Marine species and climate change: using modelling techniques to investigate effects on species distributions

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

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Abstract

Anthropogenic climate change is one of the main challenges affecting the globe, with particular implications for the oceans. Marine climate change research has moved forward rapidly in recent years, and a range of physical model outputs are available that can be used by ecologists to help predict how species might be affected into the future. Policy makers require a level of understanding of how certain species and their ranges might change so that they can respond with sustainable management actions. This thesis aims to make use of a number of modelling techniques to explore implications of past and future conditions for marine species, and to appraise those tools that can be used under differing circumstances. Policy questions are answered relating to changes in the abundance and distribution of marine species. The links between historical climatic conditions and Barents Sea cod abundance are explored using Generalised Additive Models using data collected in the middle of the 20th century. This valuable historical data indicated that cod have temperature preferences and expand and shift their distributions based on environmental conditions. A simpler modelling technique is used to examine how oxygen conditions have changed in recent decades in the North Sea, how they might change in the future, and what implications this has for commercial fish species. The models show that oxygen conditions have improved recently and that they will not decrease to levels that result in large negative effects in the coming century. Species distribution modelling using a combination of global and downscaled model outputs shows that the UK will become more suitable for some non-native and harmful algal species in the 21st century, and less suitable for others. The model outputs contribute to the understanding of climate change effects and development of management tools to ensure the resilience of marine ecosystems into the future.

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Chapter 1

General Introduction

In recent years anthropogenic climate change has become accepted as a phenomenon that is affecting the globe, and which will continue to do so for decades to come. Climate change research has increased in complexity and output, with impacts, adaptation and mitigation all at the forefront of science. In the marine realm, what was once considered simply as climate warming, is now understood to be much more complex. Changes are being seen not only to temperature, but also salinity, oxygen levels, pH, sea level, waves, sediment transport and circulation, with subsequent impacts to marine life and society. The Intergovernmental Panel on Climate Change (IPCC) is the global authority on climate change, providing up to date information on its physical, human and environmental effects (IPCC, 2015). The IPCC has gone from its relatively short First Assessment Report of climate change in 1990 (414 pages in Working Group I) to the Fifth Assessment Report (AR5) in 2013 and 2014 (IPCC, 2014), which comprehensively (1535 pages in Working Group I) describes the most recent evidence and detailed consequences of climate change (Pörtner *et al*., 2014). Effects described include impacts on the physical environment, microbes, plants, higher animals and benthic and pelagic ecosystems, and AR5 is the first Assessment Report to consider the effects on and of hypoxia in detail. In AR5 (working Group II) two chapters (6 and 30) were included specifically on the oceans. In 2018, a special report on ‘Oceans and Cryosphere’ is planned showing the importance of this area of research.

North western Europe is an interesting region within which to study climate change, with the North Sea in particular being considered a ‘hot spot’ of maritime change (Hobday and Pecl, 2014). Sea surface temperatures in the southern North Sea have risen more than the global average over the past 50 years (Hobday and Pecl, 2014) and by 2099 there is projected to be a temperature increase of approximately 1.7°C (Mathis, 2013), with mean bottom temperatures increasing by 0.15°C and coastal waters by 5°C (Weinart *et al*., 2016). For the wider north western shelf seas area, a mean sea surface temperature increase of 2.9°C and a reduction in salinity of 0.41 psu are projected by the end of the 21st century (Tinker *et al*., 2016). These changes are already having effects on marine organisms and will likely do so into the future (e.g. Pearce-Higgins and Holt, 2013; Pinnegar *et al*., 2013). A recent assessment of changes in the distributions of 65 North Sea benthic invertebrates found that between 1986 and 2000, many species' ranges shifted north west and deepened (Hiddink *et al*., 2015). Some cold water fish around the UK and northern Europe have moved into deeper, cooler waters (Dulvy *et al*. 2008) and some warmer water species are occurring more frequently in new areas (Simpson *et al*., 2013). For example mackerel are now occurring in larger numbers around Iceland and anchovies have become established in the southern North Sea and English Channel (Simpson *et al*., 2013). This has management implications for existing fisheries and may create opportunities for exploitation of species arriving into new areas, or challenges where intensive fishing can no longer be sustained. There have also been changes to some cetacean populations within northern Europe that may shift their ranges in the future due to increased temperature and changes in food availability (Evans and Bjørge, 2013). While it may be relatively easy to observe the changes in populations of fish and mammals, there are also consequences for smaller organisms. For example, it is thought that a number North Atlantic phytoplankton species will shift their distribution northward and eastward over the next century, consistent with changes in isotherm positions, circulation and surface conditions (Barton *et al*., 2016). Changes in zooplankton, with colder-water species such as *Calanus finmarchicus* disappearing, and warmer water species such as *Calanus helgolandicus* proliferating, are also widely cited (Beaugrand *et al*. 2002; Edwards *et al*., 2013).

This introduction explores the global and regional physical climate change models which are in use along with some of the physical-biogeochemical models. It then discusses the range of observed and predicted ecological responses to climate change, and how different modelling techniques are available to investigate effects. The aims of this thesis will then be described in a context of existing policy-relevant research and knowledge gaps.

Physical models

Environmental projection data are available from many sources and at varying resolutions globally and regionally. Global oceanic data are widely available for some parameters, for example for salinity and temperature, but other data can be more limited in spatial area, such as oxygen and pH. The most recent group of global physical models were produced to coincide with the IPCC AR5. The Coupled Model Intercomparison Project runs in parallel with the IPCC reporting periods; the most recent of which is the Fifth Phase (CMIP5). CMIP5 has provided a multi-model, standardised context within which to examine climate predictability and the differences between global climate models (CMIP5, 2016). In order to standardise future projections, four carbon emission scenarios were developed known as Representative Concentration Pathways (RCPs) which represent four different futures based on emissions, land use and mitigation. These replace the previous IPCC-SRES scenarios (Special Report on Emissions Scenarios), which are still used in many downscaled regional models. Twenty-nine modelling centres across the world produced CMIP5 models, including the Met Office Hadley Centre in the UK which developed the HadGEM and HadCM (SRES scenarios) model families (CMIP5, 2016). The US National Oceanic and Atmospheric Administration (NOAA) Geophysical Fluid Dynamics Laboratory (GFDL) and Australian CSIRO ACCESS 1.0 scenarios are also widely used in ecological climate modelling (Cheung, 2009; 2013; Fernandes *et al*., 2013; Jones *et al*., 2013a; b; Burrows, 2014). Ocean components of the GFDL and CSIRO models have a one degree resolution (GFDL, 2015), and the ocean component of HadCM3 has a resolution of 1.25 degrees with 20 depth levels (Figure 1) (Lowe *et al*., 2009; Met Office, 2016a).

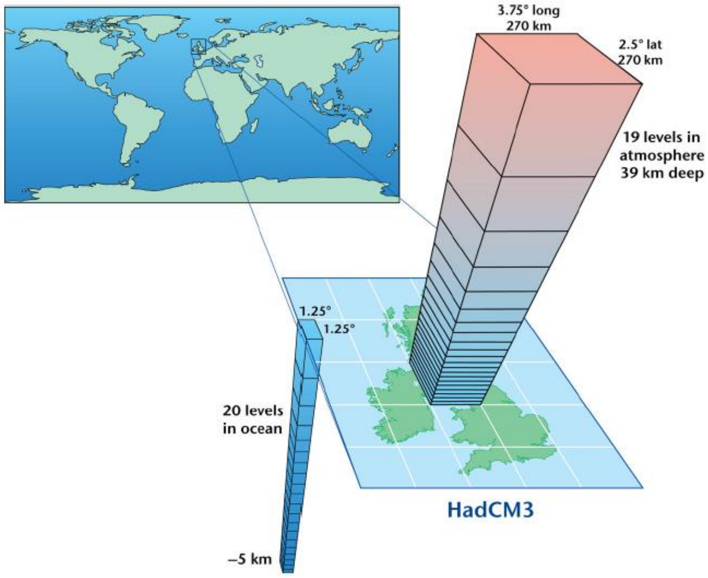

Figure 1*:* Schematic of the HadCM3 Met Office Hadley Centre climate model. Taken from UKCP09 (Lowe *et al*., 2009).

These global climate model outputs are subsequently used to produce downscaled regional climate models, which are particularly useful in understanding local and regional-scale implications of changes in the oceans. HadCM3 was used in the 2009 UK Climate Projections project (UKCP09), where it was downscaled and a single ensemble member used to project the UK shelf seas' hydrography at a resolution of 12 km using a 'medium' emissions scenario (SRES A1B) (Lowe *et al*., 2009). Since 2009, UKCP09 has been the government endorsed authority on projected climate for the United Kingdom, and impact studies have used outputs from these models many times in studying the impacts of climate change (Bell *et al*., 2012; McColl *et al*., 2012; Taylor *et al*., 2012; Clark *et al*., 2013a; Palin *et al*., 2013). In 2014, The Met Office Hadley Centre produced an ensemble run for the 'medium' emissions scenario, expanding on the one UKCP09 model run (Tinker *et al*., 2015). This time a Perturbed Physics Ensemble (PPE) of HadCM3 was downscaled using the shelf seas model POLCOMS, which enabled the authors to consider aspects of uncertainty in the model projections – previously not possible for the single ensemble member within UKCP09. These model projections are used in Chapters 5 and 6 of this thesis. In early 2016, the UK's Department for Environment, Food and Rural Affairs (Defra) announced that its next generation of regional outputs, UKCP18, will be produced in 2018, to update these 2009 projections. The marine aspects of UKCP18 are yet to be fully defined but are likely to include more detailed modelling of the shelf seas using a downscaled version of the CMIP5 models, including the HadGEM3 model, however the analysis of these simulations will focus on changes in the sea-level rather than changes in temperature and salinity.

For parameters other than those provided by the climate models themselves, physical-biogeochemical models can be forced with climate model outputs. There are many examples of this across Europe, including: POLCOM-ERSEM (Butenschön *et al*, 2016); NEMO-ERSEM (Edwards, *et al*., 2012); NORWECOM (Skogen, 1993); ECOHAM (e.g. Stegart *et al*., 2109), MARS3D (e.g. Bennis *et al*., 2011) all of which have been applied in waters around the UK. In chapter 4, for the north west European continental shelf, the coupled model GOTM-ERSEM-BFM (General Ocean Turbulence Model-European Regional Seas Ecosystem Model-Biogeochemical Flux Model) is used to replicate the hydrodynamics and biogeochemistry of the system, and when forced by the HadRM3 climate model, to provide biogeochemical properties of the shelf seas to the end of century, including oxygen and nutrients (van der Molen *et al*., 2013). In this instance the future biogeochemical projections have been provided for three point locations rather than in a gridded form, and are used in Chapter 4 of this thesis. Ecological modellers now have a range of climate models to use, but due to the nature and limitations of each model, there are often compromises to be made between the geographic coverage, resolution and parameters which are available for use. Nonetheless, there have been many studies looking at how climate change may affect marine ecosystems, including changes in food webs and diets, distribution shifts and phenology of key life history events.

Ecological effects

The oceans are complex systems, and therefore predicting the effects of climate change is non-trivial. Many modelling studies have been carried out recently that show interlinking of the different components of the system, and which demonstrate the range of effects which are being seen, or are expected to be seen. The complexity of the effects is easy to comprehend in the illustration by Sydeman *et al*. (2015; Figure 2), which shows the effects of climate change on marine vertebrates in four different systems. There are direct climate controls on some species and communities, but this then has knock-on effects (either top down or bottom up) on other components of the ecosystem.

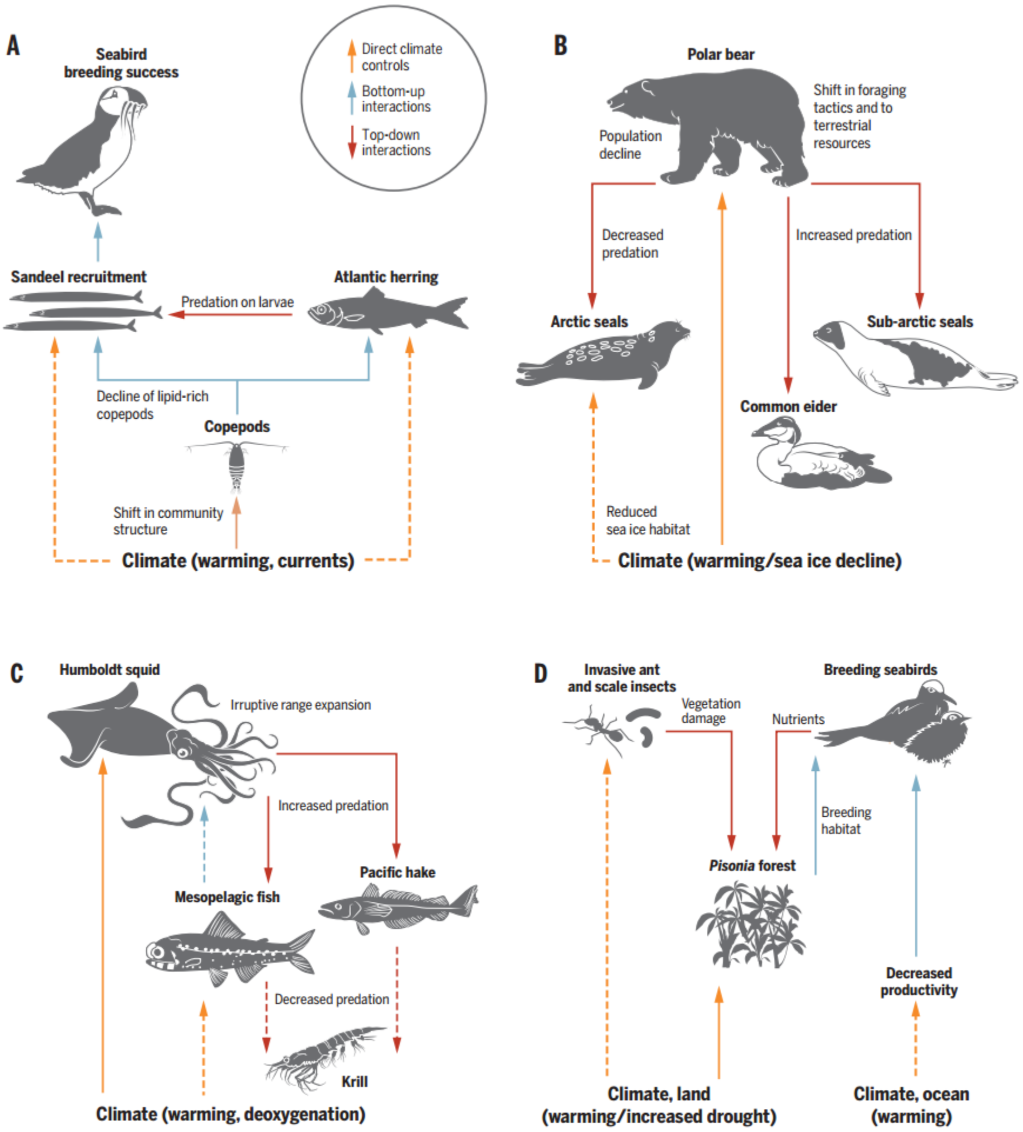

Figure 2: Schematic showing examples of the complexities of climate effects on marine vertebrates. A: the bottom up effects in the North Sea; B: the top down effects in the Arctic; C: trophic cascade in the California Current System; D: ocean-land links and cascades on coral sea islands. Taken from Sydeman *et al*. (2015).

Distribution shifts are one well-documented, relatively straight-forward, climate change impact. In simple terms, as the local climatic and environmental conditions in which a species is living change, populations follow those conditions so that the distribution of the species shifts over time, but the conditions that they experience remain approximately the same. Many species' ranges have already changed in northern Europe. There are constraints to this that may make this shift problematic, such as food availability, depth and suitable benthic habitat availability (Rutterford *et al*., 2015) and physical ability of gametes, juveniles or adults to spread. However, in the North Sea Hiddink and Ter Hofstede (2008) suggested that species richness of fish increased from 1985 to 2006 as a result of warmer sea temperatures. Hiddink *et al*. (2015) found that distributions did not change as fast as the temperatures themselves, and so the overall thermal habitat that the species experienced increased slightly. Climate velocity is a term that is used to describe the speed and direction with which climatic conditions may shift due to climate change (Loarie *et al*., 1009). Species distribution models tend to assume that a species is able to follow its niche, but if conditions change faster than a species or its life stages can physically move, or there are no connection routes, then that species may indeed become extinct from an area (Lenoir *et al*., 2011; Burrows *et al*., 2014). If one species moves or becomes locally extinct, it does not necessarily leave a niche that can be filled by other species because there may be no connection routes, and so species richness may be lost in some areas (Burrows *et al*., 2014).

Models are increasingly being used for predicting how climate change might affect production and distribution of marine species in the UK and worldwide. There are many different models available that predict different types of effects, from relatively simple mechanistic models, to more complex statistical models incorporating many environmental variables, and ultimately towards detailed ecosystem models that incorporate many likely interactions. Mechanistic models tend to look at the physiological responses of an organism and determine the *fundamental* niche (i.e. where the species could survive and persist based on those environmental limitations included in the model) (Pearson and Dawson, 2003). Other empirical models use detailed information regarding the *realised* niche of a species (i.e. where they are actually found) and use this data combined with environmental parameters to determine the bioclimate envelope of the species. Multi-model approaches can also be used to account for the variability between models (Araujo and New, 2007). These complementary modelling approaches can all be used under different circumstances, depending on availability of data and resources, to investigate how species, populations and ecosystems may respond to climatic changes, with results differing in accuracy and application. More worldwide climatic projections are becoming available, such as from the IPCC or NOAA and the Met Office in the UK, with more time slices and emissions scenarios being considered. By using these refined projections, ecological response predictions may offer more useful insights to marine managers, and focus on near term timescales as well as the long term. Such models can be used in designing marine protected areas, guiding restoration of habitats, managing invasive species, conducting risk analyses and identifying potentially endangered species (Jarnevich *et al*., 2015). Jarnevich *et al*. noted that no single model is best for all species everywhere and so the most appropriate model or an ensemble of different models (e.g. Reiss *et al*., 2011; Jones *et al.,* 2012; 2013a; 2013b) must be used depending on the question to be answered and the data available (Hijmans and Graham, 2006). For some species there is detailed information available, such as commercial fish species, for which long-term spatially-explicit abundance data has been collected. For other species, only presence data is available, sometimes at course resolution, and the only environmental data for those locations is modelled rather than measured *in situ*. Therefore the model chosen should reflect this data availability, quality and the associated limitations. For example, presence data are likely to be biased and incomplete (Jarnevich *et al*., 2015), but are likely to be better than no data at all. Table 1 shows some of the modelling techniques available to investigate species distribution and abundance changes, the types of data required and some detail of each approach.

Table 1: A selection of different methods for determining the ecological and distribution effects of marine climate change and examples where these have been used. Includes information summarised from Reiss *et al.* (2011) and Jarnevich *et al*. (2015).

Modelling method	**Detail**	**Examples**
Ecological niche factor analysis	Suitable habitat is determined using the mean distribution at presence locations and the difference between the variance of the species globally.	Galparsoro *et al*., 2008; Skov *et al*., 2008
Maxent (Maximum entropy)	Finds probability distribution that is most spread out (maximum entropy). Defines the environmental preferences based on the location of presence records. Presence only.	Hijmans and Graham, 2006; Cheung *et al*., 2009; Jones *et al*., 2012; 2013a, b
Generalised Linear Models	Regression models, using linear relationships between presence, absence and environmental data. Redundancy is removed by using a stepwise procedure.	Montero-Serra *et al*., 2015
Generalised Additive Models	Non-parametric smoothers model non-linear trends between species presence or absence and environmental predictors.	Rutterford *et al*., 2015; Hijmans and Graham, 2006
Generalised Boosted Models/Boosted Regression Trees	Multiple regression tree models are sequentially combined and the poorly predicted data is re-weighted each time.	Elith and Graham, 2009
Random Forest	Regression model generating multiple trees using randomised predictors.	Oppel and Huettman, 2010
Aquamaps	Uses simple descriptors of relationship between presence and	Jones *et al*., 2012; 2013a, b

Modelling method	**Detail**	**Examples**
	environmental variables, specified by a trapezoid distributional function. Presence only.	
Bioclimatic Envelope (BIOCLIM)	Envelope model using mean and standard deviation for each environmental variable. Presence only.	Hijmans and Graham, 2006
Genetic Algorithm for Rule-set Production (GARP)	Machine learning model.	MacLeod *et al*., 2008
Mechanistic model	A species' physiology data is used to predict suitable distribution.	Hijmans and Graham, 2006; Fly *et al*., 2015

An important consideration when presenting and communicating modelling is being aware of what the model outputs will be used for, i.e. what question is being asked and with what confidence is it being answered. The model one uses and the choices made within that model should be determined by the quantity and quality of data available, the output required, the type of organism being considered and how the level of uncertainty to be communicated. Some models are data hungry, and so can be used for species for which there are plenty of high quality data or where a species is of considerable economic value, e.g. Atlantic cod. Other models require only presence data and so are more appropriate for understudied non-native and HAB species. Where high resolution outputs are required, this can lead to a paucity of data needed to test the model fit, for example when using downscaled shelf seas models; in contrast, lower resolution outputs such as those from global climate models can lead to a better fit, but be of limited use if species are highly habitat-specific (e.g. intertidal species). Ideally models should provide assessments of the risk of something occurring coupled with the severity of that occurrence, leading to some understanding of the uncertainty around these risks. For example species distribution models are not absolute, but they do give an estimate of the relative suitability of habitats (Jarnevich *et al*., 2015) or the relative changes between species. These models are sometimes dismissed as being too uncertain, without appreciating this inherent value. While we do not have a crystal ball, we can optimise use of available data and techniques to build predictions of future changes. In some cases more complex models are used to try to incorporate many different variables and scenarios, but they often require heroic assumptions to be made due to computational power, leading to further error (Fernandez *et al*., 2013). In some cases the simplest model is best, because with fewer assumptions and parameters they can be easier to interpret.

Policy-relevant research

Many research studies are carried out on species with which a scientist or a laboratory has a background of research, often using a model species that is relatively easy to keep and reproduce under laboratory conditions. Of immediate interest to policy makers however is research which identifies the potential impacts of climate change on 'important' species; i.e. those that are of commercial, conservation or ecological interest, or nuisance species which could cause potential economic impacts. For the UK, species distribution modelling on commercial and vulnerable marine species, and one species of non-native invertebrate has been carried out by Jones *et al.* (2012; 2013a; 2013b). Beaugrand *et al*. (2011) and Lenoir *et al.* (2011) have used similar approaches to look at commercial fish around the UK, whereas Fly *et al*. (2015) and Reiss *et al.* (2011) have attempted to predict future distributions of marine invertebrates. More recently, Rutterford *et al.* (2015) have used Generalised Additive Models (GAMs) to measure the importance of environmental variables on the distribution of commercial fish species. They concluded that over the next 50 years many species will be strongly constrained by availability of suitable habitat, especially in terms of preferred depths. This was suggested to be of particularly impact on shallow-water flatfish species that, if forced northwards by warming seas, will run out of suitable habitat, leading to a requirement for rapid ecological niche shifts, or else population declines. There are however many aspects of climate change which have not been incorporated into these models, such as the role of low oxygen (e.g. Cheung *et al*., 2009; 2011; 2012; Margonski *et al*., 2010; Reiss *et al*., 2011; Diamond *et al*., 2013), and there are many species, particularly non-native and nuisance species, which are yet to be modelled at all. Despite a large body of scientific literature on the physiological and behavioural responses of marine species to changing environmental conditions at the individual level, there is currently a lack of studies helping to explain how these changes will affect commercial or nuisance species at the stock and population level, and hence the industries and ecosystems that rely on or are affected by them.

There are many different aspects to climate change which pose different problems to the environment and to human activities. Thus, there are many policy questions that need answering regarding climate change, and different types of data available with which to answer these questions. A suite of approaches has been developed to answer these questions and predict how environmental changes might affect species. However the most suitable method for the question or availability of data is not always used, and indeed it is not always clear what the correct method is. Only with an understanding of the potential future changes can policy makers respond with suitable sustainable management actions. This thesis explores some of these questions, and applies a number of different methods to climate questions that have not been previously explored.

Policy makers are able to use the outputs of climate models and distribution projections to understand and anticipate the range of responses that could be seen in the species with which they are concerned (Fernandez *et al*., 2013). In this thesis, the responses of species to climatic changes in the past, present and future are tested in order to answer relevant questions for policy makers and environment managers. First, the past climatic conditions in the Arctic are explored to consider how variability in the environment may have affected abundance of Atlantic cod (*Gadus morhua*) and their prey. The remainder of the chapters contrast environmental conditions in the present with those projected in the future. Most of the existing studies so far of European species have tended to use high resolution global climate datasets because they are readily available, cover a number of parameters and allow the ocean-wide distribution of a species to be considered. High resolution data are more frequently being made available for new areas and for new parameters, and the use of these data in ecological predictions is of great value to policy makers and environment managers as they can see the potential local and regional scale changes, over which they might have some control. Here, high resolution, downscaled models outputs are used to project how commercial and nuisance species might respond to future climate change.

The aim of this PhD is to apply a variety of different modelling tools (from very simple to complex) to explore past and future changes in marine species distributions, in order to appraise the various techniques that can be used under a variety of circumstances. Generalised Additive Models (GAMs), a simple overlay method and bioclimate envelope models (also called ecological niche models and species distribution models) are applied to ecologically and commercially important species within Europe demonstrating a toolbox of approaches for different applications, ranging from data-poor to relatively data-rich. Modern techniques will also be used on historical data, giving a new insight to past changes. A very simple technique is used to explore the effects of oxygen in the recent past, the present and into the future. Finally, existing published modelling methods are developed, based on recently available downscaled climate data.

The four main topics covered within the thesis are:

- Chapter 2: Historical Arctic logbooks, climatic changes and cod diets
- Chapters 3 and 4: Fisheries, low oxygen and climate change
- Chapter 5: Non-native species in north west Europe
- Chapter 6: Harmful algal blooms and climate change

The Arctic has experienced significant warming in recent years, however it has previously undergone distinct periods of warm conditions, notably in the middle of the last century. Currently, cod stocks in the Barents Sea are at high levels which was also the case in the 1950s. It is not fully understood why the stock size fluctuates in this way, what causes the abundance changes and which prey species can sustain such high numbers of predatory fish. It is hypothesised that marine species distributions and abundances have been affected by past environmental changes. It is expected that historical changes in environmental conditions would have effects on Atlantic cod abundances in certain locations and the availability of prey species on which they feed. This hypothesis was tested using GAMs which are able to test the relationship between and importance of a number of spatial, temporal and environmental variables on the catch per unit effort. GAMs determine the interactions between these variables and makes allowance for non-linear relationships between a number of dependent variables. Cefas holds historical fisheries research records for the Barents Sea from the 1930s to the 1970s, collected from cruises when the UK had distant-water cod fisheries interests in the region. The data are incomplete and the surveys were not designed in a traditionally statistical manner, yet using modern analytical techniques on this historical data, unique insights can be gained as to how and why the cod stocks fluctuate in relation to climate. The data can contribute to our understanding of what causes the stocks to become so high, and so help managers to understand the stock and what affects it, and so put in suitable fisheries management techniques to maintain the stock into the future. No other cod abundance and diet data are available for this part of the Barents Sea over the same historical period, and so by analysing the Cefas dataset I am able to determine how the climatic conditions at the time affected the cod stock. This GAM approach takes into account the range of variables available and the incomplete and non-statistically designed dataset. GAMs determine how much of the independent variable can be predicted by the data vailable, and so acknowledging that there are other influences on the cod and prey abundances. Within Chapter 2, analyses were carried out on historical data to explore the links between the environment, fish abundance and prey preferences, using GAMs, and these are presented in a context of fisheries management.

Oxygen availability is a key factor that determines habitat suitability for marine fish (Cheung *et al.*, 2012; Zambonino-Infante *et al.*, 2013). As a result of climate change, low oxygen conditions are predicted to occur more frequently and over a much greater geographic extent in the oceans in the future (Diaz and Rosenberg, 2008). Several authors have highlighted how oxygen concentrations, low pH and elevated temperature interact and determine a species' 'scope for growth' (e.g. Pörtner and Knust, 2007). Chapter 3 is an initial literature review of the effects of low oxygen on commercial fish and concludes that much research has already been conducted with regard to the effects of acute hypoxia on the physiology of marine species, but far less on long-term, chronic effects, especially concerning commercially important fish and shellfish. In order for policy makers to fully understand how climate change might affect commercial species in the future, the impact of oxygen needs to be considered, but until now it has been largely left to one side in favour of assessing temperature and pH. The IPCC AR5 working group II report highlighted low oxygen conditions as a critical, under-researched topic and Chapters 3 and 4 of this thesis are working to bridge this research gap. The review (Chapter 3) concludes that more work needs to be done, as a matter of urgency, to make use of experimental results and modelling techniques, particularly around the UK. Chapter 4 comprises a first step to integrating experimental results with climate modelling following the earlier examples of Cucco *et al.* (2009) and Marras *et al*. (2015). It is hypothesised that recent changes in oxygen conditions in the North Sea are likely to have affected commercial fish species, with the magnitude of effect linked to their physiological attributes. Likewise, reductions in oxygen conditions in the coming century in certain areas are expected to create certain areas which limit the activities of certain fish species. A simple overlay method is used to test these hypotheses, identifying areas and years when modelled oxygen levels will be limiting to fish, based on the physiological parameters that are available in the published literature. This method is able to identify certain areas in which certain fish may have been affected in the past, and whether these conditions have improved or worsened, and to identify trends in limiting oxygen conditions in the coming century. The modelled oxygen concentrations used here are the most recently available for the North Sea, allowing the effects of climate-induced oxygen changes on commercial fish to be tested for the first time. This research technique allows policy makers to understand how existing environment management measures, such as changes in nutrient run-off from land and elevated temperatures, can affect commercial fish, and how future climate change may alter oxygen conditions further and what the consequences might be for commercial fisheries.

In addition to gaps in climate change research on certain parameters, such as low oxygen, since most research is carried out on model, commercial or threatened species, there is a lack of studies on other groups of importance to policy makers, for example nuisance species. Non-native, introduced or invasive species and harmful algal species cause economic and environmental damage around the world and have been recognised as a major threat to natural ecosystems and coastal economies. Human activity has enabled and accelerated the spread of many non-native species, and anthropogenic run-off affects the occurrence of algal blooms. Large amounts of money are spent each year in monitoring these species, in eradicating non-natives, in forecasting harmful algal blooms and in toxicity testing in order to classify shellfish as being safe to eat. Little is known about the potential changes that climate change might have on these species, in terms of their spread and the associated costs. Previous studies have found that in north west Europe, the suitable habitat of marine species will shift further north with climate change, and so it is hypothesised that the same will be true for non-native and harmful algal species.

Habitat suitability models are used in climate research to determine the potential area that is theoretically suitable for a species, both in the present and into the future as conditions change. These models use grids of climate data to assign environmental preferences to a species based on presence records. A species distribution modelling approach (Maxent) is used here, which has been proven as one of the most robust methods (Bučas *et al*., 2013) and is suitable for the organisms being considered. For example some species distribution models, sucha sthe Dynamic Bioclimate Envelope Model are only suitable for modelling fish and invertebrate species (Cheung and Pauly, 2008). Habitat suitability models to date typically use medium or low resolution climate data, however these data can not fully represent local oceanographic features (Bedia *et al*., 2013) and so where possible, higher resolution downscaled modelled data should be used. Global climate models of approximately 1 km resolution are available for terrestrial distribution modelling (WorldClim dataset, Hijmans *et al*., 2005), but this can still be considered too low in some cases (e.g. Bedia *et al*. 2013). For the marine realm, global projections tend to be much coarser in resolution; typically at 1.5 degrees. Downscaled regional models then are able to increase resolution and incorporate mesoscale processes such as tides, rivers and smaller currents (Tinker *et al*., 2015). In Chapters 5 and 6 of this thesis, state-of-the-art, downscaled regional models produced by the Met Office are nested within a global climate model output in order to determine how climate change may affect the habitat suitability of these species. By using this novel technique, the species distribution models were trained on global species occurrence data (necessary for non-native species, or algal species which are not constrained to a small area) to ensure that all suitable environmental conditions of that species are captured. The habitat suitability is then projected into the future, and the focus when interpreting the model is on the downscaled region, in this case north western Europe. By interpreting the model in this way, it is possible to assess how smaller-scale changes in tides, currents and riverine inputs affect the local conditions that a species could experience, and thus build a more detailed understanding of the suitable future habitat around the UK specifically. Lower resolution climate data may lead to a better model fit, but are likely to be of limited to use to policy makers and marine managers who work in certain regions and habitats. Freely available species presence data is used from international databases. Presence data from these databases is not perfect as it can be biased towards locations which are easily accessible or which are more studied that others, however access to this data has allowed a number of species to be modelled reasonably rapidly, and Maxent compares well against other modelling techniques when using such species data (e.g. Elith et al. 2006; Phillips et al., 2006; Reiss et al., 2011). The advantage of running the model on a number of species is that their future distribution changes can be compared and prioritised for management. For non-native species, policy makers can then make decisions on which species to prioritise in monitoring or eradication, based on the species with the most potential to thrive in areas in the future or cause the most damage. For harmful algal species, early warning of which species are more likely to occur around the UK in the future can be used when deciding which species to monitor on a regular basis, and knowledge of the conditions that these species need can be used in forecasting. Forecasting is especially important to shellfish farmers and fishers to ensure that their harvest is safe to eat.

The thesis then concludes with Chapter 7 in which the main chapter themes are brought together, and the similarities, differences, challenges and future directions discussed.

Chapter 2

Historical Arctic logbooks provide insights into past diets and climatic responses of cod

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Abstract

Gadus morhua (Atlantic cod) stocks in the Barents Sea are currently at levels not seen since the 1950s. Causes for the population increase in the last century, and understanding of whether such large numbers will be maintained in the future, are unclear. To explore this, we digitised and interrogated historical cod catch and diet datasets from the Barents Sea. Seventeen years of catch data and 12 years of prey data spanning 1930–1959 cover unexplored spatial and temporal ranges, and importantly capture the end of a previous warm period, when temperatures were similar to those currently being experienced. This study aimed to evaluate cod catch per unit effort and prey frequency in relation to spatial, temporal and environmental variables. There was substantial spatio-temporal heterogeneity in catches through the time series. The highest catches were generally in the 1930s and 1940s, although at some localities more cod were recorded late in the 1950s. Generalised Additive Models showed that environmental, spatial and temporal variables are all valuable descriptors of cod catches, with the highest occurring from 15–45°E longitude and 73–77°N latitude, at bottom temperatures between 2 and 4 °C and at depths between 150 and 250 m. Cod diets were highly variable during the study period, with frequent changes in the relative frequencies of different prey species, particularly *Mallotus villosus* (capelin). Environmental variables were particularly good at describing the importance of capelin and *Clupea harengus* (herring) in the diet. These new analyses support existing knowledge about how the ecology of the region is

controlled by climatic variability. When viewed in combination with more recent data, these historical relationships will be valuable in forecasting the future of Barents Sea fisheries, and in understanding how environments and ecosystems may respond.

Introduction

Many studies predict that climate change will modify ecosystems in the future (e.g. Beaugrand *et al*., 2003; Stempniewicz *et al*., 2007; Engelhard *et al*., 2011a), or have detected impacts of climatic variability on ecosystems in the past (Simpson *et al*., 2011; Tamanouchi, 2011, Engelhard *et al*., 2014). However, historical ecological data are often limited in quantity and quality, and can be piecemeal and difficult to access, greatly restricting the power of models for predicting future conditions. Historical data are essential for understanding how environmental factors influence ecosystems over long periods of time and for training models that predict the effects of future climatic changes. Understanding how ecosystems have been modified by past environmental change informs future projections. It is valuable to digitise historical information before it is lost (Vines *et al*., 2014) and probe non-standardised historical data to investigate effects of previous climatic influences (e.g. (Sagarin and Micheli, 2001).

Due to its inaccessibility the Arctic's marine systems are relatively under studied compared with other regions such as the North Sea (Perry *et al*., 2005; Hiddink and Ter Hofstede, 2008; Genner *et al*., 2010), although the Barents Sea region has received more attention than much of the Arctic due to Russian and Norwegian fisheries interest. Atlantic cod *Gadus morhua* in the Arctic region around Norway and Russia (also described as Barents Sea, Northeast Arctic and Arcto-Norwegian cod (Ottersen *et al*., 2014), is a major predatory species. Barents Sea cod is the most economically important Barents Sea species, with landings of 432,314 and 438,734 tonnes for Russia and Norway respectively in 2013 (ICES, 2014a), from where it is then exported around Europe. Cod stocks in the Barents Sea are currently at high levels not seen since the 1950s (ICES, 2014b), when temperatures were similar to those today. Recent studies have attempted to explain how cod and spawning sites are distributed, how such large numbers of fish are sustained, and how available prey resources are exploited (e.g. (Drinkwater, 2011; Ottersen *et al*., 2013; Kjesbu *et al*., 2014; Orlova *et al*., 2015)). Scientists have known for over a century that the cod stock in the region can fluctuate greatly (Hjort, 1914; Jensen, 1939), and research in the early 20th century attributed fluctuations to warming in the Barents Sea and the Arctic (e.g. (Jensen, 1939; Zubov, 1948; Steffensen, 1969)) and changes to currents and hydrography (Agenorov, 1946). Researchers appreciated the importance of changing environmental conditions; for example an ICES Special Scientific Meeting assessed how climatic changes relate to fluctuations in northern fish stocks (ICES, 1948), leading to a number of publications focusing on the issue (Lee, 1956; Beverton and Lee, 1965; Corlett, 1965; Harvey, 1965; Beverton *et al*., 1944).

Atlantic cod has become emblematic of climate influences in fish and fisheries (Brander, 2010), and Barents Sea cod are of particular interest, being at the northernmost boundary of the species range at some of the lowest temperatures experienced by the species (Sundby and Nakken, 2008; Wang *et al*., 2014). Temperature directly relates to population size, with a period of warmer temperatures in the Kola section of the south-eastern Barents Sea from 1930–1960 corresponding with high cod catches and biomass, and a cooler period from 1960–2000 corresponding with lower catches and biomass (Kjesbu *et al*., 2014; Stiansen *et al*., 2006). Barents Sea cod tend to produce stronger year classes in warmer years (Bogstad *et al*., 2013), and there is evidence of a 50% increase in growth rates from the pre-1920s to the 1960s (Drinkwater, 2006; 2011). When warm copepod and euphausiid-rich Atlantic water is brought in from the Norwegian Sea, the warmer temperatures may increase the habitable area for plankton and associated fish stocks, increasing local abundance of cod prey such as capelin *Mallotus villosus* and herring *Clupea harengus* (Stenevik and Sundby, 2007). Following cod spawning, spatial distribution depends on annual ocean currents that carry the larvae and juveniles from spawning grounds along the coast of northern Norway, north and east into the Barents Sea. Current-driven spatial distributions of juvenile cod determine the depths and temperatures experienced later through to the immature stages, thus affecting growth rates and ultimately adult size (Helle *et al*., 2002). In cold years, the size of feeding areas appears to be reduced, with effects on year class strength (Sætersdal and Loeng, 1987). Since the 1990s, Kola section annual mean temperatures have increased to ~5 °C, and spawning stock biomass (SSB) and total biomass have rapidly risen to levels even higher than the previous warm period. The environmental conditions in the Barents Sea, as illustrated by a Climate Index in Figure 3 based on air temperature, Atlantic water temperature and ice cover (Boitsov *et al.*, 2012), correlate closely with these trends in cod biomass (Hylen, 2002; ICES, 2014a).

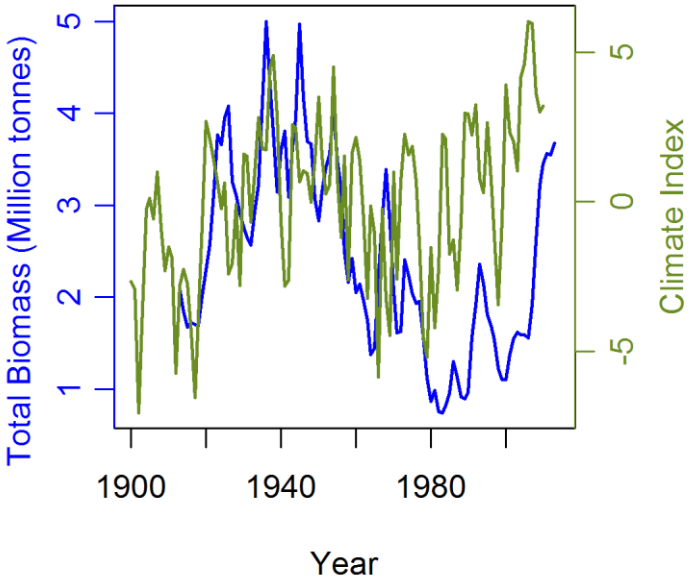

Figure 3: Total cod total stock biomass (blue) in the Barents/Norwegian Sea (ICES sub-areas I and II) from 1916–2013 (1916-1945 from Kjell Nedreaas, IMR, Bergen pers. comm., (Hylen, 2002); 1946-2013 from ICES, 2014a)), compared with a Climate Index (green) for the Barents Sea (1900–2009) (Boitsov *et al.*, 2012).

Historical data have proved valuable in assessing past impacts of climate (Rose, 2004; Engelhard *et al.*, 2011b; 2014). Here, we use newly digitised historical datasets for the Arctic to investigate changes in the distribution of Barents Sea cod, and assess changes in consumption of different prey types. Surveys mainly focused on recording catches of cod and linking catches with environmental variables, but also included stomach content analysis to assess prey that cod and other predators were consuming, and a more general assessment of the distribution of benthic invertebrate species (see Blacker, 1957). These rescued datasets are particularly valuable because they provide detailed station information alongside the catch and stomach data, in comparison with the more intensive Russian and Norwegian surveys. Russian scientists made initial observations of stomach contents from the 1920s, and collected stomach data from 1930–1960, with at least some of these surveys further south and east of those digitised here (Zatsepin and Petrova, 1939; Dolgov *et al*., 2007). Stomach analysis from British expeditions in 1936 and 1937 have been previously published (Brown and Cheng, 1946) although not the full dataset. Norwegian scientists later began analysing stomach samples and cod catches from 1984 (Johannesen *et al*., 2007) as part of the joint Norway-Russia research programme on trophic relationships in the Barents Sea (Dolgov *et al*., 2007).

This study uses analytical techniques which were not available at the time to consider historical changes in Barents Sea cod catches and diets in the wider context of warm and cool periods. Specifically, we use statistical models to test for: (a) environmental and spatial conditions in which cod catches were higher; (b) periods and times of year at which cod catches were higher; and (c) differences in prey frequencies attributable to environmental, spatial and temporal variables.

Materials and Methods

During the period 1930–1960, British researchers carried out marine surveys in the Arctic, initially boarding commercial fishing vessels to measure length distribution of cod near Bear Island, in the Svalbard (Spitsbergen) region (Graham, 1953). No surveys were carried out during World War II, but thereafter the scale of the surveys was increased from 1949 when a dedicated research ship (the RV *Ernest Holt*) was custom-built for the Svalbard-Barents Sea area by the UK Ministry of Agriculture and Fisheries (now part of Defra). Surveys were predominantly carried out in the western Barents Sea and Norwegian Sea, but also included sites around Greenland, Iceland, the Faroe Islands and the North Sea. Surveys have taken place during each of the seasons, but especially during summer and autumn when ice cover in the Barents Sea is lowest.

