

# Impacts of climate change on dissolved oxygen concentration relevant to the coastal and marine environment around the UK

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## EXECUTIVE SUMMARY

- The decline in dissolved oxygen and onset of oxygen deficiency and hypoxia are naturally occurring phenomenon in aquatic environments, typically occurring on seasonal timescales.
- Over decadal timescales, there has been a measurable decline in dissolved oxygen concentrations in the global ocean due to warming caused by anthropogenic activity.
- Approximately 15% of the global decline in oxygen has been attributed to reduced solubility in response to ocean warming, with the remaining 85% due to intensified stratification. The relative contribution of these factors in coastal and shelf-sea waters is currently unknown.
- In UK waters, sustained observations in the North Sea reveal the recent onset of oxygen deficiency in late summer, partially due to ocean warming.
- Models designed to represent coastal and shelf sea processes suggest there are large parts of the Celtic Sea, English Channel and Irish Sea that are prone to oxygen deficiency, but data is too sparse in time and space to support these findings. In addition, the ability of models to accurately represent oxygen dynamics is still under debate due to correct representation of physical and biological processes within models.
- Physical processes play a key role in the development of oxygen deficient regions and thus understanding how oxygen concentrations will respond to climate change requires a coupled physical and biogeochemical approach.

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- Coastal and shelf wide sustained observations are required in order to detect and better understand conditions controlling the depletion of dissolved oxygen in UK marine waters.

## 1. INTRODUCTION

Oxygen is the most important gas in the marine environment because it is essential for breathing or ‘respiration’ by all bacteria, protists, plants and animals that live in the sea. Dissolved oxygen concentrations in the global ocean have declined by 2% since the 1960s (Rhein *et al.*, 2013; Schmidtko *et al.*, 2017; Oschlies *et al.*, 2018). While excessive nutrient loading or ‘eutrophication’ may be the driver for the decline in dissolved oxygen concentrations in 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 that in the future, the rate of oxygen decline will increase globally in response to warming (Bopp *et al.*, 2013; Keeling *et al.*, 2010; van der Molen *et al.*, 2013). Depletion of dissolved oxygen can lead to a region being defined as either oxygen deficient, which occurs when dissolved oxygen concentrations are less than 6 mg/litre (equivalent to  $\sim 192 \mu\text{mol/kg}$ ) or hypoxic, which occurs when oxygen concentrations are less than 2 mg/litre (equivalent to  $\sim 64 \mu\text{mol/kg}$ ). The development of oxygen deficiency, or hypoxia, can have deleterious effects on the marine ecosystem (Vaquer-Sunyer and Duarte, 2008; Breitburg *et al.*, 2018). While the decline in dissolved oxygen in the 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 Rosenberg, 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 in order to accurately assess the future risk of oxygen deficiency or hypoxia in response to climate change (Oschlies *et al.*, 2018). Here, we focus on the processes controlling oxygen concentrations in the North-West European Shelf sea water, which encompasses UK coastal and shelf seas.

### What controls oxygen in the marine environment?

Oxygen constitutes 20.95% of our atmosphere and it 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). 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, 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. Biological activity produces dissolved oxygen via photosynthesis and consumes dissolved oxygen via breathing or respiration by marine plants and animals and decay of organic matter back to nutrients (herein referred to collectively as ‘biological oxygen consumption’). 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*, whereas in the dark layers of the ocean, oxygen consumption is typically greater than oxygen production leading to net biological oxygen *consumption* (Figure 1b).

There is an important link between nutrients and oxygen in the marine environment. An increase in nutrients will increase biological activity, causing an increase in dissolved oxygen production in surface waters, but oxygen consumed during decay of biological organic matter leads to a subsequent decrease in dissolved oxygen. Enhanced nutrient inputs into coastal regions have been shown to cause eutrophication (Painting *et al.*, 2013), the side effect being a decline in dissolved oxygen. Hence, dissolved oxygen is used as an indicator of the status of ecosystem health within several directives and conventions designed to protect the UK marine environment. This includes the Water Framework Directive (WFD, Best *et al.*, 2007), the Marine Strategy Framework Directive (MSFD, Ferreira *et al.*, 2011), OSPAR Common Procedure (Foden *et al.*, 2010), and monitoring carried out under the Urban Waste Water Treatment Directive (91/271/EEC) and Nitrates Directive (91/676/EEC). However, dissolved oxygen concentrations within these directives and conventions are only used to identify undesirable disturbance from the indirect effect of nutrient enrichment (OSPAR Common Procedure, Foden *et al.*, 2010) or as an indicator within the eutrophication quality descriptor (MSFD Descriptor 5) as an indirect effect of nutrient enrichment (MSFD Criterion 5.3; Ferreira *et al.*, 2011). There is no specific requirement to monitor dissolved oxygen concentration under such directives 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.

