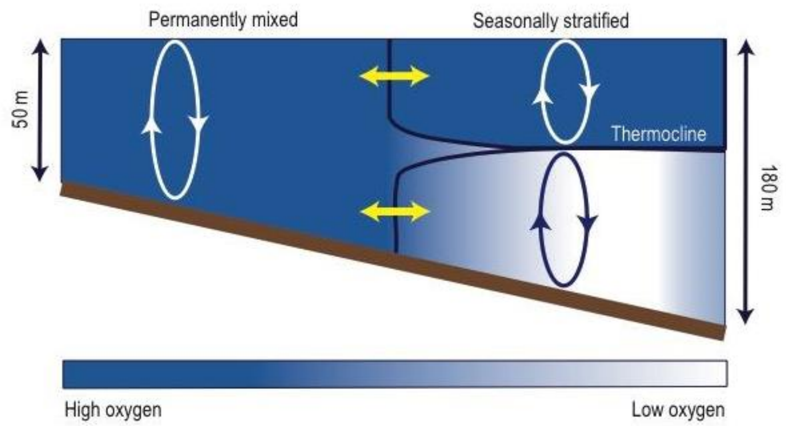
While salinity-driven stratification is generally restricted to near coastal regions around the UK, there are large areas of UK shelf seas that undergo seasonal thermal stratification when near surface waters and bottom waters are separated by a temperature gradient, or thermocline (Figure 2b, Sharples *et al.*, 2020). Such regions include, but are not limited to, the central and northern North Sea, the Celtic Sea, the western Irish Sea, the Malin Sea and Outer Hebrides region (Sharples *et al.*, 2020). During winter, the shelf seas are mixed by convection (driven by surface water cooling) and wind (Figure 2b) and become well oxygenated as waters mix and are ventilated by air-sea gas and heat exchange (Figure 2c). Winter mixing acts to homogenise surface and bottom water and their associated oxygen concentrations (Figure 2c). Critically, the water temperature in winter places a first-order control on the dissolved oxygen concentration in coastal and shelf seas because of the temperature dependence of oxygen solubility, with warmer winters leading to lower dissolved oxygen concentrations.

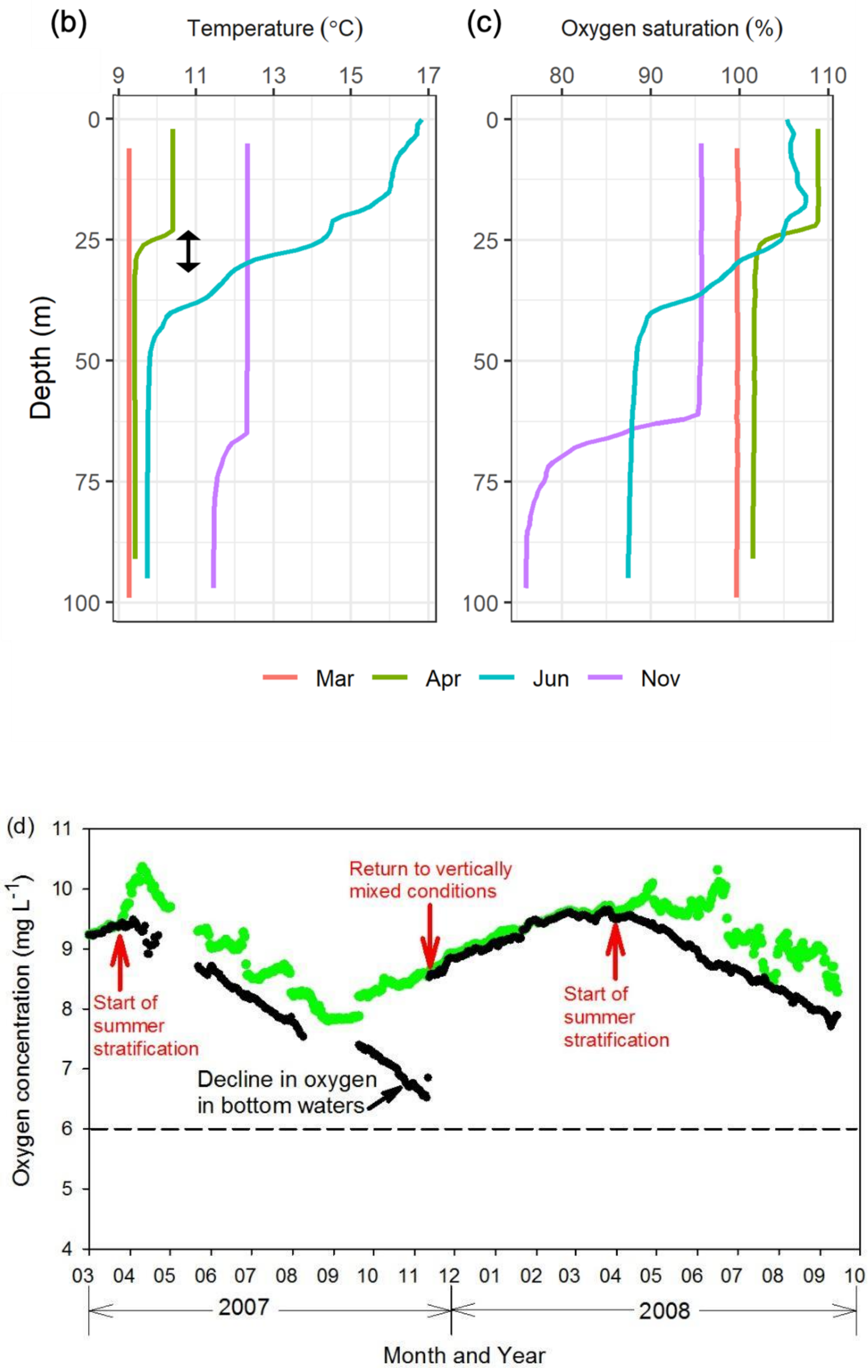
Seasonal stratification occurs over much of the UK shelf seas when there is sufficient solar heating of surface waters to overcome the combined effects of tidal and wind mixing. This coincides with spring, typically in March or April in UK waters (Figure 2d and 2e) and persists until winter storms and reduced solar heating in autumn months return the water column to winter mixed conditions, typically between October and December, although there is significant spatial variability in both the onset and breakdown of stratification. During this period of seasonal stratification, a thermocline separates the well-mixed near-surface waters and bottom boundary layers. This thermocline significantly reduces mixing between the two layers and results in different oxygen dynamics in each layer (Figure 2c, 2d and 2e).

In the surface waters, net biological oxygen production and air-sea gas exchange act to maintain dissolved oxygen concentrations at close to or above 100% saturation (Figure 2c). In contrast, the thermocline restricts mixing of bottom waters with surface waters and prevents direct air-sea gas exchange. There is also net biological oxygen consumption in the bottom waters (Figure 2c, 2d and 2e). If oxygen consumed in the bottom waters is not replenished by episodic mixing events across the thermocline, such as by enhanced mixing from strong tides and storms or by horizontal exchange with oxygenated waters (Hull *et al.*, 2020), then the bottom layer oxygen concentration may decline to levels at risk of oxygen deficiency, hypoxia or anoxia. However, the strong seasonal cycle in the UK temperate coastal and shelf seas means that no regions experience year-round stratification and so any depletion of oxygen during the summer stratified period is temporary, as dissolved oxygen will be replenished during autumn and winter mixing (Figure 2d and 2e). This seasonal pattern is in contrast to many oxygen minimum zones (OMZs) found elsewhere in the marine environment where oxygen deficiency, hypoxia or anoxia can be persistent features over many years (e.g. the Baltic Sea).

In regions of UK coastal and shelf sea waters where there is sufficient energy from tides and currents to permanently mix the water column (left region of Figure 2a), the dissolved oxygen concentration in the entire water column is relatively homogenous, with the absolute concentration changing primarily due to seasonal changes in temperature and therefore solubility. Regions that are classed as permanently mixed include the shallow regions of the central and eastern English Channel, southern North Sea and central Irish Sea. There are also areas that undergo periodic stratification due to the variable nature of the tide, for instance in the eastern Irish Sea influenced by river inputs from North-west England and the far south of the North Sea influenced by the River Rhine. Bottom layers in such regions are typically not at risk of oxygen depletion since stratification is short-lived.

(a)




(b)
Temperature (°C)
Depth (m)
(c)
Oxygen saturation (%)
Mar
Apr
Jun
Nov
(d)
Oxygen concentration (mg L-1)
Start of summer stratification
Return to vertically mixed conditions
Start of summer stratification
Decline in oxygen in bottom waters
2007
2008
Month and Year