Cod catch weights, stomach content and hydrographic data were digitised from scientific survey logbooks held in the Centre for Environment, Fisheries and Aquaculture Science (Cefas) archive. Catch weights and hydrographic data were archived in the Cefas Fisheries Survey System (FSS) database, and stomach content data were archived in the DAPSTOM online database (Cefas, 2014; Pinnegar, 2014a). Data were checked for quality purposes by mapping sequential sampling stations, plotting the data to identify outliers and unlikely records, and subsequently revisiting logbooks and removing clearly erroneous records if necessary (approximately 0.5% of species records). Sampling campaigns were not always designed in a statistically robust way, but instead the vessels ‘chased’ high cod catches, thus operating in a similar way to commercial vessels. Therefore data stations were not gridded according to a statistically stratified design, rather they were often focussed on areas where high catches were known to be found and thus data gathered was more akin to commercial cod catch per unit effort (CPUE) than to traditional scientific abundance measures. All ships used an otter trawl. Information is very sparse on exact gear design for initial cruises, however after 1949 the *RV Ernest Holt* used a standard otter trawl with a 78 ft (23.7 m) headline, 116ft (35.4 m) groundrope, and 110mm cod end mesh, with and without Vigneron-Dahl gear (Graham, 1953). Trawl durations were generally two hours. Stomach analyses, although comprehensive, were also not as statistically robust as on current surveys. No data on stomach content mass or stomach fullness were recorded; instead only frequency of occurrence of each prey item or presence data were recorded. In order to convert units of CPUE to modern equivalents it was necessary to transfer catch estimates from numbers of ‘baskets’ or hundred-weight (cwt) and pounds (lbs) to kilograms, assuming that one basket of cod is equivalent to 84 lbs (0.75 cwt) or 38 kg (Graham, 1953), and accepting that there would be variation around this average.

In this study, stations within the Norwegian and Barents Seas (62–80°N 5–55°E) were selected for analyses, with data available for 17 years (1930, 1937, 1938, 1939, 1945, 1948-1959). Environmental parameters available for each station included location, depth, duration of haul, bottom and surface temperature and salinity. Temperature and salinity measurements were not taken at all stations, and bottom salinity (11% of stations) was more commonly recorded compared to surface salinity (0.2% of stations). The mass of the cod catch was used, except where only counts had been recorded (9% of cases), in which case each individual cod was assumed to weigh two kilograms (based on the mean mass of cod where both were recorded), again accepting that there would be variation around this. Cod CPUE in kilograms per hour was then calculated at each station by dividing catch weight by haul duration.

In order to determine the most important variables for explaining cod abundance, the relationship between annual, monthly and daily cod CPUE with longitude, latitude, bottom and surface temperatures, bottom salinity and depth were examined for explanatory trends. These relationships were investigated further using Generalised Additive Models (GAMs) implemented in the *mgcv* package (Wood, 2006) of the statistical software *R* (version 3.0.3; R Core Team, 2013). A GAM determines the interactions between variables using a flexible model that allows for non-linear relationships between several potential predictors and dependent variables using smoothing functions. In this case cod CPUE was the dependent variable in each model and the explanatory variables considered were categorised as either ‘temporal’ (year, month, day of year) or ‘environmental’ (bottom and surface temperatures, bottom salinity and depth), with longitude and latitude included in each case. A third ‘spatio-temporal’ model was also produced using a combination of longitude, latitude and year. The optimal temporal, environmental and spatio-temporal models were chosen by selecting the most suitable distribution through visual assessment of the residual and smooth plots produced by the *mgcv* package, and balancing selection of a high model deviance, a low number of degrees of freedom, and a low UGCV/UBRE score as suggested by guidance (Wood, 2006). Visual assessment of the plots was essential in model choice to ensure that models had sufficient explanatory power and were not overfitting the data.

The negative binomial distribution family was chosen in the final three models as it allowed for increased variability at larger values of CPUE and dealt more effectively with the high occurrence of zero-values in CPUE data than the other families tested (Gaussian and Tweedie), thus providing a higher explanation of deviance (Table 2). The negative binomial dispersion parameter theta (θ) was selected automatically during model fitting. Within *mgcv*, tensor smooth ‘te’ was used for the three-way interaction term within the spatio-temporal model, while the more common ‘s’ smooth was used for one- and two-way interactions in all three models. The smoothing base of ‘ts’ (thin plate regression spline with shrinkage; (Wood, 2006)) was used within the interaction terms for the environmental and spatio-temporal models, as it allows the GAM to smooth with any number of covariates and drops covariates that do not improve the model fit by setting their degrees of freedom to zero. For the interaction between longitude and latitude in the temporal and environmental models, ‘sos’ (splines on a sphere; (Wood, 2014)) was used. This fits latitude and longitude to a sphere and so allows for the narrowing of the lines of longitude as is the case nearer to the poles, such as in the Barents Sea. It was necessary to use the smoothing base ‘cc’ (cyclic cubic regression spline; (Wood, 2006)) for the day of year variable as this enabled the beginning and the end of adjoining years to be linked. Salinity was removed from the final models as it did not significantly help to explain the variance in CPUE or improve the environmental model. Month was also not included in the final models as day of the year performed better in the models.

Table 2: CPUE and Prey GAM families and variables. Each of the three prey models were produced for the prey types euphausiids, cod, capelin, herring and for empty stomachs.

Name	**Family**	**Variables**
Temporal CPUE GAM	negative binomial	s(latitude, longitude, bs="sos") + s(year) + s(dayofyear, bs="cc")
Environmental CPUE GAM	negative binomial	s(latitude, longitude, bs="sos") + s(surfacetemp, bottomtemp, bs="ts") + s(depth)
Spatio-temporal CPUE GAM	negative binomial	te(longitude, latitude, yr, bs="ts")
Temporal Prey GAM	Quasi binomial	s(latitude, longitude, bs="sos") + s(year) + s(dayofyear, bs="cc")
Environmental Prey GAM	Quasi binomial	s(latitude, longitude, bs="sos") + s(surfacetemp, bottomtemp, bs="ts") + s(depth)
Spatio-temporal Prey GAM	Quasi binomial	te(longitude, latitude, yr, bs="ts")

Cod stomach content data from the DAPSTOM database for stations in the Barents and Norwegian Seas were combined with CPUE data and temporal, environmental and spatial variables for the same research cruises. Stomach content data were available for 12 years (1930 and 1949-1959), 992 stations, comprising 18,006 cod stomachs in total. The most frequently occurring stomach record (21.4% overall) was ‘empty’. Of the cod that had prey in their stomachs, the most frequent prey types were euphausiids (krill; 21.3%) and capelin (5.6%). Other important prey types included in further analyses were herring (2.3%) and cod (cannibalism; 3.0%), based on the reported importance of these prey types in previous studies (Zatsepin and Petrova, 1939; Johannesen, 2012) and on frequency of occurrence in the DAPSTOM dataset. Frequency of occurrence of these five stomach content categories (hereafter ‘prey’) was converted to a proportion of occurrence at each station and used to develop GAM models exploring the influence of temporal, environmental and spatio-temporal variables on prey choice. The quasibinomial family was used for the frequency of occurrence or absence of each prey type at a station because prey choices were not necessarily independent for each fish at a station; we assumed that if one fish was eating a certain prey species e.g. capelin, it was likely that the other fish in the catch at that station would also be eating that prey. Hyperiid amphipods, the prawn *Pandalus borealis*, the ctenophore *Beroë sp.* and pteropod mollusc *Limacina helicina* were occasionally important prey types at certain localities and times of year, but due to their relative rarity were not included in statistical analyses. Similar to the GAMs for CPUE, salinity was removed from the final GAMs for stomach content as it did not improve explanations of prey frequency; likewise day of year was used rather than month (variables, splines and smooths in Table 1).

Results

Cod CPUE varied considerably on an annual, seasonal and spatial basis. The largest overall CPUE was in the 1930–1940s (Figure 4). Directly south of Svalbard, where cod were typically caught during spring, summer and autumn, the highest absolute catches were recorded in the 1930–1940s, 1950, 1954 and 1955, while to the west of the archipelago the highest catches were recorded later in the time series, in 1958 and 1959. Around the coast of Norway, close to the main cod spawning grounds around the Lofoten Islands where cod were sampled during winter, the highest catches were in the 1940s, and also in 1958 and 1959, with a high frequency of low or zero CPUE records at stations in 1951 and 1952. When all stations were combined, there were peaks in CPUE from 1945–1949, followed by a sharp decline in CPUE in the early 1950s (Figure 5). This was followed by a slight increase through the mid-1950s and decrease again to the end of the decade. Typical of any fish survey, there was a large amount of variability in CPUE data, with a large number of zero values, but also many very high CPUE values (up to several thousand kg/hr, especially during the late 1940s). A seasonal trend in CPUE was clearly evident from the data, with highest CPUE, and most variation in catch occurring during the summer months (June to August) and in the winter (November and December).

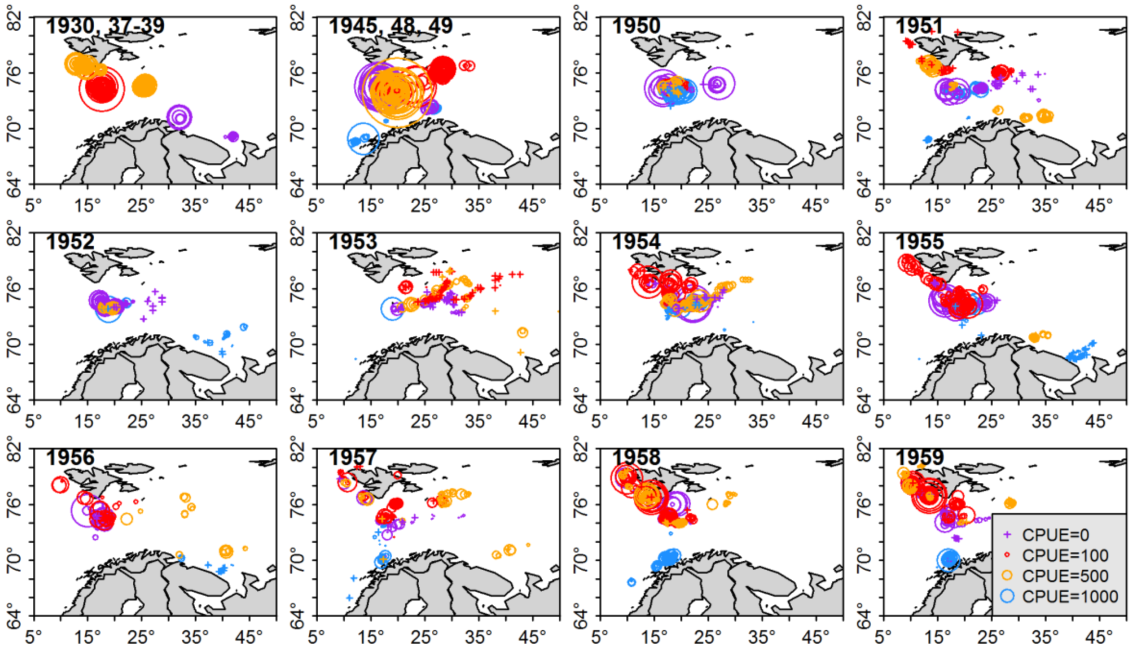

Figure 4: Cod CPUE at each station from 1930–1959. Crosses represent stations where no cod were caught. Size of the circles represent CPUE. Blue = winter, purple = spring, red = summer, orange = autumn.

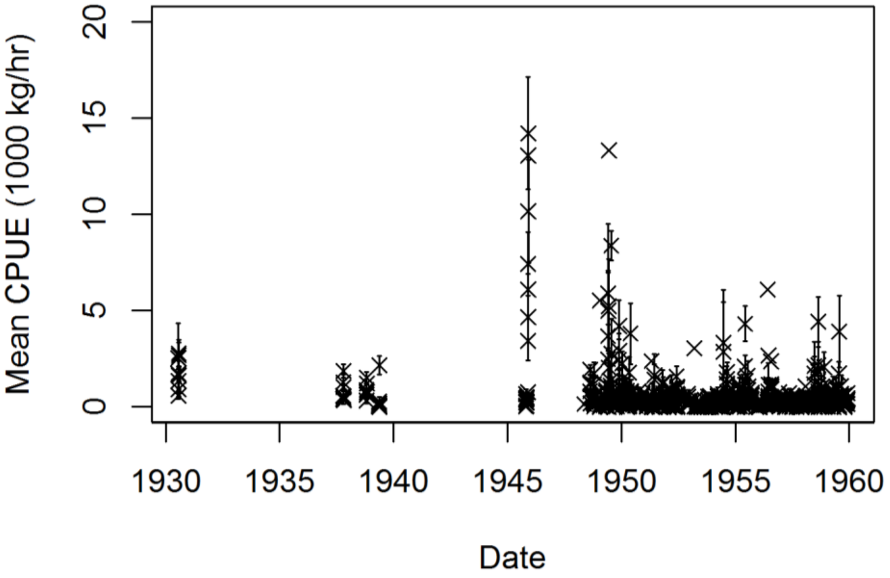

Figure 5: Long-term change in cod CPUE (kg/hr) averaged by day (±SE) for all stations combined. Note the large number of zero and near-zero CPUE values, but also very high CPUE values in some years.

Environmental variables and spatial parameters mirrored trends in cod catches, with the highest CPUE seen when bottom temperatures were 2–4 °C and surface temperatures 0–6 °C (Figure 6a and b). Cod CPUE was greatest from 15–45° E longitude, and 73–77° N latitude (Figure 6c and d), from 150–250 m depth (Figure 6e) and with bottom salinities in the range 34.8–35.2 psu (Figure 6f). Drivers for changes in cod CPUE were explored using GAMs. The optimal models found that longitude, latitude, year, day of year, bottom and surface temperature, and depth were important in explaining cod CPUE (Table 3). Deviance explained by each model was 25–29%, suggesting that other factors and natural stochasticity not captured by the models were also influencing CPUE.

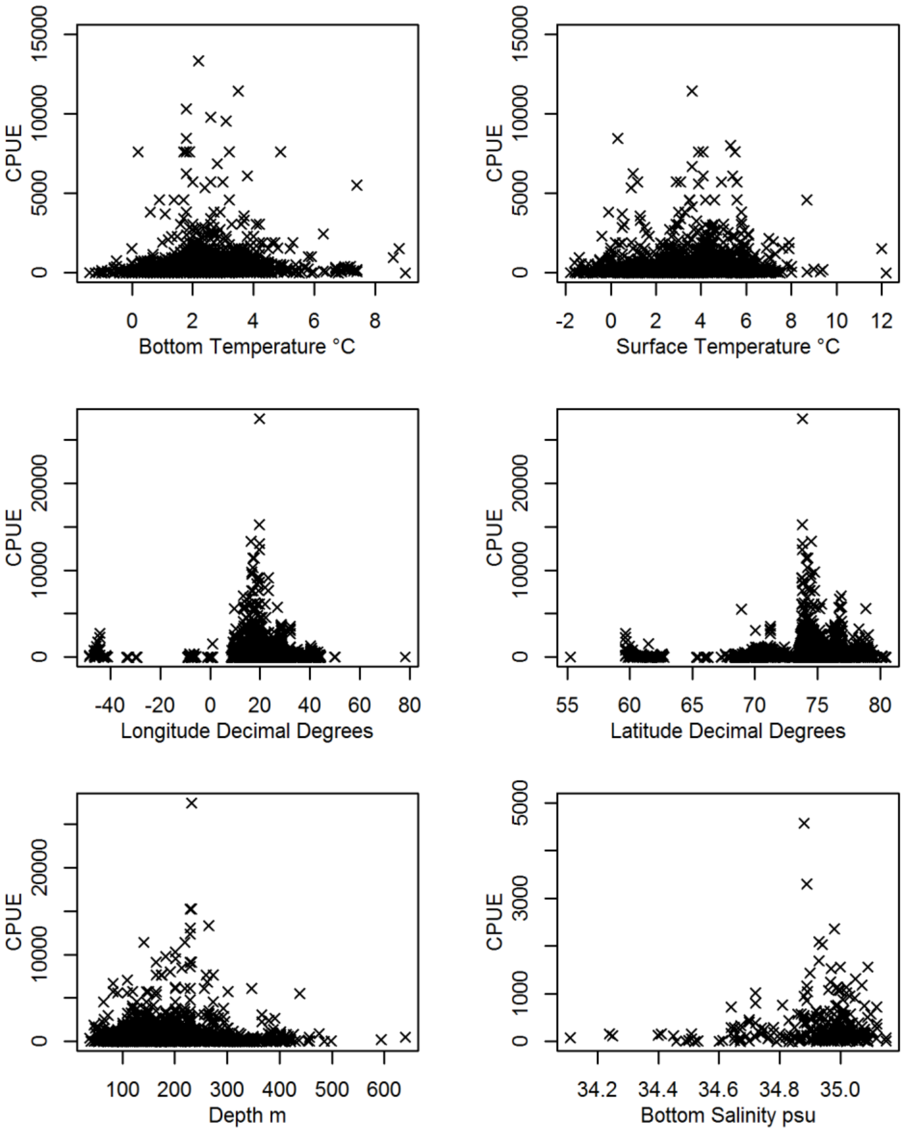

Figure 6: Relationship between CPUE and spatial and environmental variables.

Table 3: Summary results from GAMs developed to predict cod CPUE. Theta (θ) measures dispersion of the negative binomial distribution. df = degrees of freedom

Name	**Adj. R-sq**	**θ**	**df**	**UBRE Score**	**Deviance explained (%)**	**n**	**Significant**
Temporal CPUE GAM	0.23	0.389	63.5	0.28	25.1	2741	All
Environmental CPUE GAM	0.06	0.692	69.26	0.32	24.9	1218	All
Spatio-temporal CPUE GAM	0.10	0.407	121.1	0.31	28.6	2741	All

The environmental model identified that surface temperature was less reliable at explaining CPUE than bottom temperature, with highest CPUE predicted at both high and low surface temperatures. Depth was a good explanatory variable for CPUE between 100–300 m, although with fewer data points at depths less than 100 m and more than 300 m, the model is less reliable at shallower and greater depths. The temporal model supported initial visual analysis of the data (Figure 4), describing high CPUE from 1930 to late 1940s followed by a decline in the early 1950s and a slight increase later in the 1950s. The temporal model suggested variation in catches throughout the year, with highest CPUE in the summer and winter months and lowest CPUE in the spring months. Development of the spatio-temporal model found latitude and longitude, along with time, were valuable descriptors of CPUE.

There was substantial interannual variation in prey items identified in cod stomachs from 1930–1959 (Figure 7). Capelin was particularly important in the diet of cod in 1949, 1951, 1952, 1953 and 1957, dominating the diet in 1953. The importance of crustaceans such as euphausiids (but also hyperiid amphipods) was highly variable, contributing a large proportion of prey items in most years except 1951, 1954 and 1956. Cod cannibalism was also variable, with the highest proportions of cod in the diet in 1952 and 1957. Herring occurrence in cod stomachs was low overall in comparison to capelin, with the highest frequencies in 1950 and 1954. The number of empty stomachs and the presence of euphausiids, was particularly low in 1953, when capelin made up the greatest proportion of cod diets.

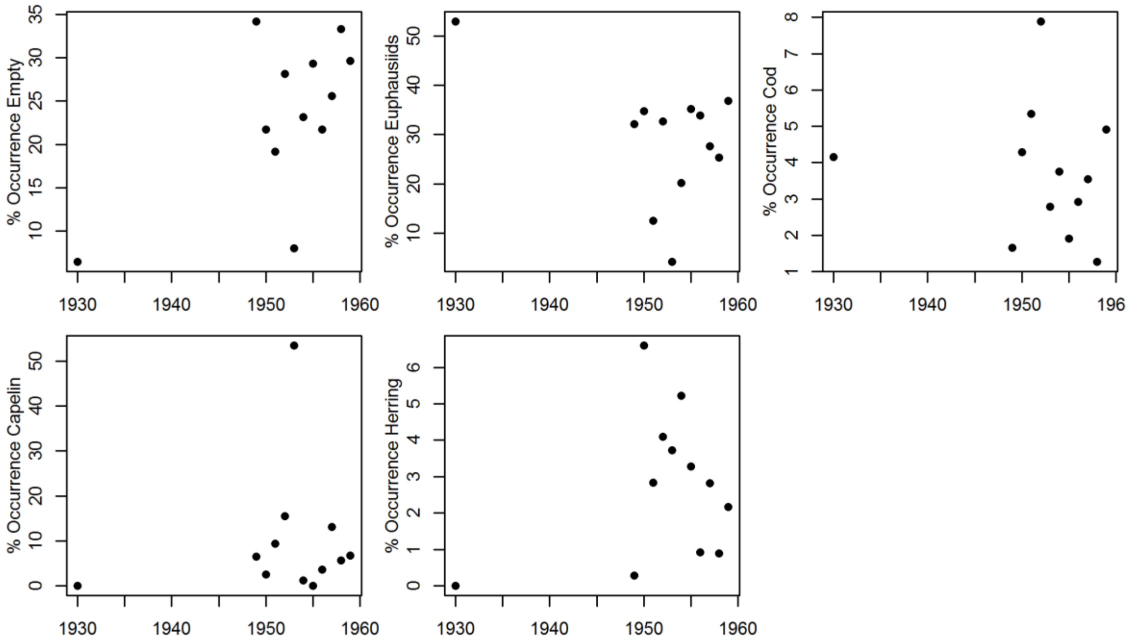

Figure 7: Annual mean percentage occurrence of the five major stomach content categories.

The GAMs found that spatial, temporal and environmental variables were all associated with cod diet. Longitude, latitude, year, day of year, bottom and surface temperatures, and depth were all valuable descriptors of cod diet (Table 4). Models predicted up to 89% of the variation in occurrence of items in the diet, indicating that these factors can dominate prey choice. Highest explanatory capability was for capelin and herring, suggesting spatio-temporal and environmental drivers, while small cod and euphausiids, and empty stomachs were explained less well by these variables (deviance explained = 26–54%). All variables were significant in all models except for depth in the environmental model for cod as prey.

Table 4: Summary results from GAMs developed to predict frequencies of prey in cod diet. df = degrees of freedom

Prey	**Model**	**Adj. R-sq**	**Total df**	**GCV Score**	**Deviance Explained (%)**	**n**	**Significant (P < 0.05)**
Euphausiid	Environmental GAM	0.44	43.44	5.98	43.3	691	All
	Temporal GAM	0.55	55.58	5.09	52.7	1025	All
	Spatio-temporal GAM	0.21	44.22	7.84	25.5	1025	All
Capelin	Environmental GAM	0.89	82.42	1.05	88.4	691	All (depth P = 0.03)
	Temporal GAM	0.91	64.37	0.83	89.6	1025	All
	Spatio-temporal GAM	0.89	98.25	0.94	89.1	1025	All
Cod	Environmental GAM	0.23	52.97	1.62	33.5	691	Not depth
	Temporal GAM	0.40	41.55	1.32	42.7	1025	All
	Spatio-temporal GAM	0.39	96.22	1.43	44.5	1025	All
Herring	Environmental GAM	0.65	82.76	1.34	68.9	691	All

Prey	Model	Adj. R-sq	Total df	GCV Score	Deviance Explained (%)	n	Significant (P < 0.05)
	Temporal GAM	0.63	66.3	1.07	71.9	1025	All
	Spatio-temporal GAM	0.56	120	1.23	71.1	1025	All
Empty	Environmental GAM	0.45	48.23	3.97	45.2	691	All
	Temporal GAM	0.56	53.96	3.74	54.1	1025	All
	Spatio-temporal GAM	0.45	80.69	4.68	45.7	1025	All

Discussion

We used previously unavailable analytical techniques to investigate underlying variables responsible for historical changes in the Barents Sea food web. Our analysis improves the knowledge base of the role of climate on the ecology of this region, and demonstrates the importance of rescuing historical datasets, even if incomplete. For example, spatial distribution in catches should be treated with some caution because the location of the sampling stations was not based on a contemporary rigorous statistical survey design; to an extent this could have affected our results on historical cod diets. In addition, because catch weights are based on assumptions of averages (both basket weights and individual fish weights) rather than absolute values, these weights should be considered as relative rather than exact. Nevertheless, analysis of this dataset shows that environmental, spatial and temporal variables were all important descriptors of prey items consumed by cod in the Barents Sea, ultimately influencing catches of cod in the region. This dataset represents a period of time when cod stocks were initially very large and subsequently declined. Catches in surveys were higher in the 1930–1940s compared to the 1950s. Catches were more variable in space and time across the Barents Sea in the 1950s. Lowest predictive power was during the 1930s and 1940s due to a paucity of data; the result of fewer cruises. Previous work has shown that CPUE was higher from 1925–1960 when compared with cooler periods before or since, coinciding with high cod recruitment (Godø, 2003). The low CPUE observed in spring is likely to be a result of cod, after their return from the winter spawning grounds, dispersing widely to commence feeding.

Cod diet varied significantly between years, with capelin and herring being strongly influenced by environmental variables. A dominance of capelin in the diet was seen in 1953, a cold year, which tends to favour capelin abundance (Orlova *et al*., 2005); in this year, few empty stomachs were recorded and there were low proportions of cod and euphausiids in the diet. This peak supports the importance of capelin as a food source for cod over other prey species when available. Analysis of cod stomachs sampled further east during Russian surveys in the 1930s found that haddock *Melanogrammus aeglefinus* and capelin were the preferred prey items, and that euphausiids were eaten only when fish were unavailable (Zatsepin and Petrova, 1939). A reported decline in capelin from 1958–1960 (Gjøsæter, 1998) coincides with the reduction of capelin in cod stomachs in 1958 in this study. Euphausiid numbers are also affected by climate, which explained 30–60% of the variation in their abundance in one study using stomach data from 1952–2009 (Orlova *et al*., 2015). Analysis of more recent stomach contents records (from 1984–2006) similarly found that capelin was the most important prey item by weight (at 30%) (Dolgov *et al*., 2007). These data have also been used to provide calculations of total prey consumption and energetics (Dolgov *et al*., 2007), to which this newly available data for earlier decades could make a valuable contribution. Cod cannibalism is known to be widespread, and Russian and Norwegian cod stomach content analyses have shown that cod cannibalism is negatively correlated with capelin abundance and varies spatially (Yaragina *et al*., 2009), also found here.

The work here largely confirms analysis from recent decades which have provided a better understanding of impacts of climate on annual movements and distributional shifts in cod. For example, climate variability influences Barents Sea cod distribution and causes a northward distribution shift in warmer years; in the 1920s and 1930s it is thought that cod, haddock and herring *expanded* farther north in the north Atlantic, whereas the range of capelin and polar cod was *shifted* to the north (Drinkwater, 2006). Water temperature during the first year of life is also a good descriptor of strong year classes; for example weak year classes from 1979 to 1982 coincided with cold years, while strong year classes from 1983–1984 in Barents Sea cod were associated with warm periods (Helle and Pennington, 1999; ICES, 2014b). Our analyses of data from preceding decades support the findings of colleagues (Helle *et al.*, 2002); that temperature and depth affect cod distribution and abundance. The 2–3°C temperature range occupied by cod in the Barents Sea is considered optimal for this stock (Orlova *et al*., 2005), corroborating our findings that catches were highest at 2–4°C. Scientists on board the *RV Ernest Holt* reported finding the largest stock at the boundary of the West Spitsbergen Current (Atlantic water) and the Bear Island Current (Arctic water), with cod being particularly concentrated where these two waters mixed (Graham, 1953). In parallel with cod, the distribution of capelin is also affected by sea temperature, with the population moving north and east in warmer years (Gjøsæter, 1998; Drinkwater, 2006).

The Atlantic Multidecadal Oscillation (AMO), derived from de-trended north Atlantic-wide sea surface temperatures, is important in characterising multi-decadal climate variability and correlates with fish production and changes to spawning sites (Drinkwater, 2011). Barents Sea warming followed by cooling during the period of this study (1930–1959), illustrates changing phases of the AMO, which has a periodicity of 60–80 years (Kerr, 2000). Thus, effects of changes in Barents Sea temperature and hydrography are the likely cause of changes in the ecosystem (Drinkwater, 2006). In more recent years there is evidence of changing climatic conditions and fisheries management affecting the ecology of the Barents Sea and the abundance of cod (Kjesbu, 2014). Zooplankton and fish populations have shifted poleward (Drinkwater, 2011), and since 2003 cod have been spawning further north along the Norwegian coast than any time in the previous 40 years (Sundby and Nakken, 2008). Inclusion of data from this study in analyses with Norwegian and Russian datasets from more recent decades would allow long term variation in fishing mortality, cod abundance, diets and hydrography to be considered in a context of climate variability. Suggestions for future analyses include testing for a time lag between temperature in previous years and subsequent catches, including fishing intensity information where available, and exploring additional data on prey availability, such as spatio-temporal variability in prey abundance (Dalpadado and Skjoldal, 1991; 1996)].

Since the Barents Sea has been fished by many nations, but is highly sensitive to climate change, these data can help inform future management of cod stocks. Understanding the influence of climatic conditions on past trends in cod abundance informs predictions of stocks in the future, but predicting climate change effects in the Barents Sea is non-trivial since climate variability is modulated by the North Atlantic Oscillation (NAO) and AMO as well as potential anthropogenic climate change. This newly available time series on cod abundance and prey provides insight into previous patterns of change in the Barents Sea ecosystem, which are relevant to future change. Climate models for the Barents Sea region predict a 5 °C air temperature rise by the end of the century (Keup-Thiel *et al*., 2006), a 1-2 °C sea temperature rise, and potential changes to ocean currents and water masses (Furevik *et al*., 2002). Under present temperature conditions the population has already expanded northwards, but it could continue eastwards and migrate for a longer period of each year (Kjesbu *et al*., 2014), depending upon depth limitations of cod. Simulations of climate change effects suggest that capelin will also move north-eastwards in the Barents Sea in the future (Huse and Ellingsen, 2008), and indeed they have moved in this direction in recent years (Prozorkevich and Gjøsæter; 2013). Simulations predict that Atlantic zooplankton production will increase 20% by 2059, while Barents Sea zooplankton may decrease (Ellingsen *et al*., 2008). Species responses to climate change, and resulting movement of prey are likely to affect cod survival and distributions, with ecosystem-wide implications if phenological changes to spawning cause mis-matches (Beaugrand and Ibañez, 2002; Beaugrand and Reid, 2003).

Our study demonstrates the value of using historical datasets that, although lacking contemporary statistical rigour and consistency of survey design, provide valuable knowledge on abundance, spatial distributions, prey selectivity and underlying climatic drivers. At a global scale, long-term spatio-temporal data are highly patchy, yet are crucial for understanding how climate change can affect marine ecosystems. With further effort, including digitising UK data from 1960–1976 and integrating Russian and Norwegian data, time series of distribution and diets of Barents Sea cod from 1930 to the present day are achievable, which could then be used in climate impact projections. These datasets are made possible by international collaboration and substantial investment in digitising the wealth of historical logbooks kept by marine scientists, fishermen and naturalists of bygone eras. Extensive time series are invaluable for understanding the influences of cyclical and directional climate change on fish stocks.

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Data Accessibility

All relevant data, including catch data and stomach contents data, are available from Cefas (https://www.cefas.co.uk/publications-data/fish-stomach-records).

Chapter 3

Fisheries, low oxygen and climate change: how much do we really know?

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Abstract

As a result of long-term climate change, regions of the ocean with low oxygen concentrations are predicted to occur more frequently and persist for longer periods of time in the future. When low levels of oxygen are present, this places additional pressure on marine organisms to meet their metabolic requirements, with impacts on growth, feeding and reproduction. Extensive research has been carried out on the effects of acute hypoxia, but far less on long-term chronic effects of low oxygen zones, especially with regard to commercially important fishes and shellfishes. To provide further understanding on how commercial species could be affected, the results of relevant experiments must support population and ecosystem models. This is not easy because individual effects are wide-ranging, for example studies to date have shown that low oxygen zones can affect predator-prey relationships as some species are able to tolerate low oxygen more than others. Some fishes may move away from areas until oxygen levels return to acceptable levels, while others take advantage of a reduced 'start response' in prey fishes, and remain in the area to feed. Sessile or less mobile species such as shellfishes are unable to move out of depleted oxygen zones. Some species can tolerate low oxygen levels for only short periods of time, while others are able to acclimatise. To advance the knowledge-base further, a number of promising technological and modelling-based developments, and the role of physiological data within these, are proposed. These include advances in remote telemetry (tagging) and sensor technologies, trait-based analyses to provide insight into how whole assemblages might respond in the future, research into long-term adaptability of species, population and ecosystem modelling techniques and quantification of economic impacts. In addition, more detailed

oxygen monitoring and projections are required to better understand the likely temporal and local-scale changes in oxygen.

Introduction

Oxygen availability is a key factor that determines habitat suitability and geographic distribution of marine fishes (Cheung *et al.*, 2012; Zambonino-Infante *et al.*, 2013). While low oxygen conditions can occur naturally, and by eutrophication particularly in coastal areas, climate change effects may also contribute to a reduction in oxygen concentration and subsequent ecosystem disturbance. As a result of climate change, reduced oxygen concentrations are predicted to occur more extensively, more frequently and for longer periods of time in the future (Matear and Hirst, 2003; Keeling *et al.*, 2010; Stramma *et al.*, 2010; IPCC, 2014). Despite a large body of scientific literature on the physiological and behavioural responses of fishes and invertebrates to low oxygen conditions at the individual level, not all of this research is helping to explain how these low oxygen levels will affect commercial fin and shellfish species at the stock and population level (Somero *et al*., 2016), and hence the fisheries that rely on them. In order to inform policy and fisheries management there is a clear need to better understand how existing knowledge about the individual physiological and behavioural responses of fishes and invertebrates can be used in population and ecosystem models to scale up to populations. This will identify further experimental evidence required, to be applied within a wider fisheries context.

The potential role of climate change in affecting oxygen levels has only been recognised in recent years. Hypoxia was highlighted in the latest IPCC (2014) Working Group II Fifth Assessment Report (WGII AR5) for the first time as an ocean system change, of importance alongside temperature and ocean acidification. Oxygen concentrations are also specifically mentioned in the European Union’s Marine Strategy Framework Directive (MSFD) (under descriptor 3), which states that governments should take action so that “*reductions of oxygen concentrations do not constitute an undesirable disturbance to the balance of organisms present in the water and to the quality of the water concerned*”. Areas of low oxygen cover a range of concentrations and are referred to by a number of terms including low oxygen, oxygen minimum zones (OMZs), hypoxia, and anoxia or dead zones (no oxygen) (Rabalais *et al.*, 2010; Hofmann *et al.*, 2011; Gilly *et al.*, 2013). No attempt has been made here to define these terms, as they are all widely used and each publication tends to define them on first use, albeit slightly differently. The IPCC's WGII AR5 report (IPCC, 2014) refers to the commonly used hypoxic oxygen concentration of 60 µmoles kg^{-1}, however a recommendation of 30% saturation (63 µmoles kg^{-1}) was cited by the Scientific Committee on Ocean Research (SCOR) Working Group on Natural and Human-Induced Hypoxia and Consequences for Coastal Areas (Rabalais *et al*., 2010). There is also no single oxygen concentration below which waters are considered to be detrimental to organisms because sensitivity varies greatly between species, populations and individuals and also depends on temperature and other factors (Chabot and Claireaux, 2008; Rabalais *et al.*, 2010; Zhang *et al.*, 2010; Rogers *et al*., 2016). In some cases low oxygen conditions are defined simply as those with oxygen concentrations above the extreme lows of hypoxia but below normal oxygen saturation levels, and it is these intermediate oxygen concentrations that are the main focus of this review.

There are numerous primary scientific studies describing how the oxygen content of water affects the physiology and energy balance of marine species (Fry, 1971; Claireaux and Lagardère, 1999; Pörtner and Knust, 2007; Zhang *et al.*, 2010; Cheung *et al.*, 2012), and it is widely known that the oxygen solubility of seawater declines as temperatures increase. A considerable body of work is available on the development of hypoxia, the toxicology of acute hypoxia, anoxia and dead zones caused by eutrophication, as well as the physiological effects on fishes and invertebrates from laboratory studies (e.g. Claireaux *et al.*, 2000; Lefrançois and Claireaux, 2003; Gamperl and Farrell, 2004; Breitburg *et al.*, 2009; Richards *et al*., 2009; McElroy *et al,* 2012; Gilly *et al.*, 2013). Many reviews have also been written on this subject (e.g. Colijn *et al.*, 2002; Camargo and Alonso, 2006; Bickler and Buck, 2007; Chabot and Claireaux, 2008; Diaz and Rosenburg, 2008; Levil *et al*., 2009; Ekau *et al.*, 2010; Zhang *et al.*, 2010; Rogers *et al*., 2016). Less work however, has been carried out on chronic sub-lethal effects of low oxygen (levels above hypoxic), including behavioural effects, or on how this then translates into population and ecosystem scale impacts (Cheung *et al.*, 2008), perhaps because monitoring of long term effects is prohibitively costly. In fact, there is very little certainty of how low oxygen levels will affect species, populations and ecosystems (Oswald *et al.*, 2011; Heath *et al.*, 2012; Gilly *et al.*, 2013) because of the difficulty of scaling up from experimental results on individual animals. It is known that an expansion of areas of low oxygen will have direct impacts on some marine organisms by affecting adult physiology and/or behaviour but it will also have impacts on populations and stocks, or indirect impacts through ecosystems and food webs (Pörtner, 2010; Cheung *et al.*, 2011; Metcalfe *et al.*, 2012). This is likely to be the case across a broad range of taxonomic groups across the globe (Koslow *et al.*, 2011).

Ecologists, molecular scientists, geneticists, modellers and conservationists are coming to realise the need to integrate their different disciplines, and incorporate physiological information into their work, in order to fully understand the impacts of projected environmental change and adaptation (e.g. Dalziel *et al*., 2009). Conservation physiology and ecophysiology are relatively new disciplines which use physiological knowledge to provide a mechanistic understanding of how animals function in their environment, and to predict the impacts of change, from either environmental or conservation interventions. Within this it tends to be the responses of an individual animal that are the focus at the experimental level. It is then usually down to ecologists and population modellers to use the new knowledge in predictive models to interpret the likely impacts of environmental change at the level of populations to ecosystems. With this in mind, research will need not only experimental results that show the effects of low oxygen conditions on individuals, but also advanced modelling techniques, in order to translate experimental data into useable predictions of population and ecosystem effects (MCCIP, 2014). Here, from a modelling point of view, a theoretical framework is presented to show how low oxygen could affect individuals, populations, ecosystems and fisheries, and to propose how experimental studies and physiological and behavioural knowledge can be used as a basis to build and improve modelling studies (Figure 8).

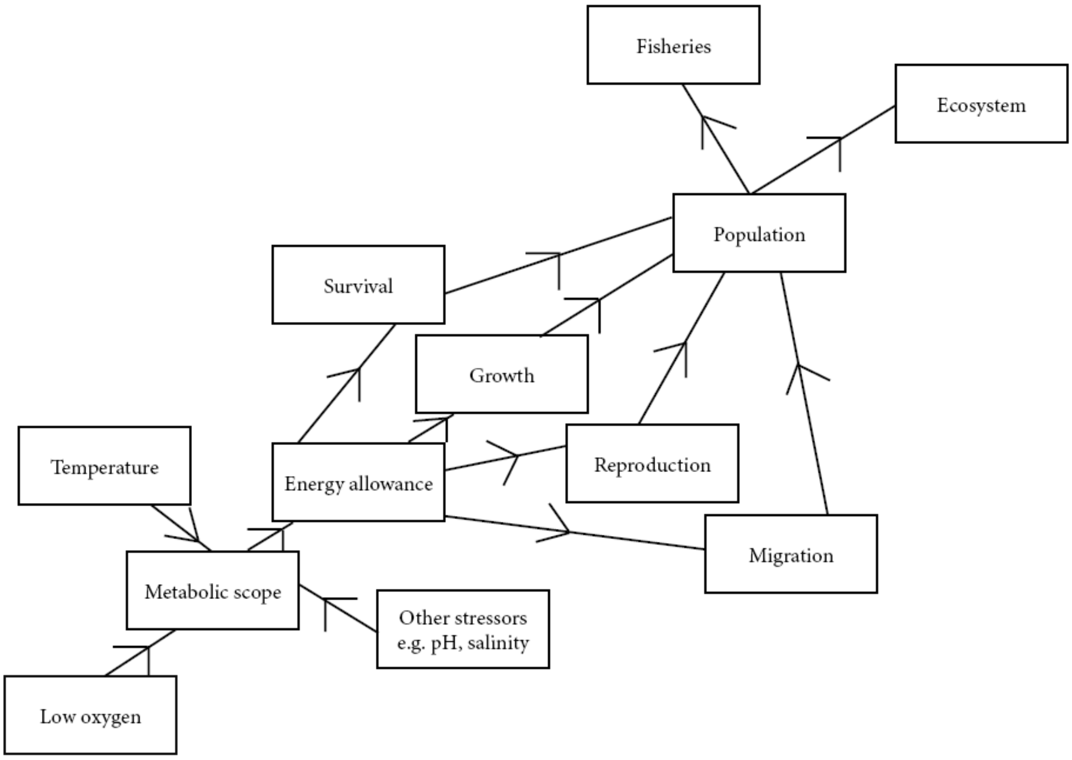

Figure 8: A theoretical framework of the effects that climate-induced low oxygen conditions may have on commercial fish and shellfish.

In this review the changes occurring in the world's oceans that influence oxygen levels are first introduced, before discussing some of the effects that low oxygen has been shown to have on early and adult life stages of marine organisms, mainly but not exclusively on fishes. Since an extensive body of literature already exists on the acute effects of hypoxia, it is important to identify what is likely to be useful from a modelling point of view, and whether and where further work is required to inform management. This review does not aim to provide an exhaustive assessment of hypoxia, or indeed of low oxygen zones. Instead the focus is on providing an overview of the range of work which is already available on individual, population and ecosystem-level effects on commercial fish and shellfish species, particularly with reference to climate-induced chronic low oxygen as opposed to acute hypoxia, and which can be taken forward for use in ecological forecast modelling. This is then used as the basis for identifying the types of experimental evidence that may be helpful, and in turn to determine how such information could be included in ecosystem and population models which incorporate oxygen concentrations and forecasts. A number of modelling techniques are described along with their potential applications in scaling up to predict the effects of low oxygen on whole ecosystems and fisheries. Lastly areas are proposed where more research should be focussed to fill gaps and advance knowledge with respect to this important topic.

Climate and oxygen

Dissolved oxygen concentrations are decreasing in many marine ecosystems around the globe, particularly in shallow areas and northerly latitudes (Matear and Hirst, 2003; Keeling *et al.*, 2010; Rabalais *et al.*, 2010; Stramma *et al.*, 2010; Cheung *et al.*, 2012; Heath *et al.*, 2012; Zambonino-Infante *et al.*, 2013). In the well-documented oxygen minimum zones of the tropical Indian, Pacific and Atlantic oceans, oxygen levels have declined since the middle of the last decade (Koslow *et al.*, 2011), and oxygen concentrations in the Pacific regularly reach lower levels than in the Atlantic (IPCC, 2014). Climate variability also contributes to changes in oxygen concentrations, alongside long-term climate change (Gilbert *et al.*, 2010). In some areas an increase in temperature, such as is caused by climate change or decadal variation, has been shown to exacerbate the observed reduction in oxygen concentration by reducing oxygen solubility and increasing strength and duration of stratification (Keeling *et al.*, 2010; Rabalais *et al.*, 2010; Hofman *et al.*, 2011; Queste *et al.*, 2013). Other factors affecting oxygen levels in the sea are the amount of organic matter, the overturning (vertical exchange of water masses due to salinity and temperature differences) and ventilation rates (the movement of oxygenated surface water into deeper areas) in certain areas (Matear and Hirst, 2003), and in coastal waters limited water exchange (e.g. Black Sea and Baltic Sea), nutrient influx, run-off (e.g. Chesapeake Bay, Mississippi River and Changjiang) and seasonal upwelling (e.g. coasts of Namibia, Chile and Peru) (Zhang *et al.*, 2010). Benthic production and associated oxygen consumption (respiration) further decrease bottom water oxygen levels (Weston *et al.*, 2008). In coastal areas, low oxygen levels triggered by climate change can be exacerbated by eutrophication (Greenwood *et al.*, 2010).