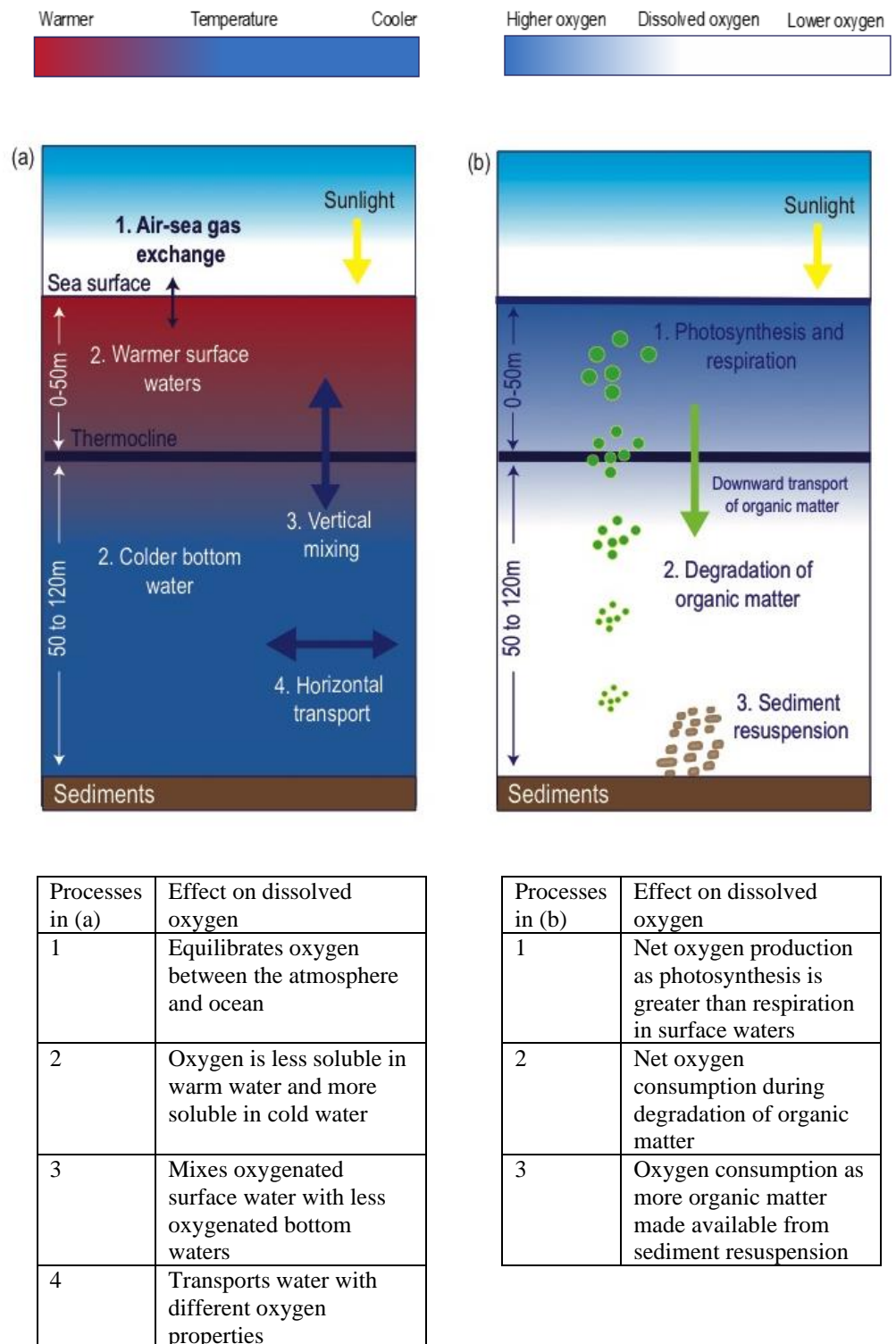


Figure 1: Schematic representation of the vertical structure of (a) temperature and the physical processes that control the distribution of dissolved oxygen and (b) dissolved oxygen and the biological processes that control the distribution of dissolved oxygen in coastal and shelf seas. Underlying tables 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, such as 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 a layer of less-dense water overlays a layer of denser water. The surface layer may be less dense due to the addition of lower salinity water, for example from freshwater run-off from rivers, or from higher temperatures, 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.*, 2013). Such regions include the central and northern North Sea, the Celtic Sea, the western Irish Sea, the Malin Sea and Outer Hebrides region (Sharples *et al.*, 2013). In winter, the shelf seas are completely mixed (Figure 2b) and therefore well oxygenated due to air–sea gas exchange (Figure 2c). Winter mixing leads to surface- and bottom-water oxygen concentrations being the same (Figure 2d). Critically, the water temperature in winter places a first order control on the dissolved oxygen concentration in coastal and shelf seas, 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 occurs in spring, typically in March or April in UK waters (Figure 2d) and persists until winter storms and reduced solar heating in autumn months returns to winter mixed conditions in October or November. During seasonal stratification, a thermocline separates the surface waters from the bottom waters which significantly reduces mixing between the two layers and resulting in different oxygen dynamics in each layer (Figure 2b–d). 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, d). In contrast, the thermocline restricts mixing of bottom waters with the well-oxygenated surface waters. In addition, there is net biological oxygen consumption in the bottom waters (Figure 2c, d). If oxygen consumed in the bottom waters is not replenished by episodic mixing events, such as by enhanced mixing from extreme tides and storms or by horizontal exchange with oxygenated waters, then the bottom layer is at risk of oxygen deficiency and hypoxia. However, the strong seasonal cycle in the UK temperate coastal and shelf seas means that the depletion of oxygen during the stratified period is temporary as dissolved oxygen will be replenished during autumn and winter mixing (Figure 2d). This seasonal pattern is in contrast to many Oxygen Minimum Zones (OMZs) found elsewhere in the marine environment where oxygen deficiency and hypoxia can be persistent features over many years.

In regions of UK coastal and shelf sea waters where there is sufficient energy from tides and currents to permanently mix the water column (Figure 2a), the dissolved oxygen concentration in the entire water column is relatively

homogenous, with the absolute concentration changing 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 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 or hypoxia since stratification is only short-lived.

