Consequences of climate-induced low oxygen conditions for commercially important fish

Article *in* Marine Ecology Progress Series · September 2017

DOI: 10.3354/meps12291

Bryony Townhill
Centre for Environment, Fisheries and Aquaculture Science

Johan van der Molen
NIOZ Royal Netherlands Institute for Sea Research

Stephen D. Simpson
University of Bristol

Adrian Farcas
Centre for Environment, Fisheries and Aquaculture Science

Vol. 580: 191–204, 2017
https://doi.org/10.3354/meps12291

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 29

Consequences of climate-induced low oxygen conditions for commercially important fish

Bryony L. Townhill[1,2,*], Johan van der Molen[1,3], Julian D. Metcalfe[1], Stephen D. Simpson[2], Adrian Farcas[1], John K. Pinnegar[1,4]

[1]Centre for Environment, Fisheries and Aquaculture Science (Cefas), Lowestoft NR33 0HT, UK
[2]University of Exeter, Biosciences, College of Life and Environmental Sciences, Exeter EX4 4QD, UK
[3]NIOZ Royal Netherlands Institute for Sea Research, Dept. of Coastal Systems and Utrecht University, Den Burg, 1797 SZ, The Netherlands
[4]School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK

ABSTRACT: Oxygen availability is key in determining habitat suitability for marine fish. As a result of climate change, low oxygen conditions are predicted to occur more frequently and over a greater geographic extent. Studies assessing the long-term chronic effects and impacts for commercially important fish are rare. To assess the potential effects of climate-induced low oxygen on fisheries, physiological data, such as critical thresholds, derived from laboratory experiments on 5 commercial fish species were integrated with hindcast and future oxygen projections from the hydrodynamic-biogeochemical model GETM-ERSEM. By using this approach, changes in habitat suitability from the 1970s to 2100 were identified. In the North Sea, the current extent of areas with the lowest oxygen levels is smaller than during the 1970s, with improved oxygen conditions having less impact on species' critical thresholds. Oxygen levels are expected to decrease again in the coming century due to climate change, although not to the minima of previous decades. In affected areas and years, intermediate oxygen levels could have temporary impacts in late summer on swimming, growth, ingestion and metabolic scope of adult fish. These results demonstrate that although physical model oxygen projections help to provide insight, they are insufficient by themselves to predict the full potential impacts of climate change on fish distribution and fisheries. Such modelling requires underpinning through experimentation, particularly of the physiological effects of climate change on different life stages so that effects on reproduction, growth and commercial catches can be determined and tailored, and robust management measures put in place.

KEY WORDS: Aerobic scope · Climate change · Critical thresholds · Fisheries · Hypoxia · Metabolic rate · Metabolic scope · Normoxia

INTRODUCTION

Dissolved oxygen levels are decreasing in the world's oceans (Rabalais et al. 2010, Cocco et al. 2013, Levin & Breitburg 2015), driven in part by both climate variability and climate change (Gilbert et al. 2010, Levin & Breitburg 2015), alongside other anthropogenic effects. Oxygen availability is important in determining habitat suitability for marine fish (Heath et al. 2012, Gallo & Levin 2016), but has not been investigated as a climate change factor to the same extent as warming and ocean acidification. Much physiological research has focussed on the effects of acute severe hypoxia of model marine species such as Atlantic cod *Gadus morhua* and Greenland halibut *Reinhardtius hippoglossoides*

*Corresponding author: bryony.townhill@cefas.co.uk

(e.g. Claireaux et al. 2000, Mejri et al. 2012), but studies on long-term chronic impacts of moderately lowered oxygen levels on commercially important fish are comparatively rare (Townhill et al. 2017). To understand the implications of low oxygen conditions (defined here as any oxygen level below full saturation) for fisheries, a greater focus on commercially exploited species is necessary. Studies designed to predict the effects of climate change on marine fish that include oxygen as a variable are currently few in number (e.g. Cheung et al. 2013, 2015). The majority of studies thus far have omitted oxygen as a variable (e.g. Cheung et al. 2009, Jones et al. 2013, Rutterford et al. 2015), likely due to a lack of information and understanding of impacts to date. With the limited availability of detailed projections of oxygen conditions, it is difficult to explore whether and how commercial fish may be affected by future changes. Therefore, an understanding of how commercial fish respond to low oxygen conditions, and whether their physiology, behaviour and distributions are likely to be affected, is required.

Oxygen is essential for most physiological processes, and so fish in low oxygen conditions can experience effects on growth, activity, survival and reproduction (Pörtner & Knust 2007, Levin & Breitburg 2015). Organisms can experience synergistic effects of low oxygen and elevated temperatures, with increased temperature exacerbating the effects of low oxygen levels, and decreasing low oxygen tolerance in many species (Schurmann & Steffensen 1992, Pörtner & Knust 2007, Pörtner 2010, 2012). The reduced solubility of oxygen in warmer water reduces the availability of oxygen to aquatic species for respiration (Pörtner & Knust 2007). If oxygen levels fall below a minimum tolerance threshold, then an organism's oxygen-demanding functions can be impaired (Claireaux et al. 2000). These thresholds include respiratory physiology metrics of oxygen tolerances (e.g. metabolic rate, oxygen uptake, metabolic or aerobic scope), critical oxygen thresholds (P_{crit}) and behavioural or physiological responses. One such threshold is metabolic or aerobic scope (MS), which is the capacity of an organism to carry out activities above its basal level activities such as reproducing, feeding or swimming (Fry 1971), measured as the difference between standard and maximum metabolic rates. When oxygen levels fall below normoxia (fully saturated oxygen conditions), MS can be reduced. It is not clear how much time fish spend at their full MS, but different species use their MS in different ways; for example, an ambush predator may need to reduce digestion to recover from a burst of swimming, while a pelagic swimmer would require more oxygen to sustain swimming over longer periods (Clark et al. 2013). Another measure is the critical oxygen threshold, i.e. the oxygen level at which a fish can no longer maintain its standard metabolic rate (Nilsson et al. 2004). If a fish remains in water with oxygen below the critical oxygen threshold over time, it will eventually lose equilibrium and die.

The experimental environment will never fully represent real-world conditions. In many cases, the aim of experimental research is measurement of these values, but the studies are rarely followed by modelling approaches which explore what these changes may mean for fish populations. Here, to explore how fish may be affected by oxygen levels experienced in their natural environment, published metrics which describe the oxygen response of a species are integrated with modelled data on past and future oxygen conditions in the North Sea.

The North Sea has been identified as a hotspot for climate change (Hobday & Pecl 2014) and has been the focus of many studies into the effects of climate change (predominantly temperature and pH changes) on fish (e.g. Blanchard et al. 2005, Perry et al. 2005, Dulvy et al. 2008, Heath et al. 2012, Jones et al. 2013, Montero-Serra et al. 2015, Rutterford et al. 2015). The North Sea is an economically important region, and fish stocks have changed in recent decades owing to fishing and climatic influences (Engelhard et al. 2014). However, there are climate change-related stressors with the potential to significantly impact fish populations, such as low oxygen concentrations, which remain to be explored. These effects are often more subtle and may be less easy to demonstrate, and fewer oxygen data are available when compared with other climatic variables, such as temperature and salinity, making assessments difficult. For example, the Intergovernmental Panel on Climate Change Assessment Report 4 (Solomon et al. 2007) global climate models generally do not include dissolved oxygen as a variable, and more recent downscaled shelf sea climate projections do not always include data on dissolved oxygen (e.g. UK Climate Projections CP09, Jenkins et al. 2009).

The aim of the present study was to integrate newly available modelled North Sea oxygen hindcast and projection data with published data on the experimentally induced physiological effects of reduced oxygen, to identify which commercial fish species may be affected by recent changes in oxygen conditions in the North Sea, and to explore the potential effects that future changes may have.

MATERIALS AND METHODS

Compilation of published oxygen metrics

Oxygen metrics for commercial North Sea fish species were collated from published studies. If figures were presented showing oxygen metrics but exact values were not available in the publication, the values were extracted using freely available Engauge software (http://markummitchell.github.io/engauge-digitizer/). The resulting dataset contained 36 studies that provided metrics describing the effects of oxygen on commercially important North Sea fish species. All units were converted to mmol m^{-3} using the Loligo System conversion tool (www.loligosystems.com/convert-oxygen-units?menu=77). Conversion depends on water temperature and salinity, and so only data including values for these were used.