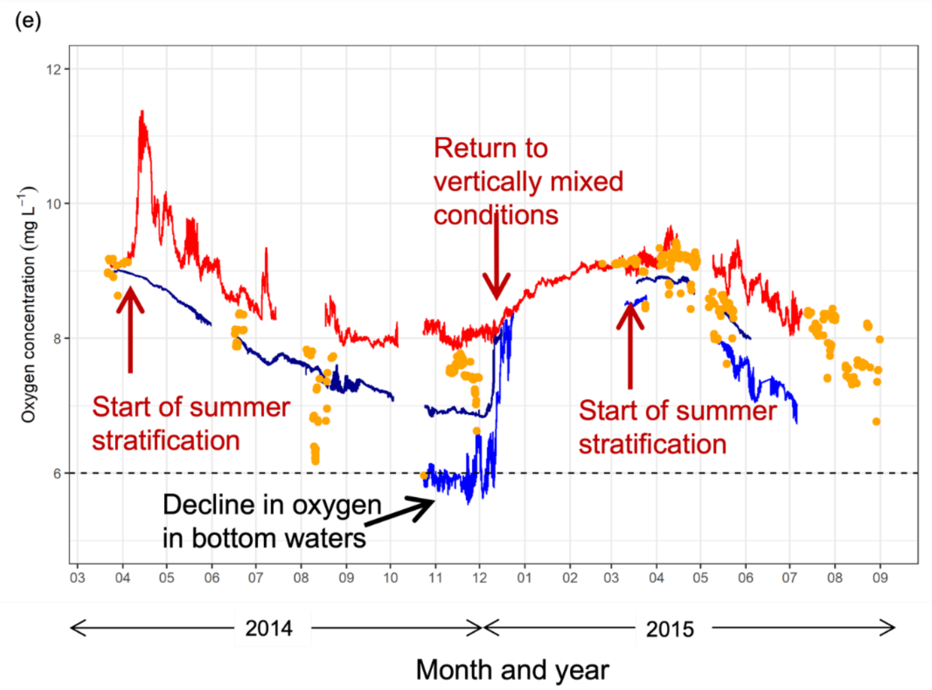


Figure 2: Schematic representation of: (a) the gradient in physical water column structure and dissolved oxygen concentrations from the shallow, permanently mixed regions (e.g. southern North Sea, English Channel) to deeper, seasonally stratifying regions (northern North Sea, Celtic Sea). Exchange between the two regions is indicated by horizontal transfer (yellow arrows). Seasonal change in (b) water column temperature (°C) and (c) dissolved oxygen saturation (%) in the seasonally stratifying central Celtic Sea at the end of winter (March, red), spring (April, green), summer (June, blue) and autumn (November, purple, data from Hull et al., 2020). (d) seasonal change in dissolved oxygen concentrations (mg/litre) at North Dogger in the North Sea from the Cefas SmartBuoy in surface waters (green) and bottom waters (black) (data from Greenwood et al.*, 2010). (e) Seasonal change in dissolved oxygen concentrations (mg/litre) in the Celtic Sea from the Celtic Deep SmartBuoy (red), Celtic Deep benthic lander (blue) and Haig Fras lander (dark blue), with discrete bottle oxygen concentrations indicated (yellow). (Data is available from https://doi.org/10.14466/CefasDataHub.38 to https://doi.org/10.14466/CefasDataHub.41. Note that the lowest oxygen concentrations in (a) are associated with intermediate rather than the deepest water column in shelf seas due to the rapid depletion of oxygen in a thinner layer which has less total oxygen available.)*

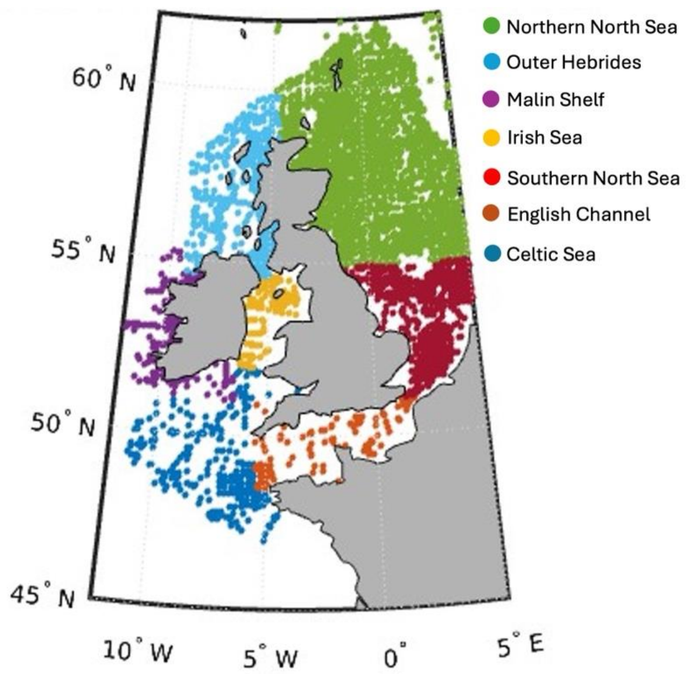
Climate change is likely to affect physical and biological processes that lead to oxygen depletion. As well as reducing the solubility of oxygen, ocean warming is predicted to increase the strength and duration of seasonal stratification over the next 50 years (Lowe *et al.*, 2009; Holt *et al.*, 2010; Sharples *et al.*, 2020). Enhanced stratification increases the isolation of bottom waters from the sea surface thus increasing the risk of oxygen deficiency and hypoxia in seasonally stratifying regions on the European Shelf. Enhanced stratification will also reduce the nutrient supply to the surface ocean, thus reducing biological productivity and the amount of organic material available for microbial respiration. In contrast, ocean warming will increase metabolic processes including biological oxygen consumption (Brewer and Peltzer, 2017). The net effect of a decline in nutrients stunting biological productivity, alongside the direct thermal enhancement of metabolic processes, is currently unknown. Particularly relevant to coastal and shelf seas systems is the change in nutrient inputs from land, which may enhance or reduce the risk of eutrophication with subsequent implications for oxygen dynamics. Changes to shelf sea and deep ocean exchange may also have major impacts on both physical and biogeochemical controls (Holt et al, 2018; Wakelin et al, 2020). Thus, understanding potential causes of oxygen depletion, and the responses of these drivers to climate change, land-use and wastewater inputs is key to predicting the likelihood of oxygen deficiency or hypoxia, and subsequent ecosystem harm, in UK marine waters.

What is already happening?

Detecting climate-driven changes in dissolved oxygen requires observations and understanding of the natural seasonal and interannual variability in surface and bottom water oxygen concentrations so that any long-term deviation from baseline conditions can be accurately assessed. Dissolved oxygen measurements in bottom waters from 1920s to 2017 in the North-west European shelf region are available from the International Council for the Exploration of the Sea (ICES) and the British Oceanographic Data Centre (BODC) databases. Synthesis of these databases reveals that the North Sea is the most intensely studied of UK marine waters for dissolved oxygen, in both space (Figure 3a) and time (Figures 3g and 3h). This level of coverage has not been replicated in other UK shelf sea regions, with a stark disparity between North Sea data coverage and the Celtic Sea (Figure 3b), Malin Shelf (Figure 3c), Outer Hebrides (Figure 3d), Irish Sea (Figure 3e) and English Channel (Figure 3f). Confidence in any results drawn from these poorly resolved regions is therefore inherently low and makes quantitative comparisons between regions, or between observations and models, extremely difficult.

Regional dynamics in dissolved oxygen concentrations

In the North Sea, oxygen concentrations typically vary from ~320 ⌠mol/kg (equivalent to ~ 10 mg/litre or over 100% saturation) in winter to ~192 ⌠mol/kg in summer (equivalent to 6 mg/litre or 70% saturation). A decline in oxygen saturation to 70% or less in bottom waters of the seasonally stratified regions in the UK waters of the North Sea during late summer conditions is well documented (Figure 2d, Weston *et al.*, 2008; Greenwood *et al.*, 2010; Queste *et al.*, 2013; Große *et al.*, 2016; Queste *et al.*, 2016; Topcu and Brockmann, 2015). High temporal resolution data from the Cefas SmartBuoy network has revealed the onset of oxygen deficiency (less than 6 mg/L) in bottom waters during the late summer period in the central and northern North Sea around the Oyster Grounds (5.2 mg/litre, 60% saturation or 167µmol/kg; Greenwood *et al.*, 2010). Re-analysis of dissolved oxygen data over decadal timescales reveals a larger spatial extent of summertime oxygen depletion across the North Sea (Topcu and Brockmann, 2015) alongside an increase in the intensity and spatial extent of oxygen depletion (Queste *et al.*, 2013). Oxygen depletion was attributed to ocean warming and increase in biological oxygen consumption (Queste *et al.*, (2013) alongside an increase in thermal stratification (Topcu and Brockmann, 2015). The lack of repeat observations of dissolved oxygen in UK marine waters means we are unable to determine the occurrence or frequency of oxygen deficiency.



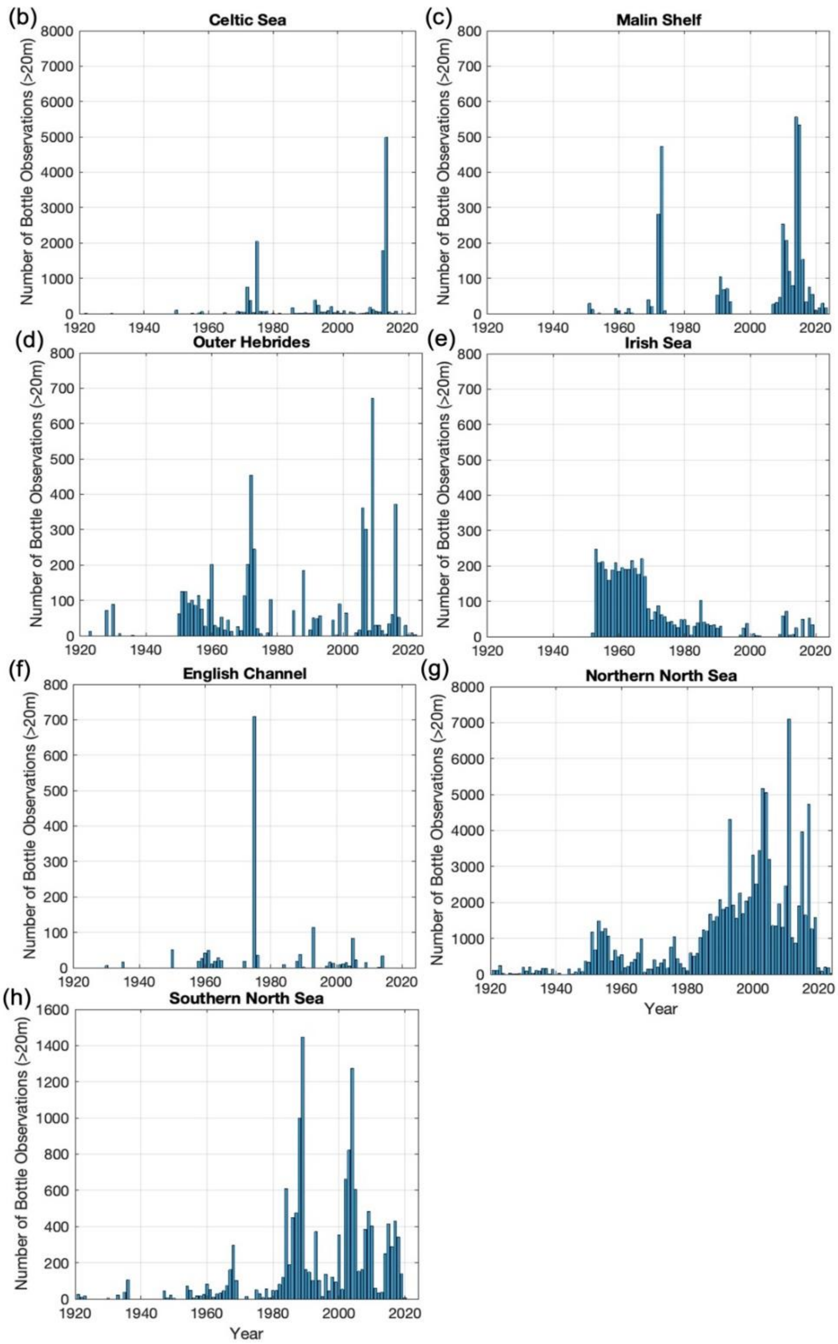


Figure 3: Synthesis of data from ICES and BODC indicating (a) the spatial distribution of measurements of dissolved oxygen below the thermocline or near the seabed from 1920s to 2024, with red lines indicating approximate boundaries between regions, and the temporal distribution of observations per year in the bottom waters from 1920s to 2024 for (b) Celtic Sea, (c) Malin Shelf, (d) Outer Hebrides, (e) Irish Sea, (f) English Channel, (g) Northern North Sea and (h) Southern North Sea. Note that the y-axis scale varies from (b) to (h) with (c), (d), (e) and (f) ranging from 0 to 800, (h) ranging from 0 to 1600 and (b) and (g) ranging from 0 to 8000.

