Investigating the ecological and economic consequences of marine climate change in UK waters

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Thesis submitted for the degree of Doctor of Philosophy
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February 2013

Contents

Abstract

Climate change is of concern for both marine biodiversity and the human societies that are supported by it. Predictive models are required to assess potential responses of socio-ecological systems to climate change, implement measures to enhance their adaptability, and ensure the persistence of marine species and the livelihoods that depend on them. This requires a combination of modelling techniques, making use of a variety of data while dealing with uncertainty at many stages of the modelling procedure. This thesis explores the impact of climate change on a marine socio-ecological system, in particular through climate-induced shifts in species' distributions. It further aims to explore sources of uncertainty in projecting models under climate change. Ecological and economic research techniques are applied to a set of species predominantly inhabiting UK waters, using projections of climate change for 2050. Ensemble projections suggest polewards shifts in species at an average rate of 27 and 42 km per decade for demersal and pelagic species respectively. Uncertainties concerning alternative, valid data sources and modelling procedures, notably species distribution models, contribute variation to predictions, and a multi-model approach is advocated to incorporate uncertainties and prevent bias through model selection. Predictions help identify increased risk of over-fishing through bycatch and indicate likely changes in environmental suitability of protected areas. Results also demonstrate how an index of agreement may be used to promote the tractability and application of projections by non-specialist communities. Furthermore, total maximum catch potential within UK waters is predicted to decrease by 2050, resulting in a median decrease in profitability between 2005 and 2050 of 10%, dependent on alterations in key costs such as fuel price. This thesis highlights the tight link between climate change impacts at ecological and socio-economic levels. Although adaptive capacity might be enhanced by switching gear or altering fishing patterns, rebuilding fish stocks to sustainable level will both improve their resilience to multiple threats and improve the resilience of fishers to withstand changes in distribution and catch.

Acknowledgements

Firstly I would like to thank the ACME project and the UK Department for Environment, Food and Rural Affairs (DEFRA)/ Centre for Environmenta, Fisheries and Aquaculture Science (CEFAS) for funding this work.

For data, I would like to thank the following: *Sea Around Us Project,* Fisheries Centre, University of British Columbia; the International Council for the Exploration of the Sea (ICES); the Joint Nature Conservation Committee (JNCC); the World Climate Research Program (WCRP) Coupled Model Intercomparison Project phase 3 (CMIP3) (http://esg.llnl.gov:8080); and the Geophysical Fluid Dynamics Laboratory (GFDL) (http://nomads.gfdl.noaa.gov).

I would like to thank my supervisors, William Cheung, Stephen Dye, John Pinnegar and Rachel Warren. They have offered tremendous support throughout my PhD, enabled me to work with multiple research centres and projects and the breadth of work they cover has been a key inspiration and driving force behind this thesis. In particular I would like to thank my primary supervisor, William Cheung for being a brilliant supervisor and inspirational researcher, even when the other side of the Atlantic.

Undertaking an interdisciplinary thesis and merging study areas, some of which my initial knowledge of was scant, has been exciting, enlightening but also challenging. This thesis has greatly benefitted from input, advice and inspiration from a wide variety of research groups and colleagues. I have been lucky enough to work with CEFAS, the Tyndall Centre for Climate Change Research, the Fisheries Centre, University of British Columbia and the Centre for Ecology, Evolution and Conservation, UEA. I would like to thank many people within these research groups not only for advice and support but for inspiration, alternative points of view and for keeping my academic interests broad. Most notably, I would like to thank Jose Fernandes, for offering unfailing support on my steep coding learning curve, and Rashid Sumaila, for teaching me economics. Also thanks to Vicky Lam, Thomas Frölicher, Andy South and Kirsten Kaschner for advice and support. I am also grateful to editors and anonymous reviewers of *Ecological Modelling, PLoS ONE and Aquatic Conservation* for providing constructive criticism on selected chapters within this thesis.

I could not have completed this thesis without the support of friends and colleagues at UEA, in the Tyndall Centre, the Fisheries Group and Strangles, an inspiring and fun group of ecologists to work alongside. In particular, many thanks to Hugh, Christina, Scott, Eveliena, Kat, Becky, Martin, Cat, Sue, Pete, Joe, Jose, Vero, Jenny, Amy and Tara. Also thanks to those at UBC who welcomed me into the Fisheries Centre and helped make my time there so productive and enjoyable.

Finally, a huge thank you to my family and friends who have supported me throughout the highs and lows of PhD life, providing advice, encouragement, chocolate and welcome distractions, and to Sarah for a beautiful fish.

Chapter 1

Introduction

The oceans cover 71 percent of the Earth's surface and are host to an estimated 50-80% of all life on Earth. They contain some of the most productive ecosystems, vast natural resources and unique habitats and further play a vital role in regulating the Earth's climate. However, the integrity of the marine environment is increasingly threatened by human-induced overexploitation, habitat destruction, pollution, and invasions by exotic species. This intensifying anthropogenic degradation of the marine environment is of concern not only due to the intrinsic value of the biodiversity that inhabits it, but also due to its critical role in supporting human societies. In 2009, 148 million tonnes of seafood from capture fisheries and aquaculture entered the human food chain, contributing 16.6 percent of the global animal protein intake by humans (FAO 2012). In 2008, commercial fisheries and aquaculture contributed over US $217.5 billion to the global economy (FAO 2012), while non-extractive uses such as marine ecotourism further contributed substantially to local economies (Dharmaratne *et al*. 2000; Gallagher & Hammerschlag 2011). Not only do marine ecosystems provide important ecosystem services, they are central to coastal peoples worldwide, their heritage, religious and cultural values. However, obtaining a detailed understanding of the effects and interactions of anthropogenic impacts can be challenging. Marine research is expensive and logistically difficult due to the size and remoteness of the biome and many marine scientists depend on technology such as boats, submersibles and scuba equipment, thereby adding costs to projects exceeding that typically experienced by terrestrial ecologists. Furthermore, not only do the effects of climate change represent added threats to the marine environment, they contribute a layer of uncertainty to the impacts of other threats, fisheries management plans or conservation measures. The development and application of models that allow exploration of the range of possible responses of the oceans and marine biodiversity to climate change is therefore a vital step in adapting and mitigating its impacts on both marine biodiversity and the human societies which depend on it. This section introduces research areas and ideas that have shaped the thesis, informed methodologies and highlighted knowledge gaps to prompt the specific research questions that will be addressed in subsequent chapters.

1. Species Response to Climate Change

1.1. Observed Effects of Climatic Variability

Species have been observed as responding to climate change throughout evolutionary history (Harris 1993). However, there is growing concern for their ability to survive under the higher temperatures and rate of climate change currently observed and predicted (Schneider and Root 1998). Global climate models (GCMs) predict significant warming around the globe, ranging from 1.1 to 6.4°C by 2100 (IPCC 2007b) and making the Earth warmer than at any point in the past 1-40 million years (Houghton *et al.* 2001). An estimation of future climate envelopes has predicted 15-37% of species in a sample spanning a range of regions and taxa to be 'committed to extinction' (Thomas *et al.* 2004), although the magnitude of such estimates have been challenged (Botkin *et al.* 2007).

In the marine environment, fishermen and scientists have observed prevailing weather conditions to be influencing the state of fish stocks for over 100 years (Cushing 1982). There is growing concern over the impact of climate change on marine systems, with longer-term shifts in the conditions caused by climate change, such as temperature and hydrological cycles, moving outside the bounds of previous climatic variability with which changes and adaptations in marine communities have been associated (Root *et al.* 2003; Beaugrand 2004; King 2005). Furthermore, climate change is likely to interact with other factors driving change in marine communities, such as removal by fisheries of predators or prey, release of endocrine disrupting substances into the ecosystem and removal of essential habitat from it. Coastal habitat is being lost and water extraction is leading to altered river-flow into estuaries. However, organisms may respond and potentially adapt to these changes in a number of ways (Rose 2005; Brook *et al.* 2008), discussed here with particular reference to marine organism

1.1.1. Phenology

Climate change may result in changes in species' morphologies, such as body size and behaviour, and a potentially linked alteration in genetic frequencies (Cheung *et al.* 2012; Thomas *et al.* 2001; Parmesan and Yohe 2003). However, evidence from Pleistocene glaciations has shown that species are more likely to exhibit ecological responses to climate change, such as shifts in range distributions, than evolutionary responses, through local adaptation (Bradshaw and Holzapfel 2006). Mechanisms promoting acclimation, such as a phenological shift in body function within an organism's lifetime, may thus be more likely than changes on a biochemical or genetic level, signifying adaptation (Parmesan *et al.* 2000). Climate change may, for example, lead to modification of phenology, periodic biological phenomena, so that critical phases remain synchronized with climatic alterations. For example, phenophases of the spawning season have been shown to be negatively correlated with mean Sea Surface Temperature (SST) the preceding winter for 27 species in the North Sea (Greve *et al.* 2005), while earlier spring migrations have also been noted (Sims *et al.* 2001; Clarke *et al.* 2003). Phenological responses are highly taxon or species specific, resulting from sensitivity to climatic fluctuations as well as factors such as temperature, light or food availability (Edwards and Richardson 2004). Altered phenology and timing of development may also lead to altered dispersal. For species whose offspring develop in the water column, for example, the duration of the larval stage will determine the length of time larvae are subject to movement by the currents (O'Connor *et al.* 2007).

1.1.2. Biogeographical Shifts

If changes in environmental conditions are too pronounced to result in acclimatisation by adjusted life cycles, a species' density at a location may change due to polewards or upwards range shifts associated with movement to areas within its metabolic limits, thereby initialising a biogeographic shift (Parmesan and Yohe 2003; Beaugrand 2009). Population-level movements, brought about by the ratio of colonisations at northern or upper altitudinal boundaries to extinctions at southern or lower altitudinal boundaries (Parmesan *et al.* 1999) have been observed across regions and taxa, both currently (Deutsch *et al.* 2008; Tingley *et al.* 2009) and in the past (Graham and Grimm 1990; Ashworth 1996). As the paleoecological record is further dominated by individualistic, species responses to climate (Hannah *et al.* 2002), this phenomenon is likely to lead to new species assemblages (Graham and Grimm 1990; Harborne and Mumby 2011). Marine examples of shifting distributions due to climate change are more striking than their terrestrial counterparts due to their greater rapidity (Parmesan and Yohe 2003; Edwards and Richardson 2004; Cheung *et al.* 2009), although it has recently been proposed that terrestrial species' distribution shifts have been greatly underestimated (VanDerWal *et al.* 2012). For example, Beaugrand *et al.* (2009) described northward movement in calanoid copepod zooplankton assemblages in the North Atlantic at a mean rate of up to 23.16 km per year over 48 years, compared to the 0.6 km yr^{-1} polewards shift observed for terrestrial species for a range of terrestrial taxa in diverse habitats (Parmesan and Yohe

2003). These changes in planktonic communities were paralleled by a northward migration of both commercial and non-commercial fish species (Brander 2003; Beare *et al.* 2004; Perry *et al.* 2005). In the European continental shelf, a response to warming has been demonstrated in the abundances of 72% of the 50 most common species UK waters (Simpson *et al.* 2011), while immigrant species such as sailfin dory, *Zenopsis conchifer,* and big-eyed tuna, *Thunnus obesus,* have also recently been recorded around the southern coast of the UK for the first time, correlated with temperature data for the North Atlantic (Stebbing *et al.* 2002). These distribution shifts reflect the influx of tropical marine species to subtropical regions that have been observed elsewhere (Arvedlund, 2009; Fodrie *et al*., 2010).