The 36 relevant studies resulted in 84 metrics that describe how fish at current or projected future North Sea temperature and salinity conditions may be affected by changes in oxygen concentrations (i.e. those carried out in warmer or more saline conditions were excluded). The 84 metrics were narrowed down by excluding those that could not be compared across oxygen conditions, for example metabolic rates calculated at different temperatures but only under 100% oxygen conditions. The remaining 16 oxygen metrics, representing 5 species (lesser sandeel *Ammodytes tobianus*, Atlantic cod, common sole *Solea solea*, European sea bass *Dicentrarchus labrax* and turbot *Scophthalmus maximus*; Table 1), were then viewed as dissolved oxygen values with which to compare the modelled oxygen outputs, to assess how past oxygen levels in the North Sea may have affected commercial fish, and from that assessment to project how much these species may be affected in the future.

Oxygen hindcast

Gridded oxygen hindcast data were used to represent the oxygen levels between 1970 and 2008. To determine the changes in oxygen levels in the North Sea over this period, the 3-dimensional, hydrodynamic-biogeochemical General Estuarine Transport Model-European Regional Seas Ecosystem Model (GETM-ERSEM) was applied to the North Sea (methods described by Lenhart et al. 2010, Tett et al. 2013, van Leeuwen et al. 2013, 2015, van der Molen et al. 2014). The freely available GETM (https://ec.europa.eu/jrc/en/publication/eur-scientific-and-technical-research-reports/getm-general-estuarine-transport-model; details in Burchard & Bolding 2002, Stips et al. 2004) was used to simulate the hydrodynamics of the North Sea. The 3D GETM model includes sea surface elevations, drying, flooding, temperature, salinity and currents. GETM was coupled with the ERSEM (www.meece.eu/library/ersem.html), which captures the chemical and biological cycles in the North Sea (Baretta et al. 1995). GETM-ERSEM was forced with 6-hourly meteorological data from ECMWF ERA 40 (www.ecmwf.int). The model simulated daily conditions in the North Sea from 1958 to 2008, with a spatial resolution of 6 nautical miles and 26 vertical general coordinate layers. For this study, modelled results for August and September (the months when oxygen is lowest) were used to generate decadal means for the seabed and sea surface temperatures and oxygen minima for the 1970s, 1980s, 1990s and 2000s (2000 to 2008). Model simulations have been previously validated with field observations from oceanographic cruises (van Leeuwen et al. 2013), and the mean, minimum and standard deviation of August oxygen concentrations for each decade are shown in Fig. 1.

Oxygen projections

Future gridded model projections for oxygen are not currently available for the North Sea, and so instead point data for 3 locations were used as published by van der Molen et al. (2013; Fig. 2). Three sites with distinct physical characteristics were chosen as the foci of our study within the North Sea (Oyster Grounds, North Dogger Bank and Southern Bight; Fig. 2), which each represent larger areas with similar seabed and water column conditions (van der Molen et al. 2013). The Oyster Grounds have a water depth of 45 m, a muddy-sand sediment with a shallow oxic layer (~1 cm), sparse fauna and seasonal stratification. The North Dogger Bank is a deeper area (~80 m) with seasonal stratification, and has a muddy-sand seabed and a very shallow oxic layer (<1 cm). Bioturbation by macrofaunal organisms is significant and controls the oxic layer depth. The Southern Bight is a shallow (<30 m), vertically mixed area, with mobile, sandy seabed which leads to a deeper oxic layer (~2–6 cm) and deeper nutrient generation than the other sites.

The coupled hydrodynamic-biogeochemical water column model GOTM-ERSEM-BFM (Biogeochemical Flux Model) was used to generate daily oxygen projection data for the 3 sites, forced by climate data from the HadRM3-PPE-UK (Met Office Hadley Centre 2012) regional climate model for 1950–2100,

Table 1. Oxygen metrics chosen for use in the analyses and the total area covered by minimum August near-bed oxygen levels below selected oxygen metrics for 5 commercial fish species. Total modelled area is 590 000 km^2. Metrics for which there was an increase in area across the decades are shown in *italics*. All metrics are for adult fish. P_{crit}: critical oxygen threshold, MS: metabolic scope, MMR: maximum metabolic rate

Metric description	Oxygen concentration (mmol m^{-3})	Total km^2 (percentage of area where oxygen is below each metric) 1970s	1980s	1990s	2000s	Reference
Lesser sandeel						
P_{crit} at 10°C	57.4	19000 (3.2)	13500 (2.3)	11600 (2.0)	8000 (1.4)	Behrens & Steffensen (2007)
Swimming reduced by 95 %	43.4	14400 (2.4)	8900 (1.5)	8400 (1.4)	5100 (0.9)	Behrens & Steffensen (2007)
Atlantic cod						
P_{crit} at 15°C	56.9	18900 (3.2)	13400 (2.2)	11600 (2.0)	7800 (1.3)	Claireaux et al. (2000)
P_{crit} at 10°C	57.3	18900 (3.2)	13500 (2.3)	11600 (2.0)	7900 (1.3)	Claireaux et al. (2000)
MS is 0 mg O_2 h^{-1} kg^{-1}	64	20900 (3.5)	15500 (2.6)	13100 (2.2)	9200 (1.6)	Claireaux et al. (2000), Chabot & Claireaux (2008
MS is lowered (32.5 mg O_2 h^{-1} kg^{-1}) at 30 % oxygen at 10°C	85	28400 (4.8)	23700 (4.0)	19900 (3.4)	13200 (2.2))	Claireaux et al. (2000), Chabot & Claireaux (2008)
MS is lowered (75 mg O_2 h^{-1} kg^{-1}) at 50 % oxygen at 10°C	142	85700 (14.5)	72300 (12.2)	63900 (10.8)	48500 (8.2)	Claireaux et al. (2000), Chabot & Claireaux (2008)
Activity constrained	159	110900 (18.8)	100200 (17.0)	103100 (17.5)	86300 (14.6)	Claireaux et al. (2000), Chabot & Claireaux (2008)
Growth and ingestion reduced	*199*	*249400 (42.3)*	*241100 (40.9)*	*273500 (46.4)*	*280400 (47.5)*	Chabot & Claireaux (2008)
MS at maximum (109 mg O2 h−1 kg−1) at 10°C	*284*	*577000 (97.8)*	*576400 (97.7)*	*579200 (98.2)*	*581500 (98.6)*	Claireaux et al. (2000), Chabot & Claireaux (2008)
Common sole						
P_{crit} at 16°C	67	21800 (3.7)	16700 (2.8)	13700 (2.3)	9600 (1.6)	Lefrançois & Claireaux (2003)
P_{crit} at 12°C	71	23200 (3.9)	18200 (2.8)	14900 (2.3)	10100 (1.6)	Lefrançois & Claireaux (2003)
Significant decrease in MMR at 16°C	*188*	*194500 (33.0)*	*186800 (31.7)*	*233500 (39.6)*	*224000 (38.0)*	Lefrançois & Claireaux (2003)
European sea bass						
P_{crit} at 15°C	69	22700 (3.8)	17400 (2.9)	14200 (2.4)	9900 (1.7)	Claireaux & Lagardère (1999)
P_{crit} at 10°C	70	22900 (3.9)	17900 (3.0)	14500 (2.5)	10000 (1.7)	Claireaux & Lagardère (1999)
Turbot						
Reduced maximal oxygen uptake	131	69600 (11.8)	55700 (9.4)	47400 (8.0)	35100 (5.9)	Mallekh & Lagardère (2002)

using the medium (SRESA 1B) emissions scenario, as described by van der Molen et al. (2013). It was confirmed (demonstrating agreement between model predictions and observations) using hindcasts forced with the meteorological hindcast forcing from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA-40 and Operational Analysis Hindcasts (http://artefacts.ceda.ac.uk/badc_datadocs/ecmwf-op/ecmwf-op.html). The bias was −5.1 % for Southern Bight, −13.0 % for Oyster Grounds and −21.9 % for the North Dogger for near-bed oxygen. The modelled values used here are therefore conservative, as they underestimate the recorded values. Projections were carried out for the Oyster Grounds (54.414° N, 4.039° E), the Southern Bight (53.167° N, 2.804° E) and the North Dogger Bank (55.671° N, 2.298° E) (see Fig. 2). The Oyster Grounds and North Dogger Bank were simulated using 40 vertical layers, and the Southern Bight using 30 layers. The modelled oxygen concentrations for the Oyster Grounds near the bed (the lowest of the 40 vertical layers) were validated against measurements from 2000–2008 of the Dutch national monitoring programme (Monitoring Waterstaatkundige Toestand des Lands; MWTL) and Cefas SmartBuoy measurements at Terschelling 135. The oxygen modelling data used in this study are available from the Cefas Data Hub at https://www.cefas.co.uk/cefas-data-hub/.