Unlike the well-studied North Sea, the Celtic Sea is poorly sampled in both time and space (Figure 3a and 3d). Data from the recent UK-Shelf Sea Biogeochemistry programme (2011-2017) has significantly improved our understanding of this region. High-resolution data from two benthic landers (Celtic Deep and Haig Fras) equipped with oxygen sensors collected between spring 2014 and autumn 2015 reveals that towards the end of seasonal stratification in late autumn 2014, oxygen concentrations in bottom waters at Haig Fras (Figure 2e, dark blue) decreased below the 6 mg/litre threshold defining oxygen deficiency (5.8 mg/litre or 62% saturation or 186 µmol/kg). Note that oxygen concentrations at the Celtic Deep site remained above 6 mg/litre (Figure 2e, blue), indicating the spatial heterogeneity in oxygen dynamics. These are the first observations indicating the development of oxygen deficiency in the Celtic Sea, albeit with a 10% error of the oxygen sensor data due to lack of geo-located discrete samples for calibration. The lack of observational data in Celtic Sea bottom waters means this important result cannot be set in a historical context and so it is not possible to verify using observational evidence whether this is a recent development or a regularly occurring phenomenon.

There is currently no evidence of oxygen deficiency in the Irish Sea or Malin Sea (O'Boyle and Nolan, 2010), but data is sparse (Figure 3c and e, respectively) and large areas known to undergo seasonal stratification have few or no observations of bottom-layer dissolved oxygen concentration in available databases, and fewer still have data available during late summer or autumn conditions when a seasonal oxygen minimum is most likely to occur.

Looking to the future, a major challenge in detecting the onset of oxygen deficiency in UK coastal and shelf sea regions is making measurements of dissolved oxygen concentrations at the appropriate scales in time and space. Benthic landers (Hull *et al.*, 2020) and autonomous underwater vehicles (Williams *et al.*, 2022, Hull *et al.,* 2021) can provide high-resolution data on dissolved oxygen in shelf sea bottom waters. Coupled physical and biogeochemical models specifically designed to represent the functioning of coastal and shelf seas have been used to predict oxygen dynamics over regional and whole shelf scales (Madec *et al.*, 2012; Butenschön *et al.*, 2016). Model re-analysis by Ciavatta *et al.* (2016) has suggested that large areas (~325,000 km^2) of the North-west European Shelf region are vulnerable to oxygen deficiency. UK regions designated as at risk of deficiency in this study include large areas of the Celtic Sea, Irish Sea and English Channel and small coastal regions around Scotland (Figure 4). A small area of the North Sea in UK waters is also identified, which forms part of a much larger area including Dutch and German waters. There is still some debate on the ability of ocean and climate models to accurately capture the myriad of processes that control seasonal oxygen dynamics. At the global scale, climate models successfully estimate the change in oxygen concentrations within 10% of observed values (IPCC, 2013; Oschlies *et al.*, 2018) but tend to underestimate the variability and decline in oxygen (Bopp *et al.*, 2013; Ito *et al.*, 2017). Assessment of model skill of a coupled hydrodynamics-ecosystem model (NEMO-ERSEM) designed to represent shelf sea processes showed that simulations underestimated oxygen by 0.6 mg/litre on average compared to observations (Wakelin *et al.,* 2020).

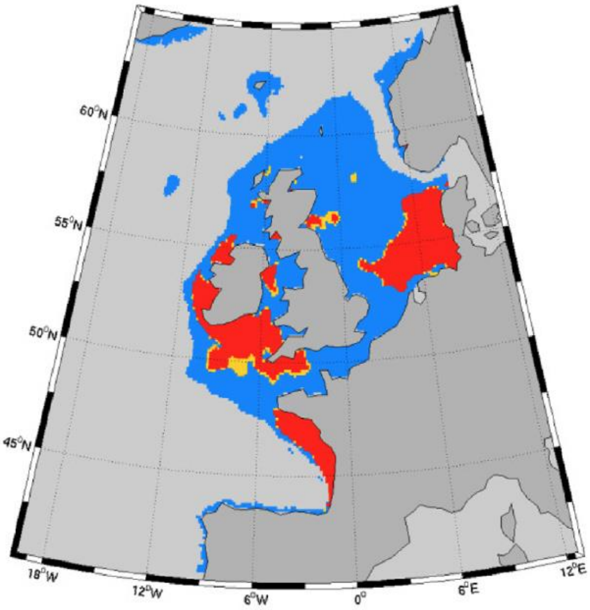


Figure 4: Model output from ERSEM indicating areas vulnerable to oxygen deficiency in bottom waters, defined as at least one daily value in 1998 to 2009 below the threshold of 6 mg/litre. Areas of the shelf where oxygen concentrations are found to be higher than 6 mg/litre at 100% confidence are highlighted in blue. Areas of the shelf where oxygen concentrations are found to be lower than 6 mg/litre at 1% confidence are highlighted in yellow. Areas of the shelf where oxygen concentrations are found to be lower than 6 mg/litre at 100% confidence are highlighted in red. (Reproduced with permission from Ciavatta et al.*, 2016.)*

Causes of oxygen depletion

While the causes for the decline in dissolved oxygen concentrations have been identified, their relative magnitude and net effect on oxygen dynamics are still poorly constrained. For example, the net effect of temperature on oxygen is complex; while warming will unambiguously reduce the solubility of oxygen, the effects of warming on the strength and duration of stratification and on biological oxygen consumption are less well known. Understanding potential drivers of oxygen depletion is key to predicting the likelihood of oxygen deficiency or hypoxia in UK marine waters. In near coastal waters, nutrient enrichment from increased rainfall and runoff can lead to eutrophication, causing acceleration of phytoplankton growth with undesirable disturbance and potentially harmful effects, including the growth of nuisance or toxic phytoplankton, red tides and dissolved oxygen depletion (Painting *et al.*, 2013).

Under the most recent assessment of near-bed dissolved oxygen concentrations under the OSPAR eutrophication assessment, UK waters were assessed as being good or high status (Devlin *et al.,* 2022). However, across the wider OSPAR region, seven areas were identified as not achieving good status with an additional five areas showing a decreasing trend in dissolved oxygen concentration. Hutchings *et al.,* (2024) assessed the long-term change in temperature and dissolved oxygen in English estuaries between 1990 to 2022. Temperature increased at an average rate of 0.037 ºC/year across all estuaries with no regional pattern. Over this period, dissolved oxygen increased in approximately half of the estuaries, likely due to regulatory changes leading to dissolved oxygen improvements e.g. a reduction in nutrient inputs through improvements in wastewater management and increases in number of primary production events causing oxygen super saturation. However, a reduction in dissolved oxygen was determined for the remaining half of studied estuaries, likely due to increased water temperature. The connectivity between estuaries and the coastal marine environment increases the potential for low oxygen waters from estuaries to be transported to near coastal regions, further increasing the risk of low oxygen.

In coastal systems, the relatively slow process of dissolved oxygen depletion is frequently interrupted by ventilation of water via physical mixing driven by wind, waves or tides, allowing replenishment of dissolved oxygen by rapid mixing with surface oxygenated waters and equilibration with the atmosphere. However, the nutrient-enhanced organic matter present in these coastal waters does have the potential to be transported away from coastal areas and contribute to biological oxygen consumption elsewhere (Topcu and Brockmann, 2015; Große *et al.*, 2017) and so still may be a problem.

UK marine waters (defined here as areas where local salinity is greater than 30) are considered to be of good to high status with respect to chlorophyll concentrations, an indicator for the risk of eutrophication (Prins and Enserink, 2022). However, eutrophication is not the only driver or precursor of dissolved oxygen depletion. The timing, duration and strength of stratification play critical roles in the seasonal depletion of dissolved oxygen because they dictate the degree of isolation of bottom waters and the potential for mixing. However, there is significant regional disparity between waters that are stratified for long periods of time and the magnitude of oxygen depletion they experience. In the North Sea, areas of prolonged stratification in the central and northern regions generally have a higher bottom-water dissolved oxygen concentration than areas that are stratified for a shorter period in the south-central North Sea region (Große *et al.*, 2016; Queste *et al.*, 2016; Topcu and Brockmann, 2015). This disparity indicates that factors other than the strength and duration of stratification play an important role in controlling oxygen depletion. The magnitude of photosynthesis in the sunlit surface layer dictates the amount of organic matter that will eventually sink below the thermocline, with more organic matter leading to greater biological oxygen consumption in deeper, dark waters. In addition, organic matter generated via photosynthesis is a food source for higher trophic levels, such as zooplankton, which graze on phytoplankton and generate sinking faecal material, which contributes to an enhanced downward flux of organic matter which could intensify biological oxygen consumption.