1.1.3. Changes in Nutrient Production and Productivity

Climate change is predicted to have a predominantly negative effect on nutrient supply and production due to reduced vertical mixing (Sarmiento *et al.* 2005). Satellite observations of ocean chlorophyll indicate that global ocean primary production has declined by more than 6% since the early 1980s (Gregg 2003). Although it has been suggested that increased stability of the water column may have a balancing positive effect on production at higher latitudes (Behrenfeld *et al.* 2006), 70% of the global decline in primary production occurred at high latitudes, especially in the northern hemisphere (Sarmiento *et al.* 2005). Using empirical models for a set of seven biomes in a comparative modelling study using six Atmosphere-Ocean Global Circulation Models (AOGCMs), Sarmiento *et al*. (2005) further predicted a small global increase in marine chlorophyll and primary production for 2050 and 2090, compared to a pre-industrial emissions control scenario. This result masked large regional differences, such as decreases in the North Pacific and increases in three of four low latitude basins (Sarmiento *et al.* 2005). However, contrasting these results, Steinacher *et al.* (2010) estimated a decrease in global mean primary productivity of between 2 and 20% by 2100, relative to preindustrial conditions. Although regional variation was also found, with increases predicted in the Southern Ocean, the predictions for a global decrease was consistent across 4 global coupled carbon cycle climate models (Steinacher *et al*. 2010). The complexity of trophic systems makes it difficult to establish reliable predictive relationships between primary and secondary production and fisheries production (Brander 2010). Furthermore, changes in production at higher trophic levels may also result from direct climatic impacts on both reproduction and growth.

Temperature may impact the success and thus locality of spawning at both local and large scales (Rose 2005; Snickars *et al.* 2010), as well as recruitment, (Pörtner 2001; Drinkwater 2005), larval development, and duration (Clarke *et al.* 2003; O'Connor *et al.* 2007). Within the Bristol Channel, the significant role of seawater temperature in determining growth and/or abundance has been identified for sea bass, *Dicentrarchus labrax,* (Henderson and Corps 1997), dab, *Limanda limanda* (Henderson & Seaby, 1994) and sole, *Solea solea* (Henderson and Seaby 2005). Significant correlations have also been found between cod, *Gadus morhua*, recruitment or growth (Brander 1995; Pörtner 2001) and temperature fluctuations, consistent with results obtained from growth experiments and rearing in enclosures (Bjornsson and Steinarsson, 2002).

1.1.4. Pathogens and Invasive species

As many pathogens are temperature sensitive, climate change is projected to impact disease in both marine organisms and humans (Harvell *et al.* 2002). Although some cold-water salmonid diseases are favoured by low temperatures (Holt *et al.* 1989), growth rates of many marine bacteria, fungi and highly toxic phytoplankton varieties, such as *Prorocentrum* and *Chattonella,* are positively correlated with temperature (Harvell *et al.* 2002). The increasing frequency and spatial distribution of phytoplankton blooms and fish kills in coastal seas globally since the 1970s have also been attributed to the eutrophication of coastal waters by human activity and increasing global temperatures (Pinnegar *et al.* 2008). The occurrence of harmful algal blooms in the North Sea is thus predicted to increase over the next 100 years due to projected increases in precipitation in Britain, the subsequent increase in the freshwater pulse released at the coast and intermittent salinity stratification (Peperzak 2003).

Greater incidence of pathogens may also have indirect effects on marine organisms. *Phaeocyctis* blooms, for example, regularly affect the coastlines of northern France, Belgium and the Netherlands. Although not themselves toxic, degeneration of the bloom leads to the formation of an anoxic, mucilaginous layer on the seabed and the mass suffocation of juvenile fish. Individuals may also become increasingly susceptible to pathogens under thermal stress (Harvell *et al.* 2002) and altered patterns of disease may release a species from, or impose, a major source of population regulation (Harvell *et al.* 2002; Brander 2010).

Although there is little data to assess whether climate change will facilitate invasions by favouring introduced over native species, as with pathogens, global warming may relax the constraints posed by inhospitable climatic conditions in a recipient region, to which novel species are already being transported by human activity (Southward *et al.* 1995; Stachowicz *et al.* 2002). For example, an increase in mean annual SST and winter water temperatures in Long Island Sound (Connecticut, USA) was found to facilitate the establishment and persistence of invaders from warmer climates due to differential responses by native and non-native ascidians to inter-annual variation in temperature. As the initiation of recruitment in the non-native species was strongly negatively correlated with early March temperature, it was able to recruit earlier with warming temperatures, conferring an advantage as the outcome of competition among sessile invertebrates is often determined by the order of habitat colonisation (Stachowicz *et al.* 2002).

1.1.5. Regime shifts

Regime shifts reflect a substantial shift from one dynamic regime to another and have been used to describe large, step-like switches in the abundance and composition of plankton and fish (Beaugrand 2004; Hjermann *et al.* 2007), often related to bottom-up changes in productivity (Drinkwater *et al.* 2010). An example of a regime shift was described in the northern Pacific Ocean, associated with changes in atmosphere circulation and temperature due to large-scale hydro-climatic changes. This involved rapid alteration of phytoplankton and zooplankton production and composition and a change in the dominant species from commercially valuable shrimp and crabs to highly productive gadoids in large areas of the Berring Sea and the Gulf of Alaska. There were also concurrent increases in salmon production in Alaskan regions and decreases in California, Oregon and Washington (De Young *et al.* 2004).

1.2. Dominant factors and mechanisms involved in the species' responses climate change

Assessment of the effects of climate change therefore involves disentangling an intricate web of climate-mediated physical variables, other external variables, and the life-history and food-web stages at which these may impact. Although temperature has been proposed as the most influential climate variable in determining large scale fish and shellfish distribution (Clarke *et al.* 2003), the effects of atmospheric climate change also manifest themselves through factors such as ocean circulation, acidity, salinity and the density structure of the water column. There is therefore considerably uncertainty in the way these oceanographic variables will act and how they might interact with one another and external factors, such as fishing pressure. Although frequently assumed to progressive, and linear (Brander 2007), responses may also be non-linear (Ottersen *et al.* 2010), for example, when exceeding a threshold value causes a major change in species composition, production and dynamics (Beaugrand 2004).

Furthermore, the biological impact of increases in environmental variables, such as temperature, will depend on the physiological sensitivity of organisms to its change (Scott and Johnston 2012). For example, species in tropical regions have narrower thermal tolerances and live closer to their tolerance limits than those in polar or temperate regions (Deutsch *et al.* 2008). Thus although it has been predicted that biological change might be concentrated in areas where temperature changes are largest, such as at high latitudes and altitudes (Root *et al.* 2003), this might not be the case if the thermal tolerance of species is proportional to the magnitude of the temperature variation they experience. Evaluating the effect of rapidly changing climate on species' survival and distributions therefore requires linking the geographic pattern of climatic change to the physiological sensitivity of study organisms (Deutsch *et al.* 2008).

The ecological effects of climate patterns and change can be categorised as direct or indirect (Ottersen *et al.* 2004, 2010). A direct effect involves a direct response to a climate pattern by a synchronized environmental phenomenon, acting on physiology, behaviour, growth, development, reproductive capacity, mortality and distribution (Brander 2007). Indirect effects, on the other hand, do not directly affect a population's biology or involve several intermediary steps between the climate pattern and ecological trait. Indirect effects might alter the productivity, structure and composition of the ecosystem on which fish depend for food and shelter (Greve *et al.* 2001; Beaugrand 2004).

1.2.1. Direct Effects

i. Temperature

Global atmospheric temperature and carbon dioxide concentrations are rising, with 11 of the last 12 years (1995 – 2006) ranking among the warmest since 1850 in terms of global surface temperature, and a 100 year trend of 0.74°C (0.56 – 0.92°C with 90% uncertainty) from 1906 to 2005 (IPCC 2007a). Although temperature increase is widespread across the globe, there is strong geographic variation between latitudes, with Arctic regions showing temperature increases at two times the global rate (IPCC 2007a). The next two decades are projected to show an increase of about 0.2°C warming per decade if greenhouse gas (GHG) and aerosol concentrations remain constant at year 2000 levels, with a further warming of about 1°C per decade expected (IPCC, 2007). Following this period, temperature projections vary depending on the emissions scenarios used, such as the 2000 IPCC Special Report on Emissions Scenario, SRES. Surface warming then varies between a 0.6 and 4.0^{o}C temperature change by 2000-2099 relative to 1980-1999) (IPCC, 2007). Air temperature rises are causing simultaneous warming of the world's ocean (Levitus *et al.* 2000; Fukasawa *et al.* 2004). Although the most significant warming is expected in the upper 500 – 800m (Bernal 1993), observations since 1961 have shown average temperature to be increasing to a depth of at least 3000m (Levitus *et al.* 2000). Regional increases in ocean temperature have also been documented in the south-west Pacific Ocean, North Atlantic (Bindoff and Church 1992; Parrilla *et al.* 1994) and the Mediterranean Sea (Bethoux *et al.* 1990). Temperature is thought to be the climatic variable which has the dominant effect on marine ecosystems (Drinkwater *et al.* 2010).

Ectothermic animals are adapted to and depend on the maintenance of a characteristic temperature window within their natural environment (Pörtner 2001). The importance of this is indicated by the fact that, contrasting mammals and birds, no ectothermic species is known to occur over the widest temperature range possible, from polar latitudes to the tropical regions. The 'law of tolerance' (Shelford 1931) was extended by Schwerdtfeger (1977) to describe the changing performance of organisms within the optimum, pejus and pessimism phases of the tolerance range, with respect to environmental factors. The pejus and pessimism temperature describes a species' or population's high and low temperature thresholds respectively and are found well within the range encompassed by the critical temperature (Frederich and Pörtner 2000). The lower heat tolerance in metazoan compared to unicellular eukaryotes and bacteria suggest that temperature limitations are imposed by complex systems rather than single molecular processes (Pörtner 2001). The increased metabolic rate and performance achieved by greater complexity (Hemmingsen 1960; White *et al.* 2006) may therefore be offset by greater thermal sensitivity. Recent comparisons of the mechanisms characterizing thermal intolerance have led to the general conclusion that oxygen limitation and a decrease in the ability to perform aerobically (aerobic scope) characterize the first line of thermal intolerance in water breathing animals at both ends of the thermal envelope (Pörtner *et al.* 2000; Pörtner 2001). At temperatures beyond the maximum critical temperature, anaerobic metabolism sets in and survival is time-limited (Frederich and Pörtner 2000; Pörtner and Knust 2007). In colder waters, oxygen supply to tissues is optimized by a shift in haemoglobin isoforms and oxygen binding properties, allowing lower oxygen affinities and higher uploading potential. Mitochondrial densities increase, allowing greater aerobic capacity and meeting energy demands (van Dijk *et al.* 1999). As temperatures decrease further, towards the lower critical temperature (Tc), ventilation and circulation become insufficient to cover mitochondrial demand, leading to the breakdown of oxygen transport and aerobic metabolism, and functional failure.

As activity and especially reproduction occur in a narrower thermal window than mitochondrial maintenance, the ecologically relevant temperature limits are those of thermal tolerance rather than the critical range (Pörtner 2001). Thermal tolerance limits may change through acclimatisation or adaptation (Scott and Johnston 2012). A trade-off between adaptation for wider thermal tolerances and reduced oxygen limitation and fecundity and growth may therefore result in reduced body size, larger individuals frequently experiencing greater thermal sensitivity than smaller ones (Pörtner and Knust 2007). These findings are supported by food-unlimited laboratory experiments where the maximum attainable weight of a 3-year old cod increased almost linearly with temperature from 3 – 6^{o}C, before levelling off and reaching a maximum at about 8.5^{o}C (Bjornsson and Steinarsson 2002). Species may also vary in their ability to adapt to temperature change because aerobic scope can be defined by motor activities. More active species of fish and octopus have a higher aerobic scope and critical temperatures compared with sessile Antarctic species (Pörtner *et al.* 2000).