Areas affected by oxygen changes in the past

A gap analysis was carried out to determine the area of North Sea that had oxygen levels below the selected metrics for each spe-

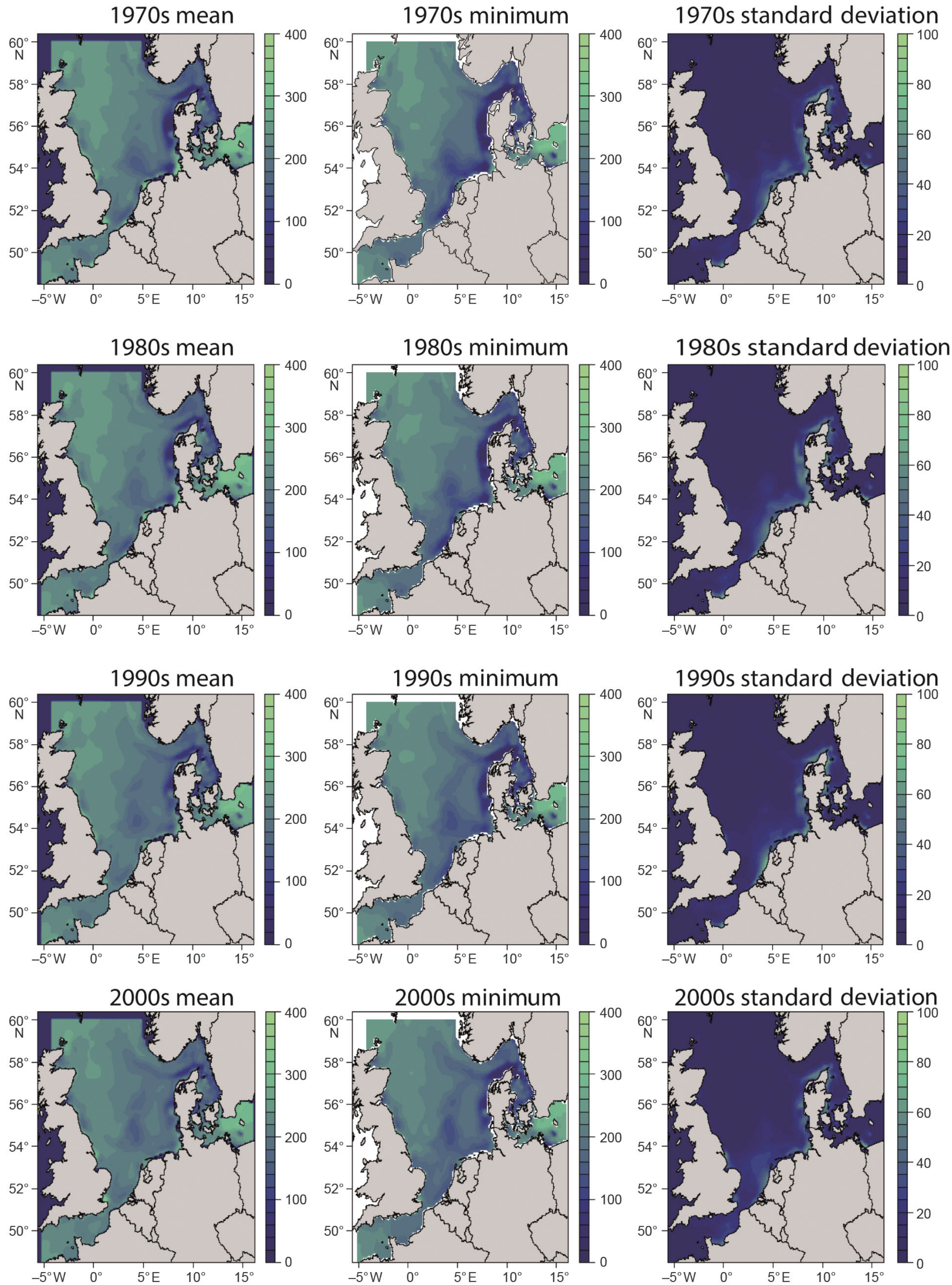

Fig. 1. Mean, minimum and standard deviation of August oxygen concentrations (mmol m^{-3}) for each decade. The minima are lowest on the eastern side of the North Sea around Denmark, and this is also the area of the highest standard deviation

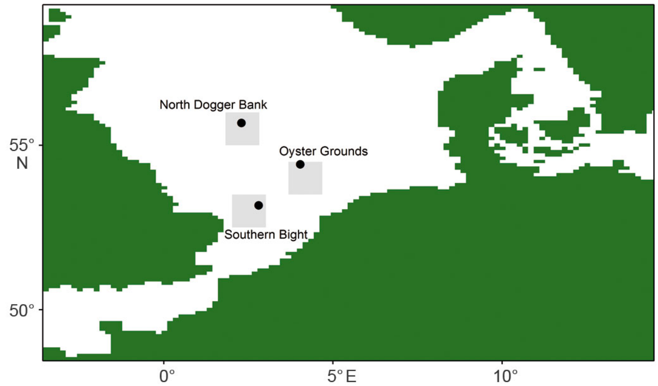

Fig. 2. Southern North Sea, showing the Oyster Grounds, North Dogger Bank and Southern Bight study areas. Grey boxes show the bounding areas for the hindcast analysis. Black dots show the point locations for future projections. Outlines of the landmass show the resolution of the model

cies. The number of modelled grid squares with oxygen minima below a given metric was calculated for each decade. Each grid square is approximately 10 km × 10 km in size, and so this calculated number of grid squares was multiplied by 100 to determine the total area in square kilometres with oxygen levels below each oxygen metric. This was done for the minimum oxygen levels for the seabed and sea surface in both August and September for each decade. In each decade, the areas below the metrics were highest at the seabed in August. Therefore, only the oxygen levels for the seabed in August are considered from here on. The modelled oxygen concentrations and areas with concentrations below a given metric were plotted using ArcMap 10.1 (ESRI 2011).

The oxygen levels in the Oyster Grounds, the Southern Bight and the North Dogger Bank were investigated in more detail to provide a comparison with the locations for which future projections are available. For the seabed in August, the areas with oxygen levels below each metric were calculated using the same analysis as above. A 1° × 1° (10 × 6 model grid cell) bounding area was used for each area (Fig. 2): Oyster Grounds: 53.5–54.5° N, 3.69–4.69° E; Southern Bight: 52.5–53.5° N, 2.02–3.02° E; North Dogger Bank: 55.0–56.0° N, 1.65–2.65° E. The areas with oxygen concentrations below the metrics for these locations were also plotted using ArcMap 10.1 (ESRI 2011).

Changes in the duration of low oxygen events in the future

Since spatial data were not available for future oxygen projections, the time that oxygen levels were below each metric was analysed at each point location. The same overlay analysis method was used to determine the percentage of days in which each of the 3 locations experienced oxygen levels below each metric in each year.

RESULTS

Oxygen metrics

The literature search yielded 16 response metrics for current or projected North Sea temperatures that were suitable for comparisons in this study (i.e. many were based on Mediterranean conditions that were not representative of the North Sea; Table 1). The metrics covered a wide range of oxygen concentrations. The lowest concentration (43.4 mmol m^{-3}) resulted in a 95% reduction in swimming speed of lesser sandeel. The highest oxygen level (284 mmol m^{-3}) was that which gave the MS of cod when measured at 100% oxygen saturation (i.e. the maximum MS). Below this concentration, the MS for cod would be reduced with a reduction in activity expected. This is the upper level used in this study, and it was assumed that no species would be adversely affected by dissolved oxygen concentrations above this level.