The volume of the bottom layer, represented by both the thickness and areal extent of bottom waters, is also a factor controlling the magnitude of oxygen depletion (Große *et al.*, 2016), with dissolved oxygen being more rapidly depleted by both water column and sedimentary processes in areas with a thinner bottom layer than a thicker bottom layer due to the lower total amount of oxygen per unit volume available in a thinner layer. As such, differences in productivity are thought to control the interannual variability in dissolved oxygen conditions in the North Sea, while spatial differences in dissolved oxygen dynamics have been attributed to variations in stratification and water depth or volume alongside tidal energy for mixing (Große *et al.*, 2016).

While stratification is an important prerequisite for bottom water oxygen depletion, other physical processes can contribute to dissolved oxygen dynamics (Queste et al, 2016; Rovelli *et al.*, 2016). Horizontal and vertical advection may transport water into different depths or regions and can lead to the exchange of water with different oxygen properties. In the central North Sea, estimates of horizontal transport or advection are low (Weston *et al.*, 2004; Greenwood *et al.*, 2010) and typically water masses are thought to be transported into areas with similar properties and so have little net effect. In the Celtic Sea, horizontal advection, tidal forcing and vertical mixing control oxygen dynamics in bottom waters at various times over the stratified period (Hull *et al.,* 2020, Rippeth *et al.,* 2024).
Vertical mixing across the thermocline has the potential to mix well-oxygenated surface waters with oxygen-deplete bottom waters (Rovelli *et al.*, 2016; Queste *et al.*, 2016; Williams *et al.*, 2022, Rippeth *et al.,* 2024). The rate of mixing across the thermocline is highly variable, depending on tides, meteorology and the proximity to banks and slopes, and the contribution from each factor is modified by the strength of local stratification. The combined effect of these processes results in thermocline

mixing in shelf seas spanning several orders of magnitude (e.g. Sharples *et al.*, 2009; Rippeth *et al.*, 2014). Extended deployments of autonomous underwater vehicles (AUVs) or 'gliders' have recently provided new insight into the importance of mixing of dissolved oxygen across the thermocline in the North Sea (Queste *et al.*, 2016) and the Celtic Sea (Williams *et al.*, 2022). Thermocline mixing is weak when compared to tidal and wind-driven mixing (Williams *et al.*, 2013; Williams *et al.*, 2022). However, these physical processes can drive a steady, albeit small, vertical flux of oxygen into the bottom mixed layer (Williams *et al.*, 2022, Rippeth *et al.,* 2024) or drive cyclic spring-neap changes in oxygen consumption driven by sediment resuspension or ventilation of the seabed (Hull et al 2020). Collectively, physical processes add to the complexity of understanding dissolved oxygen dynamics in shelf seas because they can both enhance oxygen depletion through stratification or act to reduce the potential for oxygen depletion via mixing between layers of the water column. Thus, understanding the role of physical processes now and in the future ocean is vital towards understanding climate change impacts on coastal and shelf sea oxygen dynamics (see Section 2.2).

Below the thermocline, biological processes continuously consume oxygen both in the water column and in the sediment (Figure 1b; Große *et al.*, 2016; Queste *et al.*, 2016; Hicks *et al.*, 2017; Hull *et al.*, 2020). Oxygen consumption in sediments has been found to be dependent on sediment type and season. The highest rates of oxygen consumption occur in cohesive sediments (such as mud) rather than permeable sediments (such as sand and gravel) (Hicks *et al.*, 2017). Increased sedimentary oxygen consumption has been observed during the spring bloom period when more organic matter is immediately available (Hicks *et al.*, 2017). Physical processes continue to play a role as organic matter can aggregate to create 'depocentres' or hot spots of benthic oxygen consumption. In addition, organic matter that is on top of or within surficial sediments can potentially be disturbed by natural mixing (e.g. tides and storms) or by human activities (e.g. trawling), thus making benthic organic matter available for remineralisation in the water column via resuspension, potentially contributing to event-driven oxygen decline (van der Molen *et al.*, 2013; Hull *et al.*, 2020). In the Celtic Sea, the spring-neap tidal cycle caused a cyclic change in oxygen consumption due to sediment resuspension enhancing oxygen consumption alongside ventilation introducing oxygen at a muddy-sandy site (Hull *et al.*, 2020). Estimates of the role of sediments in driving oxygen consumption on bottom waters span from less than 20% (Rovelli *et al.*, 2016; Hull *et al.*, 2020) to over 50% (Große *et al.*, 2016). The range likely reflects region specific productivity, remineralisation rates, sediment types or choice of parameters in models.

What could happen in the future?

Results from a regional shelf seas model, the Proudman Oceanographic Laboratory Coastal Ocean Modelling System (POLCOMS), predict an average rise in temperature over the century (in 2069-2089 relative to 1960-1989) of over 3°C for most of the North Sea, English Channel, Irish and Celtic Seas using a medium emissions scenario (SRES A1B) (Tinker *et al.*, 2016; Hughes *et al.*, 2017). The trajectory of atmospheric CO_2 concentration in the SRES A1B scenario is comparable to those in more recent climate scenarios RCP 6.0 and SSP4-6.0. The predicted increase in temperature will lead to a decrease in dissolved oxygen in the whole water column due to a reduction in solubility (Table 1), a decrease in dissolved oxygen in bottom waters due to an increase in the strength and duration of stratification (Table 1: Conley *et al.*, 2007; Keeling *et al.*, 2010; Rabalais *et al.*, 2010; Hofmann *et al.*, 2011; Queste *et al.*, 2013) and impose a greater risk of oxygen deficiency in summer due to lower oxygen in the preceding winter/spring due to warmer waters. Further model projections for the period 2070 to 2098 relative to 1961 to 1990 predict the period of stratification will increase by 10 to 15 days over the entire North-west European shelf region (Lowe *et al.*, 2009; Holt *et al.*, 2010; Sharples *et al.*, 2020).

Table 1. Potential implications of climate change related processes on oxygen dynamics in the coastal and shelf sea environment, including an indication of the timescale over which the process will act and the level of confidence.

Process	Direction	Timescale	Confidence
Decrease in solubility due to ocean warming	**Decrease in oxygen concentration** in surface and bottom waters	Decadal	High
Increase in stratification due to ocean warming	**Decrease in oxygen concentration** in bottom waters due to reduced mixing	Decadal	Medium
Decrease in nutrient supply to the surface mixed layer due to increased stratification	Decrease in phytoplankton growth and amount of organic matter that reaches bottom waters, decrease in oxygen consumption in bottom waters causing a relative **increase in oxygen concentration**	Seasonal	Low
Increase in biological	**Net effect unknown** due to increase in both oxygen production via photosynthesis and oxygen consumption via	Decadal	Low

processes due to ocean warming	respiration and other processes. Nutrient availability not considered		
Increase in frequency and intensity of storms	Localised change in water column stratification and **increase in oxygen concentration** due to water column mixing	Seasonal	Low
Change in large scale circulation altering the characteristics of water supplied to the UK shelf sea	**Net effect unknown** depending on the circulation patterns and change to characteristics of source water	Decadal	Low
Resuspension of sediments due to storms	Increase in organic matter available for oxygen consumption causing a **decrease in oxygen concentration**	Seasonal	Low
Increase in frequency and intensity of Marine Heatwaves	**Decrease in oxygen** due to decrease in solubility and reduced mixing to bottom waters. Increase or decrease in biological activity and production or consumption of oxygen	Episodic	Low
Increased precipitation and river runoff	Increase in nutrients will increase the risk of eutrophication and associated **decrease in oxygen concentration**	Annual	Low

Although we describe individual processes and consequences for oxygen dynamics in Table 1, the reality is that these processes occur at the same time and may exacerbate the gain or loss of oxygen or cancel each other out resulting in no net change. For example, while enhanced stratification may reduce mixing between bottom waters and the sea surface, it may also reduce the supply of nutrients, decrease phytoplankton growth, the amount of organic matter that reaches bottom waters, which will likely decrease the demand for oxygen in the bottom waters. The net effect of these two competing processes and consequences for oxygen is uncertain (Table 1). In addition, biological processes are thermally sensitive and will likely increase in response to an increase in temperature but their net impact on oxygen dynamics is unknown (Table 1). Increased storm activity driven by a warming atmosphere will enhance ocean mixing. While this will further be modified by a change in stratification from a warmer atmosphere, a likely scenario is an increase in surface layer depth, an increase in energy available to mix bottom waters and a reduction in areal extent of seasonal stratification, and thus a reduction in the risk or extent of oxygen depletion (Table 1). Other contributing processes from this enhanced mixing include resuspension of sediments, which may increase biological oxygen consumption in bottom waters or reduced light and therefore reduced primary production in upper layers (Capuzzo *et al.*, 2017). Changes in the circulation pattern and intensity may also indirectly affect oxygen concentration over large regions on annual timescales by changing salinity and therefore altering solubility and stratification (Galli et al., 2024). Disentangling the importance of these competing processes requires good monitoring of bottom water oxygen, alongside development of mechanistic understanding and improved numerical models.

On shorter timescales, oxygen solubility may be affected by marine heatwaves, defined as extreme warming events where the sea surface temperature exceeds a seasonally varying threshold (SST > 90th percentile, Hobday et al., 2016) for at least 5 consecutive days. Marine heatwaves have been observed over the southern North Sea (Cornes et al., 2023) and across the Northwest European Shelf (Berthou et al., 2024). Marine heatwaves are expected to increase in frequency and intensity over much of the global ocean. While UK marine waters are not a hotspot for marine heatwaves, the southern North Sea and English Channel may experience marine heatwaves and anomalously low near-bottom oxygen compound events year-round in future (Jacobs et al., 2024). Thermal stress to marine life (Wernberg et al., 2025) alongside low oxygen availability has the potential to adversely affect the benthic marine ecosystem.