The effect of sea water warming on marine life will depend on the position of the current habitat in the thermal tolerance range of each species or population, and whether a change in ambient temperature falls within adaptable limits. While increases in water temperature may promote growth and reproduction in cooler regions, similar increases may have negative consequences in warmer regions. In Cod, for example, increasing SST corresponding to increases in recruitment at baseline temperatures less than 5^{o}C, but decreases in recruitment at baseline temperatures greater than 8.5^{o}C (Drinkwater 2005). Tolerance limits may further depend on the extent of diurnal and seasonal temperature fluctuation already experienced. For example, cold-adaptation in polar stenotherms has led to fewer red blood cells, oxygen binding proteins (Nikinmaa 2002), and enzymes that are especially sensitive to temperature. These species are thus likely to be ill-prepared to cope with even minor increases in environmental temperature (Pörtner *et al.* 2000).

Temperature may also act indirectly on a species' survival and distribution by influencing phenology and dispersal. As temperature affects the rate of egg and larval development, warmer temperatures decrease the chance of predation at this phase in the life cycle. As the duration of the larval stage will determine the length of time they are subject to movement by currents, increased temperature will indirectly affect population connectivity, community structure and regional to global patterns of biodiversity (O'Connor *et al.* 2007). Although coupled physical-biological models have been used to suggest that larval transport can establish the range of marine species regardless of local environmental conditions, such as temperature, (Gaylord and Gaines 2000) care would need to be taken in predicting possible range shifts if establishment in a particular habitat does not result in reproduction.

ii. Salinity

In most fish species, salinity determines key factors of reproduction, such as egg fertilisation, yolk sac reabsorption, early embryogenesis, swim bladder inflation and larval growth, and is also a controller of growth in larger fish (Boeuf and Payan 2001; Mountain and Kane 2010). Climate-induced changes in salinity are hypothesised as becoming increasingly important. Although ground water discharge, projected to increase with increasing precipitation, contributes only 6% of influx to the ocean floors, its salt load is 50% greater than that of rivers. If the increased salt load is not offset by increased water volume, ocean salinity could increase, with projected implications for the thermohaline circulation and formation of dense water (Peterson *et al.* 2002). This increase, and its interaction with temperature, is hypothesised to have important consequences for aquatic ecosystems, with lower and higher relative salinities resulting in higher development and growth rates in marine and freshwater species respectively (Boeuf and Payan 2001) and influencing distribution (Maes *et al.* 1998). Salinity varies with freshwater input, showing both seasonal variation and long-term trends. For example, in Bridgewater Bay, UK, the total number of fish species was found to decline with increasing salinity, with fish distribution also being affected. Conversely, a 2^{o}C increase in average shallow water temperature in Bridgewater Bay, combined with increased river flow, decreasing salinity by 2 ppt, was projected to increase the average number of fish species caught by 6.3 per annum, a 10% increase (Henderson 2007).

As with temperature, preferred ranges and response to change in salinity are highly species specific (Boeuf and Payan 2001). In tilapia (*Oreochromis spilurus*), a salinity change from 0 to 36.6 psu in salt water had no effect on growth when increased progressively over 120 hours (Jonassen *et al.*, 1997). In chum salmon (*Oncorhynchus kata*), however, increasing salinity to 33.5 psu during rearing resulted in increased growth (Kojima *et al.* 1993). Higher growth rates are almost always observed in intermediary saline conditions (brackish water, 8-20 psu) for both freshwater and saltwater species, and are usually correlated with a lower standard metabolic rate. This preference is reflected in the use of coastal waters as nurseries for many fish species. Although the cause of increased growth is unclear, hypotheses for the mechanism of responses include: control of food intake (many species adapting food ingestion to external water salinity) and thus the central nervous system; better food conversion efficiencies and control of hormones, involved in both growth control and osmoregulatory processes (Boeuf and Payan 2001).

However, the effects of salinity change observed in lab experiments have frequently been brought about by changes greater than those observed in nature. Once outside the river plumes of incoming freshwater, the North Sea mostly varies between 33 and 34 psu, with much of the ocean being about 35psu. Upper and lower values are likely to be found in the Mediterranean, which may reach 38 psu, and the Arctic, at around 24.8psu (S. Dye, pers com.). The direct effects of salinity may therefore be negligible in comparison to those of other climatic variables. However, a greater impact may be exerted indirectly or in synergy with variables such as temperature and acidity; although ocean mixing and stratification are predominantly temperature mediated, lower salinities may increase stratification of the water column in areas such as the North Sea (S. Dye pers com.), increasing phytoplankton and zooplankton production (Pershing *et al.* 2005).

iii. Acidification

Ocean acidification describes the change in ocean calcium chemistry and the decrease in pH in response to rising atmospheric CO_2. Over the last 200 years, the oceans have absorbed about 25% of CO_2 released into the atmosphere by human activities (Sabine *et al.* 2004). Following dissociation of CO_2 to H^+ and OH^- ions, this has affected ocean surface pH, the concentration of bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}) ions, reduced the saturation state, and moved the saturation horizons of calcium carbonate ($CaCO_3$) minerals to the ocean surface (shoaling) (Beadman *et al.* 2009). Seawater currently has an average pH of 8.1 (7.8 - 8.2), 0.1 units lower than before the industrial revolution (Caldeira and Wickett 2003). Predictions based on realistic scenarios for future CO_2 emissions suggest that ocean pH will decrease by a further 0.3 - 0.4 units by 2100, and 0.77 units by 2300 (Caldeira and Wickett 2003). The rate of change in oceanic pH this century is therefore likely to be the most rapid experienced by marine organisms for 65 million years (Turley *et al.* 2009). Although effects on marine organisms are varied (Turley *et al.* 2009; Kroeker *et al.* 2010), their magnitude and importance is highlighted by their potential socio-economic impacts. For example, the reduction in growth and calcification caused by a doubling in atmospheric CO_2 has been projected to lead to a 10 - 25% loss in shellfish landings. This equates to a loss of £24.4 – 61 million per year and 1000-3000 job losses (Turley *et al.* 2009).

Ocean acidification is predicted to most significantly impact calcifying organisms, with observations in naturally acidified ecosystems indicating shifts away from calcareous species (Fabricius *et al.* 2011; Kroeker *et al.* 2011), which are impacted both physiologically and by dissolution of their calcium carbonate structures. Susceptibility to dissolution will depend on a structure's mineral form, the ampophous calcite laid down by some species having a greater susceptibility to dissolution than aragonite and calcite (Turley *et al.* 2009). For example, studies have found reduced calcification and increased incidence of shell malformation in the microscopic plants coccolithophores when grown at high CO_2 level (Langer *et al.* 2006; Feng *et al.* 2008; Beadman *et al.* 2009). Future projections of the global aragonite saturation state also indicate that 70% of cold-water corals may experience under-saturation and dissolution of aragonite skeletons, in some areas as early as 2020 (Orr *et al.* 2005; Guinotte *et al.* 2006). This might further cause breakdown of reef structure and habitat loss (Turley *et al.* 2007).

All marine species maintain an internal homeostasis by exchange of ions with the environmental. The influence of CO_2 levels on this process may affect maintenance costs in both calcifies and non-calcifies (Pörtner 2008). Deep sea fish and cephalopods are known to be particularly sensitive to increases in external CO_2 and disruption of their pH homeostasis is predicted to lead to respiratory stress, reduced aerobic capacity and impaired function with reduced oxygen binding (Ishimatsu *et al.* 2004). Studies on sea urchins, which have no impermeable membrane to isolate them from the surrounding water, have shown an inability to compensate for longer-term changes in ocean acidification, or maintain their internal pH balance for longer than 7 days at pH 7.4, resulting in loss of body functions (Miles *et al.* 2007). At CO_2 levels 220 ppm higher than current levels, they exhibited reduced growth rates and survival over several months (Shirayama and Thornton 2005). Brittlestars exhibited muscle wastage at pH 7.7, due to a trade-off to increase calcification rates (Wood *et al.* 2008), and reduced juvenile success, fertilisation, larval growth and development have also been documented with decreasing pH (Dupont *et al.* 2008; Havenhand *et al.* 2008). Conversely, despite being vulnerable at early life stages, crustaceans have been shown to be better able to compensate for changes in pH (Pane and Barry 2007) and organisms such as *Neries* worms are thought to be less vulnerable due to compensation mechanisms developed to cope with periodic drops in pH in their current environment (Widdicombe and Needham 2007).

Acidification may also impact species indirectly, through the food chain, and altered growth rates and thus competitive dynamics in acidified conditions have been shown to drive significant ecosystem shifts (Kroeker *et al.* 2012). Furthermore, acidification may alter various biogeochemical processes and pathways. For example, the performance and distribution of key benthic organisms, such as bioturbating species, which mediate nutrient cycling within the sediment and their supply to the pelagic community may be affected (Wood *et al.* 2008). A change in structure and function of microbial communities may also reduce nitrification (Widdicombe and Needham 2007) and ammonia oxidation rates, causing accumulation of ammonia instead of nitrate. A shelf-ecosystem model has, for example, been used to predict a 20% decrease in pelagic nitrification by 2100 (Blackford and Gilbert 2007). Although large uncertainties exist in future projections, with other studies predicting increases in photosynthesis, nitrogen fixation and growth rates in the nitrogen fixer *Trichodesmium* with increasing CO_2 (Levitan *et al.* 2007), the physiological responses of individual species to acidification could indirectly lead to profound ecosystem changes in an acidified ocean.

Despite the ability of the ocean to buffer CO_2 change and neutralize the increase in H+ ions by calcium carbonate sediments, this process takes tens of thousands of years (Ridgwell and Zeebe 2005; Archer and Brovkin 2008). It may be possible that species will adapt to acidification despite its rapid rate, as is suggested by investigation of responses to the best analogue for current ocean acidification, the Palaeocene-Eocene Thermal Maximum (PETM). The PETM was one of the Palaeogene hyperthermals, a series of events between 58 and 52 million years ago which have left sedimentary records indicative of large carbon inputs associated with a transient temperature rise (Dickens *et al.* 1995). Although these biogeochemical changes were associated with migratory responses in plankton such as foraminifers and coccolithophorids, (Sluijs *et al.* 2007), this adaptive response was not paralleled in the benthic community, which faced extinction dependent on the degree of calcification (Turley *et al.* 2009). As marine organisms normally regulate their internal pH levels at a particular level (e.g. pH 7.4 – 7.9 for haemolymphs) they have evolved a number of mechanisms that allow pH changes to be buffered, thereby preventing damages to internal processes and functioning. However, these have only been observed on short time scales and it is unclear how long such energetically costly mechanisms can last (Turley *et al.* 2009) or their implications on the energy budget and key aspects of population dynamics (Wood *et al.* 2008).

Further to the uncertainty surrounding projected effects of ocean acidification, they will likely be exacerbated by temperature change. Not only are organisms stressed by increasing temperatures less likely to acclimatize, adapt or recovery from lowered pH levels, acidification is exacerbated at higher temperatures, when a greater proportion of water molecules dissociate to H^+ and OH^- ions (Roessig *et al.* 2004). A more intimate link between these two variables was seen in the edible crab *Cancer pagurus,* where a 1% CO_2 increase caused significant reduction in oxygen partial pressure in the haemolymph, as well as a 5°C downwards shift of the upper thermal limits of aerobic scope (Metzger *et al.* 2007).