Past oxygen conditions

Modelled hindcast outputs show that since the 1970s, oxygen conditions in the North Sea have generally improved, as shown by a decrease in the areas affected by the lowest response metrics for cod from the 1970s to the 2000s (Fig. 3). In the 1970s, some areas around Denmark had very low oxygen conditions, whereas in the 2000s, minimum concentrations never reached these levels. When response metrics and model outputs of oxygen conditions are overlaid, the area likely to be affected by the lowest oxygen levels decreased over the decades (see Table 1). However, threshold responses at the higher oxygen concentrations (such as growth and ingestion in cod, and decrease in maximum metabolic rate [MMR] in common sole), increased from the 1970s to the 2000s, covering almost half of the model extent in August in the 2000s (see Fig. 3 for Atlantic cod thresholds). In the 2000s, near-bed oxygen concentrations in 99% of the area would somewhat restrict the MS of cod (i.e. they were below cod MS when oxygen concentrations are at 100%; Table 1). For the lesser sandeel, areas that could affect their P_{crit} and swimming decreased

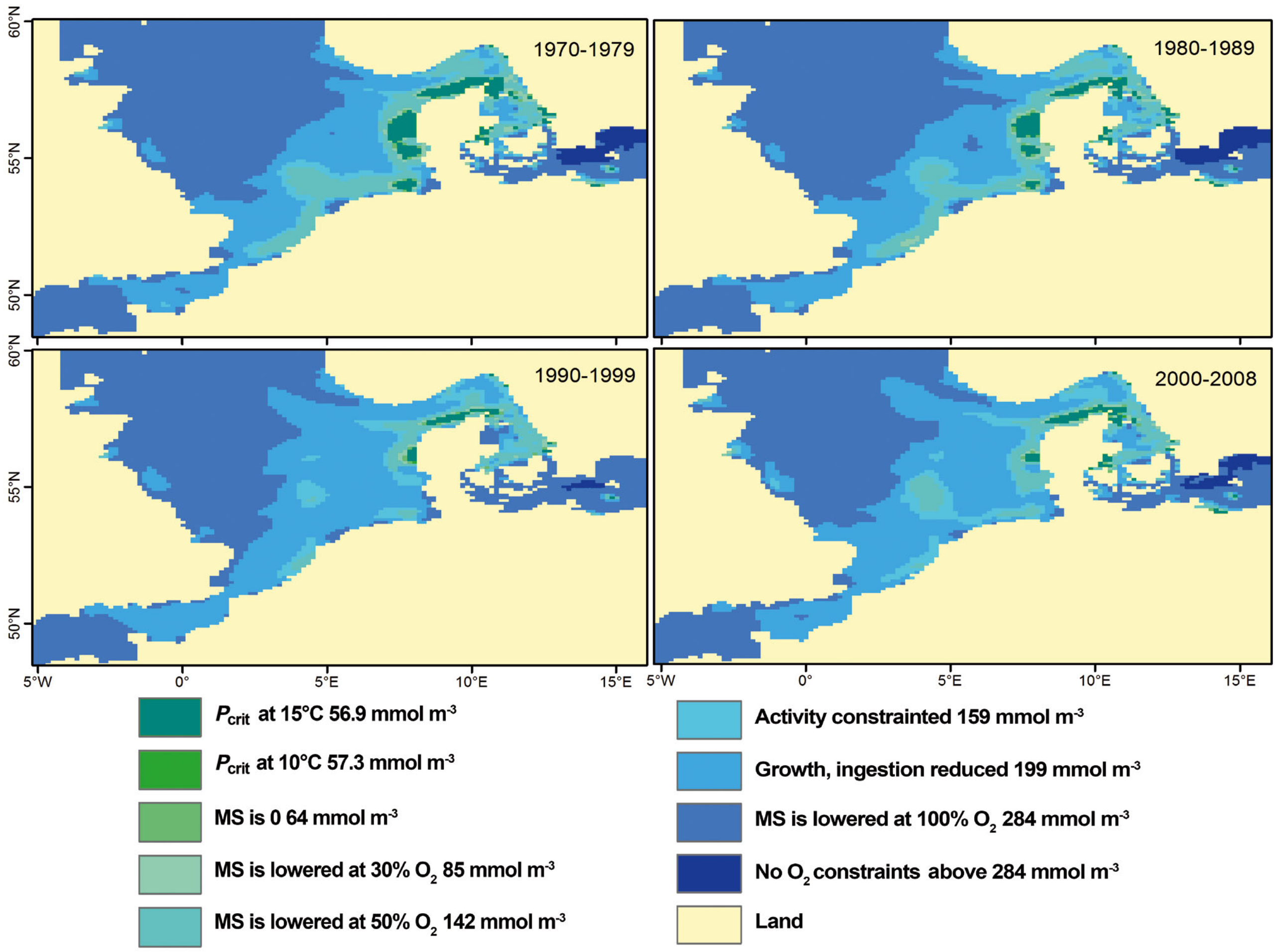

Fig. 3. For Atlantic cod *Gadus morhua*, the areas where minimum August near-bed oxygen levels are below each metric, averaged over each of the 4 decades. The metric description and oxygen concentrations are shown. The areas affected by the lowest metrics are around the east of the North Sea and around Denmark, with effects further north only seen at the higher metrics. P_{crit}: critical oxygen threshold, MS: metabolic scope

from the 1970s to the 2000s. Areas with oxygen levels below those affecting European sea bass and turbot also decreased.

There were differences between the 3 separate regions (Southern Bight, Oyster Grounds and North Dogger Bank) in the areas likely affected by low oxygen conditions (Fig. 4). The North Dogger Bank had the highest oxygen levels throughout the 4 decades, with oxygen levels lower than the highest metric of cod MS measured at 100% oxygen, but not sufficiently low to significantly affect cod growth and ingestion. In the Southern Bight, the oxygen levels were slightly lower, with some of the region having levels below 188 mmol m^{-3}, which could affect sole MMR. In the Oyster Grounds, levels were as low as 131 mmol m^{-3}, which would also affect turbot maximal oxygen uptake, but the area of lowest oxygen levels decreased from the 1970s to the 2000s.

Future oxygen conditions

The model projected that future near-bed oxygen levels for August will gradually decrease over the coming century in all 3 areas. Substantial interannual variation is projected at all sites (Fig. 5). The validation against measured bottom oxygen concentrations from 2000–2008 showed that the model matched well with known data (from Cefas Smart Buoy and the Dutch national monitoring programme MWTL), with a root mean square difference of 1.162, correlation of 0.775 and bias of −0.712 (Fig. 6).

The percentage of days during the year when near-bed oxygen was below each response metric was calculated for each decade and for each of the 3 locations (Fig. 7). Oxygen levels in the Southern Bight are not predicted to go below the lowest metrics of the focal species. In the Southern Bight, cod growth and ingestion would be reduced for an average of 3

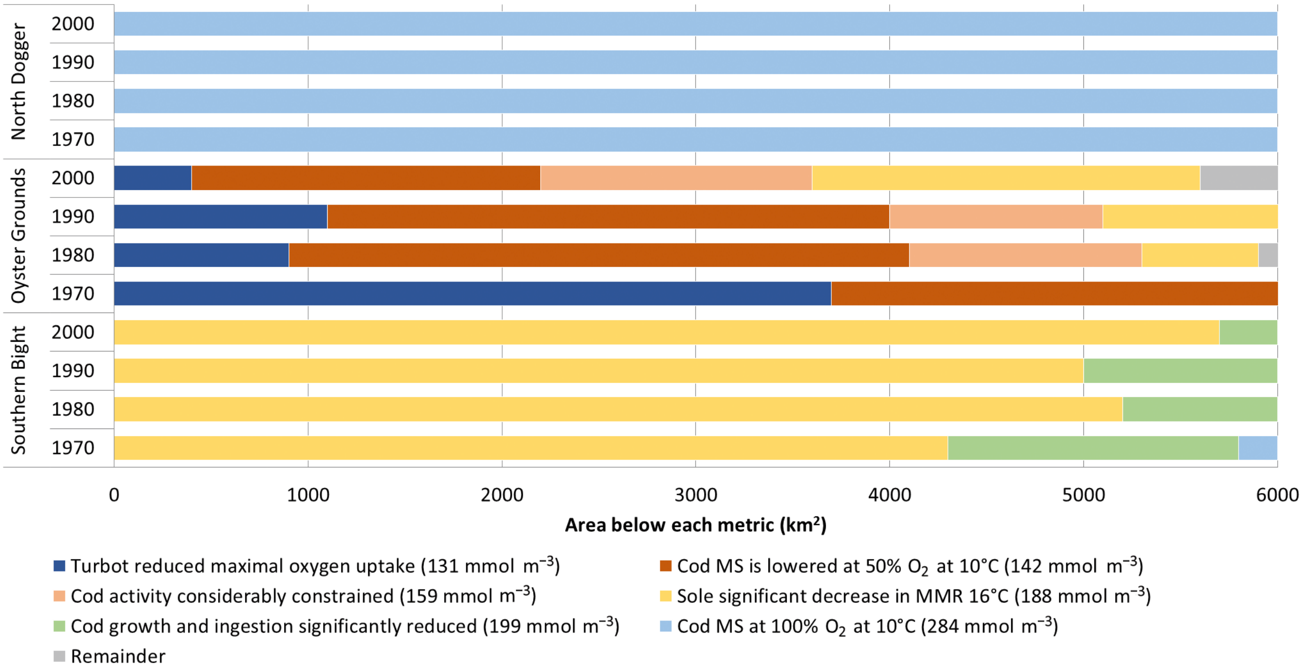

Fig. 4. Areas over which the August minimum near-bed monthly oxygen level is below each of the metrics in the North Dogger Bank, Oyster Grounds and Southern Bight areas (grey boxes in Fig. 2). No metrics other than those shown would be affected based on the oxygen levels for these regions. MS: metabolic scope, MMR: maximum metabolic rate