Over the coming century, there is projected to be an increase in thermal stratification of the ocean during the summer, particularly in northern latitudes, creating a barrier that prevents oxygen getting to lower depths, and so reducing oxygen levels in deeper waters (Keeling *et al.*, 2010). Climate change may worsen natural and eutrophication-induced hypoxia by increasing precipitation, rainfall run-off and nutrient-loaded freshwater discharge in some areas (Rabalais *et al.*, 2010; Zhang *et al.*, 2010). Simulations for the Baltic Sea, an area where low oxygen levels are a regular occurrence, suggest that by the end of the twenty-first century oxygen concentrations may be lower than at any time since 1850 (Meier *et al.*, 2012). Outputs of physical hydrodynamic models suggest that oxygen levels in the global ocean will decrease further in the future as a result of changes in hydrological and biological regimes (Table 5). However the Table illustrates that the differences will vary across the globe, with some areas experiencing much higher reductions than others, and with oxygen in the deep ocean having a much greater depletion. The changes will not be uniform within each ocean as the averages suggest, with local-scale processes affecting the patchiness and temporal occurrence of low oxygen areas (e.g. van der Molen *et al*., 2013).

Table 5: Examples of the projected average reductions in oxygen concentration in a number of oceans, and globally. Some regions show much larger reductions to the end of century than others.

Region	**Projected reduction in oxygen concentration (%)**	**Years modelled**	**Reference**
Global	4-7 averaged over the whole water column 20-40 in deep water (2000 – 4500 m)	To 2100	*Sarmiento et al.*, 1998; *Matear et al.*, 2000; *Plattner et al.*, 2001; *Bopp et al.*, 2002; Matear and Hirst, 2003
Global	1-7	To 2100	Keeling *et al*., 2010
Global	2-4	1870-2100	Cucco *et al*., 2013
Pacific Ocean	1.6	1820 to 2100	Frölicher *et al*., 2009
Atlantic Ocean	3.7	1820 to 2100	Frölicher *et al*., 2009
Indian Ocean	3.1	1820 to 2100	Frölicher *et al*., 2009
Central North Sea	11.5	To 2100	Meire *et al.,* 2013
North Sea	5.3-9.4	To 2100	van der Molen *et al.*, 2013
Global	1.81-3.45	To 2090s	Bopp *et al*., 2013

Physiological effects

Oxygen is required to sustain vital metabolic processes of marine organisms and also essential activities such as muscular activity, growth and reproduction (Pörtner and Knust, 2007). Scientists have long realised that low oxygen zones inhibit movements of fishes and shellfishes and affect predator-prey relationships, and recent work has shown the many different ways in which organisms can be affected, ranging from becoming stressed, moving out of the area to dying (e.g. Fry, 1947; Fry, 1971; Schurmann and Steffensen, 1992; Prince *et al.*, 2010; Stramma *et al.*, 2010; Urbina *et al*., 2011). Some organisms (both species and individuals) are affected more than others and the effect depends upon the strength of depletion and the time exposed. Ekau's (Ekau *et al*., 2010) review of hypoxia impacts on pelagic ecosystems provides a comprehensive table of the oxygen concentrations at which impacts on physiological functions of various marine species have been observed. Factors included range from effects on egg development, to spawning and survival, demonstrating how important oxygen is for fundamental processes which enable a species to persist in an area. A number of studies have described the different ways in which some fish species are adapted, or are able to tolerate these low oxygen conditions including body size adaptations, haemoglobin types, anaerobic metabolic abilities and behavioural adaptations (e.g. Pörtner, 2002; Chapman and McKenzie, 2009; Nilsson 2010; Pörtner, 2012; Zhu *et al.,* 2013; Somero *et al*., 2016). However the difficulty lies in understanding how these mechanistic tolerances and adaptations are reflected in population and ecosystem processes because not every individual, population or stock of a species is adapted to the same extent. This challenge can begin to be addressed by using the various modelling techniques available, and considering chronic low oxygen as well as the more frequently considered acute hypoxia. Examples of oxygen impacts on individuals are given here for illustrative purposes and are often from short-term experiments, but they are able to show the range of effects seen in marine organisms.

There are certain thresholds below which oxygen levels affect the aerobic performance of marine organisms (Pörtner, 2010) although this is very much dependent upon the exposure time, species or type of organism, respiration mode, and metabolic and physiological requirements, with highly active species being generally less tolerant of low oxygen conditions (Stramma *et al.*, 2011). It has been shown that lowering oxygen concentrations only a relatively small amount may have little or no effect on metabolic activity, but lowering further below a threshold, can curtail or impair certain oxygen-demanding functions (Claireaux *et al.*, 2000; Claireaux and Chabot, 2016). Even at relatively high oxygen levels, subtle effects begin to occur (e.g. Urbina *et al*., 2011). For example, metabolic or aerobic scope (a measure of the difference between the maximum and standard metabolic rates, i.e. the scope for activity above standard metabolic rate) becomes reduced when oxygen levels drop below normoxia (Fry, 1971; Claireaux and Chabot, 2016). Then a fish has a reduced capacity to carry out activities such as movement, reproduction, predator escape or digestion (Fry, 1971; Dutil *et al.*, 2007). Animals with smaller metabolic scope may experience limits to their activity sooner than those with larger scope. Some organisms are able to prioritise activities when oxygen levels are sufficiently low to limit their metabolic scope, for example European sea bass *Dicentrarchus labrax* (L. 1758) can prioritise aerobic exercise over digestion (Dupont-Prinet *et al.*, 2009).

The ability of an organism to tolerate low oxygen can be affected by other stressors such as sea temperature, salinity and ocean acidification, which may also become more problematic as a result of future climate change (Chabot and Claireaux, 2008; Keeling *et al.*, 2010; Vaquer-Sunyer and Duarte, 2011; Heath *et al.*, 2012; Pörtner, 2012). Critical oxygen concentrations or tensions (P_{crit}) are the lowest partial pressure at which an animal can maintain its resting metabolic rate. It has been shown that many fishes which tolerate increasing temperatures have higher critical oxygen concentrations or require an increase in oxygen concentration (Pörtner and Knust, 2007), although among species this relationship is highly variable (Rogers *et al*., 2016). A review of the hypoxia responses in fishes by Rogers *et al*. (2016) found that increased temperature caused an increase in P_{crit} in 19 species, but a decrease in four species. They also found that other factors including salinity, food, pollutants and pCO$_2$ concentrations affect the P_{crit} of species differently. A rise in sea temperature may reduce hypoxia tolerance of benthic marine invertebrates and decrease the oxygen thresholds which cause mortality (Vaquer-Sunyer and Duarte, 2011; Dupont-Prinet *et al.*, 2013a). Increased temperature exacerbates an organism's oxygen vulnerability not only by increasing oxygen demand, but also because oxygen is less soluble in water at higher temperatures, making less oxygen available for respiration (Pörtner and Knust, 2007). These factors mean that an increase in temperature caused by global warming may have effects on animals even before their lethal thermal limits are reached (Wang and Overgaard, 2007). At both ends of an organism's thermal tolerance levels, metabolic scope is limited by oxygen supply. This is known as 'oxygen and capacity dependent thermal tolerance' (Pörtner, 2010). If an animal experiences a reduction in its capacity to perform aerobically, thermal limitation begins because the circulatory and ventilatory systems struggle to match oxygen demand (Pörtner and Knust, 2007). The effects of temperature and oxygen on metabolic rates and scope can be most easily understood diagramatically (Figure *9*). The evolution of fishes has resulted in a metabolic scope that is maximised within a certain temperature range, within which performance (growth, feeding, reproduction, movement etc.) is maximised (Clark *et al.,* 2013b). At higher temperatures, standard metabolic rate increases more than maximum metabolic rate causing a narrowing of the metabolic scope. Maximum metabolic rate decreases with lower oxygen levels, further decreasing metabolic scope (Figure 9), and reduces the temperature with the optimal scope (Figure 9). These complex relationships with metabolic scope and optimal temperatures mean that it is difficult to separate the effects of temperature, oxygen and also pH/carbon dioxide concentrations. Low pH reduces tissue functional capacity, narrowing the organism's thermal window again and making them more vulnerable to increases in temperature. To complicate issues further, some species have the ability to supress their metabolism when exposed to hypoxia. For example, under hypoxic conditions, the oxygen consumption of the jumbo flying squid *Dosidicus gigas* (d'Orbigny 1835) is 20% lower than under normoxic conditions, giving the animal an energetic advantage over competitors (Seibel *et al.*, 2014). Another way in which species are able to acclimate and broaden or shift their thermal window is by changing mitochondrial densities, but there are limits to how far they are able to do this (Pörtner and Knust, 2007). Some fishes become conditioned if exposed to hypoxia or environmental variability at an early life stage (Norin *et al.*, 2013; Zambonino-Infante *et al.*, 2013). For example individuals that experience wide ranges of temperatures, such as those in sub-polar regions, are thought to have a higher resting metabolic rate, and a wider thermal tolerance (Pörtner, 2012).

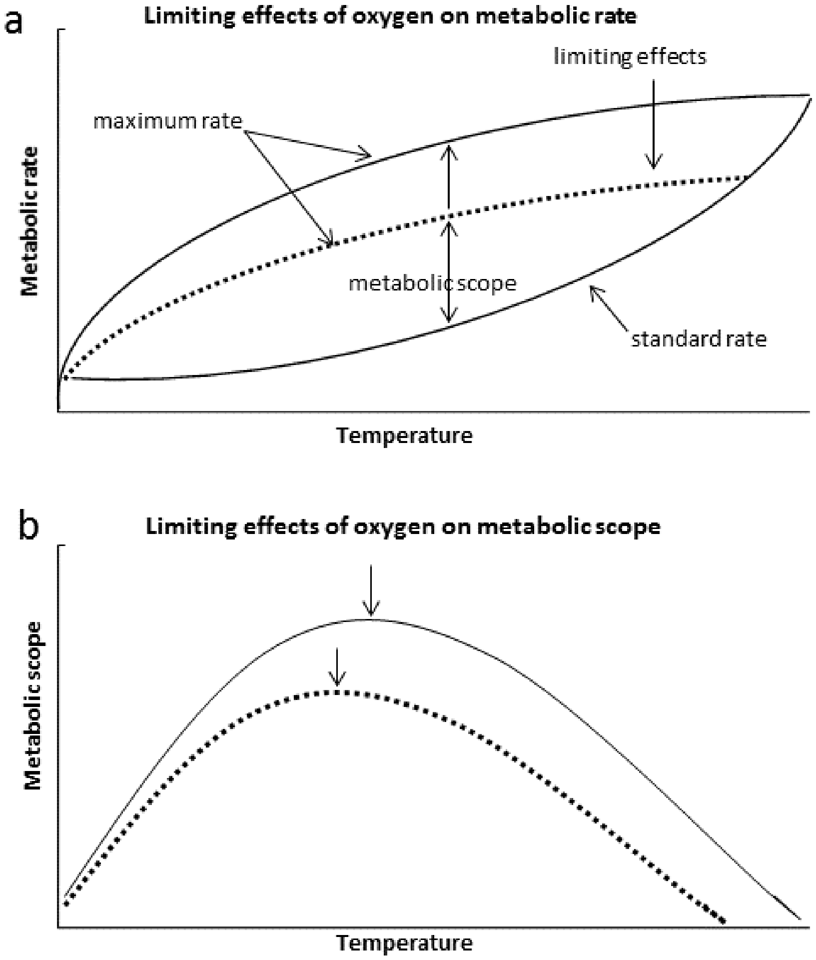

Figure 9: (a) The limiting effects of reduced oxygen on the maximum metabolic rate. Reduced dissolved oxygen will cause limiting effects on the maximum metabolic rate (dotted line), reducing the metabolic scope. (b) The limiting effects of reduced oxygen on metabolic scope. As oxygen is reduced, the metabolic scope is also reduced at any given temperature. Adapted from Fry (1947).

If the scientific community is to fully understand the ecosystem and fishery consequences of climate change induced low oxygen levels, the impacts on not only adult marine organisms, but also other life stages, must be taken into account. Many of the results of experiments on early life stages could be incorporated into models. They could be used to show how reductions in fecundity, growth or survival at early life stages will result in effects on populations and also up the food chain, causing changes at the ecosystem and fishery level. For example, if climate change increases the occurrence and duration of hypoxic events in coastal areas, as predicted, this will impact on shallow nursery areas where many commercial fishes spend their early life stages, ultimately resulting in fewer recruits to the population (Zambonino-Infante *et al.*, 2013). Healthy egg development is also important in maintaining sustainable populations. The conditions necessary for successful egg development, sometimes known as reproductive volume (Plikshs *et al*., 1993), have been studied for Atlantic cod *Gadus morhua* L. 1756 using incubation experiments based on conditions found in the Baltic Sea (Köster *et al.*, 2005). Oxygen concentrations below a threshold of 2 ml l^{-1} resulted in no successful egg development. In the wild these changes in oxygen concentrations are related to the strength of the inflow of water from the North Sea into the Baltic Sea. Herring *Clupea harengus* L.1758 could be particularly susceptible to low oxygen conditions in the future because this species lays its eggs on the seabed. Under prolonged sub-lethal hypoxic conditions, fish embryos experience significant impacts on their development, leading to higher rates of malformations (Braum 1973; Shang and Wu, 2004). Greenland halibut *Reinhardtius hippoglossoides* (Walbaum 1792) is a highly important commercial fish in Canada, representing 52% of the total biomass of fishes in the estuary and Gulf of St. Lawrence between 2005 and 2010 (Youcef *et al.*, 2013) and so it is important to consider as many influences on the fish's productivity as possible in fishery models. This species was the focus of a study in which egg development and hatching success was monitored under different oxygen conditions (Mejri *et al.*, 2012). While the eggs were highly tolerant to hypoxia and hatching occurred at 20% saturation, at 10% saturation development was impaired and hatching did not take place. Information such as this can be useful in climate models when considering future changes in oxygen concentration. For instance, the authors concluded that if dissolved oxygen concentrations continue to decrease in the Gulf of St. Lawrence, and levels drop to between 10 and 20%, recruitment of *R. hippolossoides* may be severely reduced and this may result in lower catches in the fishery. Spawning individuals and growing fish larvae may be affected more by low oxygen levels because of their higher metabolic rates (Pörtner and Farrell, 2008). Development of animals in prolonged low oxygen conditions can be severely impacted, with observed consequences for body size and growth (reduced 'scope for growth') because feeding rates and food assimilation are reduced (Secor and Gunderson, 1998; Pichavant *et al.*, 2000; Foss *et al.*, 2002; Pauly, 2010; Metcalfe *et al.*, 2012). The growth rate of turbot *Scophthalmus maximus* (L. 1758) for example is reduced at 45 days below 64% oxygen saturation (Pichavant *et al.*, 2000; Mallekh and

Legadere, 2002). These affects in turn will affect population metrics such as age at first maturity, maximum size and reproductive success of the organism.

It is not only fishes that are affected by oxygen changes, but invertebrates can also be vulnerable, and so should be considered in modelling studies. In terms of ecosystem and fishery effects on commercially important invertebrates, some experimental results, such as survivability, reproductive and mortality thresholds, may be of use to modellers, while others such as planktonic dispersal are more complex and require delicate integration of physical and ecological techniques. In a review of experiments on benthic marine organisms, Vaquer-Sunyer and Duarte (2011) found that if atmospheric temperature rises by 4 °C as predicted in some modelled climate scenarios for the 21st Century (IPCC, 2007a), organisms would be able to survive for an average of approximately 36% fewer days in hypoxic areas, and that if sea bottom temperatures rise by the same amount, mortality thresholds of hypoxia would increase by an average of 26%. For example the American cupped oyster *Crassostrea virginica* (Gmelin 1791) will have its survival time under hypoxic conditions halved from 20 days to 10 in waters that are 4 °C warmer, potentially leading to significant population changes. Experiments conducted on another invertebrate, the commercially important Indo-Pacific green-lipped mussel *Perna viridis* (L. 1758) over six weeks show that some bivalves are able to partially regulate their respiration in relation to the oxygen concentration of the surrounding water (Wang *et al.*, 2011). This species shows strong resistance to hypoxia by lowering their metabolic activity and energy use, however, below certain thresholds of oxygen, the animals' growth slows (reduced 'scope for growth') and mortality increases. The observed effects were intensified in lower salinities, highlighting the importance of considering multiple stressors. Critical oxygen thresholds (P_{crit}) of a number of decapod crustaceans were collated by Leiva *et al*. (2015) showing the range of oxygen tolerances for these animals. For example, Norway lobster *Nephrops norvegicus* (L. 1758) has a P_{crit} of 5.2 kPa (Hagerman and Uglow, 1985), the long-clawed squat lobster *Munida rugosa* (Fabricius 1775) 6.6 kPa, the galatheid squat lobster *Munida sarsi* Huus 1935 7.4 kPa *(*Zainal *et al.*, 1992*)*, the edible crab *Cancer pagurus* L. 1758 7.8-10.4 kPa (Bradford and Taylor, 1982) and the southern king crab *Lithodes santolla (*Molina 1782) 4-9 kPa *(*Paschke *et al.*, 2010). Some non-commercial species have lower values for example the bay ghost shrimp

*Neotrypaea californiensis (*Dana 1854) had a P_{crit} range of 1.3-2.6 kPa *(*Thompson and Pritchard, 1969*)*. Intertidal invertebrates may be more tolerant as they are adapted to fluctuating environmental *conditions (Leiva et al*., 2015). By contrast, Vaquer-Sunyer and Duarte (2011) found that crustaceans were the least tolerant to hypoxia of all organisms they tested, and that some tolerant groups such as bivalves may benefit from hypoxia due to reduced predation and competition, in a similar way to *R. hippolossoides* as mentioned previously (Mejri *et al.,* 2012; Dupont-Prinet *et al.*, 2013b). Although bivalves may be more tolerant, sessile organisms will be generally more vulnerable as they cannot usually move to localities with higher oxygen concentrations if they need to, unlike mobile species such as fin-fishes. These organisms may only be able to escape low oxygen conditions by advection of fertilised eggs or larvae (IPCC, 2014). Egg and larval dispersal are complex processes which can be difficult to capture accurately in models, however, they may be important mechanisms by which populations can survive in adverse conditions.

Behavioural responses

There have been many laboratory studies aimed at investigating the physiological and metabolic effects of hypoxia and anoxia particularly in coastal areas (e.g. Hochachka, 1986; Hochachka and Lutz, 2001; Timmerman *et al.,* 2012) however there have been far fewer studies, on the chronic sub-lethal behavioural effects of low oxygen. Useful measures of behaviour for modellers are those which might affect predator-prey interactions, reproductive behaviour and catchability. To be of particular use for climate modelling, these are necessary for both acute but also sustained changes in oxygen levels, including extreme hypoxia but also, just as importantly, low oxygen levels. A number of studies are included here as examples to illustrate the range of work available, which could be of use to modellers. As with physiological effects, much of the research to date shows the effects of acute hypoxia rather than chronic low oxygen but results are illustrative of the different behavioural responses that can be seen in marine organisms, some of which are more tolerant than others.

Effects at certain oxygen thresholds can be usefully interpreted in climate projection models by adjusting feeding, growth and predation parameters at times and in areas when these oxygen levels are found. The range of studies on behavioural changes and sub-lethal effects seems to suggest that many of the most important commercial fin-fishes and shellfishes could be seriously impacted if there are changes in seawater oxygen saturation in the future. For example *G. morhua* reduces swimming and food digestion when in water below 45% oxygen saturation for a few hours (Claireaux *et al.*, 2000; Chabot and Claireaux, 2008). *Dicentrarchus labrax* show reduced feeding behaviour below 40% oxygen saturation, and show more risk-taking behaviours after one day below 20% saturation (Killen *et al.*, 2012). Behavioural aspects such as these can be less straight-forward to include in models than physiological effects, but nonetheless should be considered when assessing the impact of low oxygen conditions. This could be done by parameterising models to fit observed behaviour where possible, to give a more realistic representation of a species' response to a stressor. Fishes may alter their activity levels or their behaviours such as feeding and avoidance strategies when exposed to hypoxia. Some fishes swim nearer the surface where oxygen levels are typically higher, or perform aquatic surface respiration (Kramer, 1987; Chapman and McKenzie, 2009); both these activities increasing their vulnerability to predators (Killen *et al.*, 2012). For example *D. labrax* have been shown to increase risk taking behaviour under reduced oxygen conditions (Killen *et al*., 2012), and New Zealand snapper *Chrysophrys auratus* (Forster 1801) experience some physiological stress and avoid waters with low oxygen levels, if the concentration is below the species' critical oxygen threshold (P_{crit}) (Cook and Herbert, 2012). Choice experiments in *G. morhua* (Claireaux *et al.*, 1995) have shown that the fish generally avoid hypoxic water, but that they will enter areas with lower oxygen for short periods, for example when food is offered or when they have a normal oxygen refuge available (Herbert *et al.,* 2011). These experiments indicate that the fish are able to tolerate low oxygen when they have a normoxic environment nearby to retreat to. Archival tagging in the Baltic Sea has shown that under natural conditions *G. morhua* do enter deeper, hypoxic water, and it is suggested that this is to feed on prey species that are more tolerant of the low oxygen conditions (Neuenfeldt *et al.*, 2009; Behrens *et al.*, 2013). The fish then move back into more oxygenated waters to digest the food, perhaps preventing any negative effects on body growth (Metcalfe *et al.*, 2012). *Gadus morhua* have been shown to select colder environments when oxygen levels decrease; this may lower their metabolic rate and so increase survival chances (Schurmann and Steffensen, 1992; Claireaux *et al.*, 1995). The species is known to completely avoid hypoxic waters in the Kattegat, Baltic Sea and Gulf of St. Lawrence when their metabolic scope approaches zero (Chabot and Claireaux, 2008). Satellite archival tagging and laboratory experiments have shown that Atlantic blue marlin *Makaira nigricans* Lacepède 1802 can also tolerate low oxygen if necessary, and dive into low oxygen waters for short durations to catch prey (Neuenfeldt *et al.*, 2009; Stramma *et al.*, 2011; Plambech *et al.*, 2013).

As with fishes, behavioural responses of invertebrates can be usefully interpreted for modelling and management. Behavioural traits which affect catchability may affect how invertebrate mortality is represented in fisheries modelling studies. In the late 1980s research was carried out on *N. norvegicus* following reports by fishermen of dead and dying animals in the Kattegat (Baden *et al.*, 1990). This area is characterised by a strong halocline and is susceptible to eutrophication during the late summer. Laboratory experiments demonstrated that individuals taken from this area and held under low oxygen conditions stood high on the substrate, with legs flexed (tiptoeing), and stopped feeding after three weeks. Under more severe low oxygen, the animals did not feed at all and died after two or three days. Another study on *P. viridis* found that low oxygen levels combined with low salinity reduced anti-predator behaviour, making them more vulnerable (Wang *et al.*, 2013). These behavioural effects caused by oxygen changes in invertebrates are of relevance to understanding the implications for fisheries. If animals spend more time out of burrows and on the mud, or show a reduction in predator-avoidance, they may be more susceptible to fishing gear.

Attempts have been made to incorporate some of these changes in activity caused by low oxygen and also temperature in modelling studies, such as those focussing on the ‘behavioural energetic hypothesis’ (Wildhaber and Crowder, 1990) and also the ‘growth rate potential model’ (Tyler and Brandt, 2001). These have not always stood up to model validation, in part due to the complexity of environmental variables that influence fish habitat and prey choice (Wildhaber and Crowder, 1990; Tyler and Brandt, 2001; Wildhaber, 2001; Wildhaber and Lamberson, 2004). As such, behavioural responses to oxygen levels are more difficult to interpret in terms of modelling than more straight-forward growth and survival responses but, nevertheless, they are important in understanding fish movements, predator-prey relationships and fisheries catchability.

Species, population and foodweb interactions

Individual responses to environmental changes may be relatively easy to measure, but some modelling techniques need information at a larger scale to understand the wider ecosystem implications. Changes to an individual's physiology or behaviour can potentially scale up and have consequences for whole ecosystems, by affecting predator-prey relationships, recruitment or vulnerability to fishing. Similarly, changes in body size could affect whole food webs as well as commercial fishing catches. Changes in the reproductive success of a species caused by climate change may impair recovery of a depleted fish stock or may reduce the effectiveness of conservation efforts (Chabot, 2013). For example, if fish nursery areas are affected by low oxygen at critical times of year, this can cause juveniles to crowd into areas of higher oxygen, and so increase density-dependent mortality (Diamond *et al.*, 2013). Low oxygen zones may be a barrier to larval dispersal as larvae are typically less tolerant of hypoxia than adults (Stramma *et al.*, 2010). In adults, reproduction may be impaired by hypoxia because females have a higher oxygen demand when brooding eggs internally (Pörtner and Farrell, 2008). It is thought that *C. harengus* require high oxygen levels to spawn, as they typically spawn in areas of highly mixed waters, and so the availability of benthic spawning sites may become limiting if mixing is reduced (Petitgas *et al.*, 2013).

Interactions between fishing and environmental conditions may affect population longevity. *Nephrops norvegicus*, a key commercial species in Europe, are also more vulnerable to fishing under low oxygen conditions because, as mentioned above, they spend more time out of their burrows on the sediment (Baden *et al.*, 1990). When numbers of *N. norvegicus* are reduced in an area after a hypoxic event, population recovery can only come from outside the area by slow adult migration or by larval settlement. Baden *et al.* (1990) estimated that population and associated fishery recovery following a fatal hypoxic event may take up to 10 years. The habitat compression of the sailfish *Istiophorus platypterus* (Shaw 1792) caused by expanding low oxygen zones in the tropical Atlantic is also expected to have implications for the catchability of the species, in this case by long-line fisheries (Prince and Goodyear, 2006; Prince *et al.*, 2010). This is because these fish are becoming increasingly limited to the oxygenated surface layer and so are more easily targeted by surface fishing gears.

Predator-prey relationships may be altered by changes in environmental conditions, with resulting food web and ecosystem effects. By analysing a historical time series from 1970 to 1995, Koslow *et al.* (2011) found that during times of low oxygen in the oxygen minimum zone of the southern California Current, the abundance of mesopelagic fishes decreased by 63% compared with times of high oxygen. The authors attributed this decline to an increase in vulnerability to predators when oxygen concentrations prevent fishes from going deep and out of reach for surface diving species. Likewise birds and marine mammals may be able to take advantage of reduced antipredator behaviour of fishes (Domenici *et al.*, 2013). The 'fast start' escape performance (ability to respond quickly to a stimulus such as a predator) directionality and responsiveness is reduced in some species in hypoxia, making them more vulnerable to predation (Chapman and McKenzie, 2009; Domenici *et al.*, 2013). Schooling behaviour may be disrupted under severe hypoxia for example by altering shuffling behaviour and school shape and volume, thereby changing anti-predator evasion efficacy (Domenici *et al.*, 2013). Conversely, predation may be reduced in areas of low oxygen by suppressing predator metabolic rates and so appetites or by decreasing predator performance (Chapman and McKenzie, 2009).

As well as forcing predators and prey together by habitat compression, low oxygen may also cause decoupling in some instances, with huge consequences for food chains (Stramma *et al.*, 2011). Animals may have to change their prey preferences if prey species are less tolerant to low oxygen zones and move out of an area. Experiments have shown that hypoxia can change whole groups of dominant predators in food chains. In two separate experiments using different species, jellyfish species became the dominant predator over predatory fishes when hypoxic conditions were introduced (Chapman and McKenzie, 2009). With jellyfishes increasing in abundance worldwide (e.g. Lynam *et al.*, 2010; Brotz *et al.*, 2012), hypoxic conditions may give them a competitive advantage.

These changes in interactions among individuals, species and fisheries, caused or exacerbated by low oxygen levels, show the complexity involved in understanding ecosystem and fisheries effects of oxygen and climate change. The examples given above illustrate the wide range of physiological and behavioural information which can be gathered to understand ecosystem and fisheries effects, and demonstrate how much work is needed to truly understand how low oxygen might affect marine organisms.

Modelling techniques

For the results of experiments to be useful to fisheries, environmental management and policy, it is necessary to scale up from individual-level effects both spatially and temporally to populations. In order to do this, modelling is required (Jørgensen *et al.*, 2012). While experiments are undoubtedly useful, the physiological changes occurring under laboratory conditions are unlikely to fully represent the range of responses of individuals and their ecosystems in the wild (Pörtner, 2010; Metcalfe *et al.*, 2012;). Scaling up physiological and behavioural responses is not, however, straightforward but confidence in model projections can be increased by including results from physiological studies (Somero *et al.*, 2016). Pörtner (2012) described the need for modelling to link physiological effects with future ecosystem projections, however, it is not yet fully understood how pH, temperature and low oxygen interact and so cautious assumptions must sometimes be made (Cheung *et al.*, 2011). Rose *et al.* (2009) reviewed seven models at different temporal and spatial scales that were used in the past to understand the population effects of coastal hypoxia on fishes. These included one physiological model, five individual-based models and one matrix population dynamics model. The authors found that the responses predicted by each technique varied and that each model predicted different interactions and indirect effects. There have been other attempts at modelling the effects of hypoxia, particularly coastal hypoxia, but few have included a range of oxygen conditions over a large area. There are many different modelling techniques available, described hereafter, which could be used to scale up information on the effects of low oxygen, each requiring their own set of parameters and data inputs, and giving outputs at different temporal and spatial scales and of varying precision. All give useful insights which can help in understanding the potential consequences for commercial species, and so should be explored in more detail. It may be appropriate to use different models in certain situations depending upon the data available and the questions asked. The parameters required for the modelling techniques are described in Table 6. Physiologists, ecologists and modellers can use these examples to design studies based on data that are already available or to explore responses of organisms where information is not known. These different techniques and the data required may make it possible to answer complex questions regarding climate and oxygen with minimal investment in experimental studies.

Table 6: Examples of the types of model parameters required for different modelling techniques that can be used to investigate the effects of changing oxygen levels on fishes.

Modelling technique	**Physiological or behavioural model parameters**	**References**
Bioclimate envelope models/species distribution models	Presence or presence/absence data	Cheung *et al.*, 2009; Margonski *et al.*, 2010; Cheung *et al.*, 2011; Reiss *et al.*, 2011; Cheung *et al.*, 2012; Diamond *et al.*, 2013
Fish growth function and Dynamic Bioclimate Envelope Model	Basal metabolic rate, maximum body weight, species presence	Cheung *et al*., 2012
Hypoxia Mass Balance Model	Biomass-size distributions, oxygen consumption rates, ingestion, egestion, respiration	Rakocinski, 2009
Individual-based model – generalised additive model	Egg and larval abundance, reproductive volume	Ustups *et al*., 2013

Modelling technique	**Physiological or behavioural model parameters**	**References**
Dynamic energy budget (DEB) models	Biomass, size, age, maturity, growth rates, reproduction, starvation survival	Kooijman, 2010; Maar *et al*., 2010; Klok *et al*., 2014
Coupled empirical–numerical model	Metabolic scope	Cucco *et al.,* 2012
Ecosystem models (e.g. Ecopath, Atlantis)	Spawning biomass, growth, reproduction, stock assessments, feeding rates, prey preferences, fishing effort	Meier *et al*., 2012; Nye *et al.,* 2013

Bioclimate envelope modelling (also called species distribution modelling and ecological niche modelling) is one technique that has been used to provide future spatial and temporal projections of animal distributions assuming various climate change scenarios. This type of modelling does not normally include oxygen as a parameter (Cheung *et al.*, 2009; Margonski *et al.*, 2010; Cheung *et al.*, 2011; Reiss *et al.*, 2011; Cheung *et al.*, 2012; Diamond *et al.*, 2013) however Cheung *et al.* (2011) did include oxygen levels in an assessment of future distribution changes in 120 fish and invertebrate species in the northeast Atlantic. These authors predicted a move northwards and into deep water for most species, and that an assumed reduction in oxygen content tended to increase the rate of range shift. The authors also looked at fishery catch potential associated with these changing distributions. This decreased because low oxygen levels along with ocean acidification reduced the temperature-related aerobic ‘scope for growth’, and so maximum body size. This was particularly the case for species at the edge of their range where they were close to their temperature tolerance limits and so had limited aerobic scope. Unfortunately, often only low resolution environmental data layers are available and hence this modelling approach has faced criticism (e.g. Sinclair *et al*., 2010). Bioclimate envelope models focusing on regional rather than global seas require a finer spatial resolution and more detailed projections of oxygen, but can potentially offer more detailed insights into species and population effects.

Many different approaches have been developed that take account of metabolic scope and how this will vary on daily and seasonal timescales (Jørgensen *et al.*, 2013). Cheung *et al.* (2012) predicted the integrated biological responses of over 600 marine fishes world-wide, and noted that although the projected rate of change in environmental temperature and oxygen content seemed to be small, the resulting changes in maximum body size were unexpectedly large (reductions of up to 24% by 2050 in some areas). The authors used physiological and bioclimatic information, coupled with climate models. The methodology has been heavily criticised (e.g. Brander *et al*., 2013), however, it remains one of the few studies which has incorporated projections of oxygen instead of relying only on salinity and temperature as the climatic variables. As more detailed oxygen projections become available in the future, particularly in shelf seas, these techniques could be relatively easily used to see the effects on a wide range of species.

Rakocinski (2009) proposed a size-based ecosystem modelling approach to link allometric macrobenthic processes to hypoxia using the Peters Mass Balance Model (PMBM) (Peters, 1983). Changes in the distribution of biomass over time result from differences between gains due to ingestion and losses due to egestion, respiration, and mortality. Rakocinski (2009) built upon this approach to develop a Hypoxia Mass Balance Model (HMBM) to demonstrate how changes in biomass-size distributions (for the East Bay, Florida region) could vary under different oxygen limitation scenarios. In pilot simulations ingestion deficits reduced total biomass and favoured large size classes of marine invertebrates. Effects were stronger under the more hypoxic scenario; total biomass was lower and the biomass-size distribution was more uneven among the size classes. Projected biomass-size distributions were visibly altered by the influence of only 32 days of fluctuations in dissolved oxygen. However, trial simulations only reflected a single hypothetical chronic effect of hypoxia. Hypoxia also imposes multiple direct and indirect effects on the growth and survival of macrobenthic organisms (Diaz and Rosenberg, 1995) that were not considered in this mass balance model. This type of approach and future refinements could be extended or used in different regions.

Individual-based models generally use more detailed information about adult or larval stages, and can be used to scale up from oxygen tolerance experiments in the laboratory (Pörtner and Peck, 2010). Rose *et al.* (2009) analysed four different individual-based models used to predict the population level effects of coastal hypoxia on fishes, which had varying degrees of predictive power. One type of individual-based model incorporates 'reproductive volume' i.e. the volume of water that provides minimum environmental conditions for spawning and successful egg development. The reproductive volume of a species can itself be incorporated into individual-based models to predict recruitment dynamics associated with oxygen concentrations, salinity and temperature (Ustups *et al.*, 2013). Similarly, Dynamic Energy Budget (DEB) models may be of use to predict future habitat suitability, by taking account of the effects of changes in food availability or temperature and consequences for growth or metabolic scope (Kooijman, 2010; Teal *et al.*, 2012). These models have been used to assess the effect of increased carbon dioxide on invertebrates (Klok *et al*., 2014) and Maar *et al.* (2010) has used this technique to study the impact of hypoxia on blue mussels *Mytilus edulis* L. 1758 in the Danish Limfjorden. These techniques can be complex but investments in this area could vastly increase scientific understanding of regional changes in oxygen in the future.

Cucco *et al.* (2012) used laboratory estimates of metabolic scope (determining the difference between standard and maximum metabolic rates) as well as oxygen projections from hydrodynamic models to predict suitable habitats for flathead grey mullet *Mugil cephalus* L. 1758 in the Mediterranean Sea. This work made use of numerical simulations of water temperature and dissolved oxygen concentrations. The coupled empirical–numerical model was then used to simulate temporal and spatial variation in metabolic scope in the Oristano Gulf and the Cabras lagoon system (Italy). Results suggest that during the spring and the beginning of summer, Cabras lagoon provides opportunity for higher metabolic scope for *M. cephalus* than the Oristano gulf. During the rest of the year, the gulf provides more suitable conditions (higher metabolic scope). This technique offers considerable promise in that it makes use of easy to determine physiological parameters and puts these together with outputs from existing biogeochemical models. Similar information is available for many species (e.g. *D. labrax* - Claireaux and Legardère, 1999; *G. morhua* – Claireaux *et al.*, 2000; *S. solea* - Lefrancois and Claireaux, 2003) and in other parts of the world, but it is understood that they have never been combined in this way.

Whole ecosystem models such as Ecopath and Atlantis have been used to look at the foodweb effects of climate change (Meier *et al*., 2012; Nye *et al.,* 2013). Ecopath with Ecosim has been applied in the Baltic Sea to determine the changes in marine food webs caused by climatic influences (Meier *et al.,* 2012). Relationships between twenty two functional groups (collections of organisms with similar trophic, behavioural and physiological characteristics) were modelled using climatic variables including the extent of the hypoxic area and *G. morhua* reproductive volume taken from physical-biogeochemical models. The authors suggest that by 2100, extensive areas of low oxygen will exist relative to the 1990s and 2000s. The food web models showed that sprat *Sprattus sprattus* (L. 1958) spawning biomass will likely increase in the area by 2100, and that the *G. morhua* stock will be limited by the low reproductive volume. The more complex 'Atlantis' model incorporates biogeochemistry, food web interactions and human effects on the ecosystem (CSIRO, 2011). This type of model requires large amounts of input data, but could be valuable in determining how changes in oxygen could have subsequent indirect effects for whole ecosystems.

The modelling of oxygen responses that has taken place until now has made use of data on physiological and behavioural responses such as metabolic scope (e.g. Cucco *et al.,* 2012), reproductive volume (Ustups *et al*., 2013) and ingestion/egestion rates (Rakocinski, 2009). However, there are a limited number of detailed oxygen projections available to provide accurate modelling on a regional basis (such as those used by Cucco *et al*., 2012 for the Mediterranean Sea or the one-dimensional projections by van der Molen *et al*., 2013 for the North Sea). Coarse-resolution global projections of future oxygen levels in the ocean are available through the IPCC AR5 reports (IPCC, 2014). When more locally relevant information becomes available, modelling options will be opened up, and it will become easier to judge the likely implications for fisheries and ecosystems.

Future directions

The literature described above shows that some modelling techniques are already available for scaling up from laboratory experiments to population and fishery-scale impacts. However, the existing work has been largely piece-meal, uncoordinated and it is still not clear how significant an impact a proliferation of low oxygen conditions could have for commercial fisheries and whole ecosystems in the future. To advance the knowledge-base still further, a number of promising technological and modelling-based developments are highlighted that should be encouraged in the near future. Furthering these techniques could fill important knowledge gaps as to the physiological (e.g. metabolic scope, growth, reproduction, development) and behavioural (e.g. predator escape, activity levels) effects of low oxygen levels on different phyla, species, life stages, populations, ecosystems and therefore fisheries. Future areas of work that would advance scientific knowledge of low oxygen impacts, and which are described in detail, include:

1) Advances in remote telemetry (tagging) and sensor technologies;
2) Trait-based analyses to provide insight into how whole assemblages might respond;
3) Research into long-term adaptability of species;
4) Application of population and ecosystem modelling techniques;
5) Quantification of economic impacts; and
6) Improved oxygen projections.

Under laboratory conditions it is near impossible to fully replicate the true responses of animals to stressors in the wild (Metcalfe *et al.*, 2012). Telemetry and archival tags have proven useful to determine responses of marine animals to hydrographic conditions, and while oxygen sensors are not currently small or stable enough to be used in tags, behaviour determined from tagging experiments can be compared with dissolved oxygen data measured by other means. As discussed above, pop-up satellite transmitting archival tags have been used to study the vertical movements of fast-swimming *M. nigricans* and *I. platypterus* in the tropical Atlantic and Pacific oceans (Prince and Goodyear, 2006; Prince *et al.*, 2010; Stramma *et al.*, 2011). These studies used World

Ocean Atlas average temperature and oxygen profiles in the same areas to determine how the fish behaved under different conditions. Similarly, in the Baltic Sea, archival tags have been used in parallel with measured oxygen profiles to show that *G. morhua* do enter deep, hypoxic waters at least for brief periods (Neurenfeldt *et al.*, 2009). Tags containing 3-axis accelerometers have also been used to estimate metabolic rate in fishes (e.g. Murchie *et al.*, 2011) and activity-specific energy use (Wright *et al*., 2014). These devices capture such information during brief periods of burst swimming where the animal is reliant on glycolytic (anaerobic) metabolism. This technology offers, for the first time, the potential to investigate the effects of environmental temperature, oxygen depletion and other stressors (alone and in combination) on both the aerobic and glycolytic capabilities of fishes, thereby providing insight into the ability to sustain an ‘oxygen debt’ as well as implications for metabolic scope. This technology could make it possible to identify how a whole organism behaves when its metabolic scope is reduced, instead of considering only certain behavioural choices, as is necessary in laboratory experiments. Miniature oxygen sensors could be incorporated into data storage tags, collecting invaluable information about how individual fish and populations make use of low oxygen zones during different life stages on a seasonal and spatial basis (Kröger *et al.*, 2009; Metcalfe *et al.*, 2012). It is only by knowing the actual levels of oxygen to which organisms are exposed in the wild, that conclusions can be drawn about how such organisms might adapt, or not, to changing oxygen levels in the future. Efforts are underway to develop a high accuracy, low power conductivity, temperature and dissolved oxygen (CT-DO) sensor for *in situ* oceanographic measurements (e.g. Huang, 2011). Initial trials have successfully been carried out in the laboratory and in the field (a 75 day research cruise in the Indian Ocean and off Greenland). Plans are now well advanced to integrate the electronics into a package small enough for fish tag applications, and so data on oxygen use may be available in the near future.

Biological Trait Analysis (BTA) is a technique that has proven particularly useful for predicting the response of communities exposed to stressors such as sewage pollution, anoxia and fishing (Beukema *et al.*, 1999; Bremner *et al.*, 2006; Bremner, 2008). The trait-based approach allows researchers to tackle the complexity of marine ecosystems in simple models. Rather than considering species per se, individual organisms are characterised by a few essential traits that describe the ensemble properties of many species. Based on the literature described above, a number of traits are apparent with regard to observed oxygen sensitivity. Sensitive organisms are typically characterised by active lifestyles, large size and species at the edge of their distribution, and so also their most suitable environmental, range. A wide variety of other traits (such as spawning season) are potentially important, but they may not all be equally useful. Physiological and behavioural studies can however contribute to determining threshold values for a species (Somero *et al*., 2016). Within the context of responses to low oxygen, a meta-analysis study, as has recently been done for ocean acidification (Kroeker *et al.*, 2010; Hendriks *et al.*, 2010), would identify those species and ecosystems which may be particularly vulnerable to low oxygen. It would also expose to where further experimental study of certain species and groups or specific traits could be directed.