1.2.2. Indirect Effects

i. Depth

Although direct changes in depth due to climate change are only likely to impact shallow water and coastal species, through sea level rise, a species' distribution is also bounded at certain depths (Close *et al.* 2006; Froese and Pauly 2011). A depth range may be characterised by particular levels of temperature, oxygen concentration, food availability and predation pressure in both freshwater and marine environments (Henderson and Seaby 2005) and changes in these factors may therefore influence distribution. Perry *et al*. (2005), for example, found that most of the 15 species observed to exhibit a shift in latitude between 1978 and 2001 in the North Sea in relation to warming also shifted in depth. Although this result was perhaps unsurprising given that depth in the North Sea is positively correlated with latitude and species may therefore only change depth following a latitudinal shift, a further six species, including plaice (*Pleuronectes platessa*) and cuckoo ray (*Leucoraja naevus*) moved deeper with warming but showed no change in latitude (Perry *et al.* 2005). Further to this, 14 of 19 demersal fish species assemblages in the

North Sea were found to show a significant deepening response over the 25 years from 1980 to 2004 at a rate of about 5.5 m decade $^{-1}$ (range: 0.6 – 14m decade $^{-1}$). Furthermore, while cold-water species deepened faster, warm water species exhibited shallowing over time (Dulvy *et al.* 2008).

If species show morphological and physiological adaptations to living at particular depths (e.g. Helfman *et al*., 1997), their capacity to shift their vertical range might be reduced. An adaptation or preference for certain depths may furthermore only be expressed at particular stages of the life-cycle, such as in perch, who select shallower water for spawning in a trade-off between the positive effects of temperature on development and the negative effects of solar radiation on the eggs (Huff *et al.* 2004). The ecological effects of deepening may therefore be more significant for ecologically or geographically restricted species which are unable to deepen or shift to stay within the preferred temperature range, such as eelpout in the Wadden Sea (Pörtner and Knust 2007) and species in the North Sea, where habitats greater than 80m in depth are restricted to relatively small areas (Dulvy *et al.* 2008).

ii. Ocean Currents and Stratification

Currents are driven by tides, wind in the upper ocean layers and the fluxes of heat, salinity and water density which drive the thermohaline circulation (the deep water (> 200) conveyed in slow, large-scale circulations. With projected increases in stratification and decreased formation of mixed layers, halting convective flow, many global climatic models predict a weakening and possible complete breakdown of the thermohaline circulation, especially in the Atlantic Ocean. Alterations in currents are likely to have important consequences for species dispersal, a key aspect of recruitment success (Drinkwater *et al.* 2010). Altered current patterns may also affect a species' ability to move, through active migrate or passive dispersal, and benefit from the potential fitness advantage conferred by changing water temperature and climate patterns (Drinkwater 2005). The impact of currents on a species' persistence and dispersal may therefore increase with altered environmental suitability; Whereas the first observation of a species in a novel area may be caused by currents or chance invasion and occurrence may therefore not always denote settlement, warming temperatures may increase the likelihood of successful establishment, with particularly important implications for the spread of invasive species. Altered currents may also influence water temperature, for example, through the slowing of the Gulf Stream (Minobe *et al.* 2008).

Although stratification is predicted to increase with warming ocean temperature, (Hegerl and Bindoff 2005), the impact on primary production may be positive or negative depending on the type of biome (Beaugrand 2009). Thus while in sub-polar regions, where strong mixing limits primary production, greater stratification may stimulates primary production, in areas which are permanently stratified (tropical regions), an increase tends to reduce primary production, with variations within seasons also being possible (Beaugrand 2009). Increased stratification in the Pacific may also increase the frequency of El Nino and thus more extreme climatic variation (Roessig *et al.* 2004).

iii. Primary production and Trophic Interactions

It may be argued that the most widespread effects of climate on the dynamics of marine systems are indirect (Walther *et al.* 2002). It may further be debated whether ecosystems and individual populations are controlled by top-down or bottom-up processes; Predators or prey resources exerting more influence on population growth rate respectively (Cury and Pauly 2000). However, as there is globally a greater proportion of fish biomass in regions with high primary productivity, such as sub-Arctic seas and upwelling areas of continental shelves (Hunt. Jr and Mckinnell 2006), the main global pattern of control is likely to be bottom-up, rather than the absence of predators, who are often abundant in the same regions. On a more regional scale, predators might be a major controlling mechanism (Ottersen *et al.* 2010).

Bottom-up control has been indicated in several studies (Henderson 2007; Hjermann *et al.* 2007; Ottersen *et al.* 2010) and supported by both modelled and empirical work (Ware and Thomson 2005; Chassot *et al.* 2010; Blanchard *et al.* 2012). In upwelling systems, for example, fish production appears to be controlled by enrichment, concentration and retention processes, which are in turn governed by climatic factors. As temperature rises should intensify upwellings, global fish production may decrease due to reductions in the concentration and retention processes (Walther *et al.* 2002). Trophic interactions may further influence the response and acclimatisation of higher trophic level species to climatic change through temporal synchrony and trophic coupling (Greve *et al.* 2001; De Young *et al.* 2004). For example, the number of fish caught in Bridgewater Bay, UK, each year was found to increase over a 25 year period, a 2^{o}C increase in inshore seawater temperature corresponding to a 10% increase in total species richness (Henderson 2007). This increase was supported by a corresponding increase in the prey resource, linked to a high North Atlantic Oscillation over this period. The subsequent food-limitation on fish abundance was indicated by a decrease in both species richness and total number in the following years (Henderson 2007).

The survival of fish larvae during the planktonic stage is thought to depend strongly on the availability of sufficient food (Brander *et al.* 2010). Hjort (1914) proposed that the year class strength in marine fish is determined at yolk reabsorption when the first-feeding planktonic larvae have not yet fully developed their foraging abilities and are therefore most vulnerable to starvation. The major prey of first-feeding fish larvae are usually copepod eggs and nauplii, which themselves are often linked to the production of diatoms (Fortier *et al.* 1995). Cushing (1974) subsequently coupled Hjort’s concept of a critical feeding period with a model explaining the movement and duration of the spring and autumn diatom blooms in temperate waters, the critical depth model (Gran and Braarud 1935; Sverdrup 1953), to propose the mismatch hypothesis, highlighting the importance of a spatio-temporal match between consumers and their resources.

The verity of the mismatch hypothesis has been debated, with Bollens *et al.* (1992) arguing that a delay between reproduction of some early spawning species and the peak reproduction of copepods in summer provides evidence that match/mismatch of early larvae to prey is only of secondary importance in determining spawning strategy. In these cases, spawning may be determined by constraints such as small larval predation and optimal feeding during metamorphosis (Bollens *et al.* 1992), and would thus force certain species to produce larvae in regions or time periods of poor feeding conditions (Fortier and Gagné 1990). It may alternatively be the case, however, that these early spawning species are especially vulnerable to match/mismatch of their prey species (Fortier *et al.* 1995) which will more strongly determine year-class strength due to their timing occurring further along the distributional tails of any peak abundance and thus increasing the likelihood of food limitation. Likewise, the timing between occurrence of fish larva and their prey may be especially critical in seasonally ice-covered arctic and sub-arctic seas, where the season of biological productivity is short (Cushing 1975). The proposed impact on year class size of climate-induced alterations in timing of spawning and the resulting trophic mismatch of predators and prey was recently confirmed on the basis of remote satellite sensing and a long-term dataset of haddock recruitment (Platt and Frank 2003).

However, adaptation to climate change may make it difficult to distinguish factors limiting species distributions and thus predict likely responses to change. Although fish show characteristic temperature preference windows, their preference may be modified by environmental factors. Fish with restricted food supplies may be more likely to occur in cooler waters, which result in lower metabolic demands (Moyle and Cech 2004) rather than exhibiting an altered distribution that coincides with maximal prey production. Increasing temperatures may also reduce the maximum attainable size of fish (Cheung *et al.* 2012) and thereby decrease the importance of food limitations on population growth.

It therefore seems difficult to make conclusions on the relative importance of direct versus indirect predictors of fish species distribution. If direct influences are stronger than the indirect ones, climate-induced responses will be independent (Greve *et al.* 2005), enhancing the specificity of species' responses rather than coupled community responses (Beaugrand and Reid 2003; Edwards and Richardson 2004). Dinoflagellates, for example, may respond both physiologically to temperature changes that affect their adult mortality, reproduction, respiration and development, and indirectly, if warming enhances stratified conditions and/or if these conditions appear earlier in the season (Edwards and Richardson 2004). If other species, such as diatoms, are less impacted by temperature-induced changes on physiology than by the variables such as day length and light intensity, their phenology may stay relatively fixed in time (Edwards and Richardson 2004), resulting in trophic mismatch. Therefore although it seems clear that climate induced changes in phenology and production will affect ecosystem functioning, with consequences for fish whose life cycles are synchronized with the seasonal production of their prey, the contribution of this factor on higher trophic level species abundance and distribution at higher trophic levels is harder to elucidate (e.g. Sims *et al*., 2001).

iv. Synergistic Effects

The relative importance of top-down versus bottom up control may be extrapolated to the anthropogenic impacts on the marine environmental, highlighting the importance of distinguishing between the effects of different drivers of change and understanding the linkages and interactions between them. Fishing may directly alter the demographic structure of populations, or act indirectly, for example by damaging breeding grounds (Planque *et al.* 2010). Its combined effect with climate has been proposed as explaining stepwise changes in fish dominance and ecosystem shifts (Beaugrand *et al.* 2003). Thus although the dominant effect of the environment on long-term fluctuations of fish stocks in upwelling systems is generally accepted (Cushing 1982), there is often uncertainty as to the relative influences on shorter term or more localised events. While Hutchings and Myers (1994), for example, used scientific reasoning to show that the northern cod collapsed solely due to overfishing, Rose *et al.* (2000) showed the same event to have a strong environmental component. Furthermore, an apparent range shift of smaller, warm-water tolerant species, for example in the North Sea, may result either from the increased availability of previously inhospitable habitat in winter and spring (Dulvy *et al.* 2008) or from predator release following over-exploitation of their commercially exploited predators (Daan *et al.* 2005). The interaction of fishing with stock reactions to environmental change may thus have implications for predicting future distributions, abundances and formulating management plans. For example, north and south regions of the North Sea may host different abundances of some commercial species due to higher rates of fishing mortality in the south (Dulvy *et al.* 2008), rather than a causal difference in habitat suitability. In this case, predictions based on assessment of environmental suitability by relative abundance may be incorrect.

The most important effects of fishing are proposed as being the depletion of spawning stock biomass and the truncation of the age-size structure of stocks (Hsieh *et al.* 2006). These decrease both the temporal and spatial window of reproduction (Beaugrand 2009) and likely reduce the resilience of a stock to environmental variability (Cury *et al.* 2003). For example, although it has been hypothesized that warming waters will enable cod to move northwards from the North Sea, along the Labrador coast, this projection is dependent on healthy cod stocks to the south. If fishing reduces cod stocks to a minimum, there may be insufficient individuals remaining to drive increased production, expand and thus derive any benefit from increasing temperatures and habitat suitability. The importance of considering the multiple, synergistic effects acting on fish stocks was also highlighted in the case of the North East Atlantic cod. The exploitation rate of this species increased steadily from the 1950s (ICES 2004), prompting concern by ICES from 1969. This concern was, however, dissipated due to the optimism expressed by scientists in 1985 based on several successive years of high survey indices of 5-month old cod (1983 – 1985) (Nakken 1998). However, the failure of expected population increase due to lack of capelin (cod's main food), and resulting high levels of cannibalism and low individual growth led to cod catch at the end of the 1980s being the lowest of record.