(0.8 %) d yr^{-1} in the 2010s, increasing to an average of 61 (16.7 %) d yr^{-1} in the 2090s, when sole would also experience decreased MMR on 3 (0.7 %) d yr^{-1}. In the Oyster Grounds, predicted effects are more frequent, with cod growth and ingestion being affected for 72 (19.7 %) d and sole MMR being affected for 32 (8.8 %) d yr^{-1} in the 2010s, increasing to 77 (21.1 %) d and 47 (12.9 %) d yr^{-1}, respectively, in the 2090s. Conditions where cod activity could be constrained in the Oyster Grounds increased from 0.3 (0.08 %) d in the 2010s to 4 (1.1 %) d in the 2090s. The North Dogger Bank had the lowest predicted oxygen concentrations. Most decades are projected to experience oxygen levels sufficiently low for cod growth and ingestion to be affected on at least 30 % of days each year. In the 2060s, oxygen conditions would reduce cod MS for 12 (3.4 %) d yr^{-1}, and turbot would have a reduced maximal oxygen uptake on 4 (1.2 %) d yr^{-1}. The oxygen concentrations did not decrease to levels affecting European sea bass or lesser sandeel at any of the sites, based on the metrics available.

DISCUSSION

The modelled oxygen hindcasts show improving oxygen conditions since the 1970s, particularly around the Danish coast. Total areas affected by most of the oxygen metrics decreased from the 1970s to the 2000s, with levels at the lowest thresholds such as the critical oxygen threshold greatly reduced. The improving situation may be due to reduced nutrient input to the North Sea since the late 1980s (van Leeuwen et al. 2013), since the main driver of year-to-year variations in oxygen in the North Sea is primary production (Große et al. 2016). Große et al. (2016) noted a 50 % reduction in nutrient loads to the North Sea from rivers in recent decades, albeit with oxygen deficiency still being high. They determined that along with stratification period, and volume below the stratified layer, the changes to supply and degradation of organic matter to the bottom waters each year are key to determining the reduction in oxygen. A decrease in nutrients to the North Sea in recent decades could have resulted in lower numbers of phytoplankton and a subsequent decrease of organic input below the thermocline. Topcu & Brockmann (2015) reported improved oxygen saturation in 1990–2004 when compared to the 1980s due to reduced nitrogen deposition, although they placed emphasis on a weak correlation between oxygen and nutrient inputs. Their analysis of a time series of oxygen measurements in the North Sea from 1980 to 2010 showed a particularly low oxygen concentration measured in 1983 in the southern North Sea and frequently low annual minimum oxygen concentrations

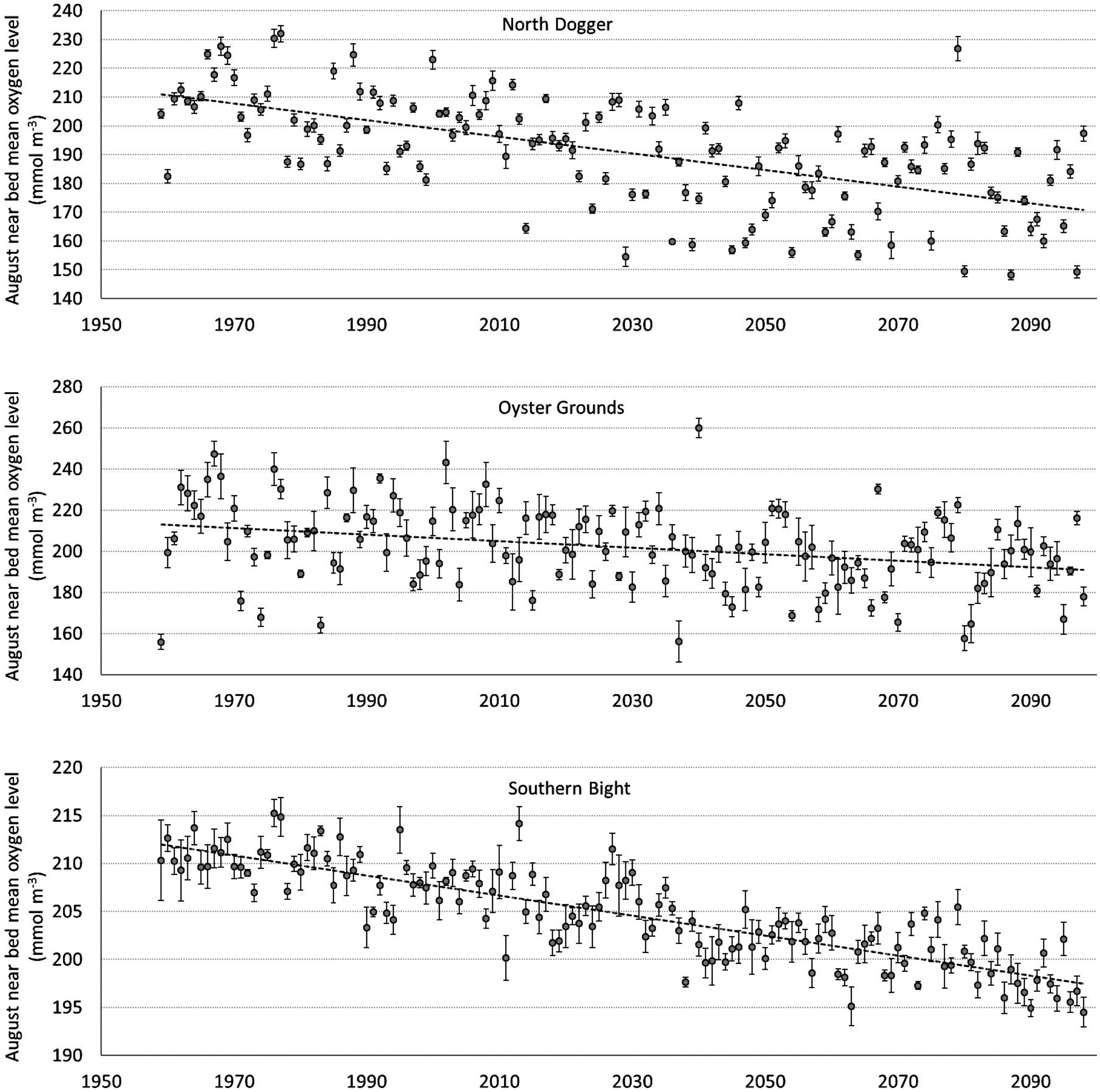

Fig. 5. Projections of August near-bed mean oxygen concentrations for the 3 study locations (black dots in Fig. 2), showing standard deviation with linear trend lines. All sites show a decreasing trend overall to the end of the century, with the Southern Bight levels not projected to get as low as the other sites

in the southern North Sea in the 1980s and 1990s when compared to the 2000s. An increase in oxygen concentrations in the southern North Sea was seen from 2003 to 2010. A different analysis of North Sea observations from 1900 showed that oxygen saturation had decreased in the central and eastern North Sea after 1990, but had increased in areas of the southern North Sea, the English Channel, the German Bight and in UK coastal waters (Queste et al. 2013), which is broadly consistent with the modelled findings here. The increased oxygen levels in the North Sea reported here suggest positive implications for commercial fish, particularly because oxygen concentrations for August were used, which correspond to the seasonal minimum and therefore the worst-case scenario. The areas affected by the 3 highest metrics (reduced growth and ingestion in cod, MS measured at 100% oxygen and decrease in MMR in common sole) increased from the 1970s to the 2000s by between 1 and 5%. This means that adult fish will have been able to maintain their metabolic rates above standard metabolic rate, yet activi-