Short-term low oxygen acclimatisation strategies in fishes have been reviewed by Zhu *et al.* (2013). This review notes that fishes produce various signalling and protective proteins whenever exposed to acute hypoxia. These proteins regulate oxygen-sensitive transcription factors which, in turn, affect the expression of hypoxia-related genes. By contrast, very little is understood about longer term evolutionary adaptation responses to low oxygen. In particular, it remains unclear whether fishes will be able to adapt over time to widespread declines in oxygen, associated with global warming. Various techniques are available to explore acclimatisation and adaptation responses, these include the analysis of ‘phenotypic plasticity’, or the influence of the environment on the development of certain, more well-suited, phenotypes (e.g. Chevin *et al.*, 2010 who suggest that more work should be done to investigate this influence and how optimum phenotypes change with environment, and ultimately to model how this affects population persistence and evolutionary change). However, it is not known that these tools have not been used in this context. Applying these techniques to the study of low oxygen effects would require improved knowledge of genetic diversity and phenotypic plasticity in populations, as well as insights into functional genomics. Further work combining laboratory studies with ecological investigation in the field would identify traits that denote adaptation to a specific environment.

A particularly promising avenue for research seems to be that taken by Cucco *et al.* (2012), combining readily-available outputs from biogeochemical models with easily measurable metabolic scope parameters from laboratory experiments. This methodology could offer an important vehicle for future climate change risk assessment, and much could be achieved even without further experimental work (making use of existing data sources, including Claireaux and Legardère (1999) and Lefrancois and Claireaux (2003)). More could be achieved by using this modelling approach to guide future experimental work, by helping to dictate the environmental conditions controlled, the parameters that are measured and the species that are targeted. Responses to multiple pressures are poorly understood (Zambonino-Infante *et al.*, 2013) and so where possible, changes in temperature, pH/carbon dioxide concentration and salinity should be considered alongside low oxygen. Metabolic scope estimates have been made for many different fish species, exposed to varying temperature and oxygen saturation conditions. Much of this work has been carried out for the purposes of commercial aquaculture (e.g. Fitzgibbon *et al.*, 2007). Outputs are available for polar and tropical fish species (e.g. Steffensen *et al.*, 1994) as well as for those more familiar species from mid-latitudes. It is only a small step to incorporate experimental results for these and other species into models to predict how organisms will react to climate change.

The main thrust within this review has been on the biological and ecological effects of low oxygen on species subject to fisheries, and not on the economic consequences per se. Beyond the work of Cheung *et al.* (2011) there have been few attempts to assess the impacts of low oxygen on fisheries yields and on the economic viability of the fishing or aquaculture sector worldwide. Climate change risks in economic terms could be quantified, so that their relative seriousness can be fully assessed alongside comparable risks elsewhere in the economy. Future work could focus on a number of different techniques available to quantify monetary losses, these include the Net Present Value (NPV) approach and partial equilibrium (PE) models. Several of these tools have recently been used to assess the likely impact of stressors such as ocean acidification (Cooley and Doney, 2009; Narita *et al.*, 2012), and so with sufficient information on stock effects and robust projections, these techniques could be similarly used to assess low oxygen impacts.

Conclusions

The challenge raised by expanding areas of low oxygen in the ocean should not be under-estimated. The United Nations Environment Programme 2003 Yearbook identified oxygen depletion as one of the most immediate future threats to global fishery resources and marine ecosystems (United Nations Environment Programme, 2004). Low oxygen is a major feature within the IPCC AR5 report (IPCC, 2014), whereas it was only mentioned in passing in the IPCC 4th Assessment (WG1 report pages 403-408) (IPCC, 2007a). The review conducted here has revealed that there is already a substantial knowledge-base concerning the physiological and behavioural responses of fishes and shellfishes to oxygen, particularly hypoxia. However, there is still a large knowledge gap of how such effects will manifest themselves as consequences for fisheries and ecosystems. After a hiatus in recent decades, fish physiology has become fashionable once more (Metcalfe *et al.*, 2012) as the challenges raised by global warming, ocean acidification and low oxygen have become apparent. Many of the techniques and tools that will be necessary to scale up from laboratory experiments to populations and ecosystems are already available, but it is clear that the disparate pieces of information and model outputs have rarely been pulled together, partly because this requires collaboration between different scientific disciplines (e.g. physiologists, hydrological modellers, ecologists, economists), who may not be accustomed to talking to one another. The availability of data is also an issue, and any initiatives which draw together existing physiological information would be hugely valuable. This review has highlighted the types of experimental data that are required to allow modelling to scale up to ecosystem and fishery effects, and the different modelling techniques which could be used. Models could include, for example, experimental data on development, growth, body size, feeding, predator-prey interactions and survival. The importance of physiologists and modellers working together should not be underestimated to ensure that assumptions are correct and that models can represent reality as closely as possible.

One of the challenges of predicting consequences for commercial species caused by reduced oxygen levels is the lack of adequate temporal projections or even current spatial information on oxygen in the marine environment. Global models are valuable but regional models would help scientists to understand the local-scale conditions that specific ecosystems, and individual fisheries, may experience in the future. A number of avenues have been described that can be explored to bring separate areas of knowledge together, the starting point being identifying knowledge gaps in physiological and behavioural data that are required for existing and newly developed modelling techniques. It is also important to acknowledge that it is not only hypoxic waters that are important, but understanding the effects of the whole range of oxygen concentrations and the length of time that areas are affected is crucial when considering climate change. On piecing together all of these separate parts, the consequences of climate change for fisheries will be made much clearer.

Acknowledgements

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Chapter 4

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

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Summary

Oxygen availability is a key factor that determines habitat suitability for marine fish. As a result of climate change, low oxygen conditions are predicted to occur more frequently and over a much greater geographic extent in the oceans. The possible effects of acute hypoxia on model marine species physiology has received much attention, however studies on long-term chronic effects and impacts for commercially important fish are comparatively rare, notably those that integrate physiological data with modelling techniques. To assess the potential effects of climate-induced low oxygen on fisheries, here physiological data from laboratory experiments on exploited North Sea species is integrated with hindcast and future oxygen model projections. By using this approach changes in habitat suitability up to 2100 were identified, which could ultimately alter reproduction, growth and commercial catches. Our findings suggest that 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 however, although not to the minima of previous decades. In affected areas, intermediate oxygen levels could have temporary impacts on digestion and metabolic scope, and may also negatively affect reproduction in summer-spawning species, although these oxygen effects may be difficult to separate from the effects of fishing, temperature and pH changes. These results demonstrate that although physical model projections help to provide insight, they are insufficient by themselves to predict the potential impacts of climate change on fish distribution and fisheries. The modelling requires underpinning through

simple experimentation, particularly through studies incorporating the combined effects of temperature, pH and low oxygen. Tailored and robust management measures can then be put in place to ensure the resilience and longevity of stocks.

Introduction

Dissolved oxygen levels are decreasing in the world's oceans (Rabalais *et al*., 2010; Cocco *et al.,* 2013; Levin and Brietburg, 2015), driven in part by both climate variability and climate change (Gilbert *et al.,* 2014; Levin and Brietburg, 2015). Oxygen availability is important in determining habitat suitability for marine fish (Heath *et al.,* 2012), 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 hypoxia of model marine species, but studies on long-term chronic impacts of moderately lowered oxygen levels on commercially important fish are comparatively rare (Townhill *et al.*, 2016). 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. The majority of studies designed to predict the effects of climate change on marine fish thus far omit 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. Studies that include oxygen are currently the exceptions (e.g. Cheung *et al.,* 2013; 2015). 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 and Knust, 2007; Levin and Brietburg, 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 and Steffensen, 1992; Pörtner and Knust, 2007; Pörtner, 2010; 2012). The reduced solubility of oxygen in warmer water reduces the availability of oxygen to aquatic species for respiration (Pörtner and Knust, 2007). There are a number of ways of measuring the tolerances of aquatic species to such oxygen conditions. These include respiratory physiology metrics of oxygen tolerances (e.g. metabolic rate, oxygen uptake, metabolic or aerobic scope), critical oxygen thresholds (P_{crit} or S_{crit}), and behavioural or physiological responses such as swimming speed, activity, ingestion and growth. Some of these tolerances have thresholds before effects are seen. If oxygen levels fall below a minimum threshold, then an organism's oxygen-demanding functions can be impaired (Claireaux *et al.,* 2000). One such threshold is metabolic or aerobic scope, which is the capacity of an organism to carry out activities above their basal level activities (Fry, 1971), measured as the difference between standard and maximum metabolic rates. When oxygen levels fall below normoxia (fully saturated oxygen conditions), metabolic scope can be reduced resulting in a fish having a reduced ability to do certain activities, for example, to reproduce, feed or swim. Another threshold used to measure fish tolerance to low oxygen is the critical oxygen threshold, measured as 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.

In physiological experiments, there are advantages and disadvantages of measuring different variables, and in using them to assess the implications of changes in oxygen levels. For example, the parameters may be relatively quick and simple to measure, but the experimental environment will never fully represent real-world conditions. In many cases, the aim of experimental research is measurement of these values. They are rarely then 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 and 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 in recent decades changes have been seen in commercially exploited fish stocks due to fishing and climatic influences (Engelhard *et al.*, 2014). However there are additional 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 less easy to demonstrate and there is less oxygen data available when compared with other climatic variables, making assessments difficult.

The aim of this work 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 how commercial fish species may have been affected by recent changes in oxygen conditions in the North Sea, and to identify 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://digitizer.sourceforge.net/). The resulting metadata contained 35 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 (http://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 35 relevant studies were narrowed down to give 82 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). Those metrics that could not be compared across oxygen conditions were excluded, for example metabolic rates calculated at different temperatures but only under 100% oxygen conditions. The remaining 14 oxygen metrics, representing five species (Table 7): (*Ammodytes tobianus* (lesser sandeel); *Gadus morhua* (Atlantic cod); *Solea solea* (common sole); *Dicentrarchus labrax* (European sea bass) and *Scophthalmus maximus* (turbot)), were then integrated with the model 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.

Table 7: Oxygen metrics chosen for use in the analyses. Metrics are presented in increasing threshold oxygen levels.

Species	**Metric and experimental temperature**	**Oxygen threshold level (mmol m^{-3})**	**Reference**
Lesser sandeel	Swimming speed reduced by 95%	43.4	Behrens and Steffensen, 2007
Atlantic cod	P_{crit} at 15°C	56.9	Claireaux *et al*., 2000
Lesser sandeel	Pcrit at 10°C	57.4	Behrens and Steffensen, 2007
Atlantic cod	P_{crit} at 10°C	57.3	Claireaux *et al*., 2000
Atlantic cod	Metabolic scope is 0 mg O_2 h^{-1} kg^{-1} (at 2–10°C)	64	Claireaux *et al*., 2000 and Chabot and Claireaux, 2008
Common sole	P_{crit} 16°C	67	Lefrancois and Claireaux, 2003
Sea bass	P_{crit} 15°C	69	Claireaux and Lagardere, 1999
Sea bass	P_{crit} 10°C	70	Claireaux and Lagardere, 1999

Species	**Metric and experimental temperature**	**Oxygen threshold level (mmol m^{-3})**	**Reference**
Common sole	P_{crit} 12°C	71	Lefrancois and Claireaux, 2003
Atlantic cod	Metabolic scope is lowered (32.5 mg O_2 h^{-1} kg^{-1}) at 30% O_2 at 10°C	85	Claireaux *et al*., 2000 and Chabot and Claireaux, 2008
Turbot	Reduced maximal oxygen uptake	131	Mallekh and Lagardere, 2002
Atlantic cod	Metabolic scope is lowered (75 mg O_2 h^{-1} kg^{-1}) at 50% O_2 at 10°C	142	Claireaux *et al.,* 2000 and Chabot and Claireaux, 2008
Atlantic cod	Activity considerably constrained (at 2 - 10°C)	159	Claireaux *et al*., 2000 and Chabot and Claireaux, 2008
Common sole	Significant decrease in MMR 16° C	188	Lefrancois and Claireaux, 2003
Atlantic cod	Growth and ingestion significantly reduced (no specific temperature given)	199	Chabot and Claireaux, 2008
Atlantic cod	Metabolic scope (109 mg O_2 h^{-1} kg^{-1}) at 100% O_2 at 10°C	284	Claireaux *et al.,* 2000 and Chabot and Claireaux, 2008

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 three-dimensional, hydrodynamic-biogeochemical model GETM-ERSEM was applied to the North Sea (methods described in: Lenhart *et al.,* 2010; Tett *et al*., 2013; van Leeuwen *et al.,* 2013; van der Molen *et al*., 2014; van Leeuwen *et al.,* 2015). The freely available General Estuarine Transport Model (GETM; http://www.getm.eu; details in Burchard and 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 European Regional Seas Ecosystem Model (ERSEM; www.nioz.nl/ersem-getm), which captures the chemical and biological cycles in the North Sea (Baretta, Ebenhöh and Ruardi, 1995). GETM-ERSEM was forced with 6-hourly meteorological data from ECMWF ERA 40 (http://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).

Oxygen projections

Future gridded model projections for oxygen are not currently available for the North Sea, and so instead point data for three locations were used as published by van der Molen *et al.,* (2013; Figure 10). 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. 1), which each represent larger areas with similar signature seabed and water column conditions (van der Molen *et al.,* 2013). The Oyster Grounds has a water depth of 45 m, a muddy-sand sediment with a shallow oxic layer (~1 cm) 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). The Southern Bight is a shallow (<30 m), vertically mixed area, with mobile, sandy seabed and deeper oxic layer (~2–6 cm).

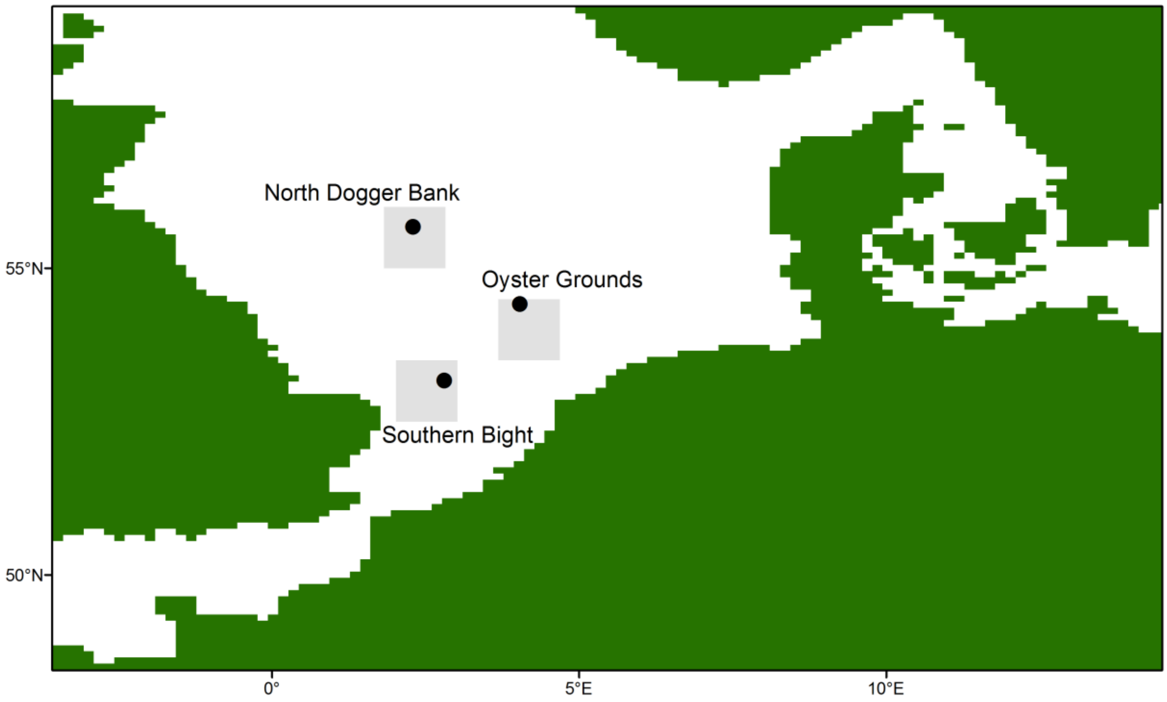

Figure 10: Southern North Sea, showing the Oyster Grounds, North Dogger Bank and Southern Bight study areas. Grey boxes show the bounding areas for the hindcast analysis. Black dots show the point locations for future projections.

The coupled hydrodynamic-biogeochemical water column model GOTM-ERSEM-BFM (Biogeochemical Flux Model) was used to generate daily data for the three sites, forced by climate data from the HadRM3-PPE-UK (Met Office, 2008) regional climate model for 1950–2100, using the medium (SRESA 1B) emissions scenario, as described in van der Molen *et al*. (2013). It was confirmed (demonstrating agreement between model predictions and observations) using hind casts forced with the meteorological hindcast forcing from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA-40 and Operational Analysis Hindcasts (http://badc.nerc.ac.uk/data/dataset_index/?source=data). Projections were carried out for the Oyster Grounds, the Southern Bight and the North Dogger Bank (see Figure 10). The Oyster Grounds (54.414°N 4.039°E) and North Dogger Bank (55.671°N, 2.298°E) were simulated using 40 vertical layers and the Southern Bight (53.167°N, 2.804°E) 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 2000–2011 of the Dutch national monitoring programme (MWTL) and Cefas SmartBuoy measurements at Terschelling 135.

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 metric levels for each species. The number of modelled grid squares with the oxygen minima below the metric oxygen levels was calculated for each decade. Each grid square is approximately 10 km x 10 km in size, and so this calculated number of grid squares was multiplied by 100 to determine the area of North Sea in square kilometres with oxygen levels below each oxygen metric. This was carried out 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 oxygen concentrations and areas below the metrics 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 x 1 degree (10 x 6 model grid cell) bounding area was used for each area (shown in Figure 10): Oyster Grounds: 53.5–54.5 N and 3.69–4.69 E; Southern Bight 52.5–53.5 N, 2.02–3.02 E; North Dogger 55.0–56.0 N, 1.65 - 2.65 E. The areas with oxygen 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 three locations experienced oxygen levels below each metric in each year.

Results

Oxygen metrics

The literature search yielded 14 response metrics for current or projected North Sea temperatures that were suitable for comparisons in this study (i.e. many were carried out under Mediterranean conditions and so were not representative of the North Sea; Table 7). The metrics covered a wide range of oxygen concentrations. The highest oxygen level (284 mmol m^{-3}) was that which gave the metabolic scope of cod when measured at 100% oxygen saturation (i.e. the maximum metabolic scope), and the lowest concentration (43.4 mmol m^{-3}) gave a 95% reduction in swimming speed of lesser sandeel.

Past oxygen conditions

Modelled hindcast outputs show that since the 1970s oxygen conditions in the North Sea have generally improved (Figure 11). In the 1970s there were areas around Denmark with very low oxygen conditions (with decadal minima frequently below 40 mmol m^{-3}), 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 reduced over the decades. 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, covering almost half of the model extent in August in the 2000s (see Figure 11 for Atlantic cod thresholds). In the 2000s, for over 99% of the area, oxygen concentrations were below those which would give a cod metabolic scope when oxygen concentrations are at 100% (i.e. levels which would not restrict the metabolic scope of cod) (Table 8).

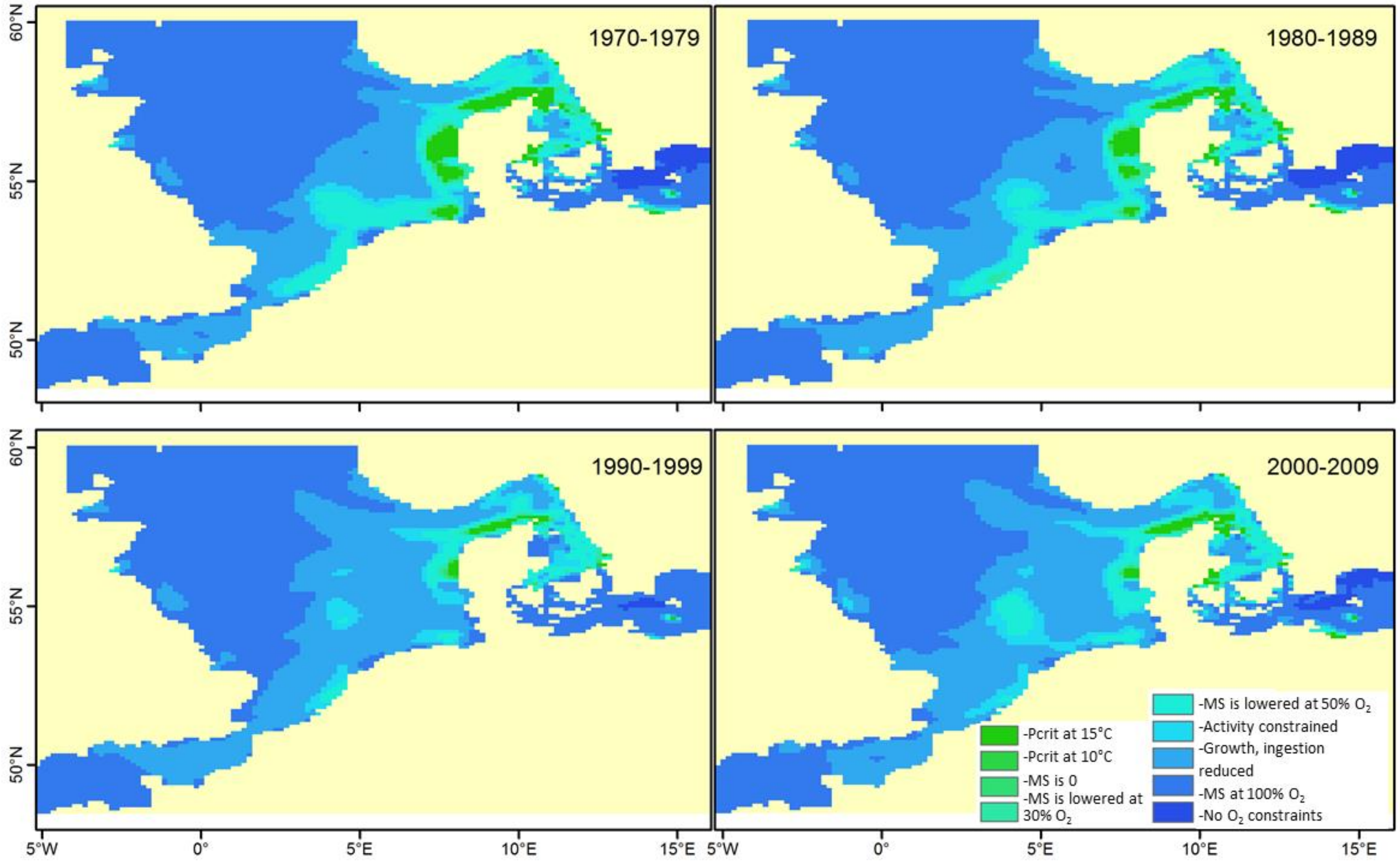

Figure 11: For Atlantic cod, the areas where minimum August near bed oxygen levels are below each metric, averaged over each of the four decades.

Table 8: The total areas covered by minimum August near bed oxygen levels below each oxygen metric for each species. Total modelled area is 59000 km^2. Metrics for which there was an increase in area across the decades are shown in bold.

Species	**Metric description**	**Oxygen concentration (mmol m^{-3})**	**Total area where oxygen is below each metric (km^2)**			
			1970s	**1980s**	**1990s**	**2000s**
Lesser sandeel	P_{crit} at 10 °C	57.4	19000	13500	11600	8000
	Swimming reduced by 95%	43.4	14400	8900	8400	5100
Atlantic cod	P_{crit} at 15 °C	56.9	18900	13400	11600	7800
	P_{crit} at 10 °C	57.3	18900	13500	11600	7900
	Metabolic scope is 0 mg O_2 h^{-1} kg^{-1}	64	20900	15500	13100	9200
	Metabolic scope is 32.5 mg O_2 h^{-1} kg^{-1} at 30% oxygen at 10 °C	85	28400	23700	19900	13200
	Metabolic scope is 75 mg O_2 h^{-1} kg^{-1} at 50% oxygen at 10°C	142	85700	72300	63900	48500
	Activity constrained	159	110900	100200	103100	86300

Species	**Metric description**	**Oxygen concentration (mmol m^{-3})**	**Total area where oxygen is below each metric (km^2)**			
			1970s	**1980s**	**1990s**	**2000s**
	Growth and ingestion reduced	**199**	**249400**	**241100**	**273500**	**280400**
	Metabolic scope at maximum (109 mg O_2 h^{-1} kg^{-1}) at 10 °C	**284**	**577000**	**576400**	**579200**	**581500**
Common sole	P_{crit} at 16 °C	67	21800	16700	13700	9600
	P_{crit} at 12 °C	71	23200	18200	14900	10100
	Significant decrease in MMR at 16 °C	**188**	**194500**	**186800**	**233500**	**224000**
European sea bass	P_{crit} at 15 °C	69	22700	17400	14200	9900
	P_{crit} at 10 °C	70	22900	17900	14500	10000
Turbot	Reduced maximal oxygen uptake	131	69600	55700	47400	35100

There were differences between the three separate regions (Southern Bight, Oyster Grounds and North Dogger Bank) in the likely areas affected by low oxygen conditions (Figure 12). The North Dogger Bank had the highest oxygen levels throughout the four decades, with oxygen levels no lower than the highest metric of cod metabolic scope measured at 100% oxygen. In the Southern Bight, the oxygen levels were slightly lower, with some of the region having oxygen levels below 159 mmol m^{-3}, which could affect cod activity. 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 gradually decrease over the coming century in all three areas, with the North Dogger Bank experiencing the steepest decline. There is projected to be substantial interannual variation at all sites, particularly at the Oyster Grounds (Figure 13). The validation against measured data from 2000–2011 showed that the model matched well with known data, with a root mean square of 1.336, correlation of 0.75372 and bias of -1.102.

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 three locations (Figure 14). Oxygen levels in the Southern Bight are not predicted to go sufficiently low in value to affect the lowest metrics of the focal species. In the Southern Bight, in the 2010s cod growth and ingestion would be reduced for an average of 3 (0.8%) days per year, increasing to an average of 58 (16%) days per year in the 2090s, when sole would also experience decreased MMR on 3 (0.7%) days per year. In the Oyster Grounds, predicted effects are more frequent, with cod growth and ingestion being affected for 40 (11%) days and sole MMR being affected for 32 (6%) days per year in the 2010s, increasing to 77 (21%) days and 47 (13%) days per year respectively in 2090s. Conditions where cod activity could be constrained in the Oyster Grounds increased from 0.3 (0.08%) days in the 2010s to 4 (1%) days in the 2090s. The North Dogger Bank had the lowest predicted oxygen conditions. Most decades are projected to experience oxygen levels sufficiently low for cod growth and ingestion to be affected on at least 146 (40%) days per year. In the 2090s, oxygen conditions would reduce cod metabolic scope for 5 (1.4%) days per year, and turbot would have a reduced maximal oxygen uptake on 4 (1.2%) days per year.

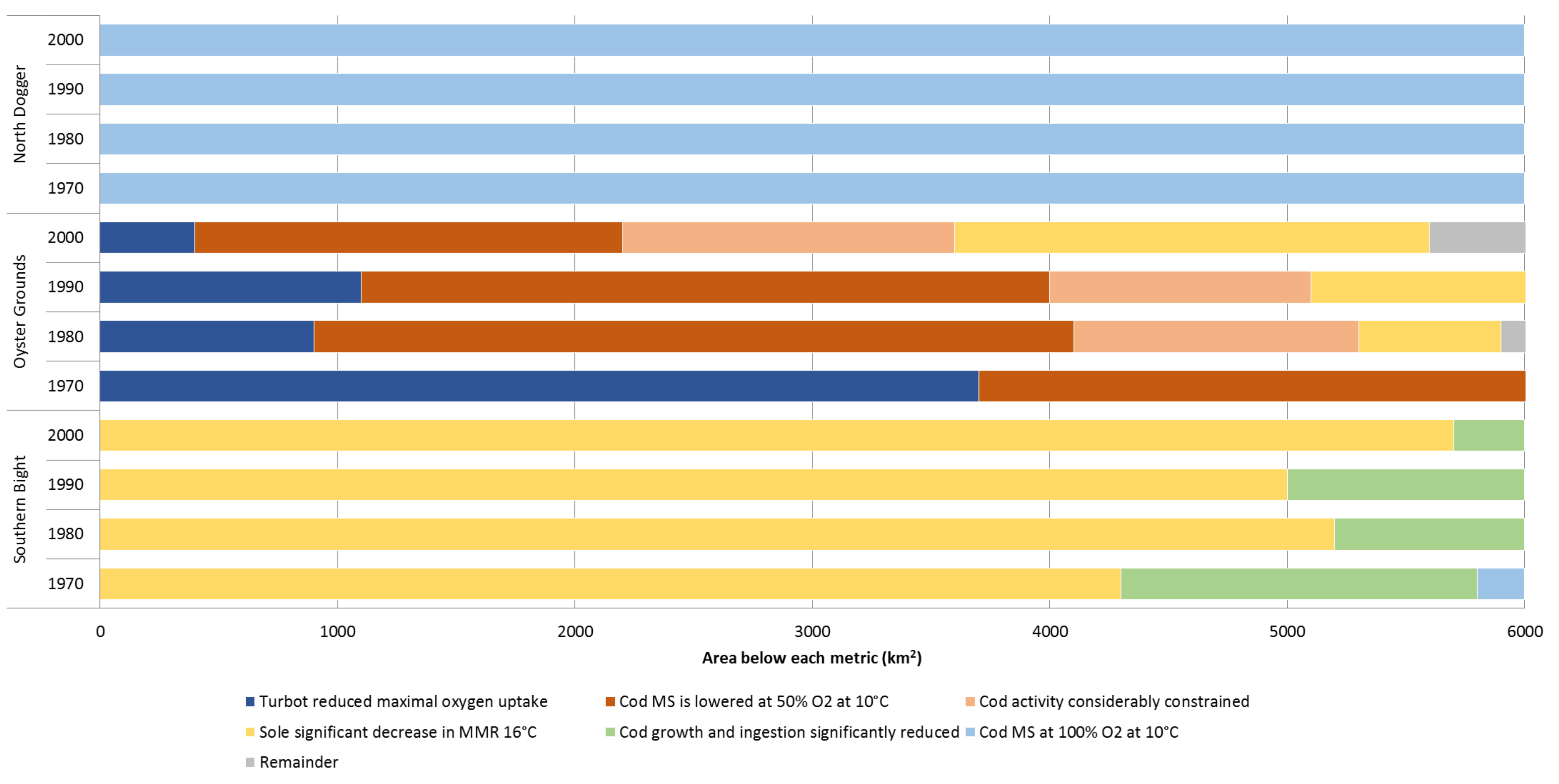

Figure 12: The areas over which the August minimum near bed monthly oxygen level is below each of the metrics in the North Dogger Bank, Oyster Grounds and Southern Bight. These regions were not affected by oxygen concentrations below the metrics shown.

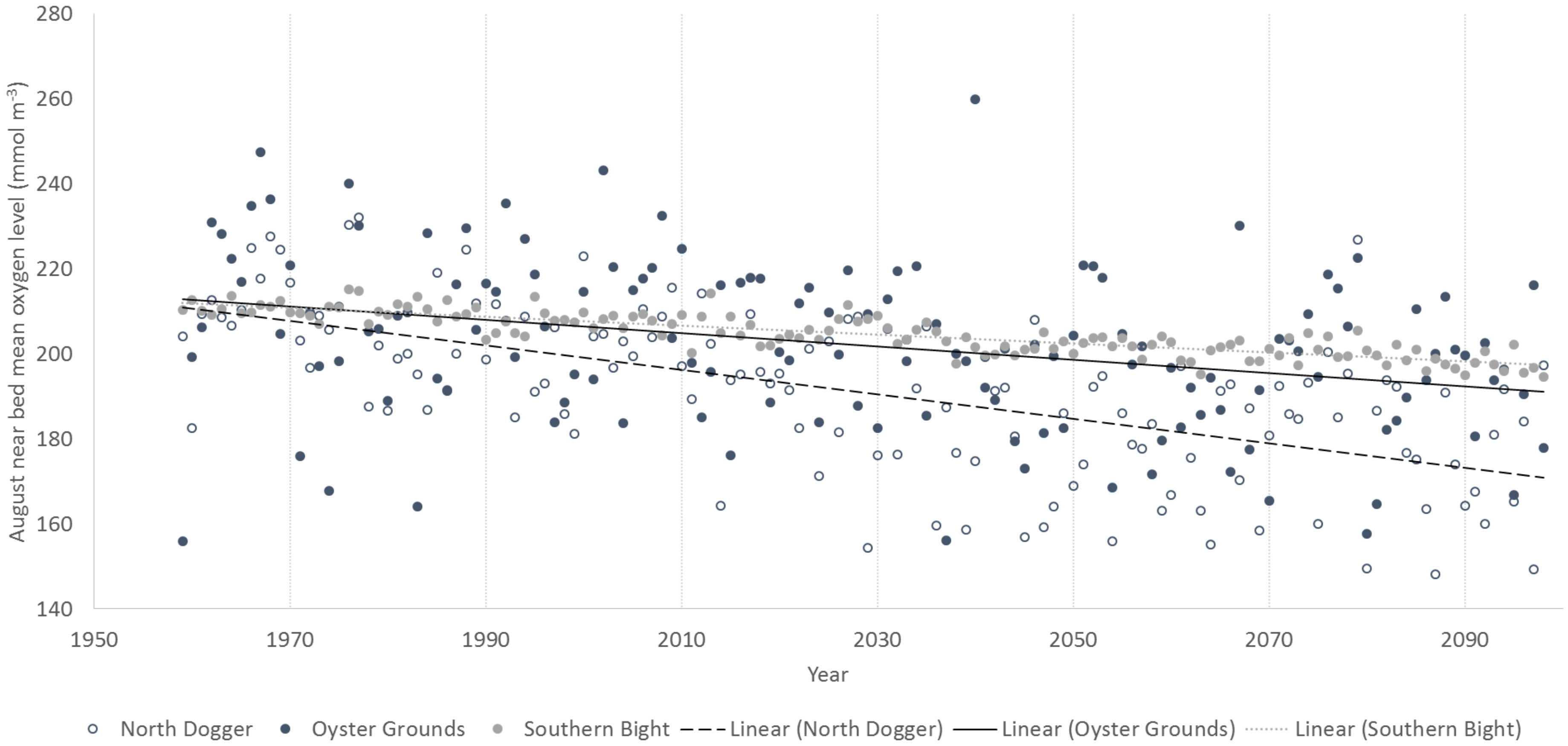

Figure 13: Projections of August near bed mean oxygen conditions for the three study locations, with linear trend lines.

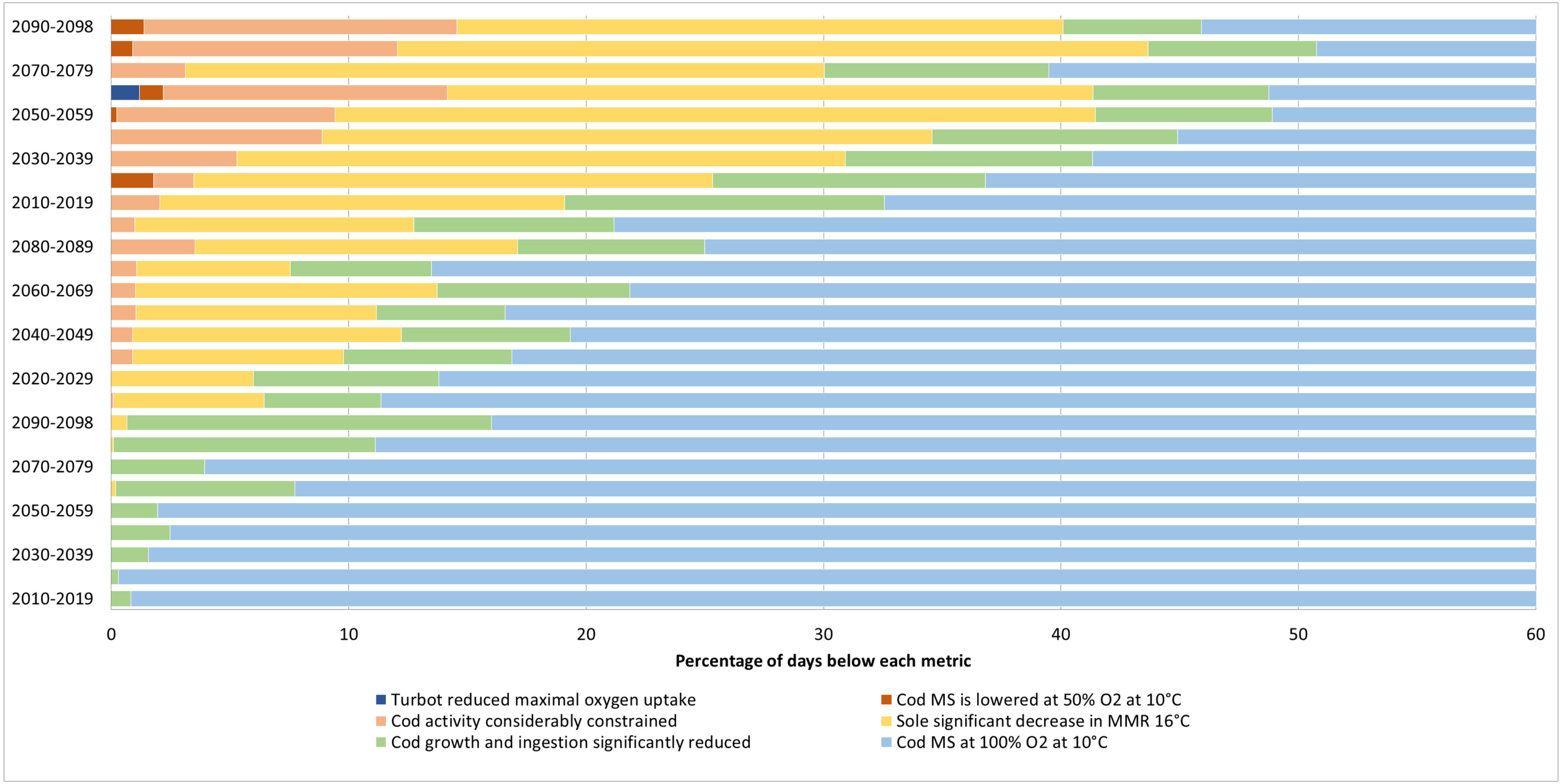

Figure 14: Percentage of days in each decade when seabed oxygen levels are predicted to be below each response metric for the North Dogger Bank, Oyster Grounds and Southern Bight.

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 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). Topcu and Brockman (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 that there was a particularly low oxygen concentration measured in 1983 in the southern North Sea and frequently low annual minimum oxygen concentrations 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 that have been found here, suggest positive implications for commercial fish. The areas affected by the three highest metrics (reduced growth and ingestion in cod, metabolic scope measured at 100% oxygen and decrease in MMR in common sole) increased in recent decades. This means that fish will have been able to maintain their metabolic rates above SMR, but their activities may have been constrained on days when oxygen was low. These effects occur at intermediate oxygen levels, which would not be considered “hypoxic”, are often excluded from work on oxygen effects on fish, and so receive little attention.

By integrating published responses with modelled hindcast oxygen conditions, it was found here that in the past, oxygen conditions are likely to have been sufficiently low to have had an impact on the activities of some fish. This is very hard to validate against fisheries data due to the other factors that act on commercial fish stocks. Since the 1970s (and indeed before then) there has been intense fishing pressure on North Sea fish (Engelhard, 2009) and will have overshadowed any effect of oxygen levels on fish populations. High resolution temperature data allowed Rutterford *et al.* (2015) to show how fish distributions in the North Sea were affected by temperature, and how they may change in the future. With detailed oxygen hindcasts and projections, similar work could be carried out to identify the role that oxygen plays in fish distribution changes, and potentially fishing pressure could be incorporated to identify if there are interactions between these two pressures. 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 (Killen *et al.* 2012), which is very difficult to quantify in the wild. Only a small number of fish could be assessed here due to the lack of experimental data, but experiments on hypoxic conditions (more severe low oxygen than discussed here) show that species are likely to react in different ways when they experience oxygen stress (Townhill *et al*., 2016). For example, *Pleuronectes platessa* (plaice) reduced their feeding rate when in water at 30% oxygen saturation (Petersen and Pihl, 1995), sea bass showed behaviours under hypoxic conditions that would make them more vulnerable to predators (Killen *et al*., 2012), and cod reduce their swimming activity and digestion (Claireaux *et al*., 2000; Chabot and Claireaux, 2008).

Integrating published responses with oxygen forecasts for future decades suggests there are unlikely to be large effects on catches of these species from oxygen effects alone. 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 (Chapman and McKenzie, 2009). 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 *Clupea harengus* (herring) and *Scomber scombrus* (mackerel), the reduced oxygen conditions could pose a problem if they were to spawn in these areas. In addition, spawning fish have increased oxygen requirements because of their higher metabolic rates (Pörtner and Farrell, 2008).

The decrease in oxygen conditions projected to the end of the century, indicate that oxygen concentrations will be lower in certain areas for longer periods of time, and so may pose more problems if fish are unable to move. 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 larger areas of the North Sea, which are deep and seasonally stratified, seasonal range shifts out of these areas could occur in the future. However the oxygen conditions of most of the North Sea are more similar to the conditions of the Oyster Grounds and 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 adapt or become tolerant to these conditions, and some populations of fish are already more tolerant than others (e.g. Zhu *et al.,* 2013). Future changes in sea temperature caused by climate change are thought to be likely to alter fish distributions in 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 and Steffensen, 1992; Claireaux *et al*., 1995). A study of mooring data in the North Sea has shown that in the Oyster Grounds, oxygen concentration in the bottom water is heavily influenced by storms and inputs of particulate and organic matter, and other short-term events (Greenwood *et al*., 2010). In the North Dogger Bank, oxygen concentrations were more influenced by more gradual temperature and organic input changes. 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 to those in the model on any day and at any depth. If oxygen metrics were available which covered a range of oxygen concentrations, alongside temperature in particular, 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 the metabolic scope of *Mugil cephalus* (flathead grey mullet) 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 and not on observational data, and so should not be treated as absolute. However, when the modelled oxygen point locations were confirmed against available observations for the period 1978 to 2008 (van der Molen *et al*., 2013) there were some negative biases (Southern Bight -5.1%; Oyster Grounds -13.9%; North Dogger -21.9%), suggesting that modelled values are underestimates of oxygen conditions. Thus the percentage of days when each fish may be affected by the oxygen values is likely to be an overestimate. Likewise, the experimental oxygen metrics relate to how captive 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. 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.

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Data Accessibility

The oxygen modelling data used in this article is available from the Cefas Data Hub at https://www.cefas.co.uk/cefas-data-hub/.