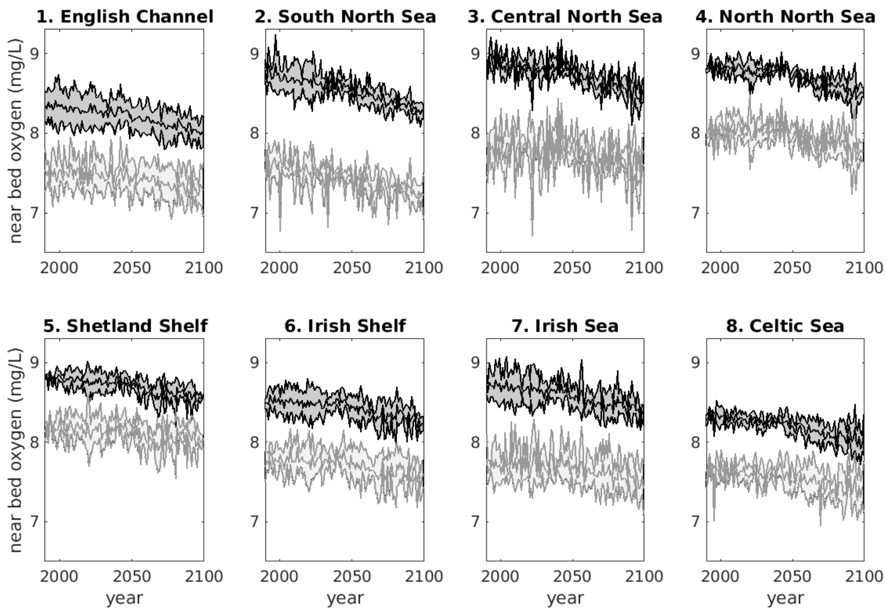
Finally, winter precipitation and river flows are projected to increase up to 30 to 50 % and up to 25%, respectively, across the UK (Robins et al., 2016), with the highest projections observed in the north and west and lowest projections in the south (Robins et al., 2016). This could increase nutrient inputs to coastal waters and enhancing the risk of eutrophication and associated oxygen depletion (Table 1, Rabalais *et al.*, 2010; Zhang *et al.*, 2010; Ockenden *et al.*, 2017). Alternatively, a reduction in summer precipitation and river flow (Robins et a., 2016) alongside improved water and land management has the potential to reduce nutrient input, reduce the risk of eutrophication and oxygen deficiency (Lenhart *et al.*, 2010; Bussi *et al.*, 2017).

The interaction between these complex processes and their combined effect is difficult to predict, however a suite of global models of varying degrees of complexity agree that dissolved oxygen concentrations in the global ocean will decline by 1.5 to 4% by 2090 or by 6 to 12 µmol/kg by 2100 (Ciais *et al.*, 2013). Model simulations specifically focused on coastal and shelf sea waters estimate that dissolved oxygen concentrations in the North Sea will decline by 5.3 to 9.5 % by 2098 (van der Molen *et al.*, 2013) or as much as 11.5% by 2100 (Meire *et al.*, 2013). Using a small ensemble of a coupled hydrodynamics-ecosystem model (NEMO-ERSEM), Wakelin et al (2020) and Galli et al (2024) investigated the potential changes in and drivers of oxygen depletion across the North-west European continental shelf seas under a high emission greenhouse gas emissions scenario (RCP 8.5). This high emission scenario is considered an unlikely scenario given the current socio-economic trends (Hausfather and Peters, 2020), however it provides an understanding of dynamics driving oxygen concentrations and a potential example of high impact low likelihood scenario. Model simulations estimate that as the shelf sea waters become warmer (between 1.3°C and 3.1°C) and less saline under RCP8.5, the mean near bed oxygen concentration will decrease by 6.3% by 2100, with monthly minimum oxygen decreasing by 7.7%. In regions that currently experience oxygen depletion, such as the central North Sea and Celtic Sea, the model predicts that oxygen depletion will intensify and last longer (see Figure 9 in Wakelin *et al.*, 2020).

For UK shelf waters (Figure 5), the mean oxygen concentration is projected to decline most strongly (3 to 4% by 2100) in the North Sea and Western English Channel while the reduction in the minimum of monthly-mean concentrations is highest (2.4 to 3.6%) in the North Sea and Celtic Sea. Deeper regions exposed to exchange with the open ocean (the Irish shelf and Shetland shelf) are less affected, with annual mean concentrations decreasing by ~2% and minimum monthly concentrations by 1.4 to 1.8%. However, in the western Irish Sea, warming of the sea surface may alter the structure of the gyre system, strengthening stratification and thus increasing the risk of oxygen depletion in bottom waters (Olbert *et al.*, 2012). These model outputs imply that the decline in dissolved oxygen in coastal and shelf seas resulting from climate change would be amplified compared to the effects in the open ocean.
According to Figure 5a, none of the regions within the UK shelf seas will reach oxygen deficiency in the future (Galli *et al.,* 2024). However, there is potential for oxygen deficiency to occur in sub-regions of UK marine waters, such as the eastern border of the Central North Sea and in the Celtic Sea (see Figure 3 in Galli *et al.,* 2024). This study also emphasised how climate change can alter stratification through changes to circulation patterns and ocean-shelf edge exchange, driving an indirect far-field influence on oxygen dynamics.

In the open ocean, 15 to 32% of the decline in oxygen is attributed to a decrease in solubility in a warming ocean, with the remaining 58 to 85% of the decline attributed to reduced ventilation due to increased stratification (Helm *et al.*, 2011; Meire *et al.*, 2013) or biological oxygen consumption (Brewer and Peltzer 2017). Observations from the North Sea suggest that one third of the historical oxygen decline is due to warming, whereas two thirds is attributed to increased oxygen consumption (Queste *et al.*, 2013). More recently, model simulations focused on the North-west European Shelf Sea suggest that 73% of the projected decline in oxygen up to 2100 at RCP8.5 is due to solubility changes with the remainder attributed to changes in the ecosystem processes (Wakelin *et al.*, 2020). Thus, it appears that the contribution of reduced solubility in reducing oxygen concentrations will become more important as the ocean warms.

(a)



(b)

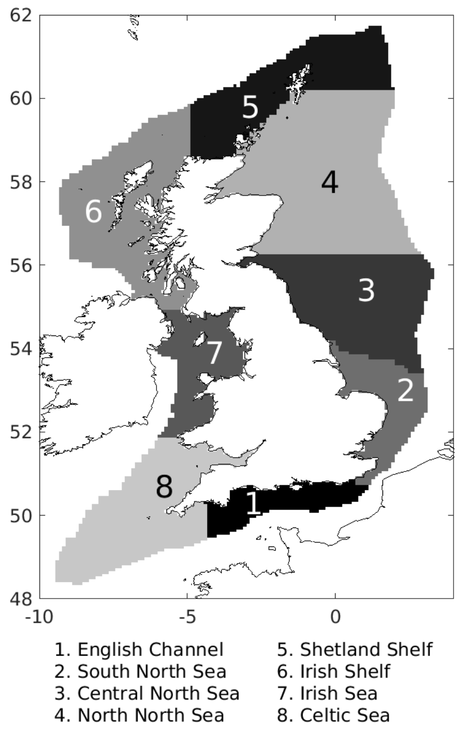


Figure 5: *(a) NEMO-ERSEM projections of near bed oxygen concentrations under a high greenhouse gas emissions scenario (RCP8.5), averaged over (b) the UK shelf regions. Lines and shading denote the mean ± the standard deviation of a three-model ensemble: black lines are annual means, grey lines are the minimum monthly-mean concentrations per year. (Adapted from Galli et al, 2024.)*

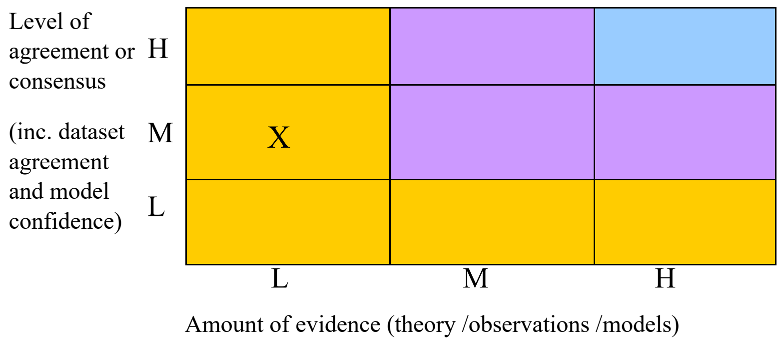
Consequences of oxygen depletion

Oxygen is required to sustain vital metabolic processes of marine organisms and is essential for activities such as muscular activity, growth and reproduction (Pörtner and Knust, 2007). Depletion of dissolved oxygen poses a serious threat to marine organisms, with the most-severe responses occurring under hypoxic or anoxic conditions. Most marine organisms have limits or thresholds to the severity of oxygen depletion they can tolerate (Vaquer-Sunyer and Duarte, 2008; Pörtner, 2010, 2017). Despite the threat posed by deoxygenation, the impact of oxygen depletion on marine life has received far less attention relative to threats posed by ocean warming and acidification (Borges et al., 2022). Meta-analysis of 721 experiments involving ocean warming, acidification and deoxygenation revealed onset of hypoxic events caused consistent negative effects on biological performance for molluscs, crustaceans and fish. Specifically, there was a decline in survival (33%), abundance (65%), development (51%), metabolism (33%), growth (24%) and reproduction (39%, Sampaio et al., 2021). Respiration rates and reproduction are considered to be most sensitive to reduced oxygen compared to growth and feeding rates (Galic et al 2019), but there is a lack of knowledge on impact of oxygen depletion of organisms at different life stages which hinders management across life stages. Other factors will affect the sensitivity of marine life to reduced oxygen including exposure time, species, type of organism, respiration mode and physiological requirements. For example, highly active and larger species living in warm water are generally less tolerant of low oxygen conditions (Stramma *et al.*, 2011, Rubalcaba et al., 2020). Oxygen depletion can be devastating for commercial fisheries. For example, during a period of oxygen deficiency (oxygen concentration of 3.7 mg/litre, equivalent to a saturation lower than 40% or 116 µmol/kg) in 1982 in German and Danish coastal waters of the North Sea, fish abundance decreased from ~400 kg per 30-minute trawl to less than 5 kg per 30 minute trawl (Westernhagen and Dethlefsen, 1983). While the focus here is on dissolved oxygen, ocean warming will also increase metabolic rates of organisms and thus it is the response to multiple stressors, not just a decline in oxygen, that needs to be understood. To delineate the role of temperature versus oxygen availability on metabolism, Deutsch *et al*. (2015) defined a metabolic index, which compares the ratio of the oxygen supply to an organism's resting oxygen demand. Using this physiological framework, projected ocean warming alongside deoxygenation would reduce the metabolic index as the increase in metabolism increases oxygen demand relative to oxygen supply. This implies that future marine hypoxia will be driven primarily by warming and not a decline in oxygen (Deutsch *et al.*, 2015).