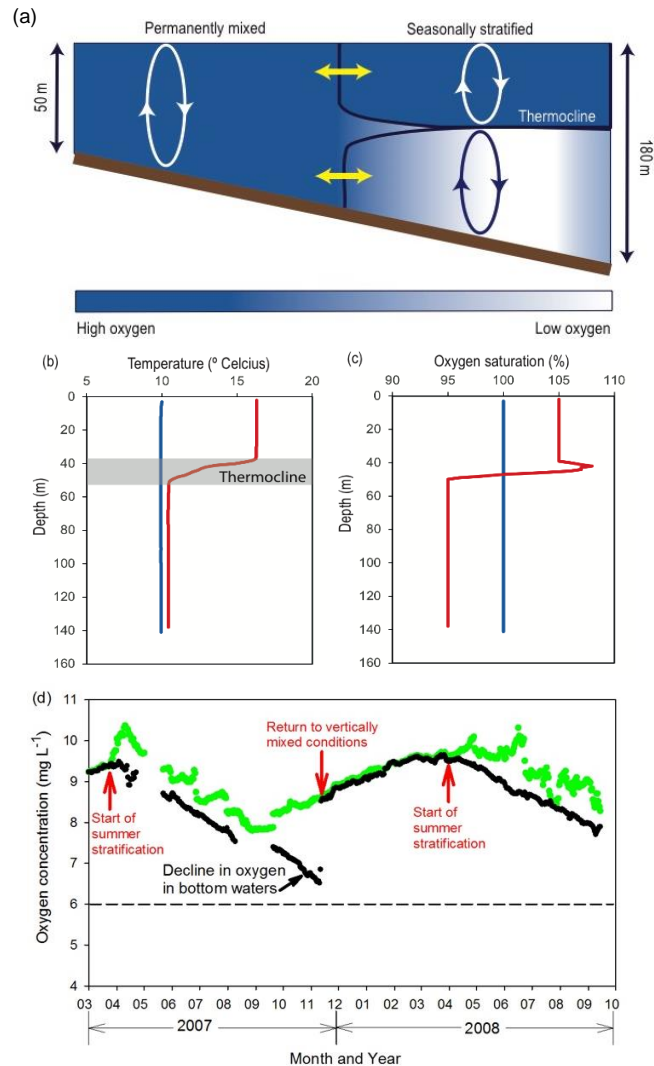


Figure 2: Schematic representation of (a) the gradient in physical water column structure and dissolved oxygen concentrations from the shallow, permanently mixed regions to deeper, seasonally stratifying regions. Exchange between the two regions is indicated by horizontal transfer (yellow arrows); (b) and (c) the seasonal change in water column temperature and dissolved oxygen saturation (%) in a seasonally stratifying shelf sea in winter (blue) and summer (red); (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.). 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.



Many factors will affect oxygen dynamics in the future. Particularly relevant to coastal and shelf seas systems is the change in nutrient inputs, which may enhance or reduce the risk of eutrophication with subsequent implications for oxygen dynamics. Climate change is likely to affect biological and physical processes that lead to oxygen depletion. Warming-induced changes in the solubility of oxygen account for less than one third of the global decline in oxygen, highlighting the relatively large contribution of warming induced changes in stratification to ocean deoxygenation (Schmidtko *et al.*, 2017). Ocean warming will affect metabolic processes including biological oxygen consumption (Brewer and Peltzer, 2017) and thus climate change will likely increase the contribution of biological processes to the decline in dissolved oxygen. In addition, seasonal stratification is predicted to increase in strength and duration over the next 50 years (Lowe *et al.*, 2009; Holt *et al.*, 2010; Sharples *et al.*, 2013), which 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. Thus, understanding potential causes of oxygen depletion, and the responses of these drivers to climate change, land-use and waste-water inputs is key to predicting the likelihood of oxygen deficiency or hypoxia, and subsequent ecosystem harm, in UK marine waters.

## 2. 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 the 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 h). 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  $\sim 320 \mu\text{mol/kg}$  (equivalent to  $\sim 10 \text{ mg/litre}$  or over 100% saturation) in winter to  $\sim 192 \mu\text{mol/kg}$  in summer (equivalent to  $6 \text{ mg/litre}$  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). Temporal high-resolution data from the Cefas SmartBuoy network has revealed the onset of oxygen deficiency (less than  $6 \text{ mg/litre}$ ) in bottom waters during the late summer period in the central and northern North Sea around the Oyster Grounds ( $5.2 \text{ mg/litre}$ , 60% saturation or  $167 \mu\text{mol/kg}$ , Greenwood *et al.*, 2010). Reanalysis of dissolved oxygen data over the past 100 years reveals that there has been an increase in the intensity and spatial extent of oxygen deficiency in the North Sea (Questo *et al.*, 2013). This period of oxygen depletion coincided with a period of ocean warming observed over the past two decades, which explains one third of the change in oxygen, with the remaining two thirds of oxygen depletion being attributed to an increase in biological oxygen consumption (Questo *et al.*, 2013).

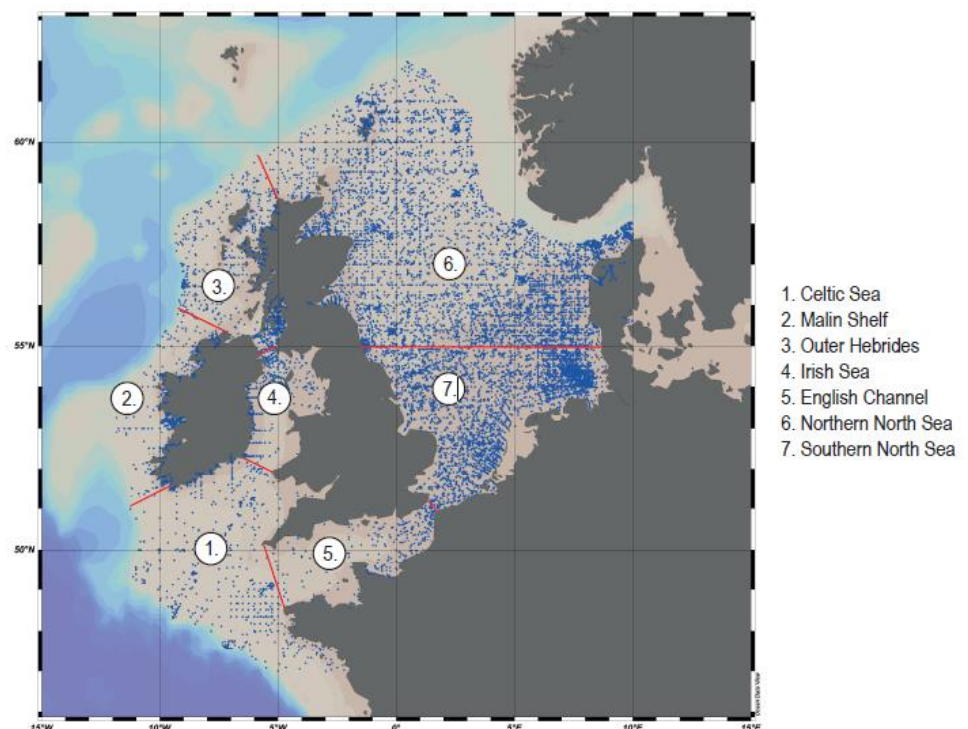


Figure 3a: Synthesis of data from ICES and BODC indicating the spatial distribution of measurements of dissolved oxygen below the thermocline or near the seabed from 1920s to 2017, with red lines indicating approximate boundaries between regions.