Chapter 5

Non-native marine species in north west Europe: developing an approach to assess future spread using regional downscaled climate projections

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Abstract

Climate change can affect the survival, colonisation and establishment of non-native species. Many non-native species common in Europe are spreading northwards as seawater temperatures increase. The similarity of climatic conditions between source and recipient areas is assumed to influence the establishment of such species, however in a changing climate those conditions are difficult to predict. A risk assessment methodology has been applied to identify non-native species with proven invasive qualities that have not yet arrived in north west Europe, but which could become problematic in the future. Those species with the highest potential to become established or be problematic have been taken forward, as well as some that may be economically beneficial, for species distribution modelling to determine future potential habitat distributions under projected climate change. In the past, species distribution models have usually made use of low resolution global environmental datasets. Here, to increase the local resolution of the distribution models, downscaled shelf seas climate change model outputs for north west Europe were nested within global outputs. In this way the distribution model could be trained using the global species presence data including the species' native locations, and then projected using more comprehensive shelf seas data to understand habitat suitability in a potential recipient area. Distribution modelling found that habitat suitability will

generally increase further north for those species with the highest potential to become established or problematic. Most of these are known to be species with potentially serious consequences for conservation. With caution, a small number of species may present an opportunity for the fishing industry or aquaculture. The ability to provide potential future distributions could be valuable in prioritizing species for monitoring or eradication programmes, increasing the chances of identifying problem species early. This is particularly important for vulnerable infrastructure or protected or threatened ecosystems.

Introduction

Non-native species can cause economic and ecological impacts in the places where they become newly established. Non-native (also non-indigenous, alien) species are considered to be those which have been introduced either directly or indirectly through human activities to areas outside their natural biogeographic range (Maggs *et al*., 2010). Some of them have harmful consequences for ecosystems, industries or human infrastructure, while some can offer opportunities in certain circumstances (Molnar *et al*., 2008; Cook *et al*., 2013). It has been estimated that non-native species could cost Europe €20 billion per year in damage caused, and in subsequent eradication programmes (Kettunen *et al.,* 2008). Distributions of non-native species are often constrained by the available vectors or mechanisms of introduction, and by the environmental conditions of the receiving areas (Libralato *et al*., 2015). The survival and reproduction of marine non-native species arriving in a new area are constrained by factors such as temperature and salinity, but also depth, substrate type and food availability; and it is thought that climate change may facilitate their persistence or reproduction in locations not previously habitable (Cook *et al*., 2013), and that some species may be ‘lying in wait’ until environmental conditions change (Ziska and Dukes, 2014). Ecosystems within north west Europe are witnessing rapid changes as a result of anthropogenic climate change (MCCIP, 2013) but also extensive habitat modification and resource use, and so are particularly vulnerable to the added impacts of non-native species. The North Sea in particular is considered to have a high degree of environmental change (Larsen *et al*., 2016), where sea surface temperatures have risen more rapidly than the global average over the past 50 years (Hobday and Pecl, 2014).

Already many marine non-native species have spread and become established in countries within north west Europe and are causing economic and biological damage (Cook *et al*., 2013). The effect of each ranges from negligible to catastrophic for native organisms and industries. They cause a range of impacts including outcompeting and displacing native species, affecting whole food chains and physical processes and damaging infrastructure (Molnar *et al*., 2008). Climate change is already known to have created conditions which facilitated an increased range of some non-native species in the UK and Ireland, including the Pacific oyster *Crassostrea gigas* and Asian club tunicate *Styela clava* (Cook *et al*., 2013). There is clearly potential that ranges will expand further in the future. One species not yet established in the UK is *Mnemiopsis leidyi*, a comb jelly that is native to the Atlantic coast of the USA, and which is thought to have been introduced to the Black Sea in the 1980s through ballast water (Didžiulis, 2013). In recent years, the species has spread to Scandinavia and Dutch and German coasts, potentially enabled by the rise in North Sea temperature (Oliveira, 2007). High numbers of the species have been associated with collapses in valuable fish stocks (Didžiulis, 2013) and so could be a major problem economically if it became established in north west Europe. Increased sea temperature could also mean that invasive seaweeds such as wakame *Undaria pinnatifida* are able to become established more successfully, and the rapa whelk *Rapana venosa*, which requires warm waters to deposit egg capsules, may be able to spread to northern areas by mid-21st century (Cook *et al*., 2013). However, climate change effects are complex (IPCC, 2014), and not all species ranges will expand because different factors affect spread (Pörtner *et al.,* 2014). Heavy rainfall and resultant decreases in salinity may reduce the spread of the carpet sea squirt *Didemnum vexillum* for example (Cook *et al*., 2013) despite favourable rising seawater temperatures, and the southward spread of the red king crab *Paralithodes camtschaticus*, which requires low temperatures, may be curtailed by further climate change (Natural England, 2009). There are a large number of non-native species within Europe, and the complexities involved in understanding how climatic change may affect where these species are able to become established means that for environment managers prioritizing the monitoring and eradication of these species is not straightforward. Roy *et al*. (2014) identified that in order for preventative action to be taken, there is an urgent need to anticipate which species could arrive and cause future problems. It is necessary then to further understand which species pose the greatest threat to north west Europe in terms of economic or biological impact, and in which areas these organisms may be able to survive and thrive in the near future and in the long term. This will enable individual species to be prioritised for management or eradication, which is particularly necessary in times of financial constraints on resources.

Some of the highest impact non-native species can be identified through risk assessment, based on information available on the effects caused in other areas and life history traits which affect likelihood of spread. Having identified these species, various species distribution modelling techniques are available to project or predict the extent of suitable environmental conditions. Some of these methodologies have been used to assess the potential future spread of non-native marine species once they have arrived at a particular destination (e.g. Herborg *et al*., 2007; Jones *et al*., 2013). Species distribution models make use of correlations between observed organism distributions and climatic or habitat variables. By looking at the current range of environmental parameters, such as depth, temperature, salinity and stratification tolerated by a species, it is possible to project future distribution using predictions of how the physical environment in an area will change in the future. Maxent is one of many, freely available, species distribution models (Phillips *et al*., 2006; Reiss *et al*. 2011) that has been applied in both terrestrial and aquatic ecosystems around the world. Previous studies using Maxent to consider future habitat distribution changes around north west Europe have used global climate model projections (e.g. Jones *et al*., 2013). Global climate models (GCMs) incorporate the physical drivers of large-scale climate change, but are less able to resolve local-scale shelf sea processes, such as currents, stratification and mesoscale processes (Tinker *et al*., 2015). While GCMs certainly produce useful projections, a new set of north west European shelf seas climate projections using an ensemble approach have recently been made available, providing much higher resolution (12 km cells) and more detail on the processes within the shelf seas (Tinker *et al*., 2015). Such changes include a centennial rise in annual mean sea surface temperature of 2.9 °C, and a freshening of 0.41 psu, of 2069-2098 relative to 1960-1989 (Tinker *et al*., 2016). By nesting the higher resolution shelf seas projections within the broader scale GCM projections (although both are based around the same HadCM3 physical model), it is possible to train a species distribution model on global species presence data, and then make use of the more detailed regional projections to understand how that species' habitat suitability may change in the future. Such an approach is particularly useful for non-native organisms as the broad-scale training dataset encompasses the original 'native' locality of the particular species, whereas the high-resolution dataset is used to characterise the potential distribution in a new area where there may be very few observations at the moment.

The aims of this study were to make use of these new climate model outputs and determine which non-native species pose the biggest risk of spread and conservation impact within north west Europe by:

- conducting a thorough risk assessment to identify species with the greatest potential to spread and consequently cause environmental or economic harm, or which could potentially be economically exploited in the UK, in the future; and
- determining future potential suitable habitat of non-native species by combining GCM projections with the most recently available north west European shelf seas climate projections.

Methods

This study involved four key steps:

1. Identify non-native species with the potential to spread and become established within the north west European shelf seas, or that are already present and have the potential to spread further.
2. Prioritise these species, using a risk assessment framework, to identify which to take forward for distribution modelling on the basis of potential impacts and invasiveness.
3. Build, train and assess the species distribution model for the present day on these key species. Combine high-resolution north west European shelf seas projections with global projections using a nesting approach to produce a useable global dataset.
4. Use the model to project future distribution change using the nested projections of future environmental conditions which have increased complexity within the shelf seas region of concern.

Step 1. Species identification

There are a number of mechanisms by which non-native species may become established, which were considered when identifying species for the risk assessment. Non-native species already present in the UK and nearby European countries, may be able to spread by natural processes (secondary colonisation) if environmental conditions (e.g. climatic changes in the future) allow. Secondary colonisation and spread can be facilitated by the movement of recreational boats between harbours, and by translocation of stock between aquaculture facilities. As seawaters warm in the future, it is likely that novel aquaculture species will be cultured in Europe and that some of these, and any accompanying species, will escape captivity. Species were not identified from this route as it is difficult to anticipate which species might be brought to Europe deliberately in the future.

In order to produce a list of non-native species to include in detailed modelling for the UK, the following qualities were considered: Non-native species already present in the UK and known to cause problems either here or in other countries, and non-native species present in north western European countries including those with a slightly warmer climate than the UK (e.g. Atlantic coasts of Portugal, Spain, France, Belgium, Holland, Germany, Denmark), and known to cause problems in those countries.

The list was compiled from a number of sources. These were the UK Technical Advisory Group on the Water Framework Directive (UKTAG, 2014), the GB Non-native Species Secretariat (NNSS, 2014); UK species lists provided by Natural England and The Marine Biological Association of the United Kingdom (MBA), the database of Delivering Alien Invasive Species Inventories for Europe (DAISIE, 2015), the global database of marine invasive species on the Conservation Gateway of The Nature Conservancy (Molnar *et al*., 2008), Cefas Priority Species Report (Cefas, 2015a), and the report on horizon scanning for invasive species in Great Britain (Roy *et al*., 2014).

From the subsequent short-list of non-native species already present in Europe (89 species in total, see Chapter 5 Appendix Table S1), the species that were scored highest by The Nature Conservancy database (Molnar *et al*., 2008) (ecological impact scores of 3 or 4) or identified on the Cefas Priority Species Report (Cefas, 2015a) were taken forward for risk assessment as described below (40 species in total, see Chapter 5 Appendix Table S2). For the Nature Conservancy database, Molnar *et al*. (2008) determined ecological impact scores by assessing how a species affects the viability and integrity of native species and biodiversity, based on documented evidence. The highest score is 4, which is achieved if a species disrupts ecosystem processes and wider abiotic influences. A score of 3 means that the species disrupts multiple species, and some wider ecosystem functions, or it affects keystone or species of conservation value. A lower score is achieved if impacts are less, for example, if only one taxon is affected. The Cefas Priority Species Report (Cefas, 2015a) contains species which have previously been assessed by Cefas or other European institutes as of high or moderate impact, or which are on European horizon scanning lists or listed by Roy *et al*. (2014).

Individuals of a species which arrive by ship (either through hull fouling or in ballast water) and are not currently able to survive in UK waters, may potentially be able to become established if conditions become more suitable with further climate change. To identify species which are not already established in Europe, current shipping routes to the UK were investigated to determine the likely ports of origin from which species could arrive and become established. Tidbury *et al*. (2014) analysed the different shipping routes for their potential to act as a vector for introduction of non-native species, and found that the ports of origin for commercial shipping to the UK with the highest number of voyages (i.e. greater than 500 voyages to the UK per year) were all in Europe or elsewhere in the UK which suggested heightened risk of secondary colonization primarily by organisms already present in the region. Regarding recreational boating, nearly all cruising routes were to continental Europe or within the UK. Thus species most likely to be introduced to the UK through current shipping and boating practices (the vast majority of which are within Europe) are highly likely captured in the species search as described above and no other species were put forward for risk assessment based solely on long-distance shipping routes.

Step 2. Risk assessment and prioritization

A thorough risk assessment was carried out on the 40 invertebrate species identified during the first process. An online “*Marine Invertebrate Invasiveness Screening Kit (MI-ISK)*” (Cefas, 2015b) was developed based on the widely used non-native freshwater fish toolkit "*Risk Identification and Assessment Methodology*" (Copp *et al.,* 2005). These toolkits include protocols and questionnaires by which species can be screened to determine their relative 'invasiveness', and thus the potential threat that they might pose in the wild. Forty-nine questions are answered about the species life history, evidence of invasiveness elsewhere in the world and whether or not they cause impacts to ecosystems or infrastructure where they have become established. An associated confidence level and a numeric score is calculated. Animals receive a high score (19 to 40) for invasiveness if there is a history of repeated introductions outside their natural range, large impacts to ecosystems or infrastructure where they become established, and/or if their life history characteristics suggest that they could be easily spread and become established in new areas. A medium score (13 to 18) is given if there is some history of invasion and some associated impacts. The species are characterized according to whether they possess undesirable traits, including reproductive strategies that enable rapid proliferation and broad dietary characteristics such as generalised feeding, that both enable species to out-compete native populations. Species information used in the risk assessment came from the GB Non-native Species Secretariat (NNSS, 2014), database of Delivering Alien Invasive Species Inventories for Europe (DAISIE, 2015), Global Invasive Species Database (2015), the Invasive Species Compendium (CABI, 2015), Cefas Priority Species Report (Cefas, 2015a) and the broader scientific literature.

Only invertebrates could be assessed due to the nature of the tool, and so aquatic plants were prioritised based on their ecological impact scores (Conservation Gateway of The Nature Conservancy, 2008) and listing on the Cefas Priority Species Report (Cefas, 2015a). Lastly, freshwater/brackish species were removed from the list, as the resolution of the climate models was considered not sufficient to allow reliable projections or outputs. Marine/brackish species were, however, included. The invertebrate species taken forward for distribution modelling were those with MI-ISK scores of 13 or over (i.e. a 'medium' or 'high' score of invasiveness), and are listed in Table 9, along with their impact scores and additional detail. The algal and angiosperm species taken forward were those which either had an Ecological Impact Score of 3 or 4, or were listed in the Cefas Priority Species Report (Cefas, 2015a).

Table 9: Species selected for distribution modelling. Species of potential commercial value are shown in bold, and species that were not modelled due to insufficient data are highlighted in grey. Information summarised from NNSS (2014), Roy *et al*. (2014), Cefas (2015a) and DAISIE (2015) except where referenced otherwise.

Scientific name	**Common name**	**Ecological impact score**	**DAISIE 100 worst**	**Cefas Priority list?**	**Impact Detail**	**Date and place of first record in Europe**	**MI-ISK Score**
Crassostrea gigas	Pacific oyster	3	Y	Monitoring	**Commercially valuable.**	France, the Metherlands and United Kingdom in 1960s for aquaculture	25
Hemigrapsus sanguineus	Asian shore crab	4	N	Monitoring	One of highest ranking by Roy *et al*., 2014.	France and the Netherlands in late 1990s (Breton *et al.,* 2002)	23
Styela clava	Asian club tunicate	4	Y	-	Outcompetes other filter feeders and causes declines in mussel production. Spray causes respiratory condition in humans. Can foul structures, shellfish and fish cages.	United Kingdom in 1950s	23
Crepidula fornicata	slipper limpet	4	Y	Monitoring	High densities, causes trophic competition, reducing growth of commercial bivalves.	United Kingdom in 1870s-1880s	22.5

Scientific name	Common name	Ecological impact score	DAISIE 100 worst	Cefas Priority list?	Impact Detail	Date and place of first record in Europe	MI-ISK Score
					Changes sediment structure. Reduces diversity of maerl beds. May reduce recruitment of fish. Fouls port structures.		
Asterias amurensis	northern Pacific starfish	-	-	Surveillance	Voracious predator, reducing numbers of native species.	Earliest record on GBIF is from Spain in 2010 (GBIF, 2017a)	20
Amphibalanus improvisus	bay barnacle, acorn barnacle	4	Y		Dominate community and compete for space and food. Foul native mussels, oysters, water intake pipes, hulls, structures.	Found in the Netherlands in 1820s.	19
Penaeus japonicus	kuruma prawn	3	Y	-	Competes with native prawn species for food and space. May change structure of native benthos, and sediment structure.	Greece since the 1920s	19
Tricellaria inopinata	bryozoan	4	Y	-	Outcompetes native bryozoans. Fouls buoys,	Italy in 1980s	19

Scientific name	Common name	Ecological impact score	DAISIE 100 worst	Cefas Priority list?	Impact Detail	Date and place of first record in Europe	MI-ISK Score
					boats, ropes. Insufficient presence data to model.		
Ruditapes philippinarum	Manila clam	4	N	-	Outcompetes native bivalves. **Could be commercially exploited.**	United Kingdom, 1980s	17.5
Garveia franciscana	rope grass hydroid	4	N	-	Blocks cooling systems in Chesapeake Bay. Insufficient presence data to model.	Germany since 1950s (OBIS, 2017a)	17
Mytilopsis leucophaeata	Conrad’s false mussel	3	N	-	Brackish biofouler of coolant systems.	Germany in 2000 (OBIS, 2017b)	17
Mercenaria mercenaria	American hard-shelled clam	3	N	-	Displaces native clams.	France in 1860s	16
Watersipora subatra	bryozoan	-	-	Monitoring	Fouling organism. Insufficient presence data to model.	First GBIF record is in United Kingdom in 2014 (GBIF, 2017b)	16
Crassostrea angulata	Portuguese oyster	-	-	Monitoring	**Commercially valuable.** Insufficient presence data.	Portugal in 16th century	15
Mnemiopsis leidyi	sea walnut, comb jelly	4	N	Surveillance	Reduces species in lower trophic levels, and reportedly can cause	Black Sea 1980s	15

Scientific name	Common name	Ecological impact score	DAISIE 100 worst	Cefas Priority list?	Impact Detail	Date and place of first record in Europe	MI-ISK Score
					collapse of planktivorous fish, dolphins and seals. One of highest ranking in Roy *et al*., 2014.		
Rapana venosa	rapa whelk	4	Y	Monitoring	Risk to oyster cultures in high densities. May compete with native *Buccinum undatum*. Mussels in Black Sea severely affected. One of highest ranking in Roy *et al*., 2014.	Black Sea in 1940s	14.5
Ensis directus	American razor clam	3	Y	Monitoring	May impact sediment structure. Shallower water than native species so can affect bathers. Can damage trawls and nets. **Could be commercially valuable.**	German Bight in 1970s	14
Didemnum vexillum	carpet sea squirt	4	N	Monitoring	Insufficient presence data to model.	France in 1990s	13

Scientific name	**Common name**	**Ecological impact score**	**DAISIE 100 worst**	**Cefas Priority list?**	**Impact Detail**	**Date and place of first record in Europe**	**MI-ISK Score**
Homarus americanus	American lobster	-	N	Monitoring	One of highest ranking future alien invasive species in Roy *et al*., 2014.	Iceland in 1960s	13
Bonnemaisonia hamifera	red alga	-	Y	Monitoring	Dominant alga in some regions, outcompeting native species.	United Kingdom in 1890s	N/A
Codium fragile	green alga	4	N	-	Alters benthic communities and increases sedimentation. Fouls shellfish beds, clogs dredges, interferes with nets, jetties etc.	The Netherlands in 1900	N/A
Sargassum muticum	wireweed	4	N	Monitoring	Outcompetes native seaweeds, fouls harbours.	France in 1960s or United Kingdom in 1970s.	N/A
Spartina townsendii var. *anglica*	cord grass	4	Y	Monitoring	Environmental modifier. Replaces *S. maritima* and excludes native *Salicornia spp*. and *Zostera spp*.. **Used to stabilise mudflats for land reclamation. May be used**	A hybrid that developed in United Kingdom	N/A

Scientific name	Common name	Ecological impact score	DAISIE 100 worst	Cefas Priority list?	Impact Detail	Date and place of first record in Europe	MI-ISK Score
					as biofuel, paper and animal feed.		
Undaria pinnatifida	wakame (seaweed)	3	Y	Monitoring	Outcompetes native seaweeds. Can grow on shellfish and impair aquaculture harvests. **Could be commercially valuable.**	France in 1980s.	N/A

Step 3. Build, train and assess the model for the present day

Using high-resolution shelf seas projections on their own would not cover a sufficiently large area or provide a broad enough range of experienced climate conditions to enable assessments of habitat suitability. For example, the shelf seas area does not include the environmental conditions experienced by a species which is native to the sub-tropics or the Arctic, and so these conditions would be excluded from any habitat suitability assessment. Therefore in order to make use of these newly-available high-resolution projections while taking account of the conditions experienced globally by each species, it was necessary to nest high-resolution regional data within a grid of coarse GCM outputs. This resulted in habitat suitability functions encompassing the entire range of each species and in particular the 'native' range of the non-native species, that could subsequently be applied at the local scale to a focal location where the species may not yet be fully established.

A set of environmental, marine climate parameters available in standard climate projections were chosen to drive the species distribution model (Maxent) as in previous work (Cheung *et al.*, 2009; Jones *et al*., 2013). To build and test the model under present day conditions the outputs of the global and regional model were used as averaged annual means from 1980–2009 (hereafter termed 'present day') taking the parameters: i) bathymetry, ii) near bottom temperature iii) sea surface temperature, iv) near bottom salinity, v) sea surface salinity, vi) bulk thermal stratification (difference between sea surface and near bottom temperature) and vii) bulk haline stratification (difference between sea surface and near bottom salinity).

Projections were obtained from the Met Office Hadley Centre. Global 1.25 degree resolution projections were from a Perturbed Physics Ensemble (PPE) (Collins *et al*., 2011) of the Atmosphere-Ocean Global Climate Model HadCM3 (Gordon *et al*., 2000; Pope *et al*., 2000). This PPE consisted of the standard version of the model (the unperturbed ensemble member) with 10 ensemble members with a number of atmospheric parameters perturbed in order to span the range of uncertainty in Climate Sensitivity (the amount of global mean warming associated with a doubling of CO_2). In this study the unperturbed ensemble member is used, which is equivalent to the standard version of

HadCM3 and HadRM3. The unperturbed member of this ensemble has been dynamically downscaled with the shelf seas model POLCOMS (Proudman Oceanographic Laboratory Coastal Ocean Modelling System; Holt and James, 2001; Holt *et al*., 2001) to produce the north west European shelf seas projection (Tinker *et al*., 2015; 2016) used in this study, with a resulting resolution of 12 km (1/9° latitude by 1/6° longitude), covering 43°N – 63°33'20"N and 18°20'W – 13°E (see Figure 15).

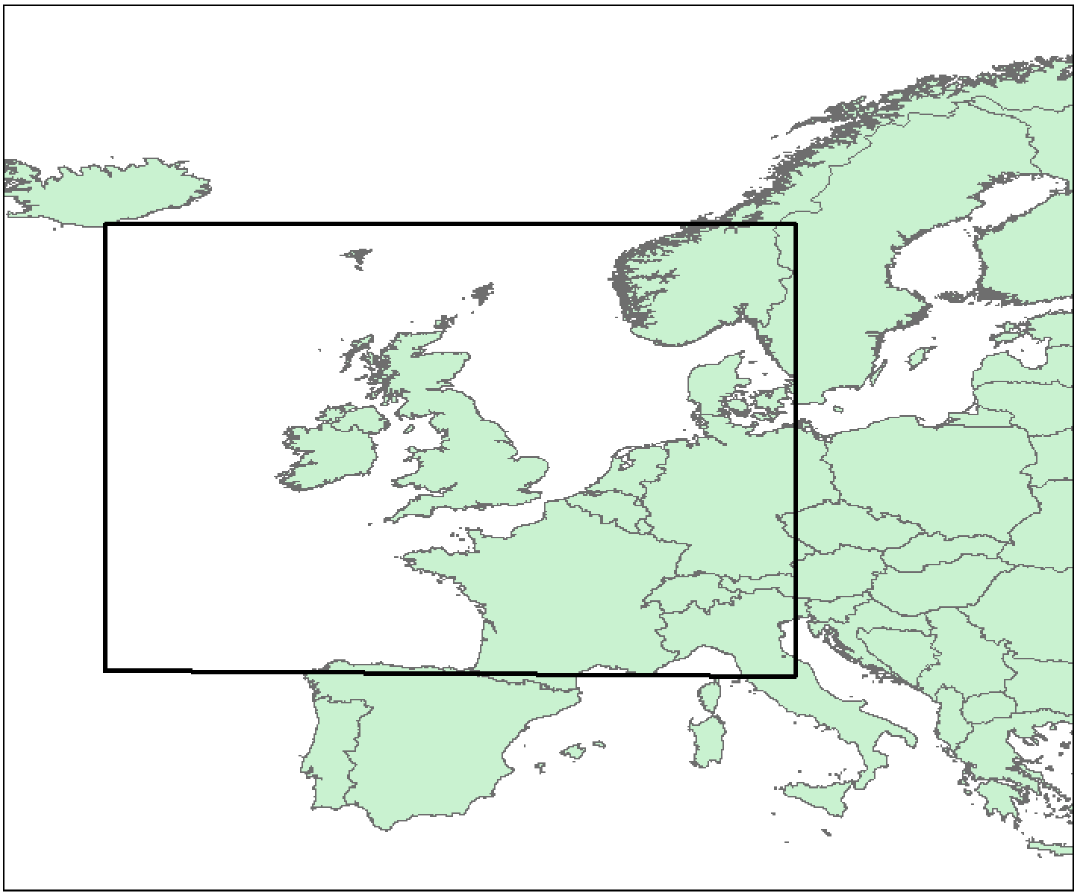

Figure 15: The extent of the dynamically downscaled regional climate projections.

The downscaled shelf seas projections were nested within the driving global projections using Python 2.7 (Python Software Foundation, 2010) (packages netCDF4 and numpy) with a resulting global dataset at 0.5 degree resolution. The global ocean fields were bi-linearly interpolated from the native 1.25° resolution to the 0.5°, while the downscaled regional fields were aggregated up (averaged) from their native 1/6°x1/9° resolution to the required 0.5°. They were then copied into the global data. As the regional data and the global data are consistent (the global data are from the run that forced the regional model), the two datasets match at the boundary. This intermediate resolution was necessary as it still captures the local-scale processes of the shelf seas model while not reducing the resolution of the GCM more than is appropriate. This intermediate resolution (0.5 degree) grid of present day environmental parameters was then used as the driver for the species distribution model.

The Maximum Entropy (Maxent) species distribution model was used (Phillips *et al*., 2006) because it provides a robust method for assessing habitat suitability (e.g. Reiss *et al.* 2011; Vierod *et al*., 2015) compared to other, similar modelling methodologies. Maxent randomly selects training data points and generates habitat suitability by combining presence-only occurrence data and chosen environmental variables and predicting the potential distribution of a species, or habitat suitability. The remaining presence data points are used to test the model fit. Projected environmental conditions are then used to force the model to predict future habitat suitability, based on the same environmental preferences. Maxent estimates the probability distribution of the grid by finding the distribution that has the maximum entropy (i.e. most uniform), subject to the constraints of incomplete information (Phillips *et al*., 2006). The probability distribution is defined by the environmental variables used in to the model. The term “habitat suitability” is used here to describe the bathymetry and the environmental hydrographic conditions of the area, and does not include characteristics of bottom substrate, or local species interactions within communities (i.e. food availability, etc.). It was not possible to include bottom substrate as a model variable because, at 0.5 degree resolution, this was too large to suitably represent the substrate type, which can change dramatically within the area.

Species occurrence data were downloaded from two databases: the Ocean Biogeographic Information System (OBIS) (http://www.iobis.org) and the Global Biodiversity Information Facility (GBIF, 2015) (http://data.gbif.org). The data were cleaned using the statistical software R (version 3.0.3 (R Core Team, 2013), to remove duplicates, occurrences outside the accepted depth and Food and Agriculture Organisation of the United Nations (FAO) area ranges, and to remove reported occurrences on land (due to mis-recording of locations). This was done by taking FAO areas and depth ranges from OBIS and Sea Life Base (http://www.sealifebase.org), with depth being rounded up to the nearest 100 m to ensure that all reasonable presence data were included. Cleaning and sense-checking the data in this way reduced the chance that species which were misidentified or mis-recorded were included in the presence dataset. The data were aggregated to the intermediate resolution 0.5 degree grid, with a value in each cell for presence or absence. This aggregation reduced the number of presence points within a small area (e.g. at a regularly sampled beach or marina). Maxent was then run for each species using the model interface (version 3.3.3k) downloaded from http://www.cs.princeton.edu/ ~schapire/maxent/. The presence data were uploaded into 'Samples' and the current environmental data (climate and bathymetry) into 'Environmental layers'. Auto features were used along with 'jacknife' which checks variable importance. Maxent automatically chooses the number of training values based on the number of presence data points available. The number of training points used across the different species varied considerably, from the highest for the American lobster (202) to the lowest for the seaweed wakame (16), with those with the higher value likely to be a better fit to reality than others. The number of training and presence points are given in Table 10. Maxent then tests the 'skill' of the resulting relationships using the Area Under the Curve (AUC) value. The AUC value (from 0 to 1) is a measure of the performance of the model; the higher the value the better the model fit. A threshold value of 0.8 or above was chosen, based on a review of published habitat suitability models by Mercks *et al*., 2011). It should be noted that this type of modelling can be subject to autocorrelation due to biased and opportunistic species sampling, and so this value of 0.8 is used as a guide rather than an absolute value of a robust output.

Step 4. Using the model: future distribution change

Projections from climate model output were obtained from the same unperturbed member of the downscaled HadCM3 model as described above, under an SRES A1B business as usual scenario, characterised as 'medium' emissions. As described above these were nested within the global climate model outputs to produce a set of intermediate resolution projections for two future timeslices: 2040–2069 and 2069–2098. Hereafter these timeslices are referred to by their middle year: 2055 or 'near future'; and 2084 or 'end of century'.

Data outputs from these projections were included as inputs into species distribution model (Maxent), as described above, but with the future environmental data entered into 'Projection layers'. This was carried out for each species in each future time scenario. This gave a global half-degree resolution grid of habitat suitability ranging from 0 to 1 for the present and future scenarios. The latitudinal centroid for each time period and species was then calculated, both globally and for the extent of the shelf seas model alone, giving the centre of the latitudinal range for each species and a measure of how it has changed from the current to the future period, both globally and around the UK. The centroid *C* was calculated using the equation from Cheung *et al*., (2009):

$$C = \frac{\sum_{i=1}^{n} Lat_i \cdot Abd_i}{\sum_{i=1}^{n} Abd_i}$$

where Lat_i is the central latitude of the spatial cell *i*, *Abd* is the predicted relative habitat suitability of the same cell, and *n* is the total number of cells. The difference between the two latitudinal centroids in the current and projected years was then calculated in kilometres (Cheung *et al*., 2011):

$$Latitudinal\ shift\ (km) = (Lat_m - Lat_n) \times \frac{\pi}{180} \times 6378.2$$

where Lat_m and Lat_n are the latitudinal centroids in the projected (*m*) and current (*n*) years, and 6378.2 is the approximate equatorial radius of the Earth in km.

Results

Steps 1 and 2. Risk assessment and prioritisation

The MI-ISK scores for the marine invertebrates showed that the Pacific oyster, the slipper limpet *Crepidula fornicata,* the Asian club tunicate, the Asian shore crab *Hemigrapsus sanguineus* and the northern Pacific starfish *Asterias amurensis* all scored ‘high’ and had the highest potential risk for spread and subsequent impact. All other invertebrates scored ‘medium’.

Step 3: Validation of the present day species distribution models

For five species, as listed in Table 9, there were insufficient presence data to either run the model or produce the robust output with an AUC greater than 0.8, and so these were not taken forward to the final modelling stage. For the remaining species which were taken forward for the future modelling, the AUC values, the variable with the highest percent contribution, the total number of presence data points and the number of training points used are all presented in Table 10.

Table 10: The Area Under the Curve (AUC) value, the variable with the highest percent contribution to the model, and the number of presence records used for training.

Species	**AUC value**	**Variable with the highest percent contribution**	**Number of presence records**	**Number of presence records used for training**
Amphibalanus improvisus	0.989	Near bed temperature	308	136
Asterias amurensis	0.987	Bathymetry	95	70
Bonnemanisonia hamifera	0.992	Bathymetry	191	145
Codium fragile	0.992	Near bed temperature	202	132
Crassostrea gigas	0.988	Near bed temperature	283	147
Crepidula fornicata	0.988	Near bed temperature	394	191
Ensis directus	0.990	Near bed temperature	266	133
Hemigrapsus Sanguineus	0.9980	Bathymetry	83	38
Homarus americanus	0.988	Near bed temperature	291	202
Mercenaria mercenaria	0.992	Near bed temperature	147	60

Species	**AUC value**	**Variable with the highest percent contribution**	**Number of presence records**	**Number of presence records used for training**
Mnemiopsis leidyi	0.994	Near bed temperature	133	86
Mytilopsis leucophaeata	0.994	Near bed temperature	89	26
Penaeus japonicus	0.985	Near bed temperature	63	32
Rapana venosa	0.971	Near bed temperature	84	25
Ruditapes philippinarum	0.984	Bathymetry	77	29
Sargassum muticum	0.991	Near bed temperature	230	123
Spartina townsendii var. anglica	0.995	Bathymetry	143	78
Styela clava	0.990	Bathymetry	97	65
Undaria pinnatifida	0.999	Bathymetry	27	16

All AUC values are above 0.9 showing good predictive power of the models. Further detail on the modelling results is provided in Chapter 5 Appendix Table S3.

Step 4. Future distribution change

Species distribution modelling found that habitat suitability ranges for all species would move poleward at a global scale by up to 843 km (9.5 km/yr) (Figure 16), and generally northward within the European shelf seas by up to 115 km (1.3 km/yr) by the end of the century (Figure 17), although American lobster *Homarus americanus* and Conrad's false mussel *Mytilopsis leucophaeata* were exceptions with predicted southwards movement. The American lobster was projected to have a distribution shifted south by 2055 and then north by 2084 while Conrad's false mussel's habitat suitability shifts south over both time periods. The species with latitudinal centroid projected to move the furthest globally by the end of the century are kuruma prawn *Penaeus japonicus* (843 km, 9.5 km/yr), American hard-shelled clam *Mercenaria mercenaria* (620 km, 7.0 km/yr), slipper limpet (615 km, 6.9 km/yr), American razor clam *Ensis directus* (572 km, 6.4 km/yr) and Manila clam *Ruditapes philippinarum* (703 km, 7.9 km/yr). Within the shelf seas area, the species with the greatest northward latitudinal centroid change by 2084 are cord grass *Spartina townsendii var. anglica* (115 km, 1.3 km/yr), wireweed *Sargassum muticum* (110 km, 1.2 km/yr), Asian club tunicate (90 km, 1.0 km/yr), Pacific oyster (86 km, 1.0 km/yr), Asian shore crab and kuruma prawn both (81 km, 0.9 km/yr). The annual latitudinal centroid shifts stated above are an average over the whole period and the actual changes are unlikely to be linear.

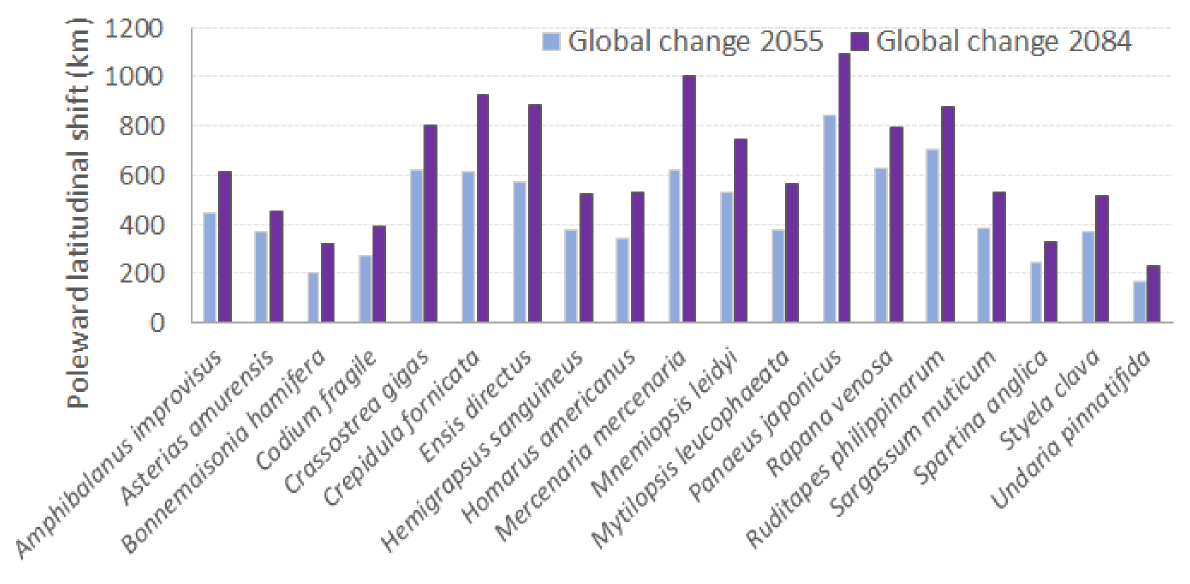

Figure 16: Poleward shifts in global habitat suitability, referenced against a baseline from 1995, as predicted for the years 2055 (light bars) and 2085 (dark bars).

For the four highest MI-ISK scoring species (Pacific oyster, Asian shore crab, Asian club tunicate and slipper limpet) and most of the species assessed, habitat suitability was projected to shift northwards by 2055 and 2084 compared with 1995, particularly in the southern North Sea and along the Scandinavian coastline (Figure 18). The American lobster showed higher habitat suitability in deeper waters, particularly along the shelf edge and in the Bay of Biscay. The habitat suitability of Conrad's false mussel decreased around the northern UK and Scandinavia in 2055 and 2084. Within these plots, the difference in resolution from the global and shelf seas models can be seen by looking at the outline of the coast. The land area covered by the GCM only is based on data at 1.25 degree resolution and so is not highly detailed. However, the area derived from the shelf seas model can be clearly seen by the more detailed coastal outline.

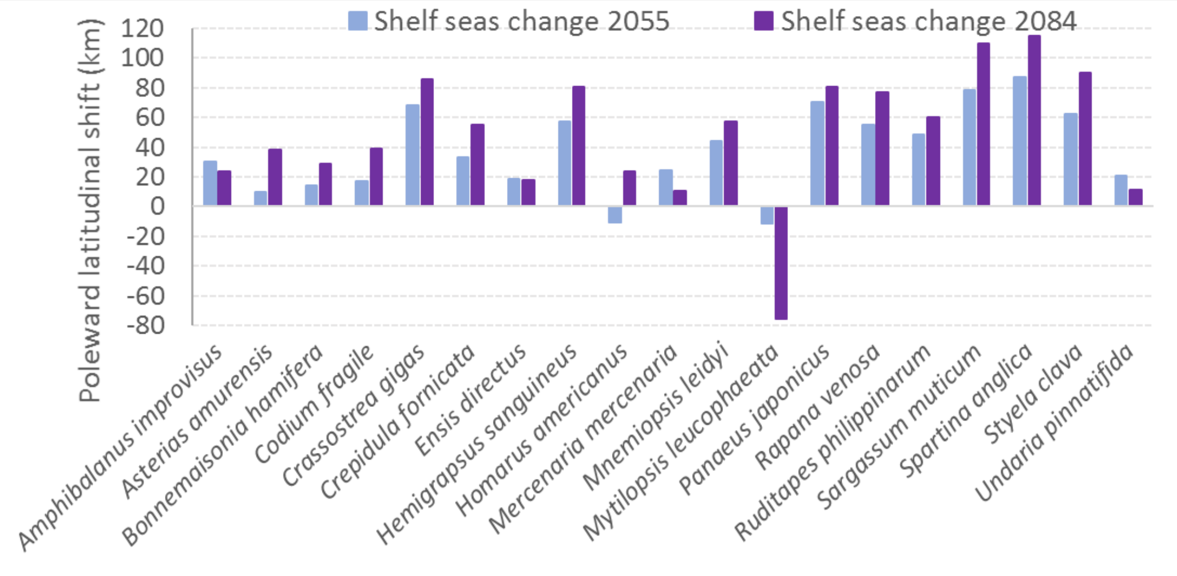

Figure 17: Poleward (northerly) shifts in habitat suitability in the shelf seas area, referenced against a baseline from 1995, as predicted for the years 2055 (light bars) and 2085 (dark bars).

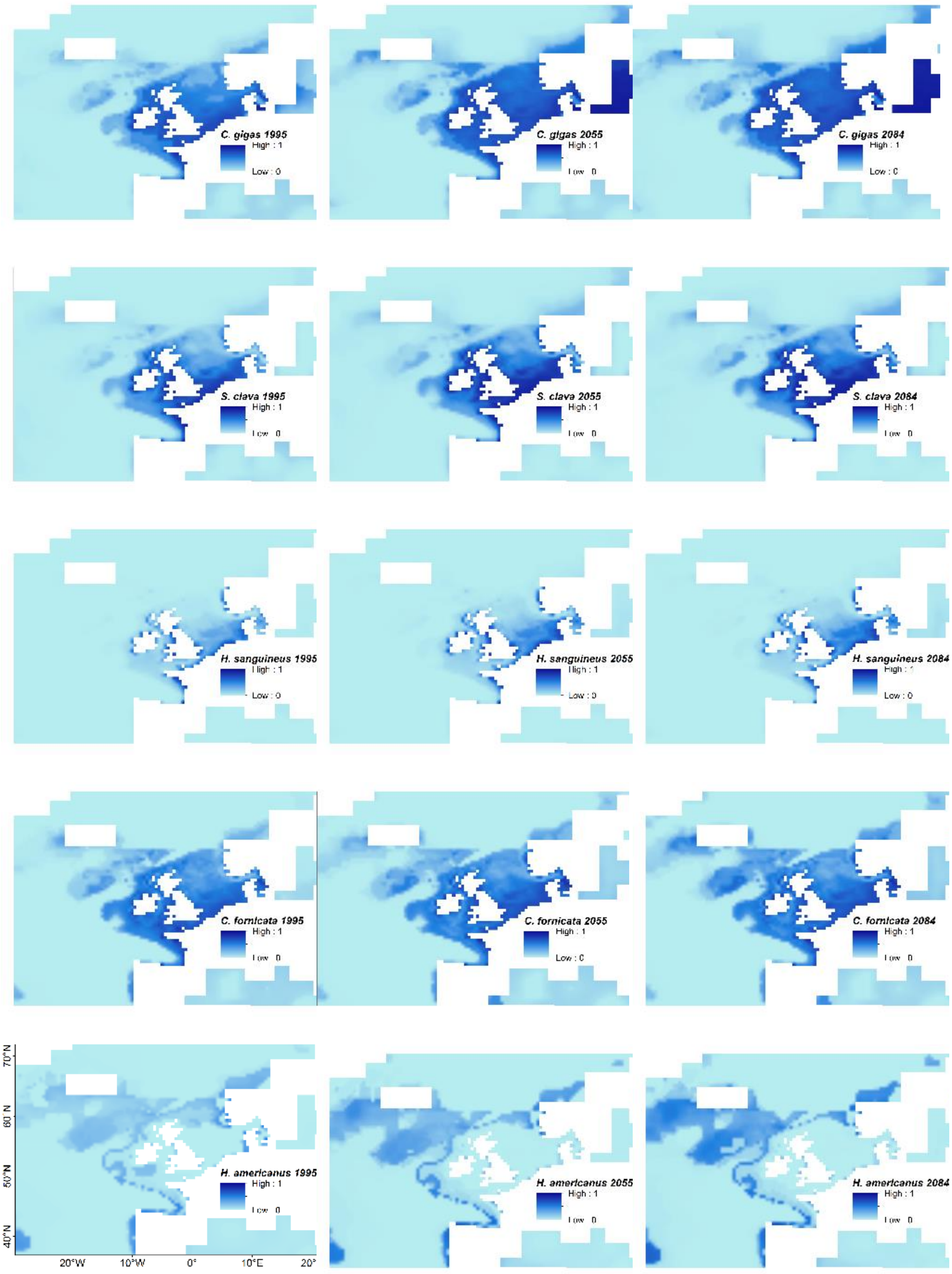

Figure 18: Habitat suitability (from 0 to 1) within the north west European shelf seas area for five species with particularly high MI-ISK risk scores, as predicted for the years 1995 (left), 2055 (middle), and 2085 (right).