The preceding sections have thus shown that there are many physical and biochemical variables involved in translating the effects of global climate change to the marine environment, its communities and populations. Furthermore, there are a variety of ways in which these variables can act, introducing considerable uncertainty into any attempt to predict their possible effects on marine species. Examples and evidence above have shown that there are two ways in which populations and thus communities may change in response to climate (Genner *et al.* 2004). The first of these will depend on the bioclimatic envelope, the climatic space, of a species, which will be directly determined by an individual's physiology, transferring to population or species level changes in abundance and distribution. The second mechanism emphasises interactions, with individual and population level change in survivorship, dispersal, fecundity and behaviour cascading to the community and ecosystem level. The challenge in predicting future species' responses to climate changes therefore seems to be the incorporation of these two areas, and this will be investigated in the following section.

2. Species distribution modelling

The earliest examples of species distribution modelling found in the literature are thought to be the niche-based crop predictions by Henry Nix (Nix *et al.* 1977). A workshop in 1988 and resulting publications (Verner *et al.* 1986; Margules and Austin 1991), prompted an increasing number of species distribution models to be developed, supported and enhanced by concurrent advances in computer and statistic sciences and by the strong theoretical support to predictive ecology as the 'more rigorously scientific, more informative and more useful ecology' (Peters 1991). Since this time, the predictive modelling of species distributions has become recognised as an innovative tool to explore a wide range of questions in ecology, biogeography, evolution, conservation science and climate change research.

Species distribution models (SDMs) are empirical models relating field observations to environmental predictor variables, based on statistically or theoretically derived response surfaces (Guisan and Zimmermann 2000). They thus predict the range of a species as the manifestation of environmental characteristics that limit or support the organism of interest and are based on ecological niche theory. The fundamental ecological niche can be defined as the environmental conditions under which a species can survive and grow Hutchinson (1957), thus defining a species' ecological properties and potentially incorporating all abiotic variables affecting it (Austin *et al.* 1990) but no biotic limiting factors, such as competition for resources. The area within a fundamental niche into which a species is restricted by biotic interactions is described as its realized niche (Austin *et al.* 1990; Guisan and Zimmermann 2000). Thus while the fundamental niche should vary spatially but remain environmentally intact, the realized niche may vary in both geographical and environmental space when subject to the same climatic variation. It has been suggested that limitations to the species distribution modelling procedure are encountered when ecological theory is not fully integrated into the modelling process and that insights from the theory should be used in a more systematic way to underpin decisions made during the modelling process (Guisan and Thuiller 2005; Stewart-Koster *et al.* 2012).

Species Distribution Models can be classified as either static or dynamic. While static models provide time-independent equilibrium predictions as a function of environmental variables, dynamic models predict time-dependent responses to a changing environment (Prentice and Solomon 1991). Within these categories, models can be described as correlative, which bases predictions on correlations between observed distributions and environmental variables, or mechanistic, which aims for a physiological simulation of the mechanism defining a species' range (Pearson and Dawson 2003). As correlative models are based on the premise that the best indicator of a species' environmental requirements is its current distribution, the species' envelope is characterized based on the realized niche. Conversely, models aiming to find a more mechanistic relationship between climatic parameters and species responses aim to identify the fundamental niche by modelling physiologically limiting mechanisms in a species' climatic requirements (Heikkinen *et al.* 2006; Beaumont *et al.* 2008). Models based on mechanistic considerations may therefore be more robust under changed environmental conditions than those based on currently observed correlations, which may not apply in the future. Jiménex-Valerde *et al.* (2008) thus defined realized and potential distributions (corresponding to realized and fundamental niches respectively) to delineate aspects of modelling methodologies, formulating a conceptual framework for model design and selection in ecology and application.

Distinction between niche types therefore implicitly involves distinction between incorporating biotic or abiotic predictors. However, it has been suggested that 'in most ecological gradients, the majority of species appear to find one direction to be physically stressful and the other to be biologically stressful' (Brown *et al.* 1996). This was subsequently demonstrated for a latitudinal gradient by McArthur (1972) and has also been investigated through *in situ* experiments in barnacles (Connell 1961; Wethey 1984) and foxes (Tannerfeldt *et al.* 2002). For example, Connell (1961) found evidence indicating that the upper limits of existence on the intertidal zone by the barnacle *Chthamalus stellatus* resulted from physical factors such as tolerance limits to heat and dessication. Lower limits, however, were principally determined by competition with the barnacle *Balanus balanoides,* which grows faster than *C. stellatus*, eliminating it by smothering, undercutting or crushing its young and thereby limiting distribution on the lower intertidal zone (Connell 1961). Although the extent of interspecific competeition between red and arctic foxes is debated, with evidence often being inconclusive (e.g. Linnell *et al*. 1999), Tannerfeldt *et al.* (2002) focussed on the level of individual territories to show that interspecific interference competition can influence the southern distribution of Artic foxes through their exclusion from breeding sites in low latitude habitat. As higher altitude sites have lower food availability, it has been suggested that this small scale behavioural effect might scale up to have a significant impact at the population level for the smaller arctic fox (Tanerfeldt *et al.* 2002).

However, although including predictor variables representing the presence or absence of known competitors in a model has been shown to significantly improve its predictive abilities (Leathwick and Austin 2001; Anderson *et al.* 2002), the inclusion of other species might also coincide with physical variables that have not been incorporated into or accounted for in the model. The question of whether a significant interaction is critical for inclusion in a model is therefore a debatable one, and one that is related to the question of scale of the study and model design.

2.1. Considerations in Model Design

The choice of methods for species' distribution modelling is extensive and increasing. Methods vary in how they model the distribution of the response, select predictor variables, weight variable contributions, allow for interactions and predict the actual geographic patterns of occurrence (Guisan and Zimmermann 2000; Elith *et al.* 2006). This variation necessarily brings considerable uncertainty into the models and the range of outputs they produce. Methodologies will further be shaped by the type of data required for specific procedures, and that which is obtainable. Model selection should be determined by study objectives, thereby ensuring the ecological theory behind certain techniques, its assumptions and inherent uncertainties are suitable and sufficient to produce realistic and accurate predictions.

2.1.1. Direct or Indirect Variables, Generality or Precision?

To obtain a species distribution prediction, a dataset of species presence or abundance must be related to one or more environmental predictors. These may be divided into those that have a *direct* or *indirect* effect on species distribution or are *resources* (Austin 2007). Whereas direct gradients are environmental parameters, such as temperature and pH, that have physiological importance but are not consumed, resource gradients refer to matter and energy consumed by plants and animals, such as nutrients and light. Indirect gradients may act through a series of steps and have no direct physiological importance to a species' growth or survival, although they correlating well to observed species patterns. Although climatic variables are recognised as being particularly useful in species distribution modelling due to their coinciding with physiological tolerances, results have been improved by addition of topographic features, such as slope and elevation, which may modify how individual organisms experience a particular climatic regime (Parra *et al.* 2004). Elevation would not, however, be suitable for modelling future projections, as elevation-temperature associations break down under climate change.

To characterise a niche mechanistically, a species' distribution should be related to direct, causal predictors. As these factors are often difficult or expensive to measure, they are often sampled from digital maps, such as for elevation-sensitive spatial interpolations of climate station data (Thornton *et al.* 1997). This process may introduce uncertainties through interpolation errors, lack of sufficient station data and the fact that standard climatic stations might not reveal biologically relevant microclimates, decreasing the precision of predictions due to spatial uncertainty. Soil, nutrient and geology maps are even more difficult to derive. Contrasting this, indirect, topographic variables may be used to replace a combination of different resource and direct gradients (Guisan *et al.* 1999) and may be generated with little loss of precision from relatively accurate digital elevation models. As equivalent topographic positions may, however, encompass a different set of direct and resource values in different locations, under the 'law of relative site constancy' (Walter & Walter, 1953, cited in Guisan & Zimmermann, 2000), a model using such predictors is geographically limited and cannot be extrapolated to different geographic areas without incurring substantial error. Conversely, models parameterized with physiological, direct and resource predictors can be applied more generally and are thus applicable to a wider geographic or temporal range, assuming negligible adaptation. The choice of model predictors may therefore involve a trade-off between precision and generality, affecting its applicability for particular uses. Although mechanistic models might involve loss of precision and perhaps accuracy, physiologically based variables are frequently used in broad scale predictions, as topographic variables might lose predictive power at such coarse resolutions.

2.1.2. Scale

Related to the issue of generality and precision is that of scale. The scale of a study and model may be expressed independently as both the *resolution* and the *extent* of a study area; modelling a large area does not necessarily imply a coarse scale. Not only must both these components be explicitly addressed, but the resolution and extent of both species and predictor datasets must also be appropriate and compatible to ensure a model's validity. There may be mismatch between the resolution of sampled species data and that of the environmental predictors, which may be at too large a resolution to be meaningfully related to the occurrence of a particular species (e.g. Guinotte *et al*., 2006). Patterns observed at one scale may also be undetectable at another, both within a study site and over a larger area including the study site (depending on resolution and extent respectively). Van Horne (2002) showed how constraining the extent of a study can result in incorrect interpretation of results if only part of an important environmental gradient is sampled. Sampling must be undertaken throughout a potentially range-limiting predictor gradient to ensure the adequate observation of the response curve (Van Horn 2002).

Pearson & Dawson (2003) proposed a hierarchical model framework, whereby distributions were influenced by increasingly local factors as resolution increased and extent decreased, providing conditions at higher levels in the hierarchy were satisfied. While climate was hypothesised as having a dominant influence on distribution at a continental scale, at more local scales, topography and land-cover types were suggested to become increasingly important given suitable climates (Pearson and Dawson 2003). Predictor variables with inappropriate resolutions but which are potentially influential in determining occurrence may be remediated by techniques of downscaling, interpolation and aggregation.

2.1.3. Complexity or Simplicity?

A trade-off running parallel to that of generality versus precision or specificity concerns model complexity and tractability (Thuiller *et al.* 2008). It has been suggested that certain newly developed techniques are better able to parameterize complex relationships, such as the interactions between predictor variables possible using GBM, MARS-INT and BRUTO (Wisz *et al.* 2008), therefore producing more robust predictions (Elith *et al*., 2006; Tsoar *et al*., 2007). However, although complex models may have greater power, inclusion of more parameters may not make them closer to the truth or improve model accuracy. They are also data hungry and can seldom be used when data is limited (Guisan and Thuiller 2005; Wisz *et al.* 2008).

It has been proposed that complex models are likely to be more accurate at finer resolutions (specificity) and would generalize poorly (Drake *et al.* 2006), whereas simple models will offer useful and parsimonious solutions at a broader scale (generality) (Thuiller *et al.* 2008). This distinction is reflected in the disparity between modelling realized and potential niches, as complex techniques may be more suitable to measure the realized distribution than simple ones, which may better estimate potential distribution (Jiménez-Valverde *et al.* 2008). It may also be argued that interpretation of results from model comparison studies (e.g. Elith *et al*., 2006; Wisz *et al*., 2008) may vary on consideration of methodological and theoretical considerations. Thus, techniques able to establish a more complex fit between dependent and independent variables will over-fit the presence data more strongly, resulting in smaller predicted extents of occurrence than those suggested by simpler techniques. If these techniques are subsequently analysed using presence/absence data, a greater number of the true absences in the validation data are likely to be predicted as absences by complex techniques, leading to the conclusion that complex techniques are more accurate than simpler ones (Jiménez-Valverde *et al.* 2008). Considerations on the appropriateness of models of different complexities must therefore be taken into account when defining SDM objectives and interpreting results (Jiménez-Valverde *et al.* 2008). Although an attempt has recently been made to compromise the trade-offs of precision versus generality and complexity versus simplicity, the resulting hybrid models are data-hungry and require a detailed knowledge of ecological processes that is rarely available for large numbers of species and regions (Thuiller *et al.* 2008).