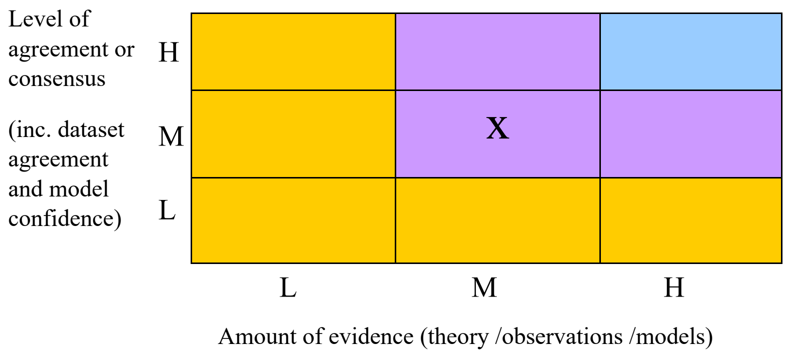
Although hypoxia has not been detected in UK marine waters, it has been detected in the wider North-west European shelf seas including the North Sea (Topcu and Brockmann, 2015) and Baltic Sea (Meier *et al.*, 2019) and thus will affect species that contribute to the ecosystem and perhaps economy of the UK due to connectivity of the marine environment and transfer of migratory species between regions. Periods of oxygen deficiency have been detected in the UK waters of the North Sea and now the Celtic Sea. While the impact of deoxygenation has been documented in non-UK waters of the North Sea (Westernhagen and Dethlefsen, 1983) and globally (Rose *et al.*, 2019) the impacts on the marine ecosystem, specifically commercial fisheries has not yet been documented in UK marine waters.

CONFIDENCE ASSESSMENT

What is already happening?



What could happen in the future?



On a global scale, there is a *high level of confidence* that the oceans are losing oxygen due to ocean warming. In UK coastal waters, there is a high level of understanding of the seasonal and interannual variability in oxygen dynamics in the permanently mixed and seasonally stratifying waters in the North Sea due to the relatively extensive sampling regime for dissolved oxygen concentrations in this region over the past four to five decades. Repeat sampling at specific sites has provided insight into the occurrence and onset of oxygen depletion, leading to risk of oxygen deficiency but the spatial extent of oxygen depletion outside of these specific regions within the North Sea is uncertain due to the paucity of direct observations.

Approximately one third of the historical seasonally focused depletion of oxygen in the North Sea has been attributed to warming but the remaining two thirds are thought to be due to enhanced oxygen consumption. The relative importance of the processes that drive enhanced oxygen consumption (e.g. more organic matter, decreased ventilation of bottom waters), however, remain poorly understood.

Finally, whereas the North Sea is well sampled in time and space, the rest of the Northwest European Shelf waters, especially the Celtic and Irish seas, are relatively poorly sampled and offer *low levels of confidence* in the occurrence or risk of oxygen depletion. Nevertheless, both observations and models agree that the UK coastal and shelf seas are losing oxygen and thus there is a *medium level of confidence* on the direction of change.

At the global scale, there is a *high level of confidence* that an increase in temperature will continue to reduce the solubility of oxygen and enhance stratification and thus lead to the ongoing decline in dissolved oxygen concentrations, especially below the thermocline. On a regional scale appropriate for coastal and shelf seas, there is a consensus that the ocean will lose oxygen. Model simulations can provide estimates of the magnitude and causes of the decline in dissolved oxygen but there is still uncertainty in how well they represent the coupling between physical and biogeochemical processes, biological processes specifically, strong seasonality in nutrient supply in a shallow water column and interaction with the sediment. Therefore, there is a *medium level of confidence* on the future of dissolved oxygen dynamics on a regional scale relevant to UK marine waters.

KEY CHALLENGES AND EMERGING ISSUES

1. We need to be able to determine the mechanisms driving spatial and temporal trends in dissolved oxygen and confidently identify when and where changes in dissolved oxygen are being driven by human-induced activity such as ocean warming or nutrient enrichment relative to background natural variability.

2. Assessing the occurrence, frequency and spatial extent of oxygen deficiency in UK coastal and shelf waters is hampered by the lack of long-term data in regions outside of the North Sea. The poor resolution of dissolved oxygen data also hampers the ability to confidently test coastal and shelf-sea models. An integrated observing system providing high resolution, continuous time-series data using new technologies such as autonomous ocean gliders or instrumented moorings would provide the means to improve detection of oxygen depletion in the future. Recent and current programmes such as the NERC-Defra Shelf Sea Biogeochemistry programme (Kröger *et al.,* 2018) NERC-Defra WWF AlterEco project (https://altereco.ac.uk) and EU H2020 AtlantOS programme

(https://atlantos-h2020.eu) are providing emerging insight into best practices on how to operate autonomous ocean gliders to study dissolved oxygen dynamics in UK marine waters.

3. There is still uncertainty surrounding the ability of models to simulate the individual processes and coupling between processes that control dissolved oxygen dynamics. To accurately predict dissolved oxygen, models need to simulate each contributing process correctly, in isolation but also coupled to other processes. This is an enormous challenge for ocean models since it is not possible to include all physical, chemical and biological processes in any model. Instead, complex processes must be parameterised to produce net effects that are close to that observed, but that may have differing levels of success dependent on local conditions. We do not yet fully understand all processes contributing to the decline in oxygen in the marine environment and thus representing these processes in models is challenging. The lack of understanding is particularly acute within coastal and shelf sea sediments. The lack of long-term time series data for testing coupled physical-ecosystem models, or the variability in functioning between sites with different conditions is also problematic.

REFERENCES

Berthou, S., Renshaw, R., Smyth, T. *et al.* Exceptional atmospheric conditions in June 2023 generated a northwest European marine heatwave which contributed to breaking land temperature records. *Commun Earth Environ* **5**, 287 (2024). https://doi.org/10.1038/s43247-024-01413-8

Best, M.A., Wither, A.W. and Coates, S. (2007) Dissolved oxygen as a physico-chemical supporting element in the Water Framework Directive. *Marine Pollution Bulletin*, **55**, 53–64. doi:10.1016/j.marpolbul.2006.08.037

Bopp, L., Resplandy, L., Orr, J.C., Doney, S.C., Dunne, J.P., Gehlen, M. *et al*. (2013) Multiple stressors of ocean ecosystems in the 21st Centure: projects with CMIP5 models. *Biogeosciences*, **10**, 6225-6245.

Borges, F.O., Sampaio, E., Santos, C.P. and Rosa, R. (2022). Impacts of Low Oxygen on Marine Life: Neglected, but a Crucial Priority for Research. The Biological Bulletin, 243, (2), https://doi.org/10.1086/721468

Breitburg, D.L., Hondorp, D.W., Davias, L.A. and Diaz, R.J. (2009) Hypoxia, Nitrogen and Fisheries: Integrating Effects Across Local and Global Landscapes. *Annual Reviews in Marine Sciences*, **1**, 329-49.

Breitburg, D., Levin, L.A., Oschilies, A., Gregoire, M., Chave, F.P., Conley, D.J. *et al*. (2018) Declining oxygen in the global ocean and coastal waters. *Science*, **359**, eaam7240.

Brewer, P.G. and Peltzer, E.T. (2017) Depth perception: the need to report ocean biogeochemical rates as functions of temperature, not depth. *Philosophical Transactions of the Royal Society A*, **375**, 20160319.

Bussi, G., James, V., Whitehead, P.G., Dadson, S.J. and Holman, I.P. (2017) Dynamic response of land use and river nutrient concentration to long-term climatic changes. *Science of The Total Environment*, 590-591, 818-31.

Butenschön, M., Clark, J., Aldridge, J.N., Allen, J.I., Artioli, Y., Blackford, J. *et al*. (2016) ERSEM 15.06: a generic model for marine biogeochemistry and the ecosystem dynamics of the lower trophic levels. *Geosciences Model Development*, **9**, 1293-1339. doi.org/10.5194/gmd-9-1293-2016.

Capuzzo, E., Lynam, C.P., Barry, J., Stephens, D., Forster, R.M., Greenwood, N., McQuatters-Gollop, A., Silva, T., vanLeeuwen, S.M. and Engelhard, G.H., (2017) A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. *Global Change Biology*, **24**, e352-e364.

Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J. *et al*. (2013) Carbon and Other Biogeochemical Cycles. In *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Stocker, T.F., Qin, D., Plattner, G,K., Tignor, M., Allen, S.K. *et al.*). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Ciavatta, S., Kay, S., Saux-Picart, S., Butenschon, M. and Allen, J.I. (2016) Decadal reanalysis of biogeochemical indicators and fluxes in the North West European shelf-sea ecosystem. *Journal of Geophysical Research: Oceans*. **121.** doi: 10.1002/2015JC011496.

Conley, D. J., Carstensen, J., Ertebjerg, G., Christensen, P.B., Dalsgaard, T., Hansen, J. L. S. and Josefson, A.B., (2007) Long- term changes and impacts of hypoxia in Danish coastal waters. *Ecological Applications* **17**: S165–S184.

Cornes, R. C., Tinker, J., Hermanson, L., Oltmanns, M., Hunter, W. R., Lloyd-Hartley, H., et al. (2023). Climate change impacts on temperature around the UK and Ireland. *MCCIP Sci. Rev.* 18:1-18. doi:10.14465/2022.reu08.temp

Deutsch, C., Ferrel, A., Seibel, B., Portner, H-O and Huey, R.B. (2015) Climate change tightens a metabolic constraint on marine habitats. *Science*, **348**, 6239.

Devlin, M., Fernand, L. and Collingridge, K. 2022. *Concentrations of Dissolved Oxygen Near the Seafloor in the Greater North Sea, Celtic Seas and Bay of Biscay and Iberian Coast*. In: OSPAR, 2023: The 2023 Quality Status Report for the North-East Atlantic. OSPAR Commission, London. Available at: https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/indicator-assessments/seafloor-dissolved-oxygen

Diaz, R.J. and Rosenberg, R. (2008) Spreading Dead Zones and Consequences for Marine Ecosystems, *Science*, 321(5891), 926-929.