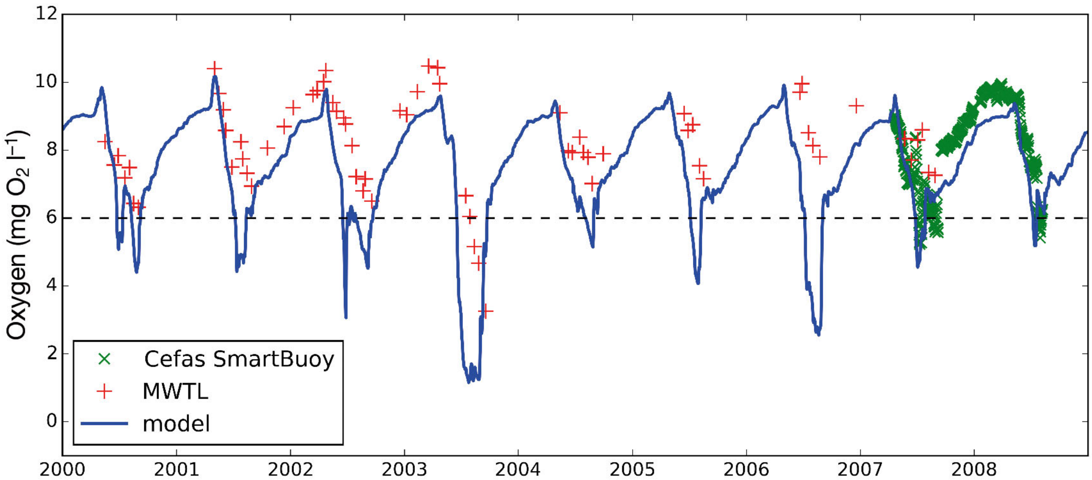

Fig. 6. Model results of the oxygen concentrations in the bottom layer of the Dutch station Terschelling 135 on the Oyster Grounds in the period 2000–2008 (blue line) together with Dutch national monitoring programme (MWTL) and SmartBuoy data. The dashed black line is the assessment level for oxygen concentration of 6 mg l^{-1}

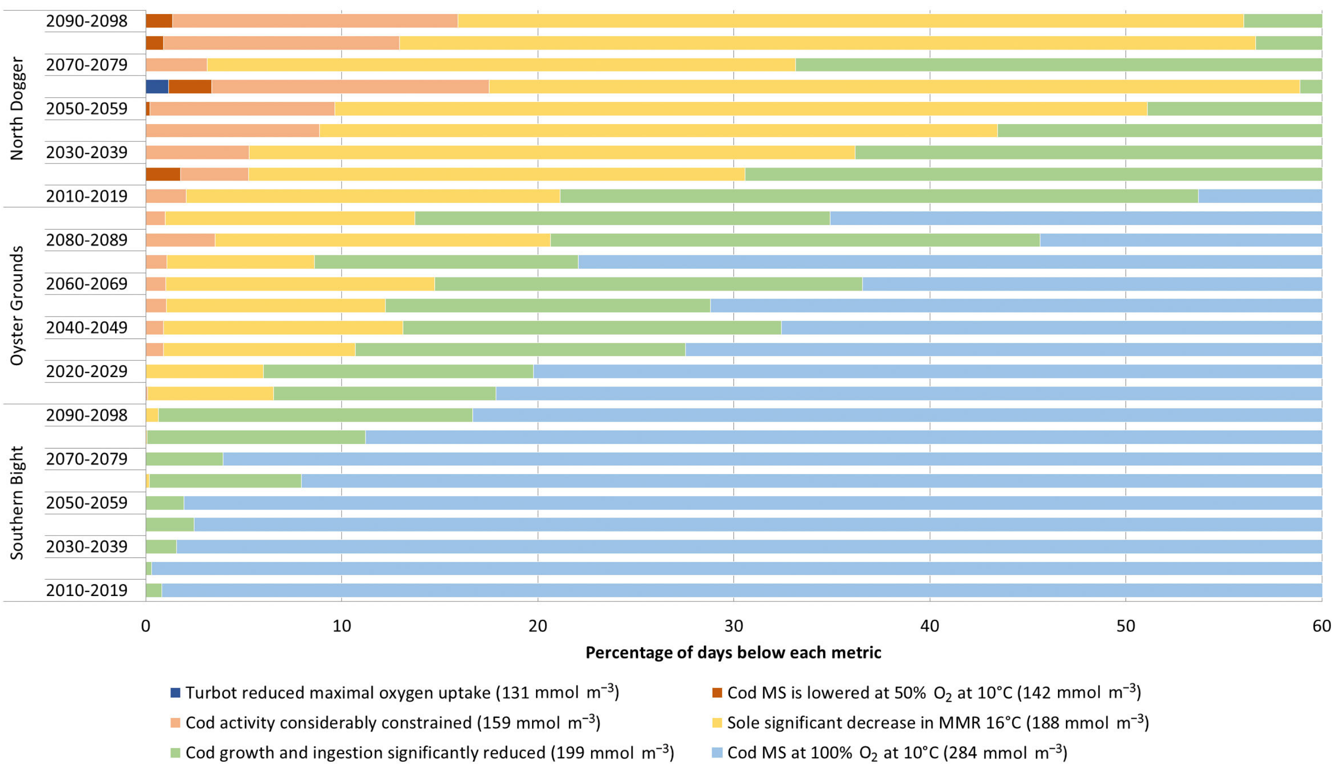

Fig. 7. Percentage of days in each decade when seabed oxygen levels are predicted to be below each response metric for the point locations (black dots in Fig. 2) on North Dogger Bank, on Oyster Grounds and in the Southern Bight. The North Dogger Bank is affected more by the lower metrics than other sites, with the Southern Bight least affected. MS: metabolic scope, MMR: maximum metabolic rate

ties fuelled by aerobic energy production, such as burst swimming, may have been constrained on days when oxygen was low. Climate projections in the North Sea show a greater reduction in oxygen compared to other parts of the world, such as the Pacific and Indian Oceans (Frölicher et al. 2009), although Matear & Hirst (2003) cited a large reduction in deep-water oxygen at the end of the 21st century.

By integrating published responses to reduced oxygen concentrations with modelled oxygen conditions, we found that in the past, oxygen conditions were likely sufficiently low to have had an impact on the activities of some fish. Since the 1970s (and indeed before then), fishing pressure on North Sea fish has been intense (Engelhard 2009), which likely over-shadowed any effect of oxygen levels on fish populations and makes it difficult to demonstrate population level effects of low oxygen concentrations. High-resolution temperature data allowed Rutterford et al. (2015) to show how fish distributions in the North Sea may change in the future. With detailed oxygen projections, similar work could be carried out to study oxygen and fish distribution changes, and interactions with fishing. Even so, certain behaviours are unlikely to be detected in abundance data, such as altered swimming speeds in Atlantic cod (Claireaux et al. 1995) or behaviour of cod in the Baltic Sea which are thought to dive into deeper, low oxygen water to catch prey, but return to higher oxygen levels to digest the food (Hinrichsen et al. 2011). Some of these behaviours may have knock-on effects such as increasing their vulnerability to predators or reducing feeding (Petersen & Pihl 1995, Killen et al. 2012), which is very difficult to quantify in the wild.

Integrating published responses with oxygen forecasts for future decades suggests moderate effects on the physiology of several fish species from oxygen limitation, but the potential impacts on catches of these species remain unknown. The areas affected are relatively small, and changes in oxygen conditions are projected to be relatively mild compared with previous decades. Cod, turbot and sole are all demersal fish and so would be affected by low oxygen in bottom waters, but may be able to move higher in the water column or into neighbouring areas, escaping to waters closer to normoxia as seen in other species such as New Zealand snapper *Chrysophrys auratus* and blue marlin *Makaira nigricans* (Chapman & McKenzie 2009, Neuenfeldt et al. 2009, Cook & Herbert 2012) and in cod in the Baltic Sea (Hinrichsen et al. 2011). Sea bass spend more time higher in the water column, and so are less likely to be affected than demersal fish. None of the fish for which indices were available spawned during August (Ellis et al. 2012). For summer spawners such as herring *Clupea harengus* and mackerel *Scomber scombrus*, the reduced oxygen conditions could pose a problem if they were to spawn in these areas. In addition, spawning fish and early life stages have different oxygen requirements because of the differences in metabolic rates and oxygen demand of gonads, growth and development (Pörtner & Farrell 2008). These fish may experience more constraints than those included here. A study of lesser sandeel in Danish waters (Behrens et al. 2009) compared sediment oxygen concentrations with the P_{crit} of the fish, and found that under a 4°C temperature increase scenario, oxygen deficiency in some enclosed areas would increase from 23% (present day) to 40%. As with the present study, these findings indicate that a greater impact will be felt in certain areas than others, depending on the circulation and substrate conditions, particularly for species which rely on the sediment, such as sandeel.