2.1.4. Number of Variables

The idea of quantity and its impact on quality must therefore be considered in the selection of predictor variables as the addition of environmental predictors may not improve a prediction’s sensitivity or precision (Elith *et al.* 2006). The models DOMAIN and BIOCLIM, for example, have shown a clear effect of the number of input variables, with results becoming less accurate with addition of predictors (Hijmans and Graham 2006). A method that takes into account the number of predictors included may therefore be beneficial. GAM and MAXENT, using variable selection and weightings, have been shown to be less influenced by number of predictors (Hijmans and Graham 2006).

Additional problems may be caused if too many predictors result in novel combinations of variables, and distribution is under-predicted because a variable is outside what is observed in the current climate (Hijmans and Graham 2006), potentially leading to inaccurate forecasts of decreasing range size. This problem might be overcome in methodologies that use both presence and absence/pseudo-absence data in predictions (e.g. GAM, Maxent). Here, some of the 'new' environmental space should be correctly identified as suitable if the conditions are closer to those found for presence observations than those sampled for predicted absences, enabling prediction under novel environmental combinations. This highlights the theoretical and technical considerations required to ensure accurate and meaningful predictions despite differences in available data and modelling technique.

2.1.5. Presence or Presence - Absence Data?

While presence-absence SDMs use presence-absence data to generate statistical functions and discriminative rules, presence-only methods define the environmental envelope around locations where a species has been recorded, which may then be compared to the environmental conditions of the background area. Presence only methods are therefore likely to predict *potential* distributions that more closely resemble the *fundamental* niche of a species, whereas presence-absence data will likely reflect the present natural distribution derived from the *realized* niche. Obtaining valid data confirming a species is absent from a locality is difficult (Gu and Swihart 2004) and frequently unaffordable. The increasing abundance of data recorded without sampling schemes or compiled from museum and herbarium collections, where absences cannot be reliably inferred and datasets contain sampling biases has thus promoted the development of methodologies that can exploit the potential of presence-only data. However, while comparative studies have concluded that no single algorithm can be identified as performing better than all others under all circumstances (Brotons *et al.* 2004), it has been proposed that algorithms able to handle 'true' datasets (eg. GLMs; ANN) perform better and are more reliable and useful than presence-only methods (eg. ENFA; BIOCLIM) (Brotons *et al.* 2004; Martinez-Meyer 2005; Lobo *et al.* 2008). Presence-only methods may also introduce inaccuracies through the interaction of ecological characteristics with species prevalence. For example, fitting presence data obtained from good quality, scarce habitat may bias models if the relative importance of a suitable habitat is over-weighted by many more observations in other habitat types. Inclusion of absence data has been found to be especially useful for modelling wide-ranging, tolerant species (Brotons *et al.* 2004), and GLMs have been found to be more accurate than presence-only ENFA models when species used all optimal habitats with a high probability and sub-optimal habitats with a low probability (Hirzel *et al.* 2002).

The advantages of absences are lost when assumptions are not upheld and their validity is questionable. Presence is a probabilistic function predominantly affected by species abundance and detectability. Failing to detect a species does therefore not confirm its true absence from a cell. The inherent assumption that absence indicates areas where species are not present due to negative species-environmental relationships may also fail to hold due to habitat population dynamics, fragmentation, dispersal or historic distribution (Brotons *et al.* 2004). Despite the greater accuracy of GLMs over ENFA mentioned above, it was also found that ENFA was likely to outperform GLM in scenarios where a species did not occupy all available, suitable habitat (Hirzel 2001). Presence only models are therefore more suitable for constructing models of potential habitat when it would not be appropriate to judge false positive predictors as failures. For example, if absence at a particular locality are caused by factors not included in the model, such as dispersal limitations, biotic interactions or incorrect assessment (Pearson and Dawson 2003; Pearson *et al.* 2007).

However, presence-absence methods have been adapted and improved, using a binomial response and random samples of the study area's background environment as 'non-use' or 'pseudo-absences' (Stockwell and Peters 1999; Zaniewski *et al.* 2002). It then becomes possible to assess how much model predictions differ from random expectations (Boyce *et al.* 2002; Hirzel *et al.* 2002). In a comprehensive comparison of modelling methods by Elith *et al.* (2006), no support was given to presence-only methods that did not attempt to classify a species' distribution relative to its background environmental. Conversely, newer modelling methods that characterize the background environment (such as Maxent) outperformed classical presence only methods (BIOCLIM, LIVES, DOMAIN) as well as regression-based models (GAM, GLM) (Elith *et al.* 2006). Care must be taken, however, in relating absence data to model output, as the kind of absence data used for model calibration condition the characteristics of the species distribution described by model results (Jiménez-Valverde *et al.* 2008). While the realized distribution cannot be characterized without true absence data within a species' environmentally suitable limits, due to biotic factors or dispersal limitations (Lobo 2008), if the aim is to estimate potential distribution, absences should come from environmental conditions known to be unsuitable for the species, avoiding those caused by non-environmental factors (Chefaoui and Lobo 2008).

2.1.6. Sample Size and Extent

A further important consideration in model design is the quantity of data required to make accurate and reliable predictions. Studies have frequently observed decreasing model accuracy and increasing variability in predictive accuracy with decreasing sample size (Kadmon *et al.* 2003; Hernandez *et al.* 2006; Wisz *et al.* 2008). This may be caused by the increasing levels of uncertainty and weight carried by outliers with decreasing sample size and the need for large samples to describe complex relationships among environmental variables. For example, It has been suggested that a sample size of 22 caused models to be descriptive and hypothesis generating only, rather than predictive (Williams and Hero 2001), and that a sample of greater than 250 independent points is required to maximise accuracy (Pearce and Ferrier 2000). However, studies of biodiversity are necessarily frequently based on incomplete data. The technique of environmental niche and species distribution modelling has emerged as a solution to this challenge (Martinez-Meyer 2005).

The efficient use of data in generating a prediction can be split into two components. The first of these describes the rate at which accuracy increases with data efficiency, while the second specifies the maximum accuracy achievable with a model (Stockwell and Peterson 2002; Hernandez *et al.* 2006), with a quick convergence to an asymptote at high accuracy being ideal. When this asymptote is reached will depend on the study areas and the species, the quality and spatial resolution of environmental and species occurrence data and the modelling method itself. The variation in model sensitivity to sample size was highlighted in a significant effect of sample size, algorithm and their interaction being observed on the AUC test statistic, in a comparison of 12 model algorithms (Wisz *et al.* 2008). The algorithms DOMAIN and LIVES, for example, were classed as insensitive to sample size, compared to MARS and BRUTO, which were classed as highly sensitive. Maxent was found to have moderate sensitivity to sample size, although still giving the highest predictive ability at low sample sizes (10) and second highest at sample sizes of 30 and 100 (Wisz *et al.* 2008).

It has been suggested that the number of species sample points is less important than their distribution and overall density, which might be especially influential for widespread species with broad niches (Stockwell and Peterson 2002; Kadmon *et al.* 2003). If distribution in space is biased and observations are clustered in a small part of a species' range, the ecological requirements of a species may be mis-represented. It has, for example, been suggested that Bioclim is unsuitable for use with small sample sizes (Tsoar *et al.* 2007) as it does not extrapolate beyond the bounds of the environmental conditions at known locations of occurrence, the envelope defining conditions therefore expanding with occurrence data (Hernandez *et al.* 2006). Variation in sampling bias for different taxa may also in part explain the variation in predictive ability of models across species (Stockwell and Peterson 2002; Kadmon *et al.* 2003; Ready *et al.* 2010). Sampling bias may be especially significant for marine offshore organisms as in-shore areas are often sampled at a higher rate than offshore areas. It was, for example, proposed that a low ROC-AUC value for John dory, *Zeus faber,* might be caused by the fact that it lives over a greater range than the other species studied, exhibiting sampling bias if data were restricted to a few regions (Ready *et al.* 2010). Modelling inaccuracies may also be introduced if taxonomic uncertainty leads to the inclusion of environments to which different populations (potentially taxa) might be adapted (Ready *et al.* 2010), as in the case of the Pacific sardine, *Sardinops sagax,* which has genetically identified sub-populations in different parts of its distribution (Grant *et al.* 1998).

2.2. Model Assumptions

As both species and environmental data reflect a snap-shot in time and space, SDMs work on the key assumption that the species is in pseudo-equilibrium with its environment (Guisan and Thuiller 2005). If this assumption is not upheld, the observed realized niches used for predictions in a model do not represent a species' environmental tolerance limits. Svenning and Skov (2004) showed that the ratio of realized to potential range size for many European tree species was 50%, with the distribution of many species being strongly controlled by dispersal constraints on post-glacial expansion (Svenning and Skov 2004). A model that closely fit observed distribution would thus underestimate the potential range. However, other modelling studies have supported the hypothesis that continental-scale distributions are principally supported by climate and that many species distributions can be assumed to be in equilibrium with current climate at the macro-scale, although the finer details of distribution may not be identified (Pearson *et al.* 2002). The main criticisms of Species Distribution Modelling stem from the inability to uphold this assumption of equilibrium, due to the following key parameters.

2.2.1. Biotic Interactions

A species' distribution is restricted by environmental limits on survival as well as competition for resources with other species. Not only are the effects of biological interactions difficult to model in a general way, future projections are complicated by the likelihood that, following range shifts, species will encounter interactions currently unobservable in nature. Incorporating indirect impacts of climate change on a species' distribution by factoring in prey species will likely improve model accuracy due to the more responsive nature of lower trophic levels to environmental variation (Ottersen *et al.* 2010), and the fact that many commercially exploited marine species are likely to be more influenced by bottom-up than top-down processes (Henderson 2007; Hjermann *et al.* 2007; Ottersen *et al.* 2010).

2.2.2. Evolutionary Change

Modelling species' distribution shifts under changed environmental conditions incorporates the assumption that adaptation rates will be slower than extinction rates and ecological niches will therefore be conserved. This assumption has been shown to be species dependent, and although some insect species have indicated an evolutionary response to climate change, with enhanced dispersal abilities (Thomas *et al.* 2001), the physiological limitations of others appear unaffected by evolutionary processes over long time scales (Huntley *et al.* 1989). There have also been examples of changes in life history and phenotypic traits of some fish species in response to fishing pressure (Law 2000), although this might have more impact on the actual rate of range shifting in response to environmental change, rather than the magnitude of shift (Cheung *et al.* 2008), causing the temporal aspect of predictions to be conservative. Bioclimatic envelope models are therefore most appropriate for species unable to undergo rapid evolution, such as long-lived species, and those that react slowly to variability, such as arctic and alpine flora (Guisan and Zimmermann 2000).