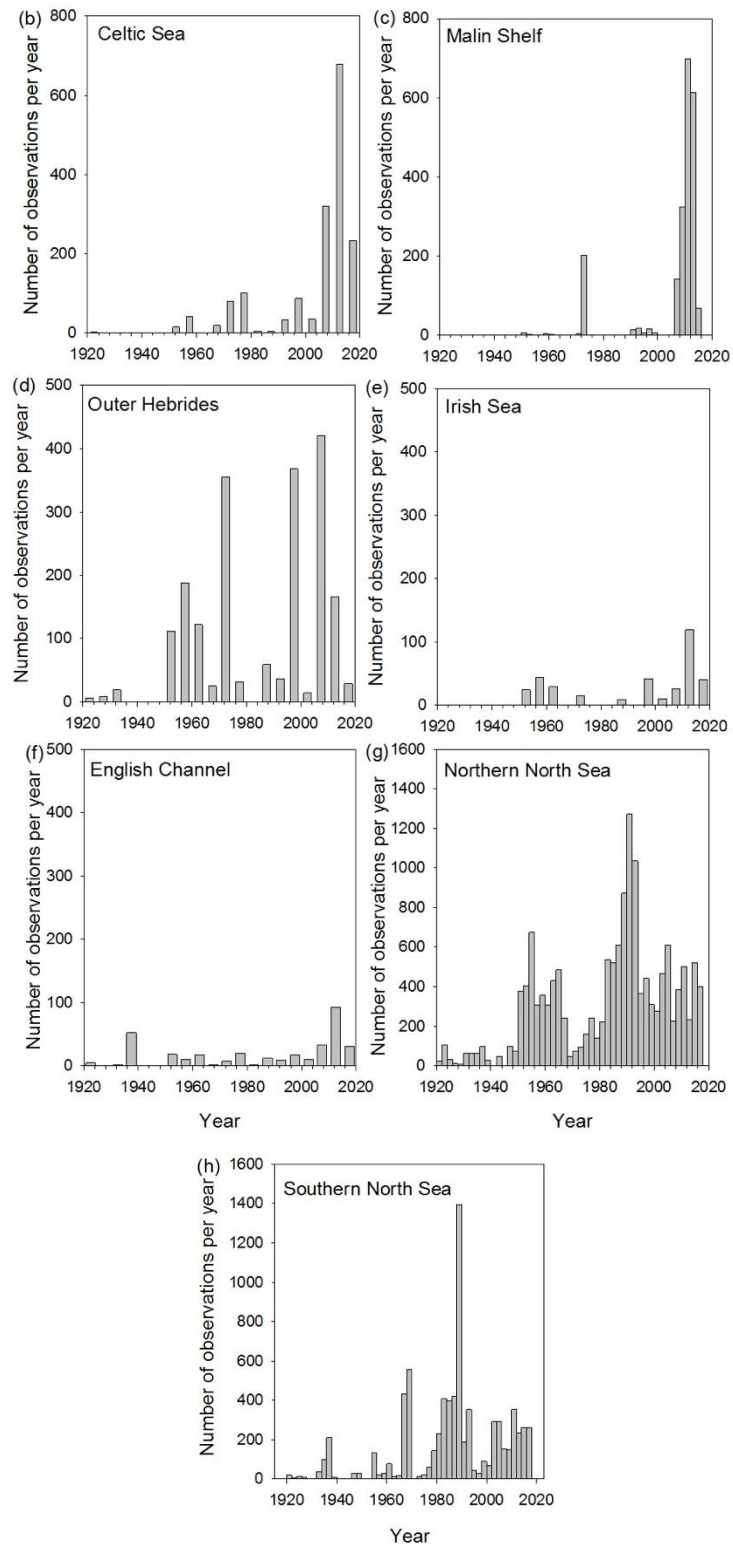


Figure 3b–h. The temporal distribution of observations per year in the bottom waters from 1920s to 2017 for (b) Celtic Sea, (c) Malin Shelf, (d) Outer Hebrides, (e) Irish Sea, (f) English Channel, (g) northern North Sea and (h) southern North Sea. Note that the y-axis scale varies from (b) to (h) with (b) and (c) ranging from 0 to 800, (d), (e) and (f) ranging from 0 to 500 and (g) and (h) ranging from 0 to 1600.

Unlike the well-studied North Sea, the Celtic Sea is poorly sampled in both time and space (Figure 3a–h). Data from the recent UK-Shelf Sea Biogeochemistry programme has significantly improved our understanding of this region. High-resolution data from a benthic study reveal that towards the end of seasonal stratification in late autumn 2014, oxygen concentrations in bottom waters decreased below the 6 mg/litre threshold defining oxygen deficiency (5.8 mg/litre or 62% saturation or 186  $\mu\text{mol/kg}$ ; Aldridge *et al.*, 2017). These are the first published observations indicating the development of oxygen deficiency in the Celtic Sea. 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 3a–h) 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. 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). Recent model re-analysis by Ciavatta *et al.* (2016) has suggested that large areas ( $\sim 325,000 \text{ km}^2$ ) 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. The reliability of ocean and climate models in accurately capturing the myriad of processes that control seasonal oxygen dynamics is still under debate. While current global climate models are able to estimate the change in oxygen concentrations due to solubility to within 10% of the estimate from observations (IPCC, 2013; Oschlies *et al.*, 2018), they tend to underestimate the variability and decline in oxygen (Bopp *et al.*, 2013; Ito *et al.*, 2017), implying that physical processes of mixing and ventilation, as well as biological oxygen consumption, are poorly represented within these models (Oschlies *et al.*, 2017, 2018).