The projections to the end of the century indicate that oxygen concentrations will be lower in certain areas for longer periods of time (as much as half the year in the case of the North Dogger Bank in the 2080s), and so may pose more problems if fish are unable to move away from these areas. In the North Dogger Bank, cod and sole may have their activities constrained for several weeks each year toward the end of the century. If these results are representative of similar areas of the North Sea that are deep and seasonally stratified, seasonal range shifts out of these areas could occur in the future. However, most of the North Sea experiences oxygen conditions that are more similar to conditions on the Oyster Grounds and in the Southern Bight and so would only be affected for a small number of days each year. For species that do not spawn during the summer months, low oxygen levels may not have an effect on overall population sizes, but it could cause changes in distributions under warm, stratified conditions. The results here indicate that low oxygen conditions will become more prevalent through the century. If this change is gradual, fish may be able to adapt or become tolerant to these conditions, as already observed in some populations of fish (e.g. Zhu et al. 2013). Future changes in sea temperature caused by climate change are thought to be likely to alter fish distributions with respect to latitude and depth (Simpson et al. 2013, Rutterford et al. 2015), if fish are able to adapt or move. It may be that changes in oxygen will also cause similar effects, with fish staying in cooler waters which have higher oxygen solubility (Schurmann & Steffensen 1992, Claireaux et al. 1995). A study of mooring data in the North Sea has shown that on the Oyster Grounds, oxygen concentration in the bottom water is heavily influenced by storms, inputs of particulate and organic matter, and other short-term events (Greenwood et al. 2010). On the North Dogger Bank, oxygen concentrations were more strongly influenced by gradual changes in temperature and organic input. More detailed observations such as used by Greenwood et al. (2010) would enable more accurate forecasts and projections of oxygen conditions, and therefore more detailed understanding of how oxygen affects fish distributions, biology and behaviour.

While it would be valuable to capture the interplay between temperature and oxygen in determining responses of fish, this current methodology does not include temperature, salinity or pH due to a lack of physiological metrics covering all of these environmental parameters. The metrics chosen were those that were tested at temperatures found in the North Sea, but it is probable that these temperatures differ from those in the model on any day and at any depth. If oxygen metrics were available that covered a range of both oxygen concentrations and temperatures, the method of integrating published responses with hindcast/forecast data could be made more robust to the thermal limitations and oxygen responses of fish. A good example is a study on MS of flathead grey mullet *Mugil cephalus* in the Mediterranean at a range of temperatures and oxygen concentrations (Cucco et al. 2012), where experimental results were used to model the effect of changes in these and other parameters, to show how the fish and their catches may be affected at different times of year.

Oxygen values used in our analyses are based on model outputs rather than observational data and should not be treated as absolute. There are differences between the hindcast over the 3 areas, and the future projections of the 3 point locations that can be seen in Figs. 4–6, as there is not a smooth progression of modelled oxygen concentrations from the 1970s to the 2090s. The conditions across each area will not be exactly the same as for the point locations, leading to the differences in the mean and minimum oxygen concentrations, and the changes between decades. Modelled oxygen concentrations at specific locations on the Oyster Grounds underestimated measured concentrations, suggesting that the areas and percentage of days when fish may be affected by low oxygen values are likely to be overestimated. Likewise, the experimental oxygen metrics relate to how captive adult fish perform under experimental conditions at certain temperatures and feeding regimes, and not necessarily to how they would respond in the wild. The small number of published oxygen metrics which were suitable for use in this study shows how few experiments have been carried out which consider the effects of oxygen changes on commercial species. However, the integrated results produced here can be used to understand trends in oxygen availability and the general pressures on fish species.

This study demonstrates that simple techniques can be used to understand how animals might be affected by their environment, both in the past and in the future. It has been demonstrated that oxygen conditions have improved to a degree over recent decades, and therefore that fish in the North Sea are experiencing fewer restrictions from oxygen limitations to their activities overall. In the future, these restrictions may increase, but future projections indicate that they will not decrease to the low levels observed in the 1970s and 1980s. This is positive news for commercial fish which experience pressure from fishing as well as from changing environmental conditions, and for the fisheries they support. In time, further development of climate models to predict dissolved oxygen levels at high spatial resolution will give valuable information on the conditions likely to be experienced by animals in the wild. Likewise, more detailed experimental or field studies, performed at a range of temperatures, salinities, pH levels and oxygen conditions, would allow us to make more accurate projections of where and by how much species may be constrained in the future, but also investigate how oxygen has affected fish in the past. Future projections will enable managers and policy-makers to better understand the pressures experienced by certain commercial species, and therefore put suitable, informed and robust measures in place to protect stocks into the future. Management measures which increase the resilience of stocks to environmental changes, including oxygen changes, are necessary if stocks and associated fisheries are to persist in the coming century.

Acknowledgements. This work was supported by the Centre for Environment, Fisheries & Aquaculture Science (Cefas) through the 2013/15 Fisheries, Low Oxygen and Climate Change (FLOX) project DP329. GETM-ERSEM-BFM was funded through Cefas Seedcorn project DP224 (Modelling the causes and consequences of environmental change in UK shelf seas). The future projections with GOTM-ERSEM-BFM were carried out as part of the Marine Ecosystem Connections project funded by the UK Department for Environment, Food and Rural Affairs (Defra), through Cefas contract ME3205. S.D.S. was supported by a NERC Knowledge Exchange Fellowship (NE/J500616/2).

LITERATURE CITED

Baretta JW, Ebenhöh W, Ruardij P (1995) The European regional seas ecosystem model: a complex marine ecosystem model. J Mar Res 33:233–246

Behrens JW, Steffensen JF (2007) The effect of hypoxia on behavioural and physiological aspects of lesser sandeel, *Ammodytes tobianus* (Linaeus, 1785). Mar Biol 150: 1365–1377