Discussion

The risk assessment found a range of non-native species which are either already impacting marine environments within the UK or north west Europe or which pose a significant threat. The species distribution models suggest a change in habitat suitability around the shelf seas over time with predicted climate change scenarios. This will potentially result in the majority of the species included in the risk assessment responding to this with a northward shift within the next 50 to 100 years and becoming established in new areas. The models predict how far the suitable habitat for these non-native species may spread including into areas where conditions are not currently suitable. Further spread may occur via natural dispersal or facilitation by further shipping movements and other human activities, but the environmental conditions that currently limit survival and reproduction will become less restrictive in the coming decades.

The risk assessment and distribution modelling identified Pacific oyster, Asian shore crab, Asian club tunicate, wireweed and cord grass as species of particular concern due to their potential future suitable habitat and the impact that they have on ecosystems or industries; evidenced by high MI-ISK scores and the greatest anticipated latitudinal shifts in habitat suitability. Changing environmental conditions could allow these species to increase their range substantially, with ecologically and economically damaging impacts. For example, the Asian shore crab is anticipated to spread north around the British Isles and along the Scandinavian coasts, where it has the potential to outcompete the native green shore crab *Carcinus maenas* (Epifanio, 2013). The green shore crab is itself an invasive species in some parts of the world, and on rocky shores in New England, USA, arrival of the Asian shore crab caused a reduction in green shore crab numbers of up to 90% (Lohrer and Whitlatch, 2002). In addition to effects on individual species, there are also likely to be changes to predator-prey interactions (such as predation pressure on native bivalves, Lohrer and Whitlatch, 2002) and consequently whole food webs, and this too can be modelled given scenarios of projected spread, population growth and ecological characteristics (e.g. Pinnegar *et al*., 2014). The Pacific oyster forms reefs when it occurs in high numbers, and these may be useful for coastal protection, such as in the Netherlands where reef accretion rates and persistence have been studied (e.g. Walles *et al*., 2015). In the UK, reefs are present in the Yealm Estuary in Devon

(S. Hawkins, pers. comm., November 2016). The presence of reefs could prevent certain protected areas from meeting ecological status levels required by legislation (Herbert *et al*., 2012). Economic problems which could be envisaged from some of these species include wireweed and Asian club tunicate fouling man-made structures such as aquaculture facilities, with consequential declines in mussel production in the case of the tunicate (NNSS, 2015).

It has been suggested that in some circumstances non-native species may enrich ecosystems rather than causing harm (Libralato *et al*., 2015), and non-native species can co-exist with natives in some instances (Gallagher *et al*., 2016). Additionally, some of the species considered in this study could represent a hitherto unexploited commercial opportunity where they have invaded. For example, shellfish such as the American razor clam, the American lobster, the Pacific oyster and the Manilla clam and seaweed such as wakame*,* are edible species which could be commercially exploited, either through wild harvest or aquaculture. Indeed, there are already commercial fisheries for the Manilla clam in the UK (Jensen *et al.,* 2004; Humphreys *et al.,* 2015). With very careful management, wild capture could provide a mechanism to limit population sizes and subsequent impacts while also providing short-term commercial gain although much caution should be taken with this approach. Detailed cost benefit analyses would be required, especially in relation to the possible loss of revenue from native species potentially impacted either directly or indirectly by climate change and the introduced non-native organisms, before the exploitation of these species should be really considered. The Pacific oyster has been harvested in the UK for a number of decades in areas where it is abundant (Davison, 1976). Herbert *et al*. (2012) state that in certain areas where wild settlement is inevitable due to the volumes of boat traffic, harvesting the species may be the only way to manage the stock. The authors suggest that fisheries support schemes could be appropriate to develop the new fishery. In the Bay of Biscay, the American razor clam is collected for human consumption and as bait (Arias and Anadon, 2012), and it is considered that densities in certain areas are high enough to sustain a fishery (Witbaard *et al*., 2013). In an ICES Alien Species Alert Gollasch *et al*. (2015) note caution with regard to establishing such a fishery due to the potential to cause further spread. Cord grass can spread rapidly within soft sediments and so its ability to thrive in new areas has been of benefit with regard to stabilising coastlines (Davidson, 1991). However, this benefit needs to be balanced with the reduced biodiversity within the cord grass monoculture, in comparison with biodiversity among the native saltmarsh plants which are slower to become established (Davidson, 1991).

The new high-resolution north west European shelf seas climate projections suggest a geographic pattern of sea temperature changes, with greater winter/spring warming in the southwestern North Sea, and summer/autumn warming in the Celtic Sea and North Sea (Tinker *et al*., 2016). The use of the downscaled model outputs allows tides, regional currents and stratification to be represented across the north west European shelf seas area (Tinker *et al*., 2016), which are important for modelling the physical conditions in this region, and for the survival and reproduction of a number of species. The GCM does not represent these processes and so if used to represent certain shelf regions, there may be deficiencies in the ability to model the underlying species distribution-habitat relationships.

It should be noted that this study is not indicative of an inevitable spread of a range of non-native species, but that it demonstrates the potential spread based on the projected environmental suitability (Jarnevich *et al*., 2015). The habitat suitabilities were compared to the present day (averaged time period), and were based on recorded occurrences and not absolute distributions. Thermal niche alone does not fully predict invasive species distributions (Parravincini *et al*., 2015), and for a complete picture there are many factors to consider other than those included in this study. For example, it is unlikely that species will thrive in large numbers at the boundaries of projected areas of habitat suitability although they may be present. It may be the case that some species may not be able to spread at the same rate as the climate changes (such as in the Mediterranean, Hiddink *et al*., 2012), and so they will not spread to all of the areas deemed suitable. Additional factors such as local hydrodynamics, substrate type, species interactions and food supply may mean that these areas remain unsuitable (Cook *et al*., 2013). Substrate type was not included in the models here because the resolution of 0.5 degrees is too large to represent the bottom characteristics in an area, which can change over small distances. Individuals need a suitable substrate to settle and establish, and can use certain substrates, including man-made structures, as stepping stones to colonise new areas, depending upon their dispersal mechanism (Adams *et al.*, 2014). Some of the species assessed here are specialists of a certain habitat (e.g. saltmarsh) and so future work could consider overlaying the habitat suitability projections here on maps of substrate type, which would show the specific areas in which the species may become established. Species interactions such as presence of native or non-native predators and competitors can be affected by climate, (Poloczanska *et al*., 2008; Hawkins *et al*., 2009) and would also affect establishment of a new species in an area. To investigate this further, specific species interactions could be considered in small areas under future scenarios, such as carried out by Poloczanska *et al.* (2008). Dispersal characteristics such as larval duration, life history traits and larval behaviour (Gaines *et al.*, 2007) were considered in the risk assessment undertaken here, but further work for each species could consider the hydrodynamics in certain areas to determine the potential for spread.

Species distribution models must be interpreted with appropriate caution (Jarnevich *et al*., 2015). Since the exact presence of every species at any one time can not be mapped, presence data used in the models are incomplete and are likely to be biased to areas where there is greater sampling effort, creating autocorrelation errors. There are more mechanistic modelling approaches available (Jennings and Brander, 2010), however the Maxent approach offers the opportunity to screen large numbers of species relatively quickly and easily and so should be viewed as complementary to more complex approaches. A study comparing different species distribution modelling techniques of benthic species found Maxent to be one of the most robust, including for small sample sizes (Bučas *et al*., 2013) and others have found it compared well against other techniques (Elith *et al*., 2006; Phillips *et al*., 2006; Pearson *et al*., 2007; Reiss *et al*., 2011; Padalia *et al*., 2014). This study focused on species of interest to the UK and north west Europe, and the climate projection dataset used was designed to be of highest possible resolution around the shelf seas. Therefore, caution should be if interpreting habitat suitability predictions for elsewhere in the globe where interpolation was used to increase the grid resolution. While the half-degree resolution used in the models is high relative to global data, much of the coastal and intertidal species presence data points are lost as a result of this action. Therefore for species that occur very close to the coast, this missing zone must be considered when using the habitat suitability scores.

Aspects of climatic change not included within the models here are changes in pH or oxygen saturation. Ocean acidification is predicted to have diverse effects on organisms. It is possible that algae and jellyfish, that do not have calcareous skeletons, may benefit while molluscs and some crustaceans may be at a disadvantage (Hall-Spencer and Allen, 2015). Therefore, with increased ocean acidification later in the century, the predicted habitat suitability for the Pacific oyster may be an overestimate, while that for the comb jelly *M. leidyi,* and seaweeds *C. fragile*, wireweed and wakame it may be overly conservative. Greater intensity and frequency of storms may also favour the spread of non-native species, particularly seaweeds and animals that attach to seaweeds (Cook *et al*., 2013). Along with longer term climate change, short-term climatic changes can also affect species distributions, with some species requiring a succession of years of warm conditions to become established. For example a series of warm summers and mild winters has led to increases in populations of the non-native barnacle *Austrominius modestus* in the North Sea (Witte *et al*., 2010), and the Pacific oyster didn't establish a large population in the eastern North Sea until 17 years after arriving, coincident with warm summer temperatures (Diederich *et al*., 2005). The effects of these parameters on individuals and ecosystems are complex and so further research will help to understand the complexities affecting spread, survival and population persistence of species.

There are a number of sources of uncertainty that will affect these results. Full quantification of this uncertainty is outside the scope of this study, however, they are briefly discussed here. These sources of uncertainty are from three areas within the methodology: the underlying climate projections; the species distribution modelling approach; and the observations used to train it. Climate projection uncertainty typically includes choice of emission scenario (here we use a single emission scenario, A1B), model structure uncertainty (we use a single GCM and shelf seas model (HadCM3 and POLCOMS), and model parameter uncertainty (the standard (unperturbed) member of a perturbed physical ensemble is used here). It is noted that these results give a plausible estimate of possible future invasive species distribution but do not necessarily characterise the full range of possibilities. However, recommend future work is to explore the implications of these underlying uncertainties, and to explore the uncertainties in distribution modelling such as through using a multi-model approach (e.g. Jones *et al*., 2013). The limitations of recording species observations should be particularly highlighted. If a species has not realised its full fundamental niche (i.e. it does not yet occur in all of the places where it could survive; a situation that is highly likely in an invasive species), then it is difficult to make predictions about its future distribution, as the predicted niche may be smaller than the full 'realisable' potential niche (Phillips *et al*., 2006). This is also a problem when species occurrence records come from only one part of the global distribution (for example if many records occur close to a research station) which does not represent the whole species niche, or when there are too few occurrence data points. Sufficient sampling effort is required to ensure that the models are robust (Phillips *et al*., 2006). For some of the species which had a high MI-ISK score, it was not possible to carry out Maxent modelling due to a low number of presence records globally. As more records are digitised and made publically available, this will help to increase the accuracy of modelling techniques and the forecasts that they give.

Prevention of establishment or arrival is recognised as the most effective management approach to combat non-native species (Caplat and Coutts, 2011; Caffrey *et al*., 2014). The Convention on Biological Diversity (CBD) and new European legislation on the prevention and management of invasive species (IAS regulations) both focus on identifying and managing the pathways and vectors of introduction and spread. These pathways and vectors can be varied and complex, such as international shipping, recreational boating and trans-shipment of aquaculture species, therefore individual countries cannot stop the spread of introduced non-native species alone, making international cooperation vital. As such, there are a number of initiatives aimed at sharing information and prioritising species for further research and monitoring, such as the North European and Baltic Network on Invasive Alien Species (NOBANIS, 2015), Delivering Alien Invasive Species Inventory for Europe (DAISIE, 2015) and Reducing the Impact of Non-Native Species in Europe (RINSE, 2014). The IAS Regulation has a target to have identified, prioritised and controlled or eradicated species which are highlighted by risk assessments as a priority and to manage the pathways of introduction and spread by 2020, likewise the European Marine Strategy Framework Directive (MSFD), which also targets the management of non-native species, has an aim of achieving Good Environmental Status by 2020.

Conservation agencies and scientists are working together to try to achieve this. However further regulations such as The International Convention for the Control and Management of Ships' Ballast Water and Sediments (BWM Convention), which has yet to be ratified, are required to help prevent further introductions of new species. Once introduced, it is very difficult to prevent spread of a species in the aquatic environment, although not impossible given sufficient resources. Some of the species assessed here were introduced as aquaculture species and were not expected to spread (e.g. Manila clam, Jensen *et al*., 2004; Pacific oyster, Minchin and Gollasch, 2008), demonstrating the need for very detailed risk assessment and consideration before new aquaculture species are farmed.

This study contributes to the growing knowledge-base available, aimed at informing the measures required to monitor, prevent introduction or slow the spread of non-native species in the marine environment, and potentially eradicate them altogether. For species that have arrived recently, their impact within European ecosystems is not yet fully understood. Ecosystems can be resilient to some changes, and the addition of one species may not always mean the loss of others. However, the impact can only be determined by sufficient monitoring and screening of both the introduced species, and the ecosystem that has been invaded. Novel techniques such as analysis of environmental DNA (eDNA) may facilitate the rapid screening of potential introduction sites (e.g. ports and harbours) for particular species (Goldberg *et al*., 2015). It is clear from these models that the habitat around north west Europe will become more suitable for certain non-native species in the coming century, and so environment managers need to be mindful of this. Early detection of non-native species is crucial to stop them becoming established (Roy *et al*., 2014; Cefas, 2015a). The risk assessments and modelling projections in this study could be used to prioritise the species for monitoring surveys and impact assessments, increasing the chances that the most dangerous species are identified early. The results of this study will enable managers of protected areas or important infrastructure, such as marinas and power stations, to identify high risk areas and priority species as soon as they arrive, and activate eradication programmes before they become fully established, thus saving money and conferring a higher chance of success. However eradication of such species may be an ongoing process until the species source or pathways of spread are removed.

Acknowledgements

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Chapter 6

Harmful algal blooms and climate change: exploring future distribution changes

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Abstract

Harmful algae can cause death in fish, marine mammals and humans, via their toxins or sheer quantity. There are many species which cause a variety of problems around northwest Europe, and the frequency and distribution of algal blooms have been changing in the recent past due to climatic changes. Species distribution modelling can be used to understand how species may respond to future climate change, by considering environmental habitat preferences and how these habitats may shift spatially and temporally; but most studies to date use only very low resolution global model outputs. In this study, high resolution, downscaled shelf seas climate projections for the north west European shelf are nested within low resolution global projections, to understand how the distribution of nuisance algal species may change in north west Europe by mid and end of century. Predictions suggest that the preferred habitat (defined by temperature, salinity, depth and stratification) of most species will shift north this century, and that suitability will increase in the central and northern North Sea. An increase in occurrence of certain species in these areas might lead to greater bloom frequency if seasonal conditions such as wind, irradiance and nutrient levels are suitable. Prioritising monitoring of species in these areas could therefore be useful in establishing early-warning and surveillance systems for aquaculture and as part of human health protection monitoring schemes.

Introduction

Climate change is altering the occurrence of marine species around the world, reorganising what has historically been considered the native and usual range of a species. There are many problem-causing species in the oceans, which can have implications for ecology, society and the economy. Single-celled marine algae are sometimes considered a nuisance, including certain species of diatoms and dinoflagellates. Harmful algae are defined as those which cause toxicity to higher trophic level species, including fish, shellfish and marine mammals (Wells *et al*., 2015). Harmful algal blooms (HABs) are high-biomass occurrences of algal species, and can include noxious, toxic and non-toxic species that cause effects on ecosystems or individuals by their sheer quantity (Kudela *et al*., 2015; Wells *et al*., 2015). Harmful algae and HABs can cause a number of different problems when they occur through direct contact or ingestion. Some species accumulate in the tissues of filter feeding organisms and cause Paralytic and Diarrhetic Shellfish Poisoning (PSP and DSP), or produce other toxic compounds which, as well as causing health problems, have economic implications for shellfish farms as they are unable to sell their products. Some species cause fish kills, with subsequent ecological problems and economic consequences for fisheries. Domoic acid, produced by diatoms, causes Amnesic Shellfish Poisoning which can cause death in humans as well as marine mammals and sea birds (Tatters *et al*., 2012). The high biomass of certain algae during a bloom can also cause reductions in oxygen and create ‘dead zones’, exacerbating impacts resulting in fish kills (Kudela *et al*., 2015). There are a number of species of algae around north west Europe which cause economic and health problems (Table 11). The consequences for health, water quality and food security mean that understanding, predicting and mitigating harmful algal occurrences are a priority for scientists and policy makers (Kudela *et al*., 2015).

Table 11: Harmful algal species found around the UK, and the problems caused (information summarised from Smithsonian (2015) unless otherwise stated).

Species	**Taxonomy**	**Distribution**	**Problems caused**
Alexandrium minutum	Planktonic dinoflagellate	Bloom-forming, coastal regions. Widely distributed.	PSP
A. ostenfeldii	Planktonic dinoflagellate	Coastal species along west coast of Europe and Canada. No blooms recorded to date.	PSP
A. tamarense	Planktonic dinoflagellate	Bloom-forming. Coastal regions of Europe, Japan, North America.	Produces a number of toxins including PSP. Not all strains toxic.
Dinophysis acuminata	Planktonic dinoflagellate	Bloom-forming. Coastal waters of North Atlantic and Pacific.	Causes DSP. Can be toxic at low concentrations.
D. acuta	Planktonic dinoflagellate	Bloom-forming. Found worldwide.	Produces a number of toxins including DSP
Gymnodinium catenatum	Planktonic dinoflagellate	Warm, temperate coastal waters.	Produces PSP
Karenia mikimotoi (Algaebase, 2015)	Planktonic dinoflagellate	Bloom-forming. Worldwide distribution.	Causes harmful blooms but exact mechanism unknown
Prorocentrum lima	Benthic dinoflagellate	Estuarine species with world-wide distribution.	Produces a number of toxins including DSP

Species	Taxonomy	Distribution	Problems caused
Pseudo-nitzschia australis (WoRMS, 2014a)	Diatom	Widely distributed in temperate and subtropical waters.	Produces domoic and isodomoic acids
P. delicatissima (WoRMS, 2014c)	Diatom	Widely distributed in Arctic, temperate and subtropical waters.	Some strains produce domoic acid
P. fraudulenta (WoRMS, 2014b)	Diatom	Widely distributed in temperate and subtropical waters.	Produces domoic acid
P. seriata (WoRMS, 2014d)	Diatom	Northern Atlantic and more recently Pacific.	Produces domoic acid poisoning in shellfish

Algal blooms have increased in frequency around the world (Glibert *et al*., 2014). Environmental conditions have an effect on the frequency, location and intensity of algal blooms and outbreaks. Around north west Europe, *Karenia mikimotoi* blooms in the western English Channel are associated with high summer rainfall and subsequent low-salinity, high-nutrient run off from land (Barnes *et al*., 2015), and around Scotland they are associated with high rainfall (Davidson *et al*., 2009). Northern Europe is already experiencing the effects of climate change, with sea surface temperatures in the North Sea having risen more than the global average over the past 50 years (Hobday and Pecl, 2014). In the north western European shelf seas area, from the end of the 20th century to the end of the 21st there is projected to be a further increase in annual mean sea surface temperature of 2.9 °C, and a freshening of 0.41 psu, (Tinker *et al*., under review). These changes make the region vulnerable to the effects of climate change and the spread of nuisance species, such as harmful algae. Shifting climatic conditions can change the composition of the phytoplankton community, and also increase the occurrence and geographic spread of blooms (Kudela *et al*., 2015; Wells *et* *al*., 2015). Warmer air and water, and increases in duration of stratification events may lengthen the suitable time period when plankton blooms can occur (Moore *et al*., 2009). There has been an increase in phytoplankton in recent decades in the North Sea and north-east Atlantic, linked to warmer temperatures rather than nutrients (Bresnan *et al*., 2013). In the North Sea dinoflagellates such as *Prorocentrum spp.* have decreased in abundance over the last decade, likely as a result of increasing temperatures and windier conditions (Hinder *et al*., 2012). Shellfish in Scottish waters have seen a decline in toxins for paralytic shellfish poisoning in the last decade (Bresnan *et al*., 2013). By contrast, diatoms such as *Pseudo-nitzschia spp*. have increased in the same area (Hinder *et al*., 2012), showing that different species are affected in different ways by changing environmental conditions. Increased occurrence of *K. mikimotoi* blooms have been seen further north around the British Isles recently, particularly since 2010 in Scotland and Ireland, potentially linked to changes in duration of stratification (Davidson *et al*., 2006; Bresnan *et al.,* 2013). Understanding how harmful algal species may respond to future environmental conditions can help us to plan surveillance and mitigation actions and reduce the impact of outbreaks.

Integrating biogeography into climate change impact studies is fundamental for better understanding effects of environmental change on biodiversity (Hannah *et al*., 2002). One of the best techniques that can be used to achieve this is deployment of species distribution modelling techniques (e.g. Jones *et al*., 2013; Weinart *et al*., 2016). By considering the bioclimate envelope of a species (the environmental conditions within which they live), the potential future distribution can be projected based on how the physical environment will change. Such species distribution modelling techniques have gained in popularity in projecting how marine species might move in response to climate change, by combining occurrence observations with environmental variables (e.g. Reiss *et al*., 2015; Rutterford *et al*., 2015; Barton *et al*., 2016; Weinert *et al*., 2016). The models' use with planktonic and algal species is relatively new and Barton *et al*. (2016) have used the maximum entropy model Maxent to assess the future suitability of 87 diatom and dinoflagellate species in the North Atlantic. They found a general north and eastward shift, causing a 'shuffle' or redistribution in community composition. Such regional-scale responses can be more relevant ecologically than the global changes (Walther *et al*., 2002) that are often the focus of modelling studies. It is important to understand how climate change might affect harmful algae at a local and regional scale, as this is where the economic effects are felt. A better understanding of how algal species and their blooms may be affected in the coming decades is important to shellfish and fishery managers in north west Europe, in helping to identify those species which require careful monitoring and for considering other human influences such as nutrient releases which could endanger human health. To investigate the spread of harmful species in a more focused local area, the use of downscaled climate models is required (Wells *et al*., 2015), which can capture fine-scale changes in shelf seas processes and tides that are not possible with lower resolution global models (Tinker *et al*., 2015). Planktonic and benthic algae are affected by regional changes in environmental conditions such as stratification, which occur on the north west European shelf. Low resolution global climate models therefore have limits to how well they can explain harmful algal species' occurrence, and higher resolution downscaled models are required. A new set of north west European shelf seas climate projections, which use an ensemble approach with a 12 km resolution, have been recently produced and are used here (Tinker *et al*., 2015).

It is important to note that no model will be able to predict the occurrence and location of an individual bloom event because these are determined by stochastic processes and discrete weather events. In this study it is intended to provide a broad-brush indication of changing geographic affinity. Other authors have attempted to use species distribution models to provide early warning systems for HABs, and they have been deployed successfully for *Pseudo-nitzschia spp.* on the Atlantic side of North America (Anderson *et al*., 2009).

In this study, global climate models are combined with dynamic downscaled north west European shelf model outputs to (1) use species distribution modelling to project how suitable environmental conditions may change in the future, and (2) quantify how much the distributions may change and therefore consider which species may be more problematic in the coming century.

Methods

Species occurrence data

Species occurrence data were downloaded from two databases: the Ocean Biogeographic Information System (OBIS) (http://www.iobis.org) and the Global Biodiversity Information Facility (GBIF) (http://data.gbif.org). Species occurrences from March to October were collated, since these are the most likely occurrences to represent large numbers of algal cells, or algal blooms in the northern hemisphere. The UK government collects algal data on a regular basis and so data were also obtained from the Scottish Association for Marine Science (SAMS), the Agri-Food Biosciences Institute (AFBI) for Northern Ireland and for England and Wales from the Centre for the Environment, Fisheries and Aquaculture Science (CEFAS), with permission granted by the Food Standards Agency. Not all data were recorded to species level, and so only the *Dinophysis acuminate* and *D. acuta* occurrence data from AFBI, and *Prorocentrum lima* from all agencies were included. The data were cleaned to remove duplicates, occurrences outside the depth and Food and Agriculture Organisation of the United Nations (FAO) range (taken from OBIS), and to remove those recorded incorrectly as being on land. Depth was rounded up to the deepest 100 m to ensure that all plausible occurrences were included. The data were then aggregated to a binary (presence/absence) 0.5° latitude x 0.5° longitude grid.

Nested climate projections

Restricting the species distribution modelling to the extent of a shelf seas modelling would exclude much of the HAB species' present day distribution and the environmental conditions experienced in these locations, and so high resolution regional downscaled data were nested into global climate model outputs (as in Townhill *et al*., accepted). This technique allows the whole range of a species' environmental exposure to be incorporated into the habitat suitability model, while also including the local-scale influences which are important in interpreting future distributions. All projections were obtained from the Met Office Hadley Centre and were for the 'medium' emissions scenario (SRES A1B). Global projections from a perturbed physics ensemble (PPE) at a global 1.25 degree resolution (Collins *et al*., 2013) of the Atmosphere-Ocean Global Climate

Model HadCM3 (Gordon *et al*., 2000; Pope *et al*., 2000) were used under an SRES A1B business as usual, medium emissions scenario (Tinker *et al*., 2016). Within this medium emissions scenario, assumptions are made that the world expects rapid economic growth, a peak in population mid-century, followed by the growing use of low carbon technologies (IPCC, 2007b). This PPE consisted of the unperturbed (standard) version of the model, with 10 ensemble members which had atmospheric parameters perturbed to span the uncertainty in climate sensitivity. The unperturbed member is used in this study, which is equivalent to the standard version of HadCM3. The unperturbed member of this ensemble shelf seas model was downscaled using POLCOMS (Proudman Oceanographic Laboratory Coastal Ocean Modelling System; Holt and James, 2001; Holt *et al*., 2001) which produced a north west European shelf seas projection run. The downscaling resulted in a 12 km resolution (1/9° latitude by 1/6° longitude), from 43°N – 63°33’20”N and 18°20’W – 13°E (Figure 19). A 30-year average of 1980–2009 (centred on 1995) annual means was used to represent the present time period, because the majority of the species records were taken between these dates. The future time horizons to which the models were applied were 2040–2069 (centred on 2055) representing the near future, and 2069–2098 (centred on 2084) representing the end of century. Variables used were those considered to affect algal occurrence: near bottom and sea surface temperature and salinity, and the differences between the surface and bottom of each (bulk temperature and salinity which gives an approximation of stratification), and bathymetry. The downscaled shelf seas projections were nested within the driving global projections using Python 2.7 (Python Software Foundation, 2010) resulting in a dataset with a resolution of 0.5 degrees. The global ocean fields were bi-linearly interpolated to 0.5 degrees, and the downscaled regional fields were averaged (aggregated) up to 0.5 degrees. These were then copied into the appropriate region within the global model. As the regional data was produced by forcing the global model, the data are consistent and match at the boundary. It was necessary to use a resolution intermediate between the two original models because the local-scale processes are still captured in the shelf seas area, but the global data is not interpolated more than is appropriate. The resulting 0.5 degree grid of environmental parameters was then used to drive the species distribution model.

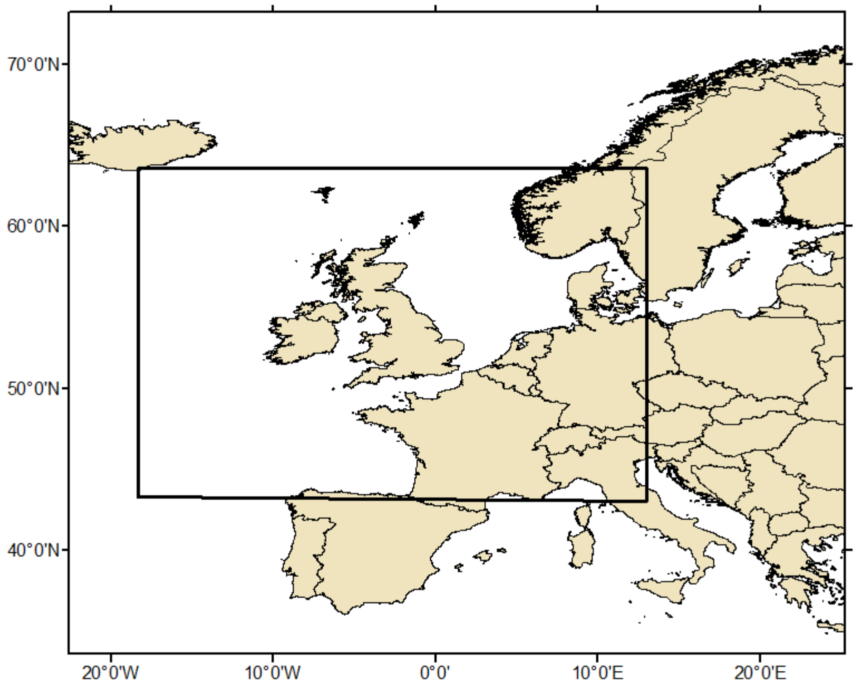

Figure 19: Extent of the north west Europe shelf seas model

Species distribution modelling

The Maximum Entropy (Maxent) bioclimate envelope model (Phillips *et al*., 2006) was used to determine the present day and future habitat suitability. This model is described in detail in Jones *et al*. (2012, 2013) and has performed well in comparison with other models in previous marine studies (Elith *et al*., 2006; Reiss *et al*., 2011; Vierod *et al*., 2015). Maxent generates habitat suitability by randomly selecting training points and combining presence-only occurrence data with chosen environmental variables, using the rest of the data points to test the model, and then predicting the future habitat suitability by forcing the model based on the same variables. Maxent estimates the probability distribution of the habitat suitability by finding the most uniform distribution (the one with the maximum entropy), within the constraints of incomplete information (Phillips *et al*., 2006). The term "relative habitat suitability" is used here to describe the bathymetry and hydrographic conditions that the species currently experience. It does not include the bottom substrate conditions or local ecosystem processes such as food availability). Maxent was run for each species in turn using the model interface (version 3.3.3k) downloaded from http://www.cs.princeton.edu/~schapire/maxent/, for the present day, near future and end of century climate data, giving a habitat suitability score between 0 and 1. Clamping was used for model fitting which ensures that the predictor variables remain within the training range (i.e. the species' habitat does not get projected outside the suitable environmental conditions) and with 'jacknife' which checks the importance of each variable. Across the species, the number of training points chosen by the model varied because there was a lot of variation in the number of available presence data points. The species with more training samples are likely to present a better fit to reality than others (numbers of presence and training data points are summarised in Table 12). Maxent used the Area Under the Curve (AUC) value to test the performance of each model, bounded by 0–1, with 1 being the best fit. A threshold AUC value of 0.8 was considered acceptable, based on Mercks *et al*. (2011) who produced a review of habitat suitability models. This modelling technique is affected by autocorrelation because the species presence sampling is inherently biased. Therefore the value of >0.8 is used as a guide rather than an absolute measure of robustness.

Latitudinal centroids

Once the bioclimate envelope models had been run and the relative habitat suitability determined, the latitudinal centroid for each time period and species was calculated. This gives the centre of the latitudinal range for each species, and can be compared between the present to the future time periods. The centroid (*C*) was calculated using the equation from Cheung *et al*. (2009):

$$C = \frac{\sum_{i=1}^{n} Lat_i \cdot Abd_i}{\sum_{i=1}^{n} Abd_i}$$

where Lat_i is the central latitude of the spatial cell *i*, *Abd* is the predicted relative habitat suitability of the same cell, and *n* is the total number of cells. The distances between the latitudinal centroids in the present and future years were then calculated in kilometres (Cheung *et al*., 2011):

$$Distance\ (km) = (Lat_m - \ Lat_n) \times \frac{\pi}{180} \times 6378.2$$

where Lat_m and Lat_n are the latitudinal centroids in the present (*n*) and projected (*m*) timeslices, and the approximated equatorial radius of the Earth is 6378.2 km.

The outputs of the different bioclimate envelope models using the global data were compared visually, and the difference in the model outputs determined and plotted using GIS. The difference between the latitudinal centroids globally and within the spatial extent of the shelf seas model were calculated, to give a value of latitudinal shift.

Results

Two species were excluded (*P. delicatissima* and *seriata*) which had more than 400 data presence points each; they were so widespread worldwide that Maxent used around 4000 training samples with resulting AUC values of 0.8. Their current widespread nature likely means that their future habitat suitability will be similarly widespread and so they were excluded from further assessment as they are present at most localities already.

Maxent provided a good fit for the remaining 10 species, with AUC values above 0.9. All species exhibited a change in habitat suitability distribution from the present day to mid and end of century. For all species, the variable with the highest percentage contribution to the model fit was either bathymetry or near bed temperature (model attributes summarised in Table 12).

The majority of the species showed a northward habitat suitability shift from the present day to mid and end of century (Figure 20, Figure 21, Table 13). All species showed a northward global shift. Most of the species had a larger northward shift at the end of the century than mid century. Three species showed a shelf seas southward shift however: *A. ostenfeldii*, *A. minutum* and *P. australis*, the first two of which had bathymetry as their highest contributing variable. Globallly, *G. catenatum* showed the greatest northward shift at more than 700 km by the end of century. For the shelf seas area, *D. acuta* and *G. catenatum* had the greatest northward shift for mid and end of century of around 800 to 100 km.

Table 12: Summary of the Maxent model attributes for each species

Species	**AUC value**	**Number of presence data points**	**Number of training samples**	**Variable with the highest percentage contribution**
Alexandrium minutum	0.996	51	31	bathymetry
Alexandrium ostenfeldii	0.977	68	48	bathymetry
Alexandrium tamarense	0.959	88	46	bathymetry
Dinophysis acuminata	0.951	853	640	near bed temperature
Dimophysis acuta	0.950	810	704	near bed temperature
Gymnodinium catenatum	0.982	26	17	near bed temperature
Karenia mikimotoi	0.990	81	56	bathymetry
Prorocentrum lima	0.979	241	149	near bed temperature
Pseudo-nitzschia australis	0.994	26	23	near bed temperature
Pseudo-nitzschia fraudulenta	0.991	17	10	near bed temperature

Table 13: Habitat suitability latitudinal centroids for the shelf seas area from the present day, near future and end of century.

Species	Latitudinal centroid		
	1980–2009	**2040–2069**	**2069–2098**
Alexandrium minutum	55.25	55.294	54.768
Alexandrium ostenfeldii	55.37	55.329	55.238
Alexandrium tamarense	55.194	55.317	55.504
Dinophysis acuminata	54.595	54.564	54.641
Dimophysis acuta	54.473	55.174	55.397
Gymnodinium catenatum	53.652	54.455	54.565
Karenia mikimotoi	55.426	55.511	55.505
Prorocentrum lima	54.319	54.686	54.734
Pseudo-nitzschia australis	55.338	55.223	55.02
Pseudo-nitzschia fraudulenta	55.221	55.319	55.322

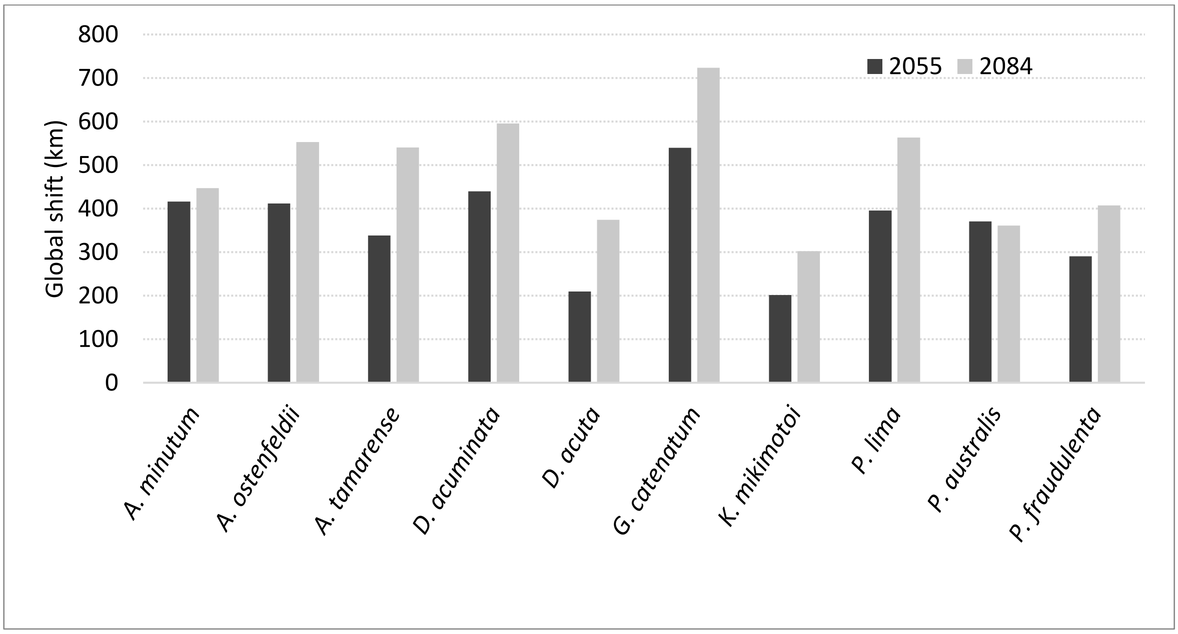

Figure 20: The global poleward shift in the habitat suitability for each species from 1995 to 2055 and to 2084.

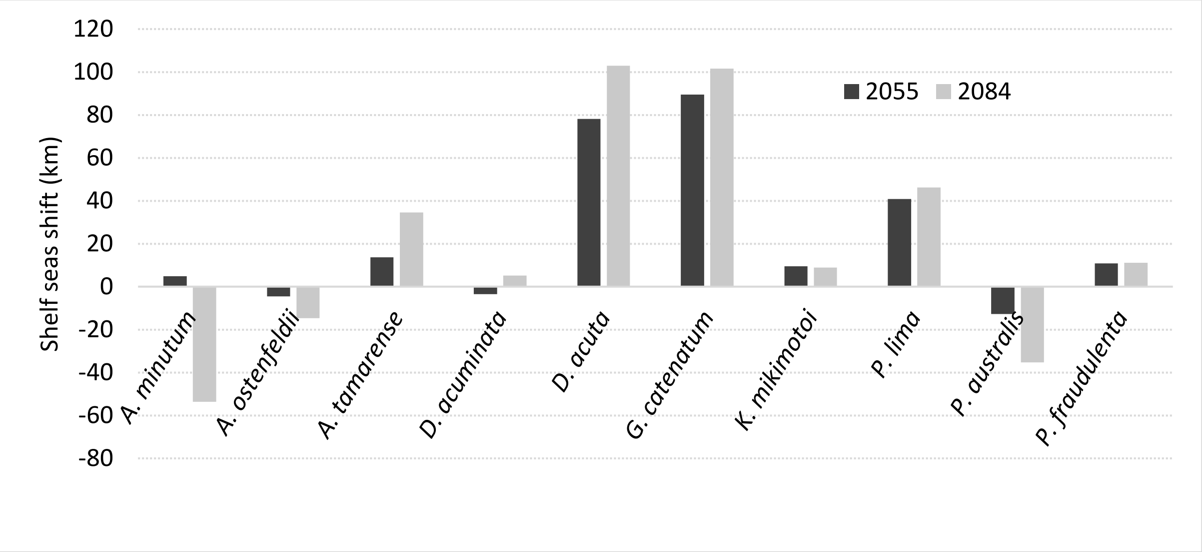

Figure 21: The habitat suitability shift within the shelf seas areas for each species from 1995 to 2055 and to 2084.

Looking in detail at the north western European shelf seas, the habitat suitability for the majority of the species increases further north; decreasing in southern countries to Scandinavia, and increasing in the Norwegian Sea (as seen in Figure 22). The maps show that the central and northern North Sea in particular witness large increases in habitat suitability, with a decrease in suitability in the Celtic Sea and the English Channel for many species. *A. minutum* is one species which has a southward latitudinal shift in the shelf seas, and it can be seen in Figure 22 that the suitability has the greatest increase along the shelf edge. Within the UK exclusive economic zone (EEZ), this species shows an overall decrease but an increase in the far north and north west. *D. acuta* shows a strong decrease in suitability off the north-east coast of Scotland and in the English Channel, while *G. catenata* has an overall increase within the UK EEZ. *P. lima* shows an decrease to the north of Scotland and Ireland, but an increase or no change in the rest of the UK EEZ.

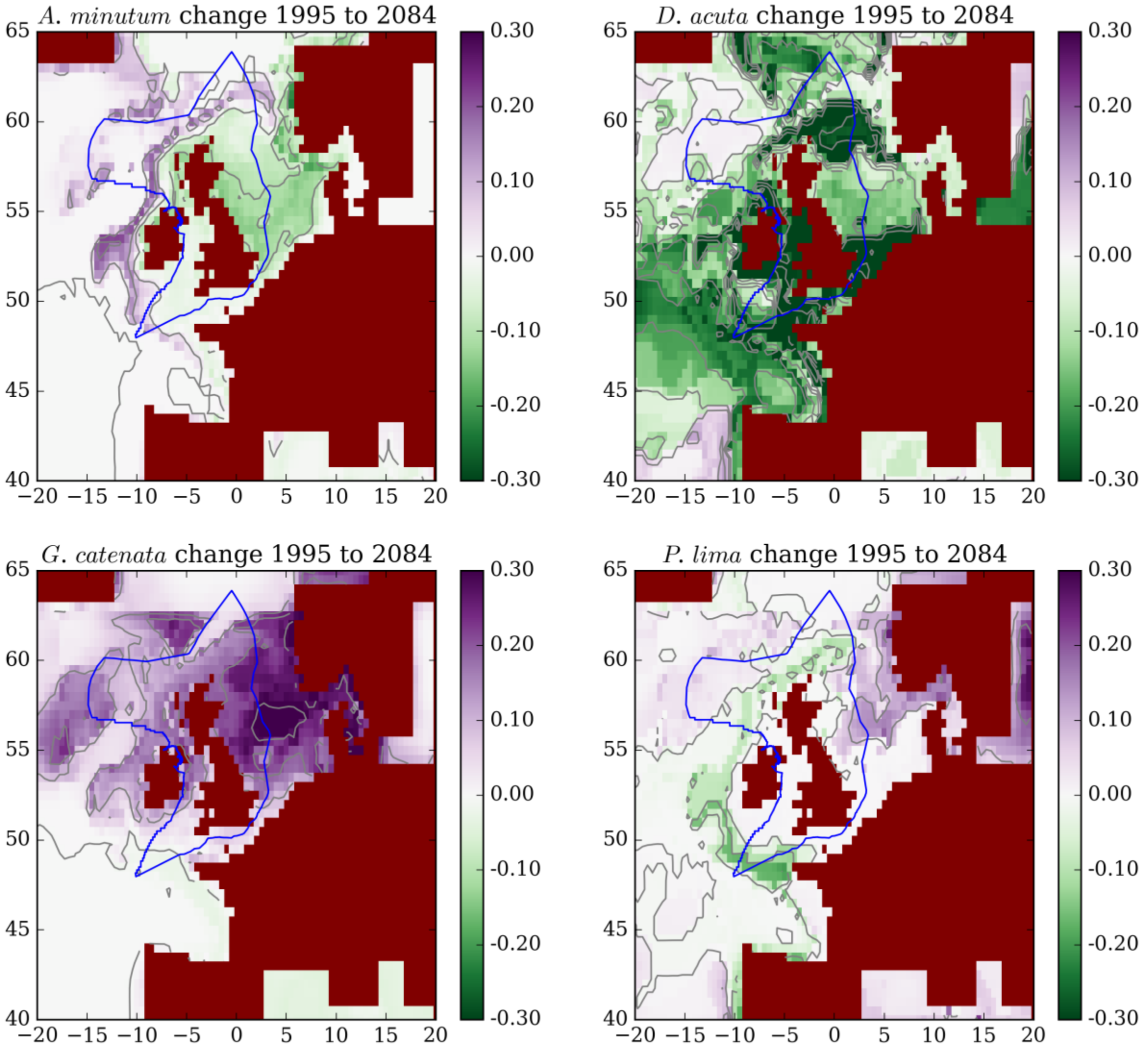

Figure 22: The spatial change in habitat suitability (ranging from 0 to 1) for four of the algal species. *A. minutum* shows a southward shelf seas shift in suitability, while the other three species illustrated are those with the largest northward shift. The blue line represents the UK EEZ.