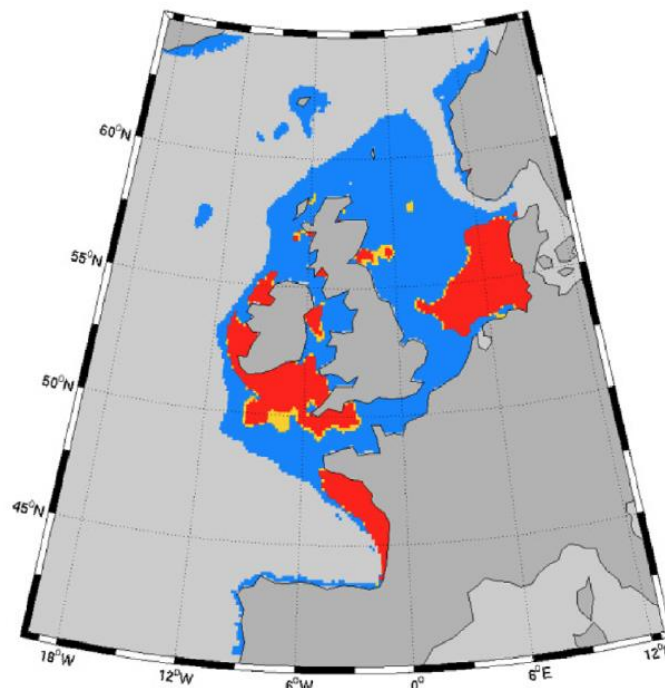


Figure 4: Model output from ERSEM indicating areas vulnerable to oxygen deficiency in bottom waters, defined as at least one daily value in 1998 to 2009 below the threshold of 6 mg/litre. Areas of the shelf where oxygen concentrations are found to be higher than 6 mg/litre at 100% confidence are highlighted 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 dynamics 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 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 EU directives, 21 UK coastal water bodies were assessed as ‘Problem Areas’ with respect to eutrophication status based on nutrient concentrations (OSPAR, 2017; Defra, 2010). 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 ‘Non-Problem Areas’ with respect to the risk and impact of nutrient enrichment (OSPAR, 2017). 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 of time 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 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 thickness or volume of the bottom waters in which biological oxygen consumption occurs is also a factor in controlling the magnitude of oxygen depletion (Große *et al.*, 2016), with dissolved oxygen being more rapidly depleted in a thinner bottom layer than a thicker bottom layer due to the lower total amount of oxygen 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 (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. However, estimates of horizontal transport or advection in the North Sea 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

contrast, 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). 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 ocean 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). While thermocline mixing is weak when compared to tidal and wind driven mixing, it is sufficient to modulate the onset of oxygen deficiency. 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 surface and bottom waters. 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 3).

Below the thermocline, biological processes continuously consume oxygen. However, only recently has the role of the sediments in consuming oxygen been identified as making a significant contribution to oxygen consumption in bottom waters (Figure 1b; Große *et al.*, 2016; Queste *et al.*, 2016; Hicks *et al.*, 2017). Output from an ecosystem model estimates that more than 50% of net oxygen consumption in bottom waters in the North Sea is due to processes occurring on or within the sea bed or benthos (Große *et al.*, 2016). Oxygen consumption in sediments has been found to be dependent upon 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 depletion (van der Molen *et al.*, 2013). The effect of sediment trawling on oxygen depletion was estimated for the Oyster Grounds and North Dogger in the North Sea and found to be non-trivial (Greenwood *et al.*, 2010).



### 3. WHAT COULD HAPPEN IN THE FUTURE?

Results from a regional shelf seas model, the Proudman Oceanographic Laboratory Coastal Ocean Modelling System or 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 (Tinker *et al.*, 2016; Hughes *et al.*, 2017). This predicted increase in temperature will directly lead to a decrease in dissolved oxygen in the sea due to a reduction in solubility (Table 1) and indirectly due to increasing 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.*, 2012). 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.*, 2013). While equivalent studies in coastal and shelf seas have not been undertaken, insights from open ocean studies reveal that these direct and indirect effects of temperature are not equally weighted. A decrease in solubility due to warming accounts for only 15 to 30% of the current global decline in oxygen. It is currently assumed that 58 to 85% of the decline in dissolved oxygen is driven by reduced ventilation due to increased stratification (Helm *et al.*, 2011; Meire *et al.*, 2013), although the role of biological oxygen consumption is not estimated (Brewer and Peltzer, 2017). Observations from the North Sea suggest that one third of the oxygen decline is due to warming, whereas two thirds is attributed to increased oxygen consumption (Questo *et al.*, 2013).

There are additional consequences of climate change that may have an impact on the magnitude and even the direction of oxygen dynamics in coastal and shelf seas. For example, while enhanced stratification acts to reduce mixing of bottom waters with the sea surface, it will also reduce the supply of nutrients to the surface ocean due to reduced mixing across the thermocline. The reduction in nutrients will decrease phytoplankton growth and the amount of organic matter that reaches bottom waters, which will likely reduce the demand for oxygen in the bottom waters. The net effect of these two competing mechanisms is uncertain (Table 1). In contrast, 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 however may include increased resuspension of sediments, which may result in enhancing biological oxygen consumption in bottom waters or reduce light and therefore reduced primary production in upper layers (Capuzzo *et al.*, 2017). Finally, winter precipitation and river

flows are expected to increase across northern Europe (EEA, 2015), potentially increasing the input of nutrients to coastal systems and thus enhancing the risk of eutrophication and associated depletion of oxygen (Table 1; Rabalais *et al.*, 2010; Zhang *et al.*, 2010). Alternatively, a reduction in nutrient input via rivers through improved water and land management has the potential to reduce eutrophication and thus reduce the risk of oxygen deficiency or hypoxia (Lenhart *et al.*, 2010).