Ferreira, J. G., Andersen, J. H., Borja, A., Bricker, S. B., Camp, J., da Silva, M. C. ET *et al*. (2011) Overview of eutrophication indicators to assess environmental status within the European

Marine Strategy Framework Directive. *Estuarine, Coastal and Shelf Sea Sciences*, **93**(2), 117-131.

Foden, J., Devlin, M.J., Mills, D.K., and Malcolm, S.J. (2010) Searching for undesirable disturbance: an application of the OSPAR eutrophication assessment method to marine waters of England and Wales, *Biogeochemistry,* **106**(2), 157-175.

Galic, N., Hawkins, T. and Forbes, V.E. (2019). Adverse impacts of hypoxia on aquatic invertebrates: A meta-analysis. Science of the Total Environment, 652, 736-743. https://doi.org/10.1016/j.scitotenv.2018.10.225

Galli, G., S. Wakelin, J. Harle, J. Holt, and Y. Artioli (2024), Multi-model comparison of trends and controls of near-bed oxygen concentration on the northwest European continental shelf under climate change, Biogeosciences, 21(8), 2143-2158, doi:10.5194/bg-21-2143-2024.

Gilbert, D., Rabalais, N.N., Díaz, R.J., and Zhang, J. (2010) Evidence for greater oxygen decline rates in the coastal ocean than in the open ocean, *Biogeosciences*, **7**, 2283-2296.

Greenwood, N., Parker, E R., Fernand, L., Sivyer, D.B., Weston, K., Painting, S.J., Kroger, S., Forster, R.M., Lees, H.E., Mills, D.K. and Laane, R.W.P.M. (2010) Detection of low bottom water oxygen concentrations in the North Sea: implications for monitoring and assessment of ecosystem health. *Biogeosciences*, **7**, 1357-1373.

Gro ße, F., Greenwood, N., Kreus, M., Lenhart, H-J, Machoczek, D., Patsch, J., Salt, L. and Thomas, H., (2016) Looking beyond stratification: a model-based analysis of the biological drivers of oxygen deficiency in the North Sea. *Biogeosciences*, **13**, 2511-2535.

Große, F., Kreus, M., Lenhart, H-F., Patsch, J. and Pohlmann, T., (2017) A Novel Modeling Approach to Quantify the Influence of Nitrogen Inputs on the Oxygen Dynamics of the North Sea. *Frontiers in Marine Sciences*, doi:10.3389/fmars.2017.00383.

Gulev, S.K., Thorne, P.W., Ahn, J., Dentener, F.J., Domingues, C.M., Gerland, S., Gong, D., Kaufman, D.S., Nnamchi, H.C., Quaas, J., Rivera, J.A., Sathyendranath, S., Smith, S.L., Trewin, B., von Shuckmann, K. and Vose, R.S.: Changing State of the Climate System, in: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Masson-Delmotte, V., Zhai, P., Priani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.N.R., Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, R., and Zhou, B., Cambridge University Press.

Hausfather, Z., Peters, G.P., (2020). Emissions – the 'business as usual' story is misleading. Nature 577, 618–620. https://doi.org/10.1038/d41586-020-00177-3

Helm, K.P., Bindoff, N. L. and Church, J. A., (2011) Observed decreases in oxygen content of the global ocean. *Geophysical Research Letters*, **38**, 23, L23602.

Hicks, N., Ubbara, G. R., Silburn, B., Smith, H.E.K., Kroger, S., Parker, E. R., Sivyer, D., Kitidis, V., Hatton, A., Mayor, D. J., Stahl, H. (2017) Oxygen dynamics in shelf sea sediments incorporating seasonal variability. *Biogeochemistry*, 135-35-47.

Hobday A. J., Alexander L. V., Perkins S. E., Smale D. A., Straub S. C., Oliver E. C., et al. (2016). A hierarchical approach to defining marine heatwaves. *Prog. Oceanography* 141, 227–238. doi: 10.1016/j.pocean.2015.12.014

Hofmann, A. F., Peltzer, E. T., Walz, P. M. and Brewer P. G., (2011) Hypoxia by degrees: Establishing definitions for a changing Ocean. *Deep-Sea Research* **1**, 58, 1212-1226.

Holt, J., Wakelin, S., Lowe, J. and Tinker, J. (2010) The potential impacts of climate change on the hydrography of the northwest European continental shelf, **86**, 361-379.

Holt, J., Polton, J., Huthnance, J., Wakelin, S., O'Dea, E., Harle, J., Yool, A., Artioli, Y., Blackford, J., Siddorn, J. and Inall, M., (2018) Climate-driven change in the North Atlantic and Arctic Oceans can greatly reduce the circulation of the North Sea. *Geophysical Research Letters*, **45**(21), 11827-11836. doi: 10.1029/2018GL078878

Hughes, S.L., Tinker, J. and Dye, S. (2017) Temperature. *MCCIP Science Review*, 2017, 22-41. doi:10.14465/2017. arc10.003-tem.

Hull, T., Johnson, M., Greenwood, N. and Kaiser, J. (2020) Bottom mixed layer oxygen dynamics in the Celtic Sea. *Biogeochemistry*, **149**, 263-289.

Hull, T., Greenwood, N., Birchill, A., Beaton, A., Palmer,M. and Kaiser, J., (2021) Simultaneous assessment of oxygen-and nitrate-based net community production in a temperate shelf sea from a single ocean glider. Biogeosciences, 18, 6167-6180. Doi: 10.5194/bg-18-6167-2021

Hutchings, A.M, de Vries, C.S., Hayes, N.R and Orr, H.G. (2024). Temperature and dissolved oxygen trends in English estuaries over the past 30 years. Estuarine, Coastal and Shelf Science, 306, 108892, https://doi.org/10.1016/j.ecss.2024.108892

IPCC Climate Change (2013) *The Physical Science Basis*. Cambridge University Press, Cambridge.

Ito, T., Minobe, S., Lng, M.C. and Deutsch, C., (2017) Upper ocean O2 trends: 1958-2015. *Geophysical Research Letters*, **44**, 9, 4214-4223.

Jacobs, Z. L., Jebri, F., Wakelin, S., Strong, J., Popova, E., Srokosz, M. and Loveridge, A. (2024) Marine heatwaves and cold spells in the Northeast Atlantic: what should the UK be prepared for? *Frontiers in Marine Science,* doi:10.3389/fmars.2024.1434365

Keeling, R.G. and Shertz, S.R. (1992) Seasonal and interannual variations in atmospheric oxygen and implications for the global carbon cycle. *Nature*, **358**, 723-727.

Keeling, R. F., Kortzinger, A. and Gruber, N. (2010) Ocean Deoxygenation in a Warming World. *Annual Reviews in Marine Science,* **2**, 199-229.

Kröger S, Parker R, Cripps G & Williamson P (Eds.) 2018. Shelf Seas: The Engine of Productivity, Policy Report on NERC-Defra Shelf Sea Biogeochemistry programme. Cefas, Lowestoft. DOI: 10.14465/2018.ssb18.pbdAll

Lenhart, H-J., Mills, D. K., Baretta-Nekker, H., van Leeuwen, S.M., van der Molen, J., Baretta, J.W. *et al*. (2010) Predicting the consequences of nutrient reduction on the eutrophication status of the North Sea. *Journal of Marine Systems*, **81**, 148-170.

Lowe, J.A., Howard, T.P., Pardaens, A., Tinker, J., Holt, J., Wake-lin, S., Milne, G., Leake, J., Wolf, J., Horsburgh, K., Reeder, T., Jenkins, G., Ridley, J., Dye, S. and Bradley, S. (2009) UK Climate Projections science report: *Marine and Coastal Projections*, Met Office Hadley Centre, Exeter, UK, 99.

Madec, G., and the NEMO Team (2012) Nemo Ocean Engine v3.4, Note du Pole de Modélisation, Inst. Pierre Simon Laplace, Paris, France. [Available at http://www.nemo-ocean.eu/27.]

Malone, T.C., Newton, A. (2020) The globalization of cultural eutrophication in the coastal ocean: causes and consequences. *Frontiers of Marine Sciences*, 7, doi: 10.3389/fmars.2020.00670

Manning, A.C. and Keeling, R.F. (2006). Global oceanic and land biotic carbon sinks from the Scripps atmospheric oxygen flask sampling network. *Tellus*, **58B**, 95-116.

Martin, D., McKenna, H. and Livina, V., (2017). The human physiological impact of global deoxygenation. Journal of Physiological Sciences, 67, 97-106, https://doi.org/10.1007/s12576-016-0501-0

McCormick LR, Levin LA (2017). Physiological and ecological implications of ocean deoxygenation for vision in marine organisms. *Philos Trans A Math Phys Eng Sci*. Sep 13;375(2102):20160322. doi: 10.1098/rsta.2016.0322. PMID: 28784712; PMCID: PMC5559417.

Meier, H.E.M., Eilola, K., Almroth-Rosell, E., Schimanke, S., Kniebusch, M., Höglund, A., Pemberton, P., Liu, Y., Väli, G. and Saraiva, S. (2019) Disentangling the impact of nutrient load and climate changes on Baltic Sea hypoxia and eutrophication since 1850. *Climate Dynamics*, **53**, 1145-1166.

Meire, L., Soetaert, K.E.R. and Meysman, F.J.R (2013) Impact of global change on coastal oxygen dynamics and risk of hypoxia. *Biogeosciences*, **10**, 2633-2653.

Naqvi, S.W.A, Bange, H.W., Farias, L., Monteiro, P.M.S, Scranton, M.I. and Zhang, J. (2010) Marine hypoxia/anoxia as a source of CH_4 and N_2O. *Biogeosciences*, **7**, 2159-2190. doi: 10.5194/ bg-7-2159-2010

O'Boyle, S. and Nolan, G., (2010). The influence of water column stratification on dissolved oxygen levels in coastal and shelf waters around Ireland. In *Biology and Environment: Proceedings of the Royal Irish Academy*, 195-209. Dublin, Ireland.

Ockenden, M.C., Hollaway, M.J., Beven, K.J., Collins, A.L., Evans, R., Falloon, P.D. *et al*. (2017). Major agricultural changes required to mitigate phosphorus losses under climate change. *Nature Communications*, **8**, 161.