Behrens JW, Ærtebjerg G, Petersen JK, Carstensen J (2009) Oxygen deficiency impacts on burying habitats for lesser sandeel, *Ammodytes tobianus* (Linnaeus, 1785), in the inner Danish waters. Can J Fish Aquat Sci 66:883–895
Blanchard JL, Mills C, Jennings S, Fox CJ, Rackham BD, Eastwood PD, O'Brien CM (2005) Distribution–abundance relationships for North Sea Atlantic cod (*Gadus morhua*): observation versus theory. Can J Fish Aquat Sci 62:2001–2009
Burchard H, Bolding K (2002) GETM: a general estuarine transport model. Tech RepEUR 20253 EN. European Commission, Ispra
Chabot D, Claireaux G (2008) Environmental hypoxia as a metabolic constraint on fish: the case of Atlantic cod, *Gadus morhua.* Mar Pollut Bull 57:287–294
Chapman LJ, McKenzie DJ (2009) Behavioural responses and ecological consequences. Fish Physiol 27:25–77
Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. Fish Fish 10: 235–251
Cheung WWL, Sarmiento JL, Dunne J, Fröhlicher TL and others (2013) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nat Clim Change 3:254–258
Cheung WWL, Brodeur RD, Okey TA, Pauly D (2015) Projecting future changes in distributions of pelagic fish species of Northeast Pacific shelf seas. Prog Oceanogr 130:19–31
Claireaux G, Lagardère JP (1999) Influence of temperature, oxygen and salinity on the metabolism of the European sea bass. J Sea Res 42:157–168
Claireaux G, Webber DM, Kerr SR, Boutilier RG (1995) Physiology and behaviour of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating salinity and oxygenation conditions. J Exp Biol 198:61–69
Claireaux G, Weber DM, Lagardère JP, Kerr S (2000) Influence of water temperature and oxygenation on the metabolic scope of Atlantic cod (*Gadus morhua*). J Sea Res 44:257–265
Clark TD, Sandblom E, Jutfelt F (2013) Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. J Exp Biol 216:2771–2782
Cocco V, Joos F, Steinacher M, Fröhlicher TL and others (2013) Oxygen and indicators of stress for marine life in multi-modal global warming projections. Biogeosciences 10:1849–1868
Cook DG, Herbert NA (2012) Low O_2 avoidance is associated with physiological perturbation but not exhaustion in the snapper (*Pagrus auratus*: Sparidae). Comp Biochem Physiol A Mol Integr Physiol 162:310–316
Cucco A, Sinerchia M, Lefrançois C, Magni P and others (2012) A metabolic scope based model of fish response to environmental changes. Ecol Model 237-238:132–141
Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. J Appl Ecol 45:1029–1039
Ellis JR, Milligan SP, Readdy L, Taylor N, Brown MJ (2012) Spawning and nursery grounds of selected fish species in UK waters. Sci Ser Tech Rep 147. Cefas, Lowestoft
Engelhard GH (2009) One hundred and twenty years of change in fishing power of English North Sea trawlers. In: Payne A, Cotter J, Potter T (eds) Advances in fisheries science: 50 years on from Beverton and Holt. Blackwell Publishing, Oxford, p 1–25
Engelhard GH, Righton DA, Pinnegar JK (2014) Climate change and fishing: a century of shifting distribution in North Sea cod. Glob Change Biol 20:2473–2483
ESRI (Environmental Systems Research Institute) (2011) ArcGIS Desktop: release 10. ESRI, Redlands, CA
Frölicher TL, Joos F, Plattner GK, Steinacher M, Doney SC (2009) Natural variability and anthropogenic trends in oceanic oxygen in a coupled carbon cycle-climate model ensemble. Global Biogeochem Cycles 23:GB1003
Fry FEJ (1971) The effect of environmental factors on the physiology of fish. In: Hoar WS, Randall DJ (eds) Fish physiology, Vol 6. Academic Press, New York, NY, p 1–98
Gallo ND, Levin LA (2016) Fish ecology and evolution in the world's oxygen minimum zones and implications of ocean deoxygenation. Adv Mar Biol 74:117–198
Gilbert D, Rabalais NN, Diaz RJ, 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 ER, Fernand L, Sivyer DB and others (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, Kreus M, Lenhart HJ and others (2016) Looking beyond stratification: a model-based analysis of the biological drivers of oxygen deficiency in the North Sea. Biogeosciences 13:2511–2535
Heath MR, Neat FC, Pinnegar JK, Reid DG, Sims DW, Wright PJ (2012) Review of climate change impacts on marine fish and shellfish around the UK and Ireland. Aquat Conserv 22:337–367
Hinrichsen HH, Huwer B, Makarchouk A, Petereit C, Schaber M, Voss R (2011) Climate-driven long-term trends in Baltic Sea oxygen concentrations and the potential consequences for eastern Baltic cod (*Gadus morhua*). ICES J Mar Sci 68:2019–2028
Hobday AJ, Pecl GT (2014) Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. Rev Fish Biol Fish 24:415–425
Jenkins GJ, Murphy JM, Sexton DMH, Lowe JA, Jones P, Kilsby CG (2009) UK climate projections: briefing report. Met Office Hadley Centre, Exeter
Jones MC, Dye SR, Pinnegar JK, Warren R, Cheung WWL (2013) Applying distribution model projections for an uncertain future: the case of the Pacific oyster in UK waters. Aquat Conserv 23:710–722
Killen SS, Marras S, Ryan MR, Domenici P, McKenzie DJ (2012) A relationship between metabolic rate and risk-taking behaviour is revealed during hypoxia in juvenile European sea bass. Funct Ecol 26:134–143
Lefrançois C, Claireaux G (2003) Influence of ambient oxygenation and temperature on metabolic scope and scope for heart rate in the common sole *Solea solea.* Mar Ecol Prog Ser 259:273–284
Lenhart HJ, Mills DK, Baretta-Bekker H, van Leeuwen SM and others (2010) Predicting the consequences of nutrient reduction on the eutrophication status of the North Sea. J Mar Syst 81:148–170
Levin LA, Breitburg DL (2015) Linking coasts and seas to address ocean deoxygenation. Nat Clim Change 5: 401–403
Mallekh R, Lagardère JP (2002) Effect of temperature and

dissolved oxygen concentration on the metabolic rate of the turbot and the relationship between metabolic scope and feeding demand. J Fish Biol 60:1105–1115
Matear RJ, Hirst AC (2003) Long-term changes in dissolved oxygen concentrations in the ocean caused by protracted global warming. Global Biogeochem Cycles 17:1125
Mejri S, Tremblay R, Lambert Y, Audet C (2012) Influence of different levels of dissolved oxygen on the success of Greenland halibut (*Reinhardtius hippoglossoides*) egg hatching and embryonic development. Mar Biol 159: 1693–1701
Met Office Hadley Centre (2012) HadRM3-PPE-UK model data. NCAS British Atmospheric Data Centre, 2008-January 2012. http://badc.nerc.ac.uk/view/badc.nerc.ac.uk__ATOM__dataent_12178667495226008
Montero-Serra I, Edwards M, Genner MJ (2015) Warming shelf seas drive the subtropicalization of European pelagic fish communities. Glob Change Biol 21:144–153
Neuenfeldt S, Andersen KH, Hinrichsen HH (2009) Some Atlantic cod *Gadus morhua* in the Baltic visit hypoxic water briefly but often. J Fish Biol 75:290–294
Nilsson GE, Hobbs JP, Munday PL, Ostlund-Nilsson S (2004) Coward or braveheart: extreme habitat fidelity through hypoxia tolerance in a coral-dwelling goby. J Exp Biol 207:33–39
Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912–1915
Petersen JK, Pihl L (1995) Responses to hypoxia of plaice, *Pleuronectes platessa*, and dab, *Limanda limanda*, in the south-east Kattegat: distribution and growth. Environ Biol Fishes 43:311–321
Pörtner HO (2010) Oxygen and capacity limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. J Exp Biol 213: 881–893
Pörtner HO (2012) Integrating climate-related stressor effects on marine organisms: unifying principles linking molecule to ecosystem-level changes. Mar Ecol Prog Ser 470:273–290
Pörtner HO, Farrell AP (2008) Ecology, physiology and climate change. Science 322:690–692
Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315:95–97
Queste BY, Fernand L, Jickells TD, Heywood KJ (2013) Spatial extent and historical context of North Sea oxygen depletion in August 2010. Biogeochemistry 113:53–68
Rabalais NN, Diaz RJ, Levin LA, Turner LA, Turner RE, Gilbert D, Zhang J (2010) Dynamics and distribution of natural and human-caused hypoxia. Biogeosciences 7: 585–619
Rutterford LA, Simpson SD, Jennings S, Johnson MP and others (2015) Future fish distributions constrained by depth in warming seas. Nat Clim Change 5:569–573
Schurmann H, Steffensen JF (1992) Lethal oxygen levels at different temperatures and the preferred temperature during hypoxia of the Atlantic cod, *Gadus morhua* L. J Fish Biol 41:927–934
Simpson SD, Blanchard J, Genner M (2013) Impacts of climate change on fish. Mar Clim Change Impacts Partnership Sci Rev 2013:113–124
Solomon S, Qin D, Manning M, Chen Z and others (eds) (2007) Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007. Cambridge University Press, Cambridge and New York, NY
Stips A, Bolding K, Pohlman T, Burchard H (2004) Simulating the temporal and spatial dynamics of the North Sea using the new model GETM (general estuarine transport model). Ocean Dyn 54:266–283
Tett P, Gowen RJ, Painting SJ, Elliott M and others (2013) Framework for understanding marine ecosystem health. Mar Ecol Prog Ser 494:1–27
Topcu HD, Brockmann UH (2015) Seasonal oxygen depletion in the North Sea, a review. Mar Pollut Bull 99:5–27
Townhill BL, Pinnegar JK, Righton DA, Metcalfe JD (2017) Fisheries, low oxygen and climate change: How much do we really know? J Fish Biol 90:723–750
van der Molen J, Aldridge JN, Coughlan C, Parker ER, Stephens D, Ruardij P (2013) Modelling marine ecosystem response to climate change and trawling in the North Sea. Biogeochemistry 113:213–236
van der Molen J, Smith HCM, Lepper P, Limpenny S, Rees J (2014) Predicting the large-scale consequences of offshore wind array development on a North Sea ecosystem. Cont Shelf Res 85:60–72
van Leeuwen SM, van der Molen J, Ruardij P, Fernand L, Jickells T (2013) Modelling the contribution of deep chlorophyll maxima to annual primary production in the North Sea. Biogeochemistry 113:137–152
van Leeuwen SM, Tett P, Mills DK, van der Molen J (2015) Stratified and nonstratified areas in the North Sea: long-term variability and biological and policy implications. J Geophys Res C Oceans 120:4670–4686
Zhu CD, Wang ZH, Yan B (2013) Strategies for hypoxia adaptation in fish species: a review. J Comp Physiol B 183:1005–1013

Editorial responsibility: Franz Mueter, Juneau, Alaska, USA

Submitted: December 12, 2016; Accepted: August 2, 2017
Proofs received from author(s): September 12, 2017