2.2.3. Species Dispersal

The extent to which a species can occupy a projected range under altered environmental conditions will rely on its ability to disperse or migrate. Persistence in a changing landscape will therefore rely on the rate of appearance and spatial arrangement of habitat patches as well as on the species' capacity for reproduction and dispersal under the altered environmental conditions. Species distribution models frequently assume 'no dispersal' or 'unlimited dispersal' (Thuiller 2004; Thomas *et al.* 2004). They therefore ignore mechanisms driving species demography, assuming that the relationship between observed occurrence and environmental conditions provides a good surrogate for demographic processes. Making an assumption on dispersal could have serious consequences from a management perspective, for example if the rate of change in local conditions outpaces the migration capabilities of species with limited dispersal abilities (Pounds *et al.* 1999). Furthermore, decreasing dispersal abilities, exacerbated by current levels of habitat modification and fragmentation, will reduce predicted potential habitat, exacerbating the disparity between a species' fundamental and realized niche. However, there have been recent advances in coupling bioclimate envelope models with dynamic population models in both terrestrial (Brook *et al.* 2009) and marine environments (Cheung *et al.* 2008).

The simplest method of incorporating dispersal into a model assumes identical dispersal rates (Midgley *et al.* 2006). However, as the migration capacity of a population depends on its individual dynamics, this assumption is seldom likely to hold. Alternatively, migration can be defined through the processes of fecundity, dispersal, recruitment and population growth (Thuiller *et al.* 2008). Dispersal will also change according to environmental suitability and therefore the carrying capacity (K) at each location (Cheung *et al.* 2008; Keith *et al.* 2008). If carrying capacity for each spatial cell of a modelled distribution is determined from the probability of occurrence per species, as defined by environmental predictors, future carrying capacity can be determined by species distribution projections models under future environmental/ climate projections. Combining modelling of carrying capacity with a dynamic population model that measures the change in relative abundance of a species in terms of, for example, its growth, extirpation and age-specific dispersal, then allows location-specific changes in abundance to be determined given constraints on dispersal and growth (Cheung *et al.* 2008; Keith *et al.* 2008). Keith *et al*. (2008) further incorporated density dependence into a species distribution models by using a ceiling model to reduce survival and growth independently for each life stages whenever a population exceeded the carrying capacity of its habitat patch (Keith *et al.* 2008).

With the greater dispersal abilities likely in the marine habitat, the extent of future distributions under alternative climatic scenarios may be dictated to a greater extent by climatic parameters than in the terrestrial environment. This was supported by the finding that the magnitude of predicted distribution range shift for over 1 200 commercially exploited fishes and invertebrate varied little under variation in intrinsic rate of population increase, larval dispersal and settlement (Cheung *et al.* 2008). The *rate* of range shifting may be more sensitive to specific population dynamics such as larval production and dispersal. However, as species distribution models under future climatic scenarios are frequently modelled over long-time scales (e.g. 30 to 100 years) the impact of population dynamics acting at a yearly time scale may have little effect on these predictions. For example, changes in the distribution ranges above were further found to be insensitive to population parameter values (Cheung *et al.* 2008).

2.3. Model Evaluation

The difficulties of model selection may be compounded by model comparison approaches and their perceived shortcomings (Jiménez-valverde and Lobo 2007; Lobo *et al.* 2008). Firstly, the meaningfulness in model comparison using an AUC value or Kappa statistic may be doubted. AUC evaluates how well model predictions discriminate between locations where observations are present and those where they are absent, and is one of the most widely use threshold-independent evaluators of model discriminatory power (Fielding and Bell 1997). AUC values range between 0 and 1, with 0.5 indicating model performance to be equal to that of a random prediction. Interpreting this value, if AUC = 0.7, the predicted value at a location where a species is present will have a predicted suitability value higher than those where the species has not been recorded 70% of the time (Wisz *et al.* 2008). Although it has been suggested that an average test gain greater than 0.75 may be considered useful, an AUC of 0.82 for 6000 presence points may still results in 41 230 pixels being incorrectly described as present (Lobo *et al.* 2008). Kappa statistics, measuring the agreement between observed and predicted distributions, are thought to indicate reliable predictions if equal or less than 0.6 (Elith *et al.* 2006; Tsoar *et al.* 2007). However, this value is still achievable with under- or over- prediction levels of 40% for a species that occupies half of the territory. In the case of a rare species occupying 5% of its territory, a kappa value of 0.6 could mean an over-prediction of 102% (a doubling of its distribution area) or an under-prediction of 44% (nearly half the distribution of the species is not predicted) (Jiménez-Valverde *et al.* 2008). Discrimination between models may therefore be based on the subjective ranges of indices that only measure whether the agreement between predicted and observed distribution is significantly different than expected by chance (Jiménez-Valverde *et al.* 2008). Evaluation of model results would therefore be biased in preference of complex techniques due to their potential to over-fit models to training data. However, AUC values remain useful in determining variation in partitioned datasets, thereby highlighting potential sampling bias in a dataset (Ready *et al.* 2010).

Secondly, evaluation of model performance may be affected by a species' relative occurrence as the probability of including false absences when selected at random increases at small extents. At large extents, random absence data are more likely to be environmentally distant from the presence domain, leading to a low commission error (false positive prediction) (Lobo *et al.* 2008). It has been argued that, as long as presence data are predicted reasonably well, it is easy to obtain high AUC values if evaluation data contain absences selected from a very large area, only part of which is occupied (Wisz *et al*., 2008*).* As widely dispersed, generalist species are present but unsampled in many grid cells, the prior probabilities in present and background sets do not differ substantially, reducing accuracy and causing generalist species to be relatively poorly predicted (Brotons *et al.* 2004, Elith *et al.,* 2006). This was highlighted in the significant relationship found between model performance (AUC) and the spatial extent of a species distribution , tolerance and marginality, which was independent of sample size (for models Bioclim, Domain, GARP and Maxent (Hernandez *et al.,* 2006).

Thirdly, differences between modelling procedures may preclude the value of model comparison. For example, in comparing presence versus absence techniques, whereas a low number of presence points may prevent presence-only evaluators assessing the overall quality of the model, presence-absence methods are still able to rely on the fit between predicted and observed absences. Scarce data would thus cause a presence-only model to be classed as poor by evaluators, whereas one using presence-absence data might obtain an intermediate score. Model choice must take into account the likely biases involved in model evaluation together with desired uses and characteristics of the sample data. In some cases, species distribution models might be better advanced by improvements in the biological occurrence data than by more complex modelling approach (Lobo, 2008).

3. Climate Modelling

Climatic variables such as maximum and minimum temperature and precipitation have been proposed as being particularly informative in species distribution modelling due to their coinciding with a species' physical tolerances (Parra *et al.* 2004). A strong foundation in physical principles and a tested ability to reproduce observed climate has given confidence to the ability of climate models to provide credible quantitative estimates of future climate change, improving the applicability of climatic variables in predicting future distributions. However, this confidence is higher for some variables, such as temperature, than for others, such as precipitation. Incorporation of climate into a model and it projection into the future will contribute sources of uncertainty additional to those surrounding the biology of an organisms and the nature of the modelling process (Beaumont *et al.* 2008).

Although current climatic data may be obtained through observation, data at a fine (≤ 1 km^2) spatial resolution are frequently necessary to capture environmental variability, especially in mountainous areas and others with steep climatic gradients. Interpolation and modelling may therefore be required to obtain a full dataset of current climate, or 'climatic surface' (Hijmans 2005). Not all climate models are equally reliable, and the quality of the surface may also vary spatially, depending on the local climate variability in an area, geographical characteristics, the quality and density of observations and the degree to which a spline can be fitted through them (Hijmans 2005).

3.1. Climate Models

Climate models are numerical models based on equations of physical laws that describe the earth's radiation budget and the dynamics of the atmosphere and ocean. Although simple energy-balance models have been used to simulate the response of the global climate system to increasing greenhouse gas (GHG) concentrations, a hierarchy of models now exists. Coupled Atmosphere Ocean General Circulation Models (AOGCMs) and nested Regional Circulation Models (RCMs) provide the most sophisticated way to make geographically and physically consistent estimates of climate change (Randall *et al.* 2007). Simple climate models (SCMs) are more computationally efficient than their more complex counterparts and have been used to investigate future climate change in response to many GHG emissions scenarios. These models have the benefit that uncertainties can be concatenated, potentially allowing the climate and sea level results to be expressed as probabilistic distributions, something that becomes more difficult with AOGCMS due to computational expense (Randall *et al.,* 2007).

An Atmospheric General Circulation Model (ACGM) may be combined with an Ocean General Circulation Model (OGCM) and those concerning sea ice and evapotranspiration over land to form the basis of full climate models such as HadCM$_3$ and CM2.X. These AOGCMs are designed to produce the best representation of a system's dynamics and their major limitation is caused by high computational costs, which prevent systematic explorations of projection uncertainties and variations both within and amongst climate models. For example, in applying data from climate models to species distribution models, projections of species ranges for 26 bio-energy crops within Europe was found to differ significantly in both magnitude and direction when using four different climatic models (Tuck *et al.* 2006). These variations may be caused by parameterization differences, such as how processes concerning water vapour and ocean mixing may be represented, or by differences in how models incorporate feedback of individual variables and their strengths.

3.2. Downscaling

General Circulation Models provide realistic representations of large-scale climatic variables, with atmospheric and ocean models frequently having horizontal resolutions of 300km and 125-250km and vertical resolutions of 10-30 vertical levels and 200-400m respectively (Beaumont *et al.* 2008). For global assessments, or those with low sub-grid scale variations, the regional information provided by an AOGCM may be sufficient. However, GCMs alone are unable to give good descriptions of local or regional processes (Benestad 2004). For example, the Hadley Centre's HadCM3 model is resolved at a spatial resolution of 2.5° latitude x 3.75° longitude (Fowler *et al.* 2007), whereas many applications by end users occur over much smaller scales. Climate data must therefore be downscaled by Dynamical Downscaling (DD), using a Regional Climate Model (RCM), or by Statistical Downscaling (SD).

Regional Climate Models use the outputs of the GCM to provide the initial conditions and lateral boundaries so that high-resolution RCM simulations can be derived for selected time periods. While the GCM simulates the response of the global circulation to large scale forcing, the RCM accounts for sub-GCM scale forcing (such as complex topographics and land cover heterogeneity) in a physically based way while also enhancing the fine-scale simulation of atmospheric circulation and climate variables. RCMs can typically decrease data predictions to a scale of 10-20km or less (Fowler *et al.* 2007). The skill of an RCM largely depends on the driving GCM and the presence and strength of regional scale forcing (Fowler *et al.* 2007; Beaumont *et al.* 2008). Studies in Europe and New Zealand, where topographic effects on temperature and precipitation are prominent, have therefore reported more skilful downscaling than those in the US Great Plains and China, where regional forcing is weaker (Wang *et al.* 2004). Further limitations include the lack of two-way interactions and feedback between the models and the tendency for RCMs to exhibit internal variability due to non-linear dynamics not associated with boundary forcings. As dynamical downscaling is also computationally expensive, models have frequently been restricted to 'time slices', usually involving a 30 year period from 1961-1990 as a baseline/control period and from 2070-2100 for a changed climate. Pattern scaling has thus been developed to allow assessment of climate for other periods. In this case, changes are scaled according to the temperature signal modelled for the intervening period, assuming a linear pattern of change (IPCC 2010).

Statistical Downscaling methods construct scenarios by adopting empirical relationships that have been calibrated from observations and applied using predictor fields from the GCM (Schmidli *et al.* 2007). They therefore rely on the concept that regional climates can be predominantly determined by a stochastic and/or deterministic function between large-scale atmospheric variables (predictors) and local or regional climate variables (predictands). Regional climate is therefore conditioned in the form R = F(X), where R = the local climate variable being downscaled, X = the set of large-scale climate variables and F = a function which relates the two and which is typically established by training and validating the models using point observations or gridded reanalysis data. The simplest method of statistical downscaling, the 'perturbation' method, involves the application of GCM-scale projections in the form of change factors (CFs) (Fowler *et al.* 2007). Here, the difference between the control run and future GCM simulations are applied to baseline observations by adding or scaling the mean climatic CF to each day. Although this method is easily applicable to several GCMs to produce a range of climatic scenarios, it assumes the spatial pattern of change will remain constant and that GCMs are more able to accurately simulate relative change than absolute values, assuming a constant bias through time (Fowler *et al.* 2007). More sophisticated SD methods included the use of regression models and neural networks, also subject to key assumptions.