Olbert, A.I., Dabrowski, T., Nash, S. and Hartnett, M. (2012) Regional modelling of the 21st century climate changes in the Irish Sea. *Continental Shelf Research*, **41**, 48-60.

Oschlies, A., Duteil, O., Getzlaff, J., Koeve, W., Landolfi, A. and Schmidtko, S. (2017) Patterns of deoxygenation: sensitivity to natural and anthropogenic drivers. *Philosophical Transactions of the Royal Society A*, **375**, 20160325.

Oschlies, A., Brandt, P., Stramma, L. and Schmidtko, S. (2018) Drivers and mechanisms of ocean deoxygenation. *Nature Geoscience*, **11**, 467-473.

OSPAR (2017). Eutrophication Status of the OSPAR Maritime Area. Third Integrated Report on the Eutrophication Status of the OSPAR Maritime Area.

Painting, S., Foden, J., Forster, R., van der Molen, J., Aldridge, J. Best, Jonas, M., Walsham, P., Webster, L., Gubbins, M.*et al.* (2013) Impacts of climate change on nutrient enrichment, *MCCIP Science Review 2013*, 219-235. doi:10.14465/2013. arc23.219-235

Pörtner, H.O. and Knust, R. (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Sciences*, **5**, 315(5808), 96097.

Pörtner, H.O. (2010) Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *Journal of Experimental Biology*, **213**, 881-893.

Pörtner, H.O., Bock, C. and Mark, F.C. (2017). Oxygen- and capacity-limited thermal tolerance: bridging ecology and physiology. *Journal of Experimental Biology*, 220, 2685-2698, doi: 10.1242/jeb.134585.

Prins, T. and Enserink, L. (2022). *Concentrations of Chlorophyll-a in the Greater North Sea, Celtic Seas and Bay of Biscay and Iberian Coast*. In: OSPAR, 2023: The 2023 Quality Status Report for the Northeast Atlantic. OSPAR Commission, London. Available at: https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/indicator-assessments/chl-a-concentrations

Queste, B.Y., Fernand, L., Jickells, T.D. and Heywood, K.J. (2013) Spatial extent and historical context of North Sea oxygen depletion in August 2010. *Biogeochemistry*, **113**, 53-68.

Queste, B.Y., Fernand, L., Jickells, T.D., Heywood, K.J. and Hind, A.J. (2016) Drivers of summer oxygen depletion in the central North Sea. *Biogeosciences*, **13**, 1209-1222.

Rabalais, N.N., Diaz, R.J., Levin, L.A., Turner, R.E., Gilbert, D. and Zhang, J. (2010). Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences*, **7**, 585-619.

Rhein, M., Rintoul, S.R., Aoki, S., Campos, E., Chambers, D., Feely, R.A. *et al*. (2013) Observations: Ocean. In *Climate Change 2013: The Physical Science Basis*. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Rice, J., Arvanitidis, C., Borja, A., Frid, C., Hidding, J.G., Karuse, J., Lorance, P., Ragnarsson, S.A., Skol, M., Trabucco, B., Enserink, L. and Norkko, A. (2012) Indicators for Sea-floor Integrity under the European Marine Strategy Framework Directive. *Ecological Indicators*, **12**, 174-184.

Rippeth, T.P., Lincoln, B.J., Kennedy, H.A., Palmer, M.R., Sharples, J. and Williams, C.A.J. (2014) Impact of vertical mixing on sea surface pCO_2 in temperate seasonally stratified shelf seas. *Journal of Geophysical Research: Oceans*, **119**(6), 3868-3882. doi:10.1002/2014JC010089

Rippeth, T., Shen, S., Lincoln, B., Scannel, B., Meng, X., Hopkins, J. and Sharples, J., (2024). The deepwater oxygen deficit in stratified shallow seas is mediated by diapycnal mixing. Nature Communications, 15: 3136, doi.org/10/1038/s41467-O24-47548-2

Robins, P.E., Skov, M.W., Lewis, M.J., Giménez, L., Davies, A.G., Malham, S.K., Neill, S.P., McDonald, J.E., Whitton, T.A., Jackson, S.E., Jago, C.F. (2016) Impacts of climate change on UK estuaries: a review of past trends and potential projections. Estuarine, Coastal and Shelf Science, 169, 119-135, https://doi.org/10.1016/j.ecss.2015.12.016

Rose, K.A., Gutiérrez, D., Breitburg, D., Conley, D., Craig, J.K., Froehlich, H.E., Jeyabaskaran, R., Kripa, V., Mbaye, B.C., Mohamed, K.S., Padua, S. and Prema, D. (2019) Impacts of ocean deoxygenation on fisheries. In *Ocean Deoxygenation: Everyone's Problem* (eds D. Laffoley, and J.M. Baxter), IUCN, Gland, Switzerland, 519-544. https://doi.org/10.2305/IUCN.CH.2019.14.en

Rovelli, L., Dengler, M., Schmidt, M., Sommer, S., Linke, P. and McGinnis, D. F. (2016) Thermocline mixing and vertical oxygen fluxes in the stratified central North Sea. *Biogeosciences*, **13**, 160901620.

Rubalcaba, J.G., Verberk, W.C.E.P., Jendricks, A.J., Saris, B. and Woods, H.A. (2020). Oxygen limitation may affect the temperature and size dependence of metabolism in aquatic ectotherms. *Proceedings of the National Academy of Sciences*, 117 (50), 31963-31968, doi: 10.1073/pnas.2003292117.

Sampaio, E., Santos, C., Rosa, I., Ferreira, V., Pörtner, H.-O., Duarte, C.M., Levin, L.A. and Rosa, R. (2021) Impacts of hypoxic events surpass those of future ocean warming and acidification. Nature Ecology and Evolution, 5, 311-321, https://doi.org/10.1038/s41559-020-01370-3

Schmidtko, S., Stramma, L. and Visbeck, M. (2017) Decline in global oceanic oxygen content during the past five decades. *Nature*, **542**, 335-339.

Sharples, J., Moore, C.M., Hickman, A. E., Holligan, P.M., Tweddle, J. F., Palmer, M.R. and Simpson, J.H., (2009) Internal tidal mixing as a control on continental margin ecosystems. *Geophysical Research Letters*, **36**, L23603, 5.

Sharples, J., Holt, J. and Dye, S. R., (2020) Impacts of climate change on shelf sea stratification. Marine Climate Change Impacts Partnership: *Science Review*, 67-70.

Stramma, L., Prince, E.D., Schmidtko, S., Luo, J., Hoolihan, J.P., Visbeck, M., Wallace, D.W. R., Brandt, P. and Kortzinger, A. (2011) Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nature Climate Change*, 2. doi: 10.1038/NCLIMATE1304

Tinker, J., Lowe, J., Holt, J., Pardaens, A. and Barciela, R. (2016) Uncertainty in climate projections for the 21st century northwest European shelf seas. *Progress in Oceanography*, **148**, 56-73.

Topcu, H.D. and Brockmann, U.H. (2015) Seasonal oxygen depletion in the North Sea, a review. *Marine Pollution Bulletin*, **99**, 5-27.

Townhill, B.L., van der Molen, J., Metcalfe, J.D., Simpson, S.D., Farcas, A., and Pinnegar, J.K. (2017a) Consequences for climate-induced low oxygen conditions for commercially important fish. *Marine Ecology Progress Series*, **580**, 191-204.

van der Molen, J., Aldridge, J., Coughlan, C., Parker, R., Stephens, D. and Ruardij, P. (2013) Modelling marine ecosystem response to climate change and trawling in the North Sea. *Biogeochemistry*, **113**, 213-236. doi:10.1007/ s1053301297637

Vaquer-Sunyer, R., and Duarte, C.M. (2008) Thresholds of hypoxia for marine biodiversity, *Proceedings of the National Academy of Sciences, USA*, **105**(40), 15,452–15,45.

Wakelin, S.L., Artioli, Y., Holt, J.T., Butenschön, M. and Blackford, J. (2020). Controls on near-bed oxygen concentration on the Northwest European Continental Shelf under a potential future climate scenario. *Progress in Oceanography*, **187**, 102400.

Wernberg, T., Thomsen, M.S., Burrows, M.T., Filbee-Dexter, K., Hobday, A.J., Holbrook, N.J., Montie, S., Moore, P.J., Oliver, E.C.J., Gupta, A.S., Smale, D.A. and Smith, S. (2025). Marine heatwaves as hot spots of climate change and impacts on biodiversity and ecosystem services. *Nature Reviews Biodiversity*, **1**, 461-479.

Westernhagen, H.V. and Dethlefsen, V. (1983) North Sea oxygen deficiency 1982 and its effects on bottom fauna. *Ambio*, **12**, 264-266.

Weston, K., Jickells, T. D., Fernand, L. and Parker, E.R. (2004) Nitrogen cycling in the southern North Sea: Consequences for total nitrogen transport. Estuarine, Coastal And Shelf Sea Sciences, **59**, 559-573. doi:10.1016/j.ecss.2003.11.002.

Weston, K., Fernand, L., Nicholls, J., Marca-Bell, A., Mills, D., Sivyer, D., and Trimmer, M. (2008) Sedimentary and water column processes in the Oyster Grounds: A potentially hypoxic region of the North Sea, *Marine Environmental Research*, **65**, 235-249. doi:10.1016/j.marenvres.2007.11.002

Williams, C., Sharples, J., Mahaffey, C. and Rippeth, T., (2013). Wind-driven nutrient pulses to the subsurface chlorophyll maximum in seasonally stratified shelf seas. *Geophysical Research Letters*, 40, 5467-5472, doi: 10.1002/2013GL058151.

Williams, C.A.J., Davis, C.E., Palmer, M.R., Sharples, J. and Mahaffey, C. (2022) The Three Rs: Resolving Respiration Robotically in Shelf Seas. *Geophysical Research Letters*, **49**, e2021GL096921.

Zhang, J.D., Gilbert, A.J., Gooday, L., Levin, S., Naqvi, W.A., Middelburg, J.J., Scranton, M., Ekau, E., Peña, A., Dewitte, B *et al*. (2010) Natural and human-induced hypoxia and consequences for coastal areas: synthesis and future development. *Biogeosciences*, **7**, 1443–1467.