*Table 1: 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	<b>Decrease in oxygen concentration</b> in surface and bottom waters	Decadal	High
Increase in stratification due to ocean warming	<b>Decrease in oxygen concentration</b> in bottom waters due to reduced mixing	Decadal	Medium
Decrease in nutrient supply 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 <b>relative increase in oxygen concentration</b>	Seasonal	Low
Increase in biological processes due to ocean warming	<b>Net effect unknown</b> due to increase in both oxygen production via photosynthesis and oxygen consumption via respiration and other processes. Nutrient availability not considered	Decadal	Low
Storms	Localised change in water column stratification and <b>increase in oxygen concentration</b> due to water column mixing	Seasonal	Low
Resuspension of sediments	Increase in organic matter available for oxygen consumption causing a <b>decrease in oxygen concentration</b>	Seasonal	Low
Increased precipitation and river runoff	Increase in nutrients will increase the risk of eutrophication and associated <b>decrease in oxygen concentration</b>	Annual	Low

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  $\mu\text{mol/kg}$  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). These model outputs imply that the decline in dissolved oxygen in coastal and shelf seas resulting from predicted climate change would be amplified compared to the effects in the open ocean.

## Consequences of oxygen depletion

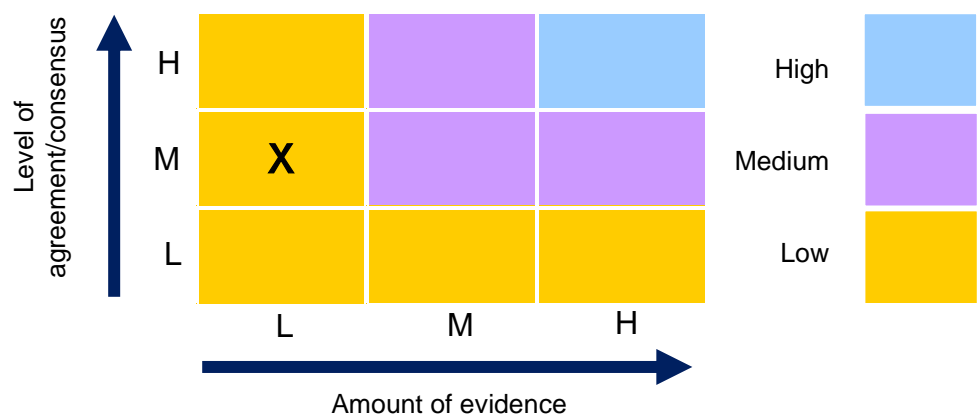
Oxygen is required to sustain vital metabolic processes of marine organisms and is essential for activities such as muscular activity, growth and reproduction (Pörtner and Knust, 2007). Thus, depletion of dissolved oxygen poses a serious threat to marine organisms, with the most severe responses occurring under hypoxic conditions ( $< 2\text{mg/litre}$ , equivalent to  $\sim 63\ \mu\text{mol/kg}$ ). All organisms have limits or thresholds to the severity of oxygen depletion that they can tolerate (Vaquer-Sunyer and Duarte, 2008; Pörtner, 2010). Even a small decrease in oxygen below a threshold can affect oxygen-demanding functions, such as movement and reproduction (Claireaux *et al.*, 2000; Claireaux and Chabot, 2016). Other key factors include exposure time, species, type of organism, respiration mode and physiological requirements. For example, highly active species are generally less tolerant of low oxygen conditions (Stramma *et al.*, 2011). Oxygen depletion can cause a reduction in survival, growth and reproduction, alter behaviour of individual organisms (Baden *et al.*, 1990; Eriksson and Baden, 1997; Chabot and Claireaux, 2008; Long *et al.*, 2008; Ludsin *et al.*, 2009), affect predator-prey relationships and in the most severe case, cause death (Shurmann and Steffensen, 1992; Stramma *et al.*, 2010; Urbina *et al.*, 2011; Townhill *et al.*, 2017b). Even brief repeated exposure to oxygen depletion can alter the immune system of macrofauna and thus increase disease and reduce growth (Stierhoff *et al.*, 2009; Keppel *et al.*, 2015). Oxygen depletion can be devastating for commercial fisheries. For example, during a period of oxygen deficiency (oxygen concentration of  $3.7\ \text{mg/litre}$ , equivalent to a saturation lower than 40% or  $116\ \mu\text{mol/kg}$ ) in 1982 in German and Danish coastal waters of the North Sea, fish abundance decreased from  $\sim 400\ \text{kg}$  per 30 min trawl to less than  $5\ \text{kg}$  per 30 min 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. For example, results from a global model indicate that a decline in oxygen alongside increased metabolism causes a decline in the vertical and poleward extent of viable habitats for a range species (Deutsch *et al.*, 2015).

In addition to the ecological risks, oxygen depletion may also have a significant effect on biogeochemical cycles. Oxygen depletion affects the transfer and storage of organic matter to the sediments (Keil *et al.*, 2016; Cavan *et al.*, 2017), biological removal of nitrate (Neubacher *et al.*, 2011; Neubacher *et al.*, 2013; Kitidis *et al.*, 2017), production of greenhouse gases such as nitrous oxide (Naqvi *et al.*, 2010; Freing *et al.*, 2012; Bianchi *et al.*, 2012), and the release of phosphorus and iron from sediments (Scholz *et al.*, 2014; Watson *et al.*, 2018). These biogeochemical responses to oxygen depletion have the potential to affect primary production locally in coastal and shelf seas and lead to feedback loops, which may have both positive and negative effects on ecosystem functioning (Niemeyer *et al.*, 2017).

Although hypoxia has not been detected in UK marine waters, it has been detected in the North-West European Shelf seas 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 but the impact on the marine ecosystem has not yet been documented.