Discussion

Our results show that around the UK the suitable areas for the occurrence of HAB species are likely to change as a result of climate change in the coming century. In the majority of cases, the suitable environmental conditions will be found further north than under present day conditions. Exceptions to this are *A. tamarense* (shelf seas distribution change to 2084), *A. minutum* (global change to 2084) and *P. australis* (global distributions to 2055 and 2084) which all showed a southward habitat suitability shift. This may be due to the differences between species in their temperature, salinity and bathymetry preferences and the interactions between these variables. For example *A. minutum* has a higher change in habitat suitability along the shelf edge, and so the habitat suitability is constrained by depth more than temperature.

The species with the highest projected northward shift in habitat suitability within the shelf seas were *D. acuta* and *G. catenatum*. These are both planktonic dinoflagellates which form blooms. *D. acuta* can cause DSP and can even be toxic at low concentrations whereas *G. catenatum* can cause PSP (Hallegraef *et al*., 2004). If these species have a large geographic shift in their ranges, then there may be more occurrences of blooms affecting shellfish fisheries and farms around the north of the UK and in Scandinavia. *D. acuta* can be retained within shellfish tissue for up to 6 months (Hallegraef *et al*., 2004), and so potentially having huge economic consequences for farmers after a bloom. Incidents of DSP have become more frequent and prolonged since it was first recorded in 1997 (Hinder *et al*., 2011), with 19 incidents between 1999 and 2009, across the whole of the UK. Hinder *et al*. (2011) report that fisheries have been closed throughout that period for up to seven months as a result of an outbreak. In 2000-2001, there was the longest closure of a shellfishery ever recorded in the UK, with aquaculture and scallop fisheries being closed throughout the year due to PSP (Hinder *et al*., 2011). For the ten years between 1999 and 2009, there has been a low level of the toxin found in England and Wales. If *G. catenatum* and other PSP species experience changes in their habitat suitabilities, then farms and fisheries further north may begin to be affected. Mapping the changes in suitability in relation to the UK EEZ shows how UK farmers and fishers may be more affected by some species than others.

There is not necessarily a strong correlation between species abundance and toxin production (Hinder *et al*., 2011), but the models in this study are useful in projecting where the species might occur in the future, and where there is potential for bloom formation. To predict individual bloom events, local environmental factors must then be considered which are required for a bloom to form, such as irradiance, cloud cover, precipitation and winds (Wells *et al*., 2015). The specific occurrence of a bloom can be affected by the timing of rainfall and subsequent land run-off, forecasting of which can be used in near-term prediction of blooms (Davidson *et al.*, 2009; Barnes *et al*., 2015). Nutrient levels in land run-off affect bloom formation and these are hard to predict for decades in advance because land management practices affect the nutrients levels. Long-term prediction of nutrients is therefore difficult, though they could be predicted in the short term based on rainfall and run-off risk. Biogeochemical modelling of the North Sea showed that primary production is expected to increase over the coming century due to climate change, and the annual growth of primary production would occur earlier in the year (van der Molen *et al*., 2013). In some areas the length of stratification and the spring blooms will be extended, while in others they remain the same, due to local conditions such as wind. A measure of stratification was included in this study but further, more sophisticated, modelling could attempt to incorporate these seasonal aspects of wind and rainfall to achieve more specific near-time predictions of bloom formation, as has been attempted for *Pseudo-nitzschia* spp. Anderson *et al.* (2009). An increased algal growth rate caused by environmental conditions may result in nutrient limitation for blooms (Hall-Spencer and Allen, 2015), adding a further complication to predictions and long-term projections.

Species distribution modelling is a useful tool for understanding the future changes in marine environments, but it is easy to over-interpret the results. Many researchers have been sceptical about the utility of such models (e.g. Bell and Schlaepfer, 2016). There are many ecological processes which are not captured by the model used here, and without consideration of these processes the modelling is oversimplified and measures of fit can be misleading (Bell and Schlaepfer, 2016). In particular for HAB species, short-term changes in environmental conditions discussed above affect the formation of discrete algal blooms and these can not be predicted by long-term climate projections. Therefore it is important that the results of the modelling from this study are taken as relative measures of the suitability of the environment in the broadest sense for a bloom to form, providing all other environmental processes come together at the local scale, and not as a definite prediction of where and when a bloom will form. Knowledge of relative suitability between species, location and time can be used to help us understand which species may become more problematic in the future and in which areas, but more detailed, short-term modelling and forecasting is required to predict blooms in the short term. Such techniques are used and are being developed around the world (e.g. Anderson *et al*., 2010) and prove valuable for managers of aquaculture and recreational facilities.

As detailed pH projections become available, these can be incorporated into future distribution models. Reduced pH is known to increase the production of domoic acid in *Pseudo-nitzschia* species, even at levels of pH that can occur today (Tatters *et al*., 2012). The authors found that silicate limitation also increases the production of domoic acid, data for which was also not available for this study. A biogeochemical modelling study of the northwest European shelf projected that in the English Channel and the Irish Sea diatoms would increase in number towards the end of the century, whereas the larger dinoflagellates would decrease because they are relatively slow and are outcompeted (Artioli *et al*., 2014). This work included the projected influences of ocean acidification, which in certain places and at certain times can cancel out the effects of other climatic factors, but in other instances can exacerbate them (Artioli *et al*., 2014). Such studies could be combined with species distribution modelling to understand the specific requirements of different groups of organisms, along with their potential spatial distribution changes.

Species distribution models assume that the tolerances and preferences of species relative to environmental conditions remain the same, and do not take into account potential for adaptation. Some HAB species may not be able to adapt to new temperature and stratification regimes or changes in variability, such as an *Alexandrium sp*. (*A. fundyense*) which in 2010 in the Gulf of Maine had growth constrained by stratification, causing an early diatom bloom and subsequent nutrient depletion (McGillicuddy *et al*., 2011). The lack of nutrients meant that the resting cysts from the previous year were unable to grow. However in laboratory experiments *A. minutum* has been found to physiologically and genetically adapt to changing pH and temperature conditions, potentially making blooms more frequent with further climate change (Flores-Moya *et al*., 2012). The findings in this study of a general northward shift for most species is similar to that found in a previous study by Barton *et al*. (2016), who found a general north and eastward shift using presence data from the continuous plankton recorder (CPR) and climate data with a one degree resolution. *K. mikimotoi* is one species that is frequently cited as moving further northwards around the UK (e.g. Davidson *et al*., 2006; Bresnan *et al.,* 2013). Our results show that it is likely to have a northwards shift within the shelf seas, and globally, but not to the same extent as most of the other species. *P. lima* however does show a much greater latitudinal shift in this study, which is similar to previous studies. Glibert *et al*. (2014) projected changes in *Prorocentrum* spp. and *Karenia* spp. in northwest Europe, based on assumptions of nutrient inputs, and found that both genera would expand in the region increasing vulnerability of coastal ecosystems and impacts of HAB events. The changes in suitability found in the present study, and the expansion of these two species found by Glibert *et al*. (2014) emphasise the importance of regional long- and near-term forecasting in reducing the impacts of these species.

This study has shown that harmful algae and HABs are likely to occur further north around north west Europe in the coming century, with some species habitat suitabilities moving faster than others. Suitability for most species increases in the central and northern North Sea. These changes have implications for aquaculture, recreation and ecosystems, as plankton composition changes and fish and shellfish farms or coastal areas experience more outbreaks. Understanding which species may become more prevalent in the future is important to marine management as it allows early intervention by implementing mitigation measures to reduce the economic and ecological harm of these species, and also raises awareness around shellfish grounds and healthcare professionals. Routine recording of these species also allows us to further understand the local conditions that cause each species to occur and produce toxins, and assess whether certain species are spreading or occurring more frequently (Hinder *et al*., 2011). Certain species can be prioritised for monitoring, and for further studies which can increase the accuracy of forecasting and shorter-term predictions. Risk assessments can be performed that take account of the likelihood, severity, consequences and probability of occurrence. Changes to harmful algae occurrence and the nuisance that they cause is already a feature of a changing marine climate, and will continue to be so, but studies such as these are highly valuable in anticipating their impacts and improving surveillance.

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Chapter 7

General Discussion

The studies in this thesis have contributed to our understanding of climate change impacts on marine ecology by investigating examples of past, present and anticipated future changes to species distributions. Several climatic drivers have been assessed through the chapters, with impacts investigated on a range of biota, with consideration of implications for management (Table 14**Error! Reference source not found.**). In this final chapter I will briefly summarise the findings and discuss implications for policy and management resulting from each study, before going on to discuss the limitations and uncertainties of the various models, but also their advantages when they are chosen correctly and interpreted well. The future directions of modelling approaches and climate change studies will then be discussed.

Synthesis

The first half of my thesis focused on the effects of climate on commercial species, looking initially at historical climatic change, moving to potential future conditions. In Chapter 2 I explored how historical climatic conditions contributed to changes in the abundance and distribution of Atlantic cod and its prey species in the Arctic, in particular capelin and herring. The value of historical data was emphasised, particularly with reference to data that were not necessarily collected in a modern, statistically designed manner and that could not be considered fit for use in a scientific paper. However, we showed that these data are not only of interest, but that they can be interrogated using modern analytical techniques to provide new insights into which variables influence fish stocks and by which mechanism. The analyses that we carried out using Generalised Additive Models supported findings of more recent data that Barents Sea cod and capelin have temperature preferences and that their distributions expand and shift based in response to the prevailing environmental conditions. Bottom temperature was more use in explaining these changes than surface temperature, perhaps because it has less short term variability, and because cod are a demersal fish. Catch rates were found to be different at different times of year, potentially revealing behavioural aspects of cod which in turn affect their

Table 14: Summary of the climatic drivers investigated in this thesis and the impacts found

Climate driver	Biota impacted	Modelling approach used	Implications for policy or management
Temperature Salinity Stratification	Atlantic cod Harmful algal species Non-native species	Generalised Additive Models Simple overlay modelling Species distribution modelling	Management of prey species and careful management of cod stock, and monitoring of environmental conditions. Forecasting of future stocks. Value in long time series and historical data. Prioritising HABs and non-native species for monitoring, and non-natives for eradication and control.
Oxygen	Commercial fish	Simple overlay	Need for continued nutrient control. Management measures need to consider pressures including effects of oxygen in certain areas. Need for better oxygen data in order to understand interactions and produce forecasts and projections.

catchability. Catches were also found to be higher in the 1930s to 1940s, coinciding with warmer temperatures and a higher climate index. Modelling approaches used in this chapter allowed us to explore the different variables for which we had data, and to identify which of those variables had the most influence on cod and their diets. Different families of parameters within the models were explored, and the most suitable suite of parameters was identified for making predictions. There was a large proportion of the deviance that was not explained by the model, which is important as it demonstrates that there are other factors at play, likely including natural variation.

In Chapters 3 and 4, the effect of oxygen conditions on commercial fish was investigated, leading to interesting results regarding changes in the recent past using hindcast data, as well as potential future changes based on projections. Chapter 3 documented the many ways in which oxygen can affect marine organisms, in terms of both physiology and behaviour. Since much research focuses only on extreme low oxygen conditions, it became evident from the review that more is needed to investigate how intermediate oxygen levels, potentially caused by future climate change, will affect commercial species. Different techniques were identified that could be used to help us understand how climate change will modify oxygen levels around the world, and one of these techniques was employed in Chapter 4. A simple technique was used in which both hindcast and future projected oxygen levels were compared spatially and temporally with known effects thresholds for commercial fish species, based on outputs from experimental studies. Only a small number of threshold levels were available which were comparable across oxygen concentrations and which represented realistic UK sea temperatures. This was made possible because there were gridded hindcasts and projections available for North Sea oxygen, which had been generated using a biogeochemical model. I found that since the 1970s, oxygen levels in the North Sea have actually improved in many areas, which could be due to improvements in land management across Europe that have meant less nutrient run-off entering the North Sea. Comparisons with measured oxygen thresholds suggest that in the latter part of the 20th century the fish were not being exposed to oxygen concentrations low enough to result in negative effects. Looking to the future, the projections for the three areas under consideration found, despite increasing temperatures, that oxygen levels would decrease again towards the end of the 21st century, but that they would not decrease to the extent of the 1970s. I concluded that fish should not be exposed to the levels of the lowest thresholds, and so will experience some oxygen stress, but not as much as in the late 20th century. While only a small number of species were considered in Chapter 4, it is encouraging to find that future oxygen levels may not be as detrimental to fish as suggested in mechanistic modelling studies (e.g. Cheung *et al*., 2013), providing other stressors, such as pollution, are appropriately controlled. As with other climate stressors, it is important that these effects are considered when managing fish stocks. Low oxygen conditions in spawning and nursery areas will put stresses on fish, making them potentially more vulnerable to fishing pressure and less able to maintain population sizes. Other human stressors that affect fish need to be managed to ensure that species retain resilience to changes in oxygen, along with other climatic factors such as increased temperature and reduced salinity. Fishing pressure can exacerbate climate responses, further reducing fish populations (Fuller *et al*., 2016), and pollution can affect the resilience or recovery of a habitat being stressed by climate change (Obura and Grimsditch, 2009). Only a small number of species were assessed here, but there could be direct or indirect implications for other species, particularly at sensitive life stages (Petitgas *et al*., 2013).

In the second half of this thesis I moved away from commercial species and considered how future changes in climate might affect species considered a nuisance, either ecologically or economically. In Chapters 5 and 6 I used a different modelling technique – the species distribution model Maxent – to predict future changes in marine conditions will affect these nuisance species, considering both non-native and harmful algal bloom (HAB) species. Maxent has been used previously to examine marine and terrestrial species distributions with climate change (Cheung *et al.*, 2009; Jones *et al*., 2013a, b; Barton *et al*., 2016). However most studies have previously used global climate change model outputs, which by necessity are low in resolution and are not able to account for local and regional oceanographic processes. For the first time, in these chapters, the outputs of high resolution, downscaled regional climate models were combined with global model outputs to produce a dataset which contained more detailed climate information for the north west European shelf seas area specifically, but which still contained the global climate data necessary for driving the species distribution model. Using this technique it was possible for models to be trained using environmental conditions that the species experience throughout their range, but then the projections provide more detail in the shelf seas area of most immediate interest and so provide insights into the suitability of regional habitat. In Chapter 5, the different routes of introductions by which non-native species could enter UK waters were considered, followed by a risk assessment to identify which of these species were more likely to become established and problematic, based on experience in other areas. Maxent was then applied on these highest risk species. We found that habitat suitability for most species shifts further north towards the mid and end of the 21st century, with suitability increasing around the UK for most species to some degree. The same was found with the HAB species, from which we can project which species are more likely to occur around the UK, and where blooms are most likely to occur. These findings, although highly uncertain, are of value for policy and management because they help to prioritise species whose suitability will change most rapidly, and establish monitoring, control and possible eradication programmes. For HABs, this will allow us to prioritise species for near-term forecasts. Ideally climate change should now be taken into account in some long-term management decisions, but this is a relatively recent addition, to ensure that fisheries, communities and economies remain resilient (Perry *et al*., 2011; Frost *et al*., 2016). The development and application of these modelling techniques will support inclusion of climate change impacts in future management decisions.

Through this thesis I have used several sources of data and a range of techniques to answer policy-relevant climate change questions, by investigating past, present and future changes in climate. I have demonstrated that existing data of varying types and quality can be used in novel ways, sometimes different to those for which they were originally collected, and analysed using statistical techniques that were not available at the time the data were collected. By combining novel techniques with the latest regional and global climate projections, and overlaying experimentally derived physiological and behavioural metrics, I have developed new insight into species distribution changes. No field or laboratory data were collected as part of this thesis and no climate model was run from scratch, but the analyses carried out have been possible because of the availability of free software and data and by digitisation of historical logbooks, the data from which has now also been made freely available through the Cefas website. By being freely available, it means that the data can be used in new ways, and to answer questions which may not even have been considered when the data was originally collected, or the original model run.

Climate modelling, such as that carried out here, allows us to predict the impact of projected environmental changes on ecosystem structure and function so that we can plan for these changes and mitigate effects on the environment and society. A level of uncertainty is however inherent in these model outputs because they cannot account for all of the pressures on a system such as fishing, habitat modification or pollution. There are also other sources of uncertainty within the models themselves which must be considered when interpreting model results and communicating them to the wider world.

Model error, uncertainty and why it shouldn't stop us

There is an often used quotation from George E.P. Box: "Essentially, all models are wrong, but some are useful" (Box and Draper, 1987).

To build an understanding of historic changes it is often necessary to use incomplete or sporadic data. In Chapter 2 I resurrected a historical time series to explore the effects of past warm climatic conditions on fish, even though the data had not been touched for decades. Historical data are not always designed in a statistically robust manner, yet they offer unique insights into environmentally driven biological responses, providing answers to ecological questions that would otherwise remain unanswered. Such data are often dismissed as incomplete or outdated, but statistical techniques can be used to interrogate them and extract valuable information. In Chapter 2 I demonstrate that GAMs can be used to test how historical environmental conditions affect cod distributions, abundances and diets, while acknowledging that there are other factors at play which cannot be accounted for by the model. In Chapter 4, an incomplete dataset of environmental thresholds from laboratory experiments was used to infer the effects of low oxygen conditions on fish species. While the fish response metrics were not originally collected for this purpose, and each was determined by a different experimental approach, nonetheless the results predict how climate change might affect the species, and also species for which no data are available. For the modelling in Chapter 4 there were no long-term datasets on oxygen conditions to compare with oxygen response thresholds, but hindcast model data were available and so were used instead.

In Chapters 5 and 6, species presence data from global databases were used, although they are likely to be inherently biased because of how they were collected. Some of the marine data came from robust surveys conducted by research agencies, but many of the records were submitted to international databases, such as OBIS and GBIF from local volunteer organisations (e.g. at nature reserves) or from university projects. Maxent, along with other similar models, has been designed such that incomplete and biased datasets can still be used. In this thesis, binning data into 0.5-degree grid cells accounted to some degree for location biases, because a large number of records in one location were still only recorded as ‘presence’ rather than being weighted by the actual number of records. This approach enables the use of data that may contain too greater degree of sampling error for more numerate approaches. In contrast, some data collected by the UK government to monitor harmful algal species could not be used in the study of HABs in Chapter 6 because other countries did not collect data for the same focal species or taxonomic resolution. While these datasets would have been collected in a statistically robust manner, species were not consistent between countries, with some only being recorded to genus rather than to species. This goes to show that sometimes it is not possible to use data which on first look is ideal.

Predictions of future climate change impacts inherently carry a degree of uncertainty. While models cannot see the future, they can make informed predictions, based on available data. Emerging research, ranging from latest measurements of atmospheric and oceanic CO_2, influence on temperature, ice melt and methane seeps, to what this will mean for society and for ecosystems, continues to build our scientific understanding. All of this new information does not necessarily mean that previous assessments of impacts are outdated, or totally incorrect. Instead, we have to understand the uncertainties around projections and assessments based upon these, and understand the data and the assumptions that are used to develop an informed, albeit imperfect, view of what may happen in the future. The modelling is not the endpoint, and this uncertainty must be communicated effectively to policy makers, environment managers and the public. There are good examples of risk communication in relation to climate change, such as those used by the Marine Climate Change Impacts Partnership (MCCIP) and the IPCC. MCCIP use a quantitative approach where experts decide how certain they are of a risk, and also how much the scientists concurr (i.e. are there experts with totally opposite views, or does all research in that area generally point in the same direction). Risk matrices are another way of expressing uncertainty, and are generally used to express two sources of uncertainty such as severity, likelihood or proximity (particularly useful for climate risks). As with descriptive uncertainty, this requires expert judgement, but it can be simpler to interpret by a non-expert, making it more accessible to managers and policy makers. However for a different audience, such as for academics, a more quantitative approach may be preferable, because they may consider a qualitative approach too vague. A simple quantitative approach is used to express flood risk, for example the magnitude of a 1:10 year flood event, but again these can be misinterpreted, particularly when considering changes in climate. The European Food Safety Authority (EFSA) Guidance on Uncertainty (EFSA, 2015) state that where possible, uncertainty should be expressed quantitatively, because decision makers are have a responsibility to resolve the impact that uncertainty has on decisions. Therefore scientists need to use an approach to assessing uncertainty that is understandable for decision makers, without requiring understanding of quantitative techniques. The guidance says that descriptive communication can be sufficient, using language such as ‘highly uncertain’, ‘may’ and ‘likely’ where it is not possible or sensible to quantitatively describe the uncertainty. For example time and budget within a project may not allow for quantitative methods to be used, but this does not necessarily invalidate the project. Or, as is the case in many studies where there may be many sources of uncertainty (e.g. from climate projections, species data, model being applied) descriptive analysis can be more meaningful. Of course, it is necessary to provide quantitative statistics of the level of uncertainty for certain aspects of the modelling (such as AUC values for Maxent), but it is recognised that in climate science, uncertainty is significant (Willows and Connell, 2003), and so putting a numerical value on that uncertainty would almost render the modelling work unusable. Figure 23 shows how the different types of uncertainty in a model change as predictions into the future are made, with the scenario uncertainty having more of an influence the further into the future a model projects. These imperfect predictions, projections and assessments can then be of great use to decision-makers and environment managers, providing they understand that predictions are not absolute. Decision makers and managers must work with the information available to them, as misinterpretation can be costly (Willows and Connell, 2003). Underestimating climate risk can lead to under-adaptation, such as protecting a certain species in a fixed location, when that species is likely to subsequently move away from that area because of changing environmental conditions, rendering the protection efforts useless. Conversely, over-adaptation can be financially costly and politically damaging, for example if a structure is built higher off the ground and away from potential storm surges which then never happen. Decision makers need to be pragmatic. A decision has to be made in a timely manner, given the best available information at that time. It is not possible to wait for perfect knowledge or a complete picture, and climate adaptation requires immediate and urgent action in many cases.

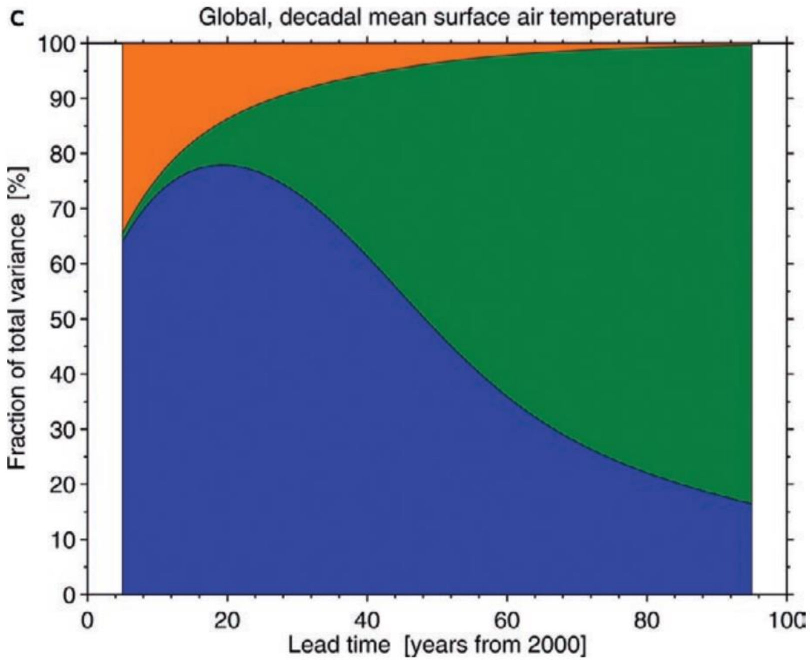

Figure 23: The relative contribution of different types of uncertainty in a model. Green represents the scenario uncertainty, blue the model uncertainty and orange represents the internal variability in a system. Taken from Hawkins and Sutton (2009).

Future directions

This thesis has contributed to the understanding of the effects of climate on species distributions and abundances, combining historic and future predictive studies. There are policy questions that remain unanswered, and some that are raised by these studies. The abundance of Barents Sea cod at the moment is similar to that in the 1950s, when cod stocks were at record highs. The study in Chapter 2 helps us to understand the drivers that affected cod stocks in the last century; information that can be used to consider what might be driving the stock now. The next steps with this work are to continue digitising the data through to the 1970s held by Cefas, and to combine this dataset with Russian and Norwegian data. This will provide a unique time series to examine how climate variability influences stock abundance and biogeography, and in turn establish the factors that affect its decline. Such a study could then inform management measures that prevent overfishing, and ensure the stock remains resilient to future unfavourable changes in climate.

Through the work in this thesis on low oxygen conditions, it emerged that oxygen levels have actually improved in recent decades, unlike the global picture that suggests a proliferation of low oxygen zones in the deep ocean (IPCC, 2014). If these trends relate to land management practices across Europe, then this is good news for policy makers because it suggests positive effects on the environment through effective policy. Further work to investigate the reasons for this reduction would help to elucidate whether this is the case. Other future work could look at the combined effects of temperature and oxygen on commercial fish, such as carried out by Cucco *et al*. (2012) who tested the effects of changes in a range of oxygen levels and temperatures on the metabolic scope of flathead grey mullet *(Mugil cephalus*). The authors also looked at the differences in response of competing species and how each might persist in the future. Some of the species considered in this thesis are found in warmer waters than others, and so while the metrics published to date did not allow me to model temperature and oxygen together, further work, including experimental work, could investigate the link between the two for different species. Different life stages are also more vulnerable to changes in oxygen conditions than others, and so experimental work could investigate the effects on eggs, larvae, juvenile and adult fish, as well as different behavioural states. There are few metrics available in the literature for different life stages and so further work would help to determine which stages are the most vulnerable, and therefore in which locations, helping to target areas for management. As with the Barents Sea cod research, another avenue to explore is the combined effect of fishing pressure and environmental changes (e.g. van der Molen *et al*., 2013). Alternative management strategies could be explored within models to determine ways to best protect marine populations from climate change.

The work on nuisance species has contributed to our understanding of which species are likely to be of concern to the UK from the middle to the end of this century. Further work in this area could focus on adding more variables to the models, particularly including effects of nutrients on algal species, and of substrate type for non-native species. Future modelling studies could focus on shorter-term changes in distribution or very specific hydrographic investigations of how species are may spread, and assess whether there are pathways that could be closed through management. Climate velocity research is increasing in popularity (e.g. Burrows *et al*., 2014; Sunday *et al*., 2015), and offers real insights into which areas may be more or less affected by climate change. This is a relatively simple technique which can be applied to different parts of the globe, potentially using downscaled model outputs, to assess vulnerabilities of different communities, and then help inform management strategies. Recent work on climate velocity has identified certain areas that are sources and sinks for species, and identified barriers to species movements such as coastlines and areas that attract species, including as cooler regions (Burrows *et al*., 2014). Within this thesis I have not discussed barriers to movement, but instead have assumed that mobile species will be able to move to areas which are more suitable, although in reality this may not necessarily be the case. My models could be compared with climate velocity maps to identify potential barriers to distributions around the British Isles, which might then prevent spread of non-native species, or which could prevent commercial fish from reaching emerging areas of suitable environmental conditions. The ambition for this work on nuisance species is that it is taken up by conservation agencies helping to target surveillance and prevent further spread of the non-native species, and for choosing which species to include in monitoring and in short term forecasts for HABs.

Modelling techniques continue to develop, furthering research into the effects of climate change on species distributions and abundances. One approach is Dynamic Energy Budget (DEB) models, which can be used to scale-up from experimental findings and physiological responses to more detailed population studies. For example DEB models have been used in studies which extrapolate physiological effects to a local or regional scale (e.g. Thomas *et al*., 2011; Klok *et al*., 2014; Muller and Nisbet, 2014) and which could be useful in continuing the research here on oxygen effects, or which could be used to include the effects of pH, temperature and salinity where data are available. Global data would not be necessary, but regional or local climate model data could be used to explore smaller scale effects. For example, DEB models were used by Klok *et al*. (2014) to assess the impact of carbon capture and storage on the cockle (*Cerastoderma edule*), adapting an earlier model produced by Wijsman and Smaal (2011). DEB models adjust constants related to metabolic processes to identify environmental conditions that match experimental findings. Klok *et al*. (2014) found that an increase in CO_2 reduced growth in cockles; reducing shell weight, length and density. Linking DEB models to mechanistic niche models in predicting blue mussel (*Mytilus edulis*) growth is described as a possible way to further research in species distribution and answer complex ecological questions (Kearney *et al*., 2010). One of the main problems with DEB modelling is estimating the many parameters needed for each species being investigated. This is less complex in Scope for Growth models (Filgueira *et al*., 2011). However comparisons of Scope for Growth, Static Energy Budget models and DEB models in fish and bivalves have shown that DEBs more closely fit real data (van der Veer *et al*., 2009; Filgueira *et al*., 2011). This again demonstrates that a balance must be found between the available information and the most accurate modelling approaches that can be applied.

In addition to new modelling techniques becoming available, new climate data are also being produced that will refine ecological studies. Although pH data was not used in this thesis, POLCOMS-ERSEM is now designed to generate pH data projections to the end of the 21st century (Artioli *et al*., 2012, 2014). Work is currently underway at Cefas and elsewhere to investigate what these modelled levels will mean for marine commercial species, using a similar technique to that in Chapter 4. Updates of UK shelf seas climate data are currently being undertaken for the UKCP18 project (an update of UKCP09). For the marine environment, this will include updates on projected sea level rise and storm surge, but potentially not other hydrographic variables.

Trait-based approaches provide another method that can be combined with modelling to predict how environmental attributes affect how a species might spread. This technique has been used to look at the effects of various stressors on communities (Beukema *et al*., 1999; Bremner *et al.*, 2006; Bremner, 2008). Instead of looking at individual species, groups of species with similar traits could be considered to determine specific traits might make species more or less vulnerable to environmental change.

All of the models described above assume that a species or population is not able to adapt sufficiently quickly to environmental changes, and that it must move with its ecological conditions in order to survive. However recently more researchers are investigating how marine organisms may be able to adapt to the conditions that they find themselves in, either by evolution or phenotypic plasticity (e.g. Hoffman and Sgrò, 2011; Reusch, 2013). In the future, this ability to adapt to environmental stressors must be taken into account in modelling and management, as some species will be able to adapt more than others and become more resilient to climate change. Some of the species which are predicted to disappear from areas which are projected to be unsuitable in the future, may actually be able to adapt and remain, with subsequent implications for fishers and marine managers.

Conclusions

Modelling climate change impacts is important so that industry, policy makers and society can understand what may happen if emissions aren't reduced rapidly, although in many cases these effects will happen regardless because of greenhouse gases that have already been emitted. These studies are only useful if they lead to the implementation of management strategies to adapt to climate change, either by communities, governments or ecosystems. Having advance warning of how species might change in abundance or adapt their ranges means that we can ensure environment management techniques are appropriate to allow these shifts to happen, rather than losing the species altogether. Europe not is one of the regions that will be affected the most rapidly by climate change in comparison to the Arctic or the tropics (Mora *et al.,* 2013), but nonetheless our marine environment could look significantly different by the end of this century. We also have the luxury of resources to adapt to climate change, so long as we commit to using them. In the case of commercial, threatened or native species, other stressors to these species can be reduced by good adaptive management such as reducing fishing pressure at certain times of year when oxygen stress is highest, or when fish are spawning, or by establishing corridors of protected areas that enable species to move without being exploited and having sympathetic management measures within these areas that can be adapted as climatic changes occur. By reducing other stressors, it gives the species more resilience to adapt to the changes that climate change will bring (Obura and Grimsditch, 2009). In the case of potential nuisance species, management could prevent further damage by removing the vectors of spread, such as improving ballast water management and cleaning boat hulls more frequently, and also where possible eradicate species that are already present. Exploiting non-native species is controversial, but it may be one way to keep populations in check when there is a lack of resources for full-scale eradication programmes. Land management techniques that reduce leaching of nutrients into the seas around Europe could help to prevent very low oxygen levels from being reached, and could reduce the occurrence of some harmful algal blooms. Advance warning of algal blooms is important for shellfish farmers and fishers to ensure that their animals are not contaminated or poisoned; these models can help inform warning systems.

This thesis has focussed on the seas around Europe for the last century, and for the next century to come, and explored implications for species and for the people that rely on them. Policy-relevant questions have been answered, with suggestions for further research to improve climate adaptation. It is necessary to integrate the objectives of communities and ecology to ensure that they are sustained (Obura and Grimsditch, 2009). For too long governments have refused to accept that climate change is something that needs consideration and investment, particularly during the recent global financial downturn (Bowen *et al.*, 2009). However the recent agreement between global governments to reduce emissions and cap global warming at 1.5 °C (United Nations, 1016) provides hope that climate change may actually be something that can be tackled using a combination of mitigation and adaptation. Scientists have a role to play alongside environment managers and policy makers in developing the knowledge and tools that will allow ecosystems and communities to be resilient, and I hope that the work in this thesis will provide a contribution to this effort.

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Appendix to Chapter 2

Two examples of news articles published following release of the Barents Sea paper.

Seafood Source

New cod data a reminder of environmental impact on stocks

By Sean Murphy, SeafoodSource online editor
Published on Tuesday, September 08, 2015

Some recently disclosed information detailing cod catch data in the North Atlantic from the first half of the 20th century may have inadvertently added fuel to the debate on just how responsible overfishing has been for harming cod stocks farther south.

The data, from U.K. survey log books ranging from the 1930s to the 1950s, are hardly a new revelation, but a recent project to digitize the data has made it easier for scientists to study the figures, and one of the conclusions they have come to is that water temperature may have played a greater role in cod stocks than previously thought.

The report, published in the scientific journal PLOS One, is behind a paywall, but just viewing the abstract is telling. “Generalised Additive Models showed that environmental, spatial and temporal variables are all valuable descriptors of cod catches, with the highest occurring … at bottom temperatures between 2 and 4°C …”

Bryony Townhill, marine climate change scientist with the Center for Environment, Fisheries and Aquaculture Science in the United Kingdom and one of the principal authors of the report, told me the study did not compare and contrast environmental factors with man-made factors such as overfishing, but that he still felt the data shows how water temperature can be a factor in cod populations.

“In this work we found that the cod distribution was affected by environmental influences, including temperature,” he said. “Other work in the area in the past and also more recently has found the same, but we have now been able to add more temperature data from that time to the picture."

Townhill also stressed that the data covers the Barents Sea in the region of Northern Norway, and could offer no comment on the decline in cod populations off the U.S. East coast. However, the data mirrors comments by other scientists made in recent years on the possibility that environment plays more of a role in cod populations, indeed stocks of most seafood, than we might realize. I recall attending a conference in 2013 in Boston where a group of scientists and industry leaders met to discuss the factors involved in the cod stock declines that have badly hurt the livelihoods of so many New England fishermen.

Svein Sundby, with the Institute of Marine Research, said in 2013 that water temperature can control, among other things, the amount of phytoplankton in the water that cod eat, and that studies have shown the amount of phytoplankton has dropped in the same waters where the cod population has plummeted.

Regulations and ongoing fishery management programs, he said at the time, need to take into account the whole biological picture, including environmental factors.

"It's a different science, so to say," he said. "This is a moving target. It's varying all the time."

No one is suggesting that overfishing is not a factor in cod's decline. Even industry leaders will acknowledge cod was massively overfished for a good part of the 20th century, but the New England fishery alone has gone from 1,900 boats in the 1980s to a mere 135 boats today, and there have also been serious cutbacks in cod fishing in the North Atlantic, which the recent report covers.

However, there is still a concern about cod stocks off the U.S. East coast, while in the colder northern waters there are different results. Just this week a number of sponsors announced a new effort to get cod fisheries in the North Atlantic labeled sustainable by the Marine Stewardship Council.

Since one of the biggest differences between the two regions is water temperature, it's hard to ignore environmental factors in cod stocks both in the North Atlantic and for New England fisheries, and regulators would do well to remember this when calculating MSY and the resulting future quotas.

World Fishing and Aquaculture

Historical data digitised

09 Sep 2015

The historical surveys were carried out by the steam vessel 'RV Ernest Holt'

Historical data collected from UK fisheries in the 1930s to 1950s has been digitised for the first time – a move that could help scientists greatly improve their understanding of climate change and variability.

The survey logbooks reveal how cod responded to changing temperatures in the last century. Scientists at the Centre for Environment, Fisheries and Aquaculture Science (Cefas) and the University of Exeter found that at the time, the warm seas experienced around Norway benefitted the cod, similar to the conditions there today.

“We know from anecdotal evidence that fisheries have varied in the past but it is rare to have such comprehensive datasets going back to the early 20th century. These logbooks, along with others still held by Cefas, reveal unique insights into the state of fish stocks and the environment in the past century, and enable us to put more recent changes into context,” said Bryony Townhill, marine climate change scientists, Cefas.

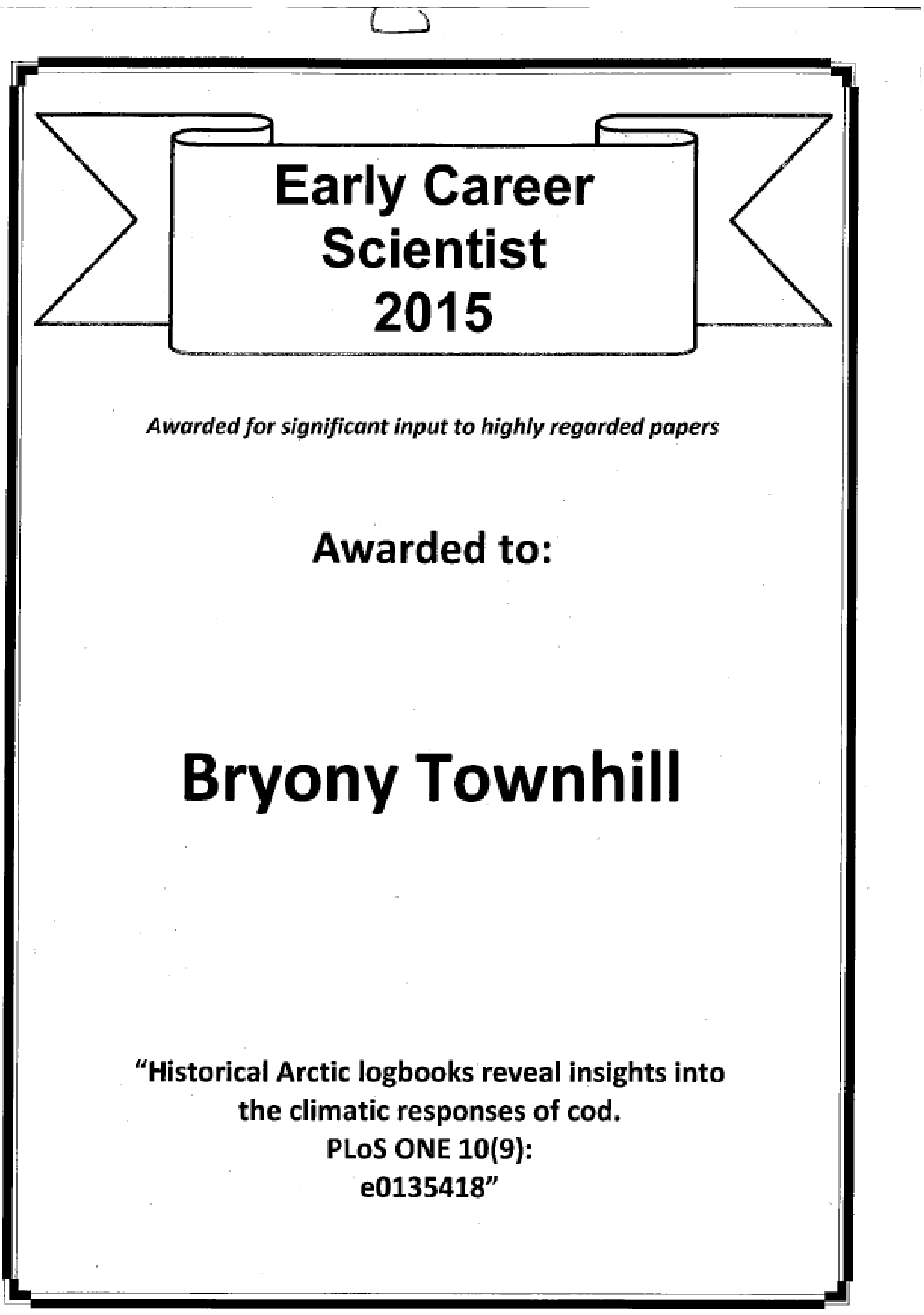
“To predict how future climate change will affect crucial fish stocks, we can learn by looking back in time,” added Dr Steve Simpson, senior lecturer in marine biology and global change, University of Exeter.

Most cod eaten by the UK comes from northern seas including the Barents Sea around Norway, because the stocks there at the moment are at record highs.

This new research also reveals that cod stocks were big in the middle of the last century, and that their food preferences each year, between capelin, herring, crustaceans and cod cannibalism, were also affected by their environment.

To ensure records from other historical survey cruises are not lost and can be made freely available, Cefas is working on cataloguing and digitising these documents where possible.