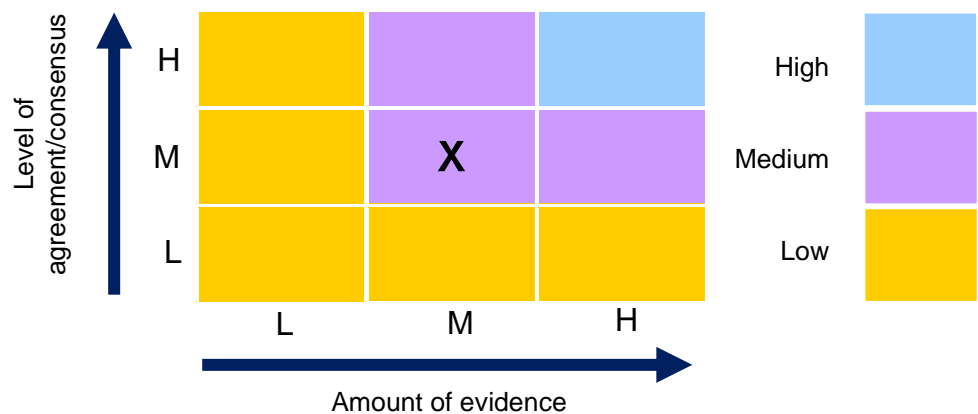
#### 4. CONFIDENCE ASSESSMENT

##### What is already happening?



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 deficiency but the spatial extent of oxygen deficiency outside of these specific regions within the North Sea is uncertain. Approximately one third of the seasonal 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. However, the relative importance of processes driving enhanced oxygen consumption (e.g. more organic matter, decreased ventilation of bottom waters) are currently unknown. Finally, while the North Sea is fairly well sampled in time and space, the rest of the North-West European Shelf waters, especially the Celtic and Irish seas, are relatively poorly sampled and so offer only *low levels of confidence* in the occurrence or risk of oxygen depletion. However, 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. It is the magnitude and causes of the decline in dissolved oxygen that are still being unravelled.

## What could happen in the future?



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. On a regional scale appropriate for coastal and shelf seas, there is a general consensus that the ocean will lose oxygen but the magnitude of loss and attribution to causes remains uncertain due to 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.

## 5. 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 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, NERC DEFRA WWF AlterEco project and EU H2020 AtlantOS programme 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

- Aldridge, J. N., Lessin, G., Amoudry, L. O., Hicks, N., Hull, T., Klar, J. K. *et al.* (2017) Comparing benthic biogeochemistry at a sandy and a muddy site in the Celtic Sea using a model and observations. *Biogeochemistry*, **135**, 155, doi.org/10.1007/s10533-017-0367-0
- Baden, S.P., Pihl, L. and Rosenberg, R. (1990) Effects of oxygen depletion on the ecology, blood physiology and fishery of the Norway lobster *Nephrops norvegicus*. *Marine Ecology Progress Series*, **67**, 141–155.
- 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
- Bianchi, D., Dunne, J.P., Sarmiento, J. L. and Galbraith, E.D. (2012) Data-based estimates of suboxia, denitrification and N<sub>2</sub>O production in the ocean and their sensitivities to dissolved O<sub>2</sub>. *Global Biogeochemical Cycles*, **26**, GB2009.
- Bopp, L., Resplandy, L., Orr, J.C., Doney, S.C., Dunne, J.P., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Seferian, R., Tjiputra, J. and Vichi, M. (2013) Multiple stressors of ocean ecosystems in the 21<sup>st</sup> Century: projects with CMIP5 models. *Biogeosciences*, **10**, 6225–6245.
- 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.
- 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.
- Cavan, E.L., Trimmer, M., Shelley, F. and Sanders, R. (2017) Remineralisation of particulate organic carbon in an ocean oxygen minimum zone. *Nature Communications*, **8**, 14847.

- Chabot, D. and Claireaux, G. (2008) Environmental hypoxia as a metabolic constraint on fish: the case of Atlantic cod, *Gadus morhua*. *Marine Pollution Bulletin*, **57**(6–12), 287–295.
- 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* [Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V. and Midgley, P.M. (eds)]. Cambridge University Press, Cambridge, UK and New York, 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
- Claireaux, G., Webber, D.M., Lagardere, J.P. and Kerr, S.R. (2000) Influence of water temperature and oxygenation on the aerobic metabolic scope of Atlantic cod (*Gadus morhua*). *Journal of Sea Research*, **44**(3–4), 257–265.
- Claireaux, G. and Chabot, D. (2016) Responses by fishes to environmental hypoxia: integration through Fry’s concept of aerobic metabolic scope. *Journal of Fish Biology*, **88**, 232–251.
- 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.
- Defra (2010) *Charting progress 2: The State of UK Seas*. Published by the Department of Environment Food and Rural Affairs on behalf of the UK Marine Monitoring Assessment Strategy community.
- 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.
- Diaz, R.J. and Rosenberg, R. (2008) Spreading Dead Zones and Consequences for Marine Ecosystems. *Science*, **321**(5891), 926–929.
- EEA (European Environment Agency) (2015) *The European environment — state and outlook 2015: synthesis report*, European Environment Agency, Copenhagen. doi:10.2800/944899
- Eriksson, S.P. and Baden, S.P. (1997) Behaviour and tolerance to hypoxia in juvenile Norway lobster (*Nephrops norvegicus*) of different ages. *Marine Biology*, **128**(1), 49–54.
- Ferreira, J.G., Andersen, J.H., Borja, A., Bricker, S.B., Camp, J., da Silva, M.C. *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.
- Freing, A., Wallace, D.W.R and Bange, H.W. (2012) Global oceanic production of nitrous oxide. *Philosophical Transactions of the Royal Society in London Biological Sciences*, **367**(1593), 1245–1255.
- 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*, doi: 10.1007/s10533-010-9475-9
- 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.
- Große, F., Greenwood, N., Kreuz, 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., Kreuz, 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*, **4**, 383, doi:10.3389/fmars.2017.00383
- 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. and Stahl, H. (2017) Oxygen dynamics in shelf sea sediments incorporating seasonal variability. *Biogeochemistry*, **135**, 35–47.
- 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. *Progress in Oceanography*, **86**, 361–379.
- Hughes, S.L., Tinker, J. and Dye, S. (2017) Temperature. *MCCIP Science Review 2017*, 22-41, doi:10.14465/2017. arc10.003-tem

- IPCC Climate Change (2013) *The Physical Science Basis*. Cambridge University Press.
- Ito, T., Minobe, S., Lng, M.C. and Deutsch, C., (2017) Upper ocean O<sub>2</sub> trends: 1958-2015. *Geophysical Research Letters*, **44**(9), 4214–4223.
- Keeling, R.G. and Shertz, S.R. (1992) Seasonal and interannual variations in atmospheric oxygen and implications for the global carbon cycle. *Nature*, **358**, 723–27.
- Keeling, R.F., Kortzinger, A. and Gruber, N. (2010) Ocean Deoxygenation in a Warming World. *Annual Reviews in Marine Science*, **2**, 199–229.
- Keil, R.G., Neibauer, J., Biladeau, C., van der Elst, K and Devol, A.H.A (2016). A multiproxy approach to understanding the ‘enhanced’ flux of organic matter through the oxygen deficient waters of the Arabian Sea. *Biogeosciences*, **13**, 2077–2092.
- Keppel, G., Mokany, K., Wardell-Johnson, G. W., Phillips, B.L., Welbergen, J.A and Reside, A.E. (2015) The capacity of refugia for conservation planning under climate change. *Frontiers in Ecology and the Environment*. **13**(2), 106–112.
- Kitidis, V., Tait, K., Nunes, J., Brown, I., Woodward, E.M.S., Harris, C., Sabadel, A.J.M., Sivyer, D.B., Silburn, B and Kröger, S. (2017) Seasonal benthic nitrogen cycling in a temperate shelf sea: the Celtic Sea. *Biogeochemistry*, **135**(1–2), 103–119, <https://doi.org/10.1007/s10533-017-0311-3>
- 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.
- Long, W.C., Brylawski, B.J. and Seitz, R.D. (2008) Behavioral effects of low dissolved oxygen in the bivalve *Macoma balthica*. *Journal of Experimental Marine Biology and Ecology*, **359**(1), 34–39.
- Lowe, J.A., Howard, T.P., Pardaens, A., Tinker, J., Holt, J., Wakelin, S. *et al.* (2009) *UK Climate Projections science report: Marine and coastal projections*. Met Office Hadley Centre, Exeter, UK, p. 99.
- Ludsin, S.A., Zhang, X., Brandt, S.B., Roman, M. R., Boicourt, W. C., Mason, D. M. and Costantini, M. (2009) Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: Implications for food web interactions and fish recruitment. *Journal of Experimental Marine Biology and Ecology*, **381**(1), S121–S131.
- Madec, G. and the NEMO Team (2012) *Nemo Ocean Engine v3.4. Note du Pole de Modélisation*, Institute Pierre Simon Laplace, Paris, France, <http://www.nemo-ocean.eu/27>
- 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.
- 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<sub>4</sub> and N<sub>2</sub>O. *Biogeosciences*, **7**, 2159–2190, doi: 10.5194/bg-7-2159-2010
- Neubacher, E.C., Parker, R.W. and Trimmer, M. (2011) Short-term hypoxia alters the balance of the nitrogen cycling in costal sediments. *Limnology and Oceanography*, **56** (2), 651–665.
- Neubacher, E.C., Parker, R.E. and Trimmer, M., (2013). The potential effect of sustained hypoxia on nitrogen cycling in sediment from the southern North Sea: A mesocosm experiment. *Biogeochemistry*, **113**(1–3), 69–84.
- Niemeyer, D., Kemena, T.P., Meissner, K.J. and Oschlies, A., (2017) A model study on warming-induced phosphorus-oxygen feedbacks in open-ocean oxygen minimum zones on millennial timescales. *Earth System Dynamics*, **8**, 357–367.
- 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*, Dublin, Ireland, 195–209.
- 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. ISBN: 978-1-911458-34-0 Publication Number: 694/2017
- Painting, S., Foden, J., Forster, R., van der Molen, J., Aldridge, J., Best, 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. (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. and Knust, R. (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Sciences*, **5**, 315(5808), 96097.
- 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* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds)]. Cambridge University Press, Cambridge, UK and New York, 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., Williams and C.A.J., (2014). Impact of vertical mixing on sea surface pCO<sub>2</sub> in temperate seasonally stratified shelf seas. *Journal of Geophysical Research: Oceans*, **119**(6), 3868–3882, 10.1002/2014JC010089
- 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.
- Schmidtko, S., Stramma, L. and Visbeck, M. (2017) Decline in global oceanic oxygen content during the past five decades. *Nature*, **542**, 335–339.
- Scholz, F., McManus, J., Mix, A.C., Hensen, C., Schneider, R.R. (2014) The impact of ocean deoxygenation on iron release from continental margin sediments. *Nature Geosciences*, **7**, 433–437.
- 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. (2013) Impacts of climate change on shelf sea stratification. *Marine Climate Change Impacts Partnership: Science Review 2013*, 67–70.
- Shurmann, H. and Steffensen, J.F. (1992) Lethal oxygen levels at different temperatures and the preferred temperature during hypoxia of the Atlantic cod, *Gadus morhua*. *Journal of Fish Biology*, **41**, 927–934.
- Stierhoff, K.L., Targett, T.E. and Power, J.H. (2009) Hypoxia-induced growth limitation of juvenile fishes in an estuarine nursery. Assessment of small-scale temporal dynamics using RNA:DNA. *Canadian Journal of Fish Aquatic Sciences*, **66**, 1033–1047.
- Stramma, L., Schmidtko, S., Levin, L.A. and Johnson, C. (2010) Ocean oxygen minimum expansion and their biological impacts. *Deep-Sea Research part 1*, **57**, 587–595.
- 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.
- Townhill, B.L., Pinnegar, J.K., Righton, D.A. and Metcalfe, J.D. (2017b) Fisheries, low oxygen and climate change: how much do we really know. *Journal of Fish Biology*, **90**, 723–750.
- Urbina, M.A., Forster, M. E. and Glover, C. N. (2011) Leap of faith: voluntary emersion behaviour and physiological adaptations to aerial exposure in a non-aestivating freshwater fish in response to aquatic hypoxia. *Physiology Behaviour*, **103**, 240–247.
- 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
- Vaquero-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

- Watson, A.J., Lendon, T. M. and Mills, B.J.W. (2018) Ocean deoxygenation, the global phosphorus cycle, and the possibility of human-caused large-scale ocean anoxia. *Philosophical Transactions A: Mathematical, Physical and Engineering Sciences*, **375** (2102), 20160318.
- 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., Sivyver, 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
- 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.