Certificate for Cefas Paper of the Year 2015



Early Career Scientist 2015

Awarded for significant input to highly regarded papers

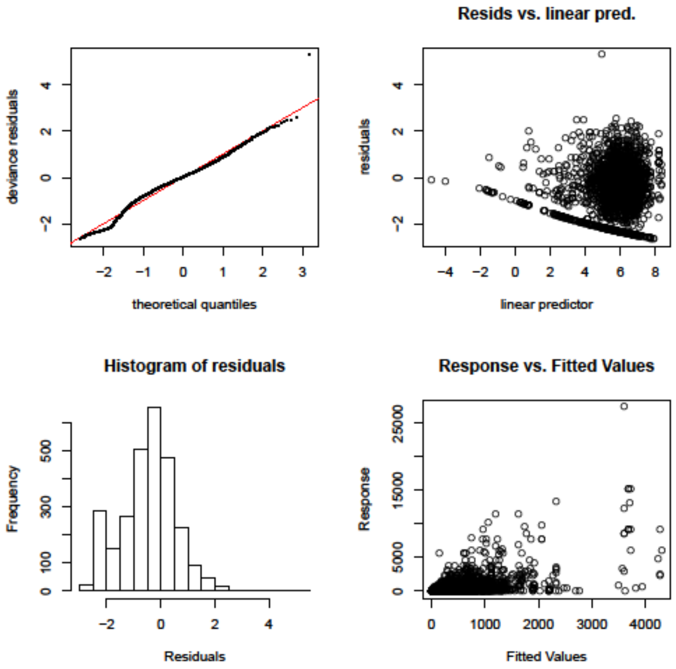
Awarded to:

Bryony Townhill

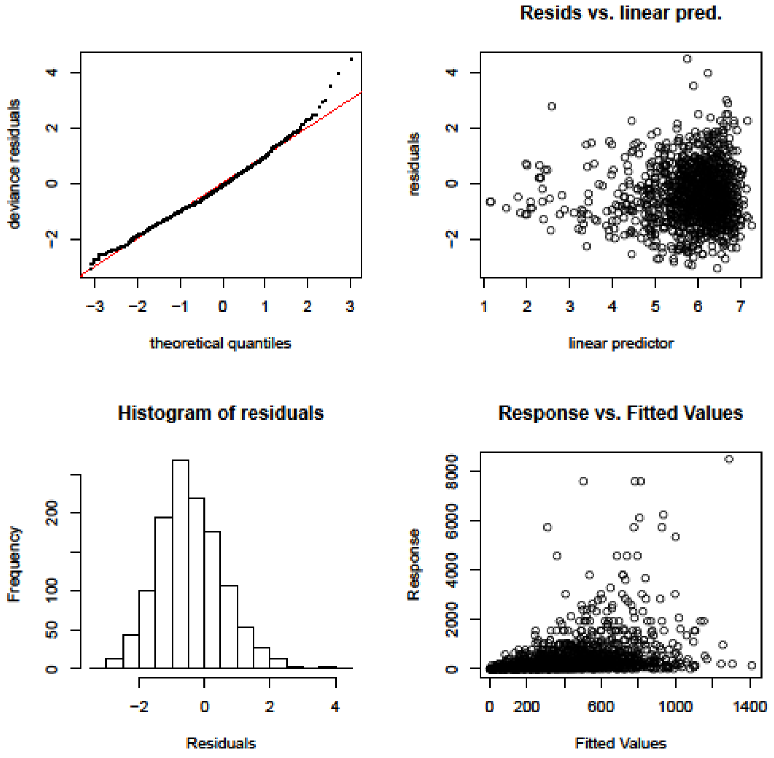
**“Historical Arctic logbooks reveal insights into
the climatic responses of cod.
PLoS ONE 10(9):
e0135418”**

Example GAM plots

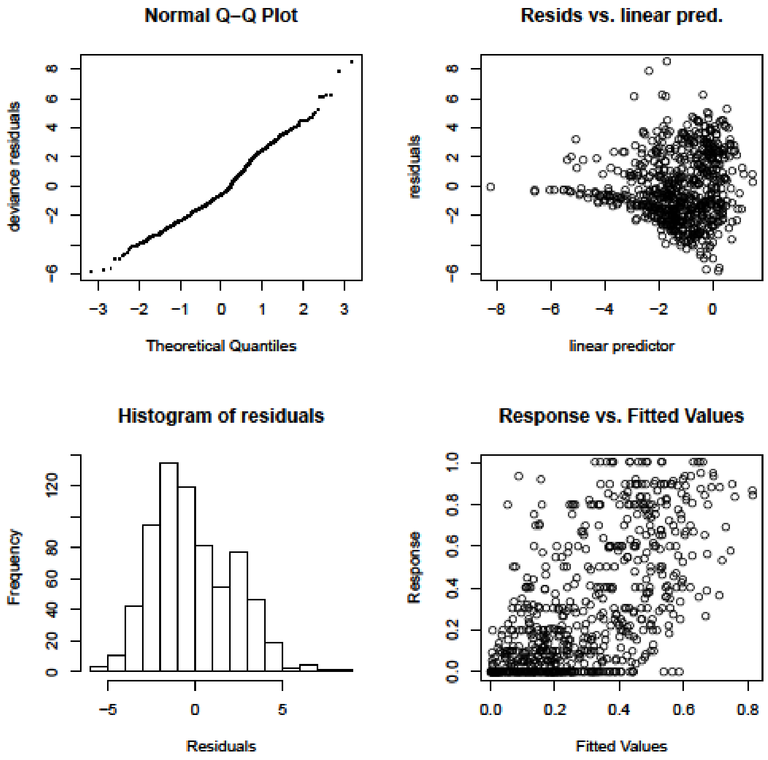
Temporal CPUE GAM



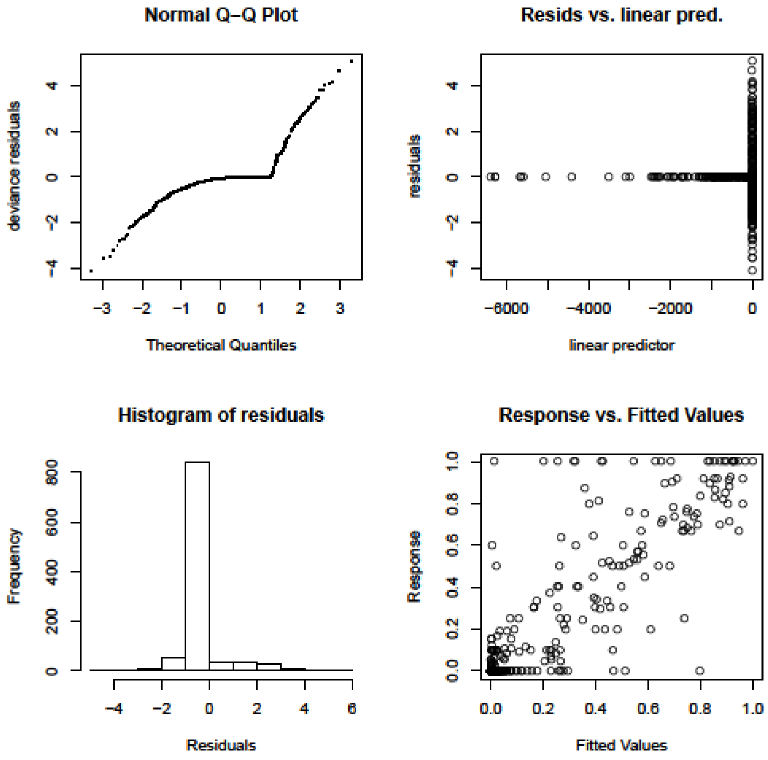
Environmental CPUE GAM



Euphausiid Environmental GAM



Capelin Temporal GAM



Appendix to Chapter 5

Supplementary Tables

Table S1. The initial short-list of species non-native species present in Europe

Scientific name	Common name
Acartia tonsa	copepod
Aglaothamnion halliae	red alga
Amphibalanus amphitrite	striped barnacle
Antithamnionella ternifolia	red alga
Asparagopsis armata	red alga
Asterias amurensis	flatbottom sea star
Asterocarpa humilis	compass sea squirt
Amphibalanus improvisus	bay barnacle, acorn barnacle
Balanus trigonus	triangle barnacle
Bonnemaisonia hamifera	red alga
Callinectes sapidus	blue crab
Caprella mutica	Japanese skeleton shrimp
Celtodoryx ciocalyptoides	sponge
Codium fragile	green alga
Cordylophora caspia	hydroid
Crassostrea angulata	Portuguese oyster
Crassostrea gigas	Pacific oyster
Crepidula fornicata	slipper limpet
Dasya baillouviana	red alga
Diadumene lineata	orange-striped sea anemone
Didemnum vexillum	carpet sea squirt

Ensis directus	American razor clam
Garveia franciscana	rope grass hydroid
Gracilaria vermiculophylla	Rough agar weed (red algae)
Grateloupia filicina var. Luxurians	red alga
Hemigrapsus sanguineus	Asian shore crab
Hemigrapsus takanoi	Brush-clawed shore crab
Hesperibalanus fallax	barnacle
Heterosiphonia japonica	red alga
Homarus americanus	American lobster
Maeotias marginata	hydrozoan
Megabalanus coccopoma	titan acorn barnacle
Mercenaria mercenaria	American hard-shelled clam
Mnemiopsis leidyi	ectoprocta
Morone saxatilis	striped bass
Mytilicola orientalis	parasitic copepod
Mytilopsis leucophaeta	brackish water zebra mussel
Neogobius melanostomus	round goby
Ocenebra inornata	Japanese sting winkle/oyster drill
Ostrea chilensis	Chilean oyster
Panaeus japonicus	red-gilled mud worm (crustacean)
Rapana venosa	Rapa whelk
Rhithropanopeus harrisii	dwarf crab
Ruditapes philippinarum	Manila clam
Sargassum muticum	wireweed
Spartina alterniflora	cord grass
Spartina anglica	cord grass

Spartina densiflora	cord grass
Spartina patens	cord grass
Styela clava	sea squirt
Synidotea laevidorsalis	isopod
Teredo navalis	common or naval shipworm (bivalve)
Tricellaria inopinata	bryozoan
Truncularìopsis trunculus	mollusc
Ulva pertusa	green alga
Umbra pygmaea	osteichthyes
Undaria pinnatifida	wakame
Urosalpinx cinerea	American oyster drill
Watersipora subatra	bryozoan

Table S2. The list of species taken forward to MI-ISK risk assessment

Species	Common Name
Crepidula fornicata	Slipper limpet
Styela clava	Asian sea squirt
Hemigrapsus sanguineus	Asian shore crab
Mnemiopsis leidyi	Sea walnut/comb jelly/ctenophore
Homarus americanus	American lobster
Tricellaria inopinata	Bryozoan
Amphibalanus improvisus	Bay/acorn barnacle
Ruditapes phillipinarum	Manila clam
Rapana venosa	Rapa whelk
Ensis directus	American razor clam
Penaeus japonicus	Kuruma prawn
Crassostrea gigas	Pacific oyster
Didemnum vexillum	Carpet sea squirt
Acartia tonsa	Copepod
Truncularíopsis trunculus	Muricid gastropod
Cordylophora caspia	Hydroid
Garveia franciscana	Rope grass hydroid
Rhithropanopeus harrisii	Dwarf crab
Ostrea chilensis	Chilean oyster/dredge oyster/New Zealand flat oyster
Balanus trigonus	Triangle barnacle
Callinectes sapidus	Blue crab
Mytilopsis leucophaeata	Brackish water zebra mussel/dark false mussel
Mercenaria mercenaria	American hard-shelled clam
Maeotias marginata	Hydrozoan

Synidotea laevidorsalis	Isopod
Celtodoryx ciocalyptoides	Sponge
Ocenebra inornata	Japanese sting winkle/Oyster drill
Teredo navalis	Naval/common shipworm
Asterias amurensis	Northern Pacific seastar
Asterocarpa humilis	Compass sea squirt
Caprella mutica	Japanese skeleton shrimp
Crassostrea angulata	Portuguese oyster
Diadumene lineata	Orange-striped sea anemone
Hemigrapsus takanoi	Brush-clawed shore crab
Mytilicola orientalis	Parasitic copepod
Amphibalanus amphitrite	Striped barnacle
Hesperibalanus fallax	Barnacle
Megabalanus coccopoma	Titan acorn barnacle
Urosalpinx cinerea	American oyster drill
Watersipora subatra	Bryozoan

Table S3. The Maxent modelling results for each species modelled

Species	Cumulative threshold	Logistic threshold	Description	Fractional predicted area	Training omission rates
A. improvisus	1.000	0.002	Fixed cumulative value 1	0.231	0.000
	5.000	0.042	Fixed cumulative value 5	0.047	0.029
	10.000	0.150	Fixed cumulative value 10	0.029	0.037
	1.500	0.004	Minimum training presence	0.161	0.000
	18.152	0.323	10 percentile training presence	0.019	0.096
	7.042	0.092	Equal training sensitivity and specificity	0.037	0.037
	10.105	0.156	Maximum training sensitivity plus specificity	0.029	0.037

	2.584	0.009	Balance training omission, predicted area and threshold value	0.094	0.007
	7.489	0.101	Equate entropy of thresholded and original distributions	0.035	0.037
A. amurensis	1.000	0.002	Fixed cumulative value 1	0.276	0.000
	5.000	0.021	Fixed cumulative value 5	0.074	0.043
	10.000	0.077	Fixed cumulative value 10	0.034	0.071
	2.520	0.007	Minimum training presence	0.142	0.000
	15.454	0.188	10 percentile training presence	0.022	0.100
	6.383	0.031	Equal training sensitivity	0.057	0.057

			and specificity		
	7.450	0.043	Maximum training sensitivity plus specificity	0.048	0.057
	2.520	0.007	Balance training omission, predicted area and threshold value	0.142	0.000
	10.674	0.094	Equate entropy of thresholded and original distributions	0.032	0.086
B. hamifera	1.000	0.006	Fixed cumulative value 1	0.040	0.007
	5.000	0.123	Fixed cumulative value 5	0.018	0.028
	10.000	0.421	Fixed cumulative value 10	0.015	0.055
	0.459	0.001	Minimum training presence	0.085	0.000

	13.574	0.464	10 percentile training presence	0.014	0.097
	3.634	0.102	Equal training sensitivity and specificity	0.021	0.021
	2.750	0.070	Maximum training sensitivity plus specificity	0.023	0.007
	1.132	0.009	Balance training omission, predicted area and threshold value	0.036	0.007
	3.299	0.088	Equate entropy of thresholded and original distributions	0.021	0.021
C. fragile	1.000	0.002	Fixed cumulative value 1	0.087	0.000
	5.000	0.121	Fixed cumulative value 5	0.019	0.015

	10.000	0.341	Fixed cumulative value 10	0.015	0.045
	1.099	0.002	Minimum training presence	0.075	0.000
	15.505	0.423	10 percentile training presence	0.013	0.098
	5.743	0.145	Equal training sensitivity and specificity	0.018	0.015
	5.743	0.145	Maximum training sensitivity plus specificity	0.018	0.015
	1.099	0.002	Balance training omission, predicted area and threshold value	0.075	0.000
	3.744	0.054	Equate entropy of thresholded and original distributions	0.022	0.015

C. gigas	1.000	0.004	Fixed cumulative value 1	0.144	0.007
	5.000	0.061	Fixed cumulative value 5	0.047	0.020
	10.000	0.167	Fixed cumulative value 10	0.030	0.054
	0.512	0.002	Minimum training presence	0.213	0.000
	17.792	0.342	10 percentile training presence	0.021	0.095
	7.529	0.103	Equal training sensitivity and specificity	0.036	0.034
	5.679	0.073	Maximum training sensitivity plus specificity	0.043	0.020
	2.151	0.012	Balance training omission, predicted area and	0.085	0.007

			threshold value		
	7.094	0.096	Equate entropy of thresholded and original distributions	0.037	0.034
C. fornicata	1.000	0.009	Fixed cumulative value 1	0.081	0.005
	5.000	0.100	Fixed cumulative value 5	0.042	0.010
	10.000	0.204	Fixed cumulative value 10	0.031	0.031
	0.689	0.002	Minimum training presence	0.112	0.000
	17.941	0.393	10 percentile training presence	0.023	0.099
	9.935	0.201	Equal training sensitivity and specificity	0.031	0.031
	6.466	0.130	Maximum training sensitivity	0.038	0.010

			plus specificity		
	1.295	0.016	Balance training omission, predicted area and threshold value	0.072	0.005
	5.873	0.116	Equate entropy of thresholded and original distributions	0.039	0.010
E. directus	1.000	0.002	Fixed cumulative value 1	0.144	0.000
	5.000	0.072	Fixed cumulative value 5	0.050	0.015
	10.000	0.149	Fixed cumulative value 10	0.034	0.030
	1.044	0.003	Minimum training presence	0.137	0.000
	22.455	0.364	10 percentile training presence	0.018	0.098
	10.215	0.151	Equal training	0.033	0.030

			sensitivity and specificity		
	7.974	0.123	Maximum training sensitivity plus specificity	0.039	0.023
	1.934	0.015	Balance training omission, predicted area and threshold value	0.079	0.008
	8.193	0.124	Equate entropy of thresholded and original distributions	0.038	0.030
H. sanguineus	1.000	0.003	Fixed cumulative value 1	0.078	0.000
	5.000	0.022	Fixed cumulative value 5	0.022	0.000
	10.000	0.083	Fixed cumulative value 10	0.009	0.000
	11.578	0.116	Minimum training presence	0.008	0.000

	15.787	0.276	10 percentile training presence	0.006	0.079
	11.578	0.116	Equal training sensitivity and specificity	0.008	0.000
	11.578	0.116	Maximum training sensitivity plus specificity	0.008	0.000
	1.605	0.004	Balance training omission, predicted area and threshold value	0.059	0.000
	9.241	0.065	Equate entropy of thresholded and original distributions	0.011	0.000
H. americanus	1.000	0.009	Fixed cumulative value 1	0.056	0.005
	5.000	0.127	Fixed cumulative value 5	0.025	0.005

	10.000	0.374	Fixed cumulative value 10	0.020	0.025
	0.032	0.000	Minimum training presence	0.346	0.000
	15.863	0.492	10 percentile training presence	0.018	0.099
	9.301	0.356	Equal training sensitivity and specificity	0.021	0.020
	5.348	0.135	Maximum training sensitivity plus specificity	0.025	0.005
	1.240	0.011	Balance training omission, predicted area and threshold value	0.049	0.005
	3.659	0.080	Equate entropy of thresholded and original distributions	0.029	0.005

M. mercenaria	1.000	0.003	Fixed cumulative value 1	0.183	0.000
	5.000	0.040	Fixed cumulative value 5	0.064	0.000
	10.000	0.098	Fixed cumulative value 10	0.039	0.017
	8.394	0.080	Minimum training presence	0.045	0.000
	16.822	0.180	10 percentile training presence	0.024	0.100
	15.134	0.159	Equal training sensitivity and specificity	0.027	0.033
	15.134	0.159	Maximum training sensitivity plus specificity	0.027	0.017
	2.471	0.014	Balance training omission, predicted area and	0.099	0.000

			threshold value		
	11.567	0.117	Equate entropy of thresholded and original distributions	0.035	0.017
M. leidyi	1.000	0.004	Fixed cumulative value 1	0.063	0.000
	5.000	0.049	Fixed cumulative value 5	0.025	0.023
	10.000	0.098	Fixed cumulative value 10	0.013	0.023
	1.001	0.004	Minimum training presence	0.063	0.000
	13.426	0.208	10 percentile training presence	0.010	0.093
	5.446	0.053	Equal training sensitivity and specificity	0.023	0.023
	10.005	0.098	Maximum training sensitivity	0.013	0.023

			plus specificity		
	1.001	0.004	Balance training omission, predicted area and threshold value	0.063	0.000
	7.918	0.078	Equate entropy of thresholded and original distributions	0.017	0.023
M. leucophaeata	1.000	0.003	Fixed cumulative value 1	0.240	0.000
	5.000	0.023	Fixed cumulative value 5	0.081	0.000
	10.000	0.071	Fixed cumulative value 10	0.044	0.000
	13.889	0.112	Minimum training presence	0.032	0.000
	19.840	0.188	10 percentile training presence	0.021	0.077
	13.929	0.112	Equal training	0.032	0.038

			sensitivity and specificity		
	13.889	0.112	Maximum training sensitivity plus specificity	0.032	0.000
	3.520	0.012	Balance training omission, predicted area and threshold value	0.108	0.000
	14.137	0.117	Equate entropy of thresholded and original distributions	0.031	0.038
P. japonicus	1.000	0.002	Fixed cumulative value 1	0.256	0.031
	5.000	0.025	Fixed cumulative value 5	0.068	0.031
	10.000	0.099	Fixed cumulative value 10	0.035	0.094
	0.892	0.002	Minimum training presence	0.273	0.000

	20.044	0.290	10 percentile training presence	0.019	0.094
	6.332	0.042	Equal training sensitivity and specificity	0.054	0.062
	6.320	0.041	Maximum training sensitivity plus specificity	0.054	0.031
	0.892	0.002	Balance training omission, predicted area and threshold value	0.273	0.000
	9.808	0.097	Equate entropy of thresholded and original distributions	0.036	0.094
R. venosa	1.000	0.002	Fixed cumulative value 1	0.483	0.040
	5.000	0.008	Fixed cumulative value 5	0.168	0.040

	10.000	0.032	Fixed cumulative value 10	0.059	0.040
	0.359	0.001	Minimum training presence	0.621	0.000
	32.357	0.462	10 percentile training presence	0.008	0.080
	12.342	0.052	Equal training sensitivity and specificity	0.041	0.040
	12.342	0.052	Maximum training sensitivity plus specificity	0.041	0.040
	6.649	0.013	Balance training omission, predicted area and threshold value	0.116	0.040
	14.014	0.072	Equate entropy of thresholded and original distributions	0.033	0.080

R. philippinarum	1.000	0.004	Fixed cumulative value 1	0.301	0.000
	5.000	0.027	Fixed cumulative value 5	0.135	0.034
	10.000	0.061	Fixed cumulative value 10	0.079	0.034
	3.941	0.020	Minimum training presence	0.157	0.000
	15.556	0.105	10 percentile training presence	0.048	0.069
	11.432	0.073	Equal training sensitivity and specificity	0.069	0.069
	10.732	0.067	Maximum training sensitivity plus specificity	0.074	0.034
	3.696	0.019	Balance training omission, predicted area and	0.163	0.000

			threshold value		
	15.114	0.102	Equate entropy of thresholded and original distributions	0.049	0.069
S. muticum	1.000	0.002	Fixed cumulative value 1	0.109	0.008
	5.000	0.072	Fixed cumulative value 5	0.031	0.008
	10.000	0.170	Fixed cumulative value 10	0.021	0.033
	0.399	0.001	Minimum training presence	0.245	0.000
	18.260	0.382	10 percentile training presence	0.014	0.098
	7.291	0.121	Equal training sensitivity and specificity	0.025	0.024
	5.922	0.089	Maximum training sensitivity	0.028	0.008

			plus specificity		
	1.906	0.010	Balance training omission, predicted area and threshold value	0.057	0.008
	6.715	0.104	Equate entropy of thresholded and original distributions	0.026	0.016
S. townsendii var. anglica	1.000	0.004	Fixed cumulative value 1	0.042	0.000
	5.000	0.070	Fixed cumulative value 5	0.015	0.038
	10.000	0.277	Fixed cumulative value 10	0.009	0.051
	2.204	0.017	Minimum training presence	0.025	0.000
	13.931	0.360	10 percentile training presence	0.008	0.090
	2.496	0.021	Equal training	0.023	0.026

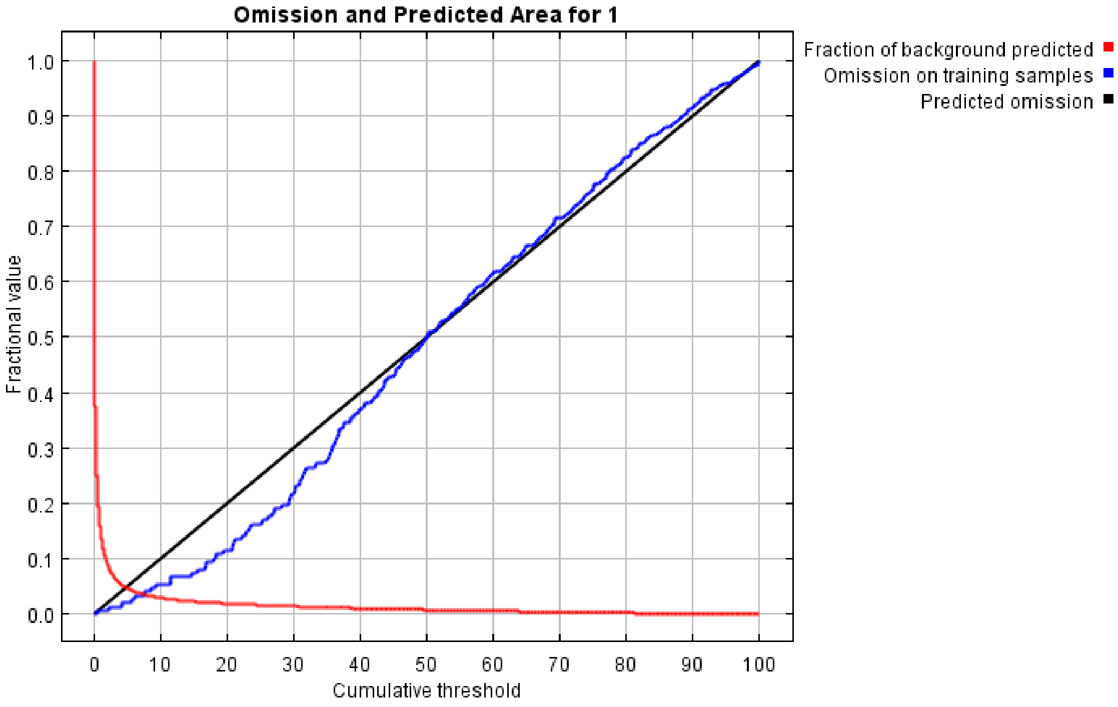
			sensitivity and specificity		
	2.204	0.017	Maximum training sensitivity plus specificity	0.025	0.000
	1.116	0.005	Balance training omission, predicted area and threshold value	0.039	0.000
	5.844	0.084	Equate entropy of thresholded and original distributions	0.013	0.038
S. clava	1.000	0.001	Fixed cumulative value 1	0.253	0.000
	5.000	0.015	Fixed cumulative value 5	0.056	0.031
	10.000	0.073	Fixed cumulative value 10	0.023	0.077
	1.556	0.002	Minimum training presence	0.186	0.000

	16.060	0.194	10 percentile training presence	0.013	0.092
	5.779	0.019	Equal training sensitivity and specificity	0.046	0.046
	5.141	0.016	Maximum training sensitivity plus specificity	0.054	0.031
	1.556	0.002	Balance training omission, predicted area and threshold value	0.186	0.000
	10.486	0.079	Equate entropy of thresholded and original distributions	0.022	0.077
U. pinnatifida	1.000	0.003	Fixed cumulative value 1	0.021	0.000
	5.000	0.053	Fixed cumulative value 5	0.006	0.000

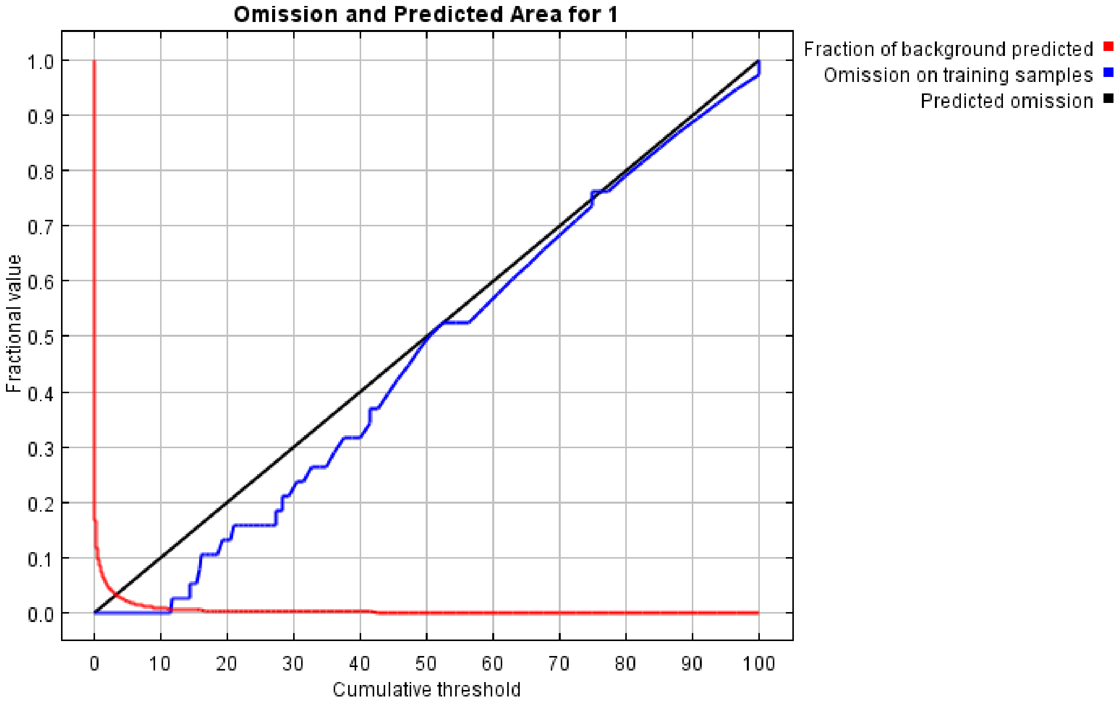
	10.000	0.131	Fixed cumulative value 10	0.004	0.062
	6.904	0.091	Minimum training presence	0.005	0.000
	22.356	0.359	10 percentile training presence	0.002	0.062
	6.904	0.091	Equal training sensitivity and specificity	0.005	0.000
	6.904	0.091	Maximum training sensitivity plus specificity	0.005	0.000
	0.714	0.002	Balance training omission, predicted area and threshold value	0.026	0.000
	8.390	0.109	Equate entropy of thresholded and original distributions	0.004	0.062

Example Maxent model plots

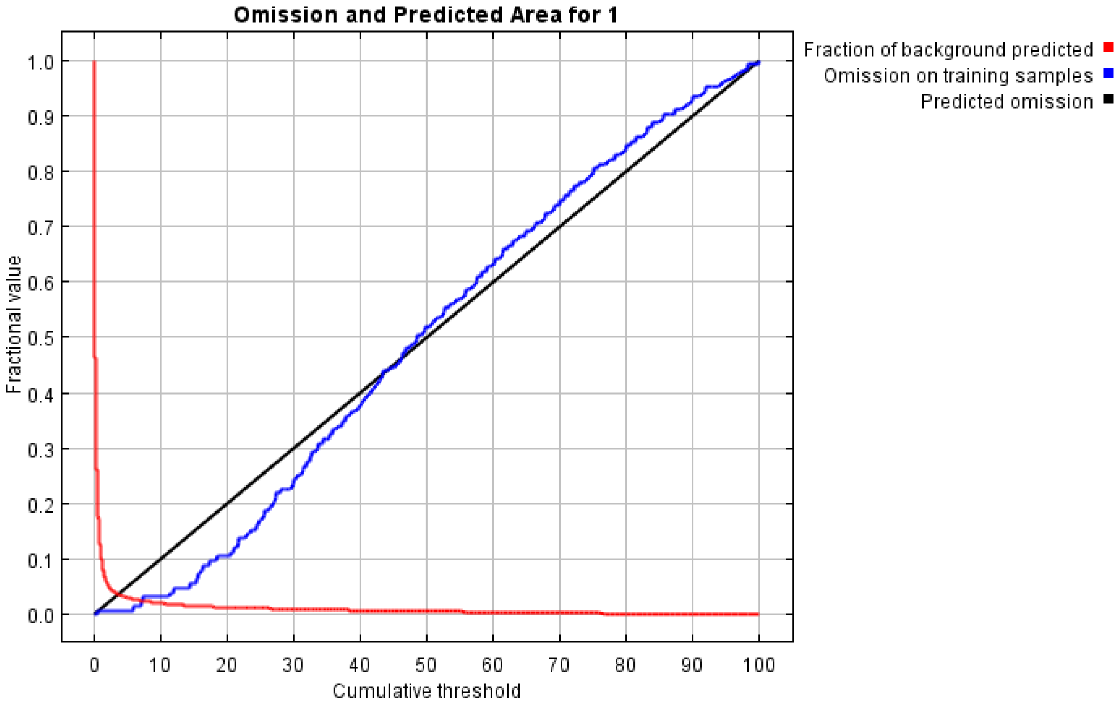
Omission rate for *Crassostrea gigas*



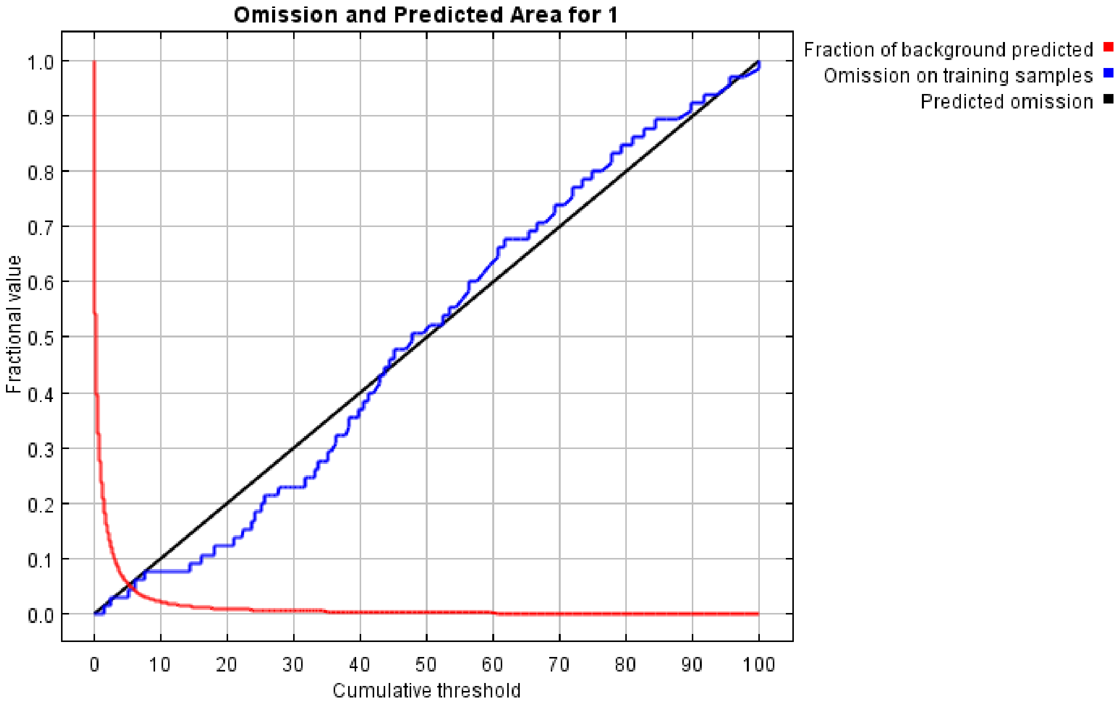
Omission rate for *Hemigrapsus sanguineus*



Omission rate for *Sargassum muticum*



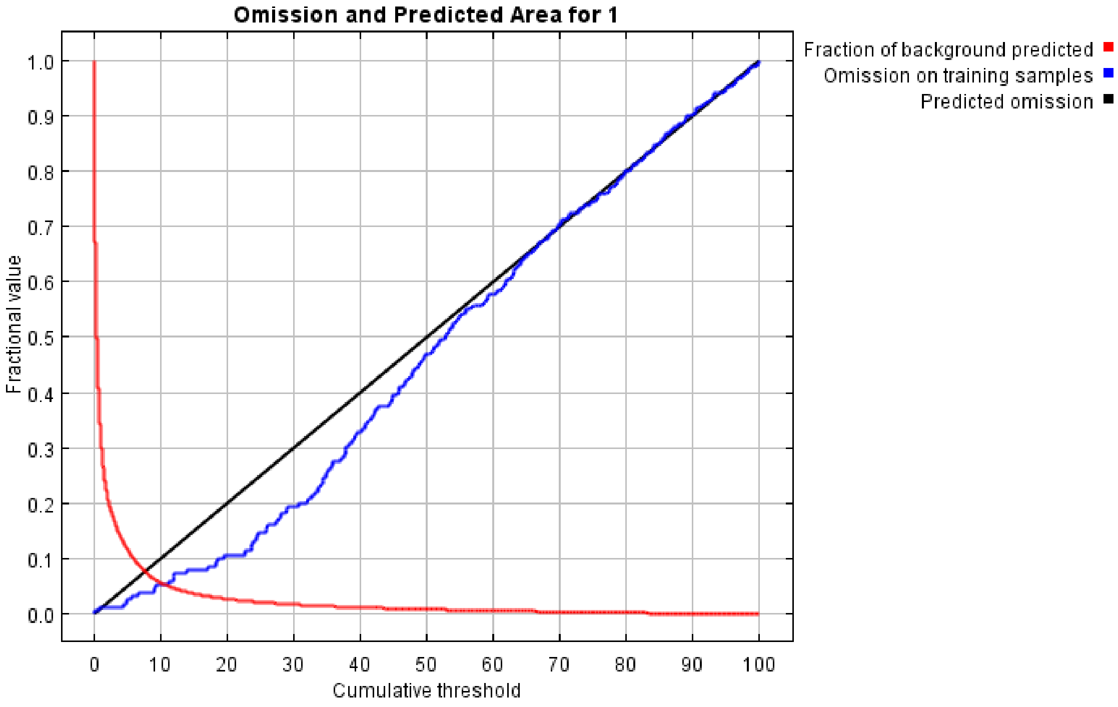
Omission rate for *Styela clava*



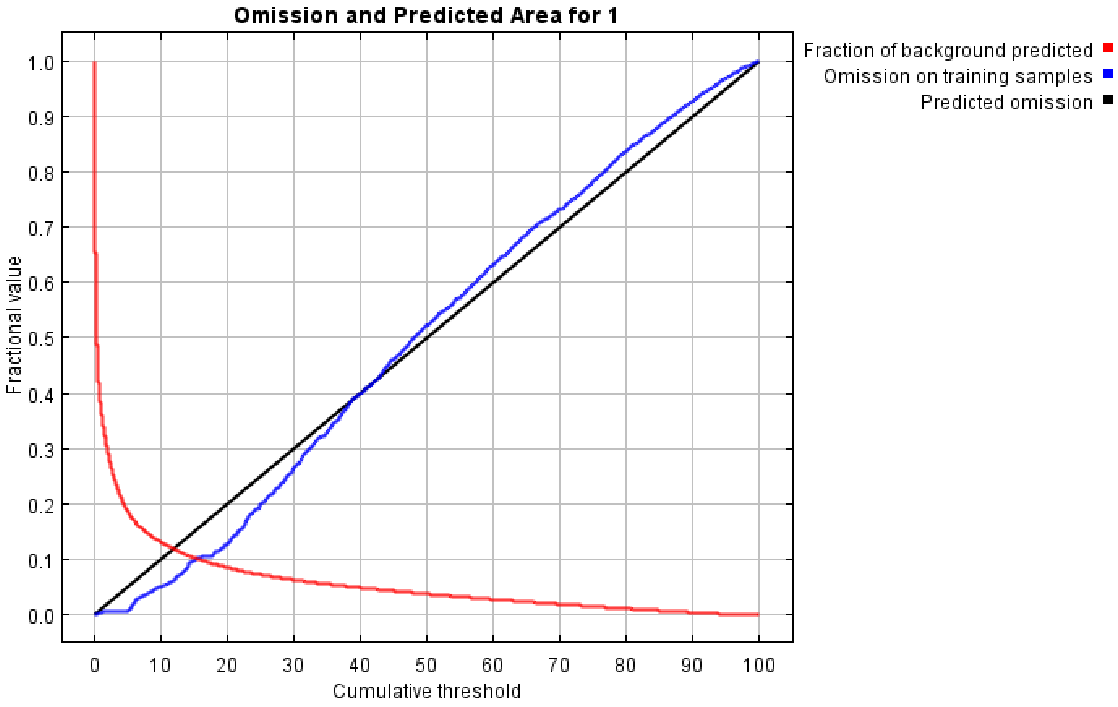
Appendix to Chapter 6

Example Maxent model plots

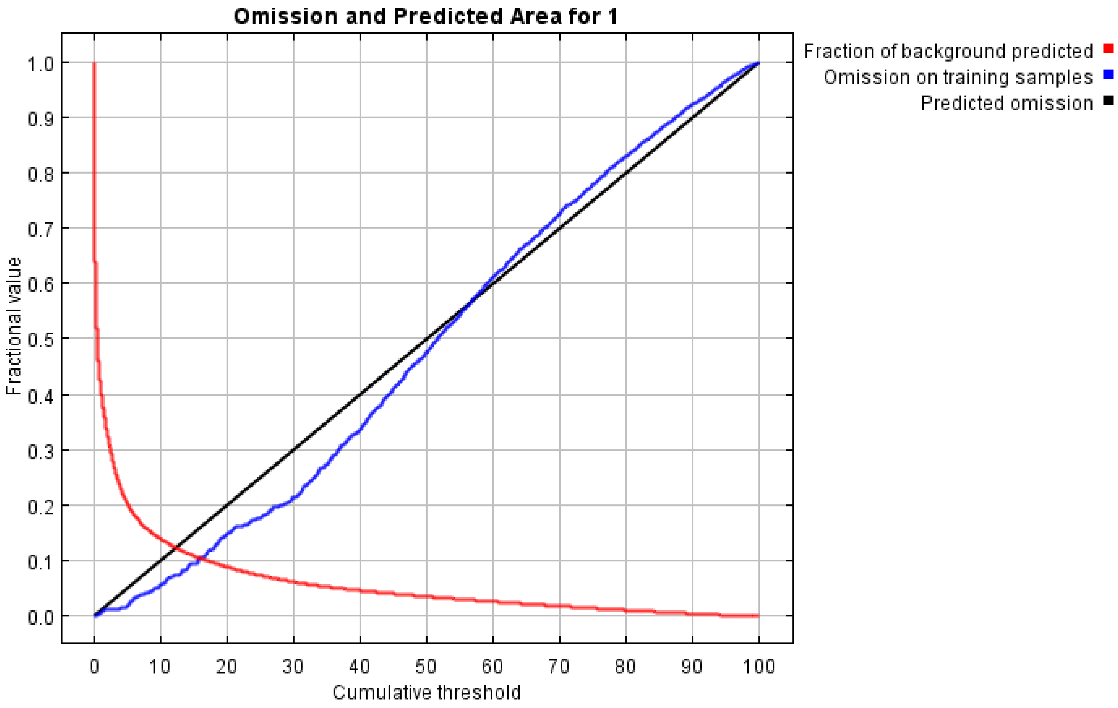
Omission rate for Prorocentrum lima



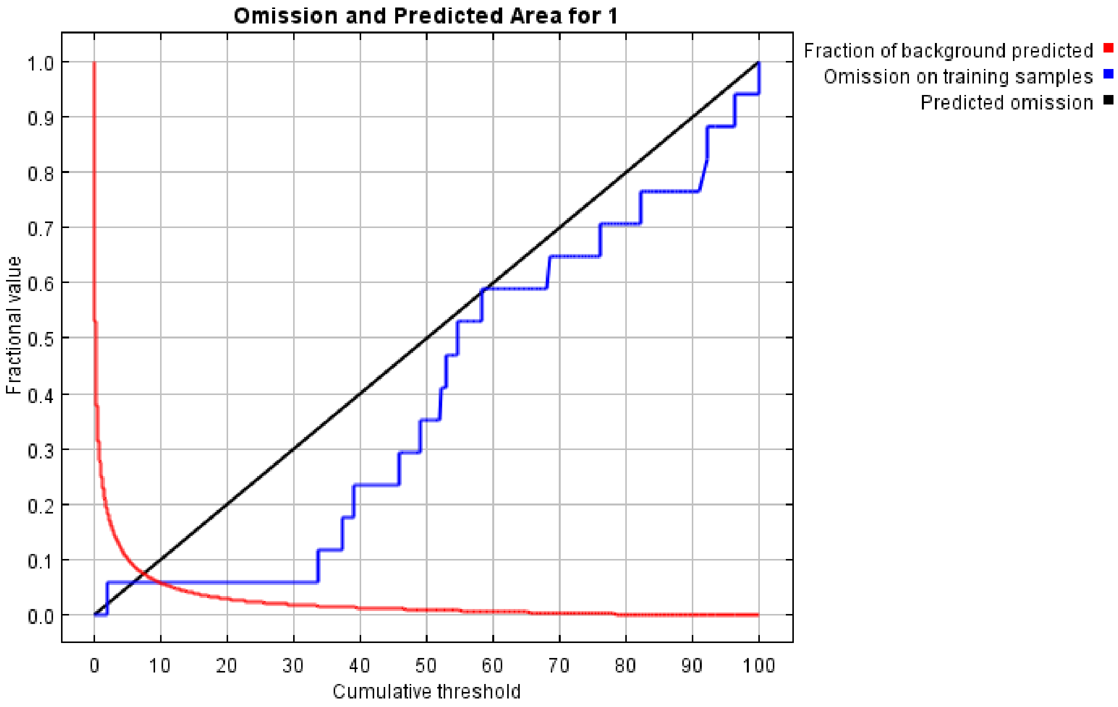
Omission rate for *Dinophysis acuta*



Omission rate for *Dinophysis acuminata*



Omission rate for *Gymodinium catenatum*



Note low number of presence data points (26) and training samples (17).