Statistical downscaling methods are more straightforward than dynamical downscaling and have frequently been used in sensitivity studies and for rapid assessments of multiple climate change scenarios when RCM outputs are unavailable. However, they have also been viewed as difficult to interpret, fail to include the uncertainties inherent in GCM projections (IPCC 2010) and have been found to underestimate variance and poorly represent extreme events (Fowler *et al.* 2007). Thus while downscaled scenarios based on one GCM or emissions scenario translated into an impact study may give the impression of increased resolution and thus confidence in the projection, alternative downscaling methods may lead to variation in climate scenario projections comparable to differences due to alternate emission scenarios (Haylock *et al*. 2006).

It is therefore being increasingly recognized that a comprehensive, reliable impact study must stem from multiple GCM outputs (IPCC, 2010). Ensemble averaging, involving the averaging of results or weighting of each simulation depending on its skill, may filter out biases of individual models, only retaining errors that are generally pervasive (Randall *et al.,* 2007). Results thus obtained may compare better with the observed climatology than individual models (Giorgi & Mearns, 2002). This technique does, however, come with its own set of uncertainties as the ensemble average may be bias by particularly poor models. High order variability, such as that brought about by extreme events may also be lost and an average may represent a state that does not exist in nature.

3.3. Scenarios of future climate change

Climate scenarios are plausible representations of the future that are consistent with assumptions about future emission of GHGs and other pollutants and with our understanding of the effect of increased atmospheric concentrations of these gases on global climate. They are constructed to determine the impacts of climate change on the environment and resources and may be either based on ‘idealized’ scenarios or on simulations derived by integrating climate models with a particular projection of GHG concentrations, or emissions scenario (Beaumont *et al.* 2008).

‘Idealized’ scenarios denote specified changes in particular climatic variables across a certain area. This may be a 2°C increase in temperature or 5% increase in precipitation. A range of scenarios may be investigated, for example to identify thresholds at which species exhibit vulnerability to climate change and thus their sensitivity (Williams *et al.* 2003). As the change in the climatic predictor is specified, idealized scenarios do not allow the temporal response of a species to be investigated. The method also implies a uniform change in climate variables across the study area (Beaumont *et al.* 2008), and may be more suitable in areas where climate models give poor simulations, such as over steep climatic gradients, or are poorly resolved, such as over islands.

Emissions scenarios are incorporated into climate models by first of all using biogeochemical models to convert estimates of future GHG emissions into changes in GHG concentrations, and then prescribing these concentrations into the future (Beaumont *et al.,* 2008). Changes to the system may be introduced through one of the following methods:

1. The Equilibrium method provides a change in climate following a doubling of carbon dioxide (IPCC, 1990)
2. The Transient method involves the evolution of modelled states (such as temperature, pressure and soil moisture) over time as GHGs gradually increase in the atmosphere. The model is initialized, usually reflecting pre-industrialized conditions around 1850 and two experiments are then run:
    a. A control model, run from 1850 to the present day without any climate forcing terms, assesses the natural variability within the model;
    b. A perturbation experiment, involving re-running the model while changing forcing variables to reflect observed or predicted changes in gases.

While different realizations of a model reflect the uncertainties in the initial state of the model, the relative differences between the realizations and the realizations and the control reflect the impact of variable forcing.

The Equilibrium method, whereby the state of a species may be assessed according to a specified change, suffers similar shortcomings to idealized scenarios (Beaumont *et al.* 2008). Transient models, on the other hand, involve the gradual changing of forcing rather than a sudden change to an alternative state. This may occur in an idealized way, such as a periodic 1% increase in carbon dioxide, or more realistically, using scenarios such as the SRES scenarios developed by the (IPCC 2007a), which describe different demographic, social, technological and environmental developments (Nakicenovic *et al.,* 2000). For example, a study may present a range of outcomes from possible climate change scenarios by modelling both a conservative and an extreme scenario (Beaumont and Hughes 2002; Thuiller *et al.* 2005). However, the variability introduced into a model by climate change scenarios will vary depending on the time frame being studied. For the first few decades of the 21st century, the choice of emissions scenario has little effect on the projected climate (Jenkins and Lowe 2003). Within this time frame, variation in a species distribution model will more likely result from uncertainty in climate models and species' characteristics (Beaumont *et al.* 2008). As the time horizon increases, so too will the variation caused by emission scenario. Therefore although these scenarios allow a range of plausible impacts of future climate change on resources and the environment to be determined, the uncertainty prevalent in the degree of GHG increase may still pose substantial challenges for environmental management and policy making. As studies undertaken in this thesis make predictions up to 2050, they focus on projections made using the SRES A2 scenario. This scenario describes a global mean surface temperature rise of around 1.7–4.4°C during the 21st century, in response to atmospheric carbon dioxide concentrations of about 700 ppm (IPCC 2000). The A2 scenario has been assessed as being the most realistic, in particular in terms of its emission intensity, per capita income and energy intensity (Tol 2005).

4. The Effect of Climate Change on Marine Fisheries in the UK

Commercial fishing is an important socio-economic activity in coastal regions of the UK and Ireland. The fishing sector in the UK directly employ approximately 12 212 people, with some coastal communities having a job dependency of over 20% on this sector. Many commercially important fish species have, however, been over-exploited, and while total landing into the UK peaked at 1.1 million tonnes in 1930, by 2009 they had decreased to 580 tonnes. This fall occurred despite a concurrent fishery expansion and increase in fishing power by an order of magnitude (Englehard 2008) and coincided with changes in the structure of fishery landings and a move in markets towards low trophic level, low prices species (Pinnegar *et al.*, 2002).

Observed and predicted ocean-atmospheric changes are further likely to affect future fish and shellfish production, bringing increasing challenges to maintaining sustainable, long-term fisheries management. As mentioned above, warming has been seen to influence the distribution of species in UK waters (Clarke *et al.*, 2003; Dulvy *et al.*, 2005), and will likely lead to the changes in the productivity and catch potential predicted elsewhere (Cheung *et al.* 2010). Species such as haddock and mackerel have responded to increasing temperatures by moving northwards, leading to the 2010 'mackerel war' between Iceland and the EU, and protests against high Icelandic quotas for mackerel. There is also evidence that warm-water species are moving into UK and Irish waters, opening up new fishing opportunities. UK waters have, for example, seen new or expanding fisheries for sea bass, red mullet, John Dory, anchovy and squid, and fisheries in Ireland are investing in new technologies to more effectively exploit the opportunities offered by boarfish, which is moving into the area (Pinnegar *et al*., 2002).

As fish and seafood are traded globally, the changes in fisheries production resulting from climate change will also impact trade patterns, markets, and access agreements. Greenland is one of a few fisheries expected to benefit significantly as result of climate change (Cheung *et al.* 2009) and the access agreements and imports, in particular to the UK and Ireland, are likely to become increasingly important to markets and consumers. A Fisheries Partnership Agreement has, for example, recently been concluded between the EU community and Greenland for the period 2007-12 which allows vessels from Germany, Denmark, UK, Spain and Portugal to fish in Greenland waters, an agreement that represents an investment of 15.8 million Euros.

The economic consequences of climate change for fisheries may further manifest themselves through changes in the price and value of catches, fishing costs, fisher's incomes, earnings to fishing companies, discount rates and economic rents (ie. The surplus after all costs, including 'normal' profits, have been covered) as well as through the global economy. Furthermore capital costs may be affected if increases in severity and frequency of extreme weather events increases damage and loss of gear, of through necessary adaptation to the quantity, composition and distribution of fisheries resources (Pauly *et al.* 2005). However, many of these costs may be complex and difficult to predict. Several studies have looked at the economic consequences for fishing fleets under increasing fuel costs. Although the contribution of fuel to overall fishery costs vary, they frequently represent a major proportion, reaching up to 60% in case such as the commercial fisheries of Hong Kong (Sumaila *et al.* 2007) and representing 25% of the value of EU live fish and shellfish landings in 2008 (COM, 2006). Further to this, the energy performance of fishing fleets has often declined over time, and may continue to do so, due to the need to search longer and fish deeper in offshore waters as coastal stocks decline (Pauly *et al.* 2002).

Fisheries and aquaculture policy makers must therefore develop strategies and decision making models to adapt to climate change under the uncertainty concerning its direct and indirect impacts, while also accounting for social and economic uncertainty. The overall impacts of CC will thus depend on the changes themselves as well as the vulnerability of a country/ region and the strategies available to a fishing community to adapt to change. Fisheries in low latitude regions such as West Africa have been predicted to be affected most by climate-related shifts in species distributions and catch potential (Cheung *et al.* 2010), a region where this sector is also a vital source of protein and income to impoverished societies with few alternative income sources and low adaptability. Insights from adaptive ecosystem management and new institutional economics suggest that building resilience into human and ecological systems is the optimal way to deal with future surprises and unknowable risks from climate change (Tompkins and Adger 2003). Societies must therefore enhance their response capacity to face the effects of future climates that might lie outside their experienced range, leading to challenges both at the level of natural resource management, as well as that of international agreements and actions.

The UK has been suggested as having a low sensitivity to climate change and a very low vulnerability of its national economy (Allison *et al.* 2009) and can therefore be described as fairly resilient. Despite this estimate, climate change related impacts on marine fishes and invertebrates will lead to both winners and losers in UK and Irish fisheries. Adaptation will involve changing patterns of production and consumption at local levels, while responding to preference patterns in the wider EU and USA (Failler 2007). As the price of fishmeal has grown in conjunction with its use in aquaculture (Merino *et al.* 2010) fish farms will further have to decrease their costs of production, replacing fishmeal with alternative protein sources. Fishing fleets will need to increase in efficiency and reducing their environmental impacts in response to the volatility of fuel prices and taxes aimed at lowering carbon emissions. It may, however, frequently be the case that 'adaptive capacity' is limited and fishers preferentially leave the sector rather than adapt (Tidd *et al.* 2011). Furthermore, although the adaptive capacity of the UK seafood industry and markets is thought to be high, there is concern that those communities with the highest economic and job dependency on fisheries will also be those to feel the physical impacts of climate change most acutely. These communities may already suffer relatively high levels of deprivation and geographic isolation and are likely to experience greater changes in flooding, temperature and precipitation than inland communities, as well as rises in sea level, wave heights and rates of erosion. It is therefore these communities that might face challenges in successful adaptation and have been suggested as a key policy priority in adaptation to climate change (Zsamboky *et al.* 2011).

5. Thesis Background, Aims and Hypotheses

Species distribution models have become important tools to explore the ecological effects of climate change. Evidence and discussion presented above have made it clear that consideration of uncertainties and variation in modelling approaches and data sources must be taken into account in study design and the application of outputs. However, the additional challenges of working in the marine environment, such as a prevalence of scare and unreliable data, has caused the development and application of SDMs, their rigorous testing, evaluation and assessment of their appropriateness to a particular research problem to lag behind that in the terrestrial sphere. For example, when applying species distribution models to address specific research questions, few studies have applied a multi-model approach to assess the effects of future climate change on marine species. Furthermore, in exploring the potential effects of climate change on a natural resource, such as fish stocks, there seems to be a great potential to link ecological, species distribution modelling with socio-economic modelling to explore how the effects of climate change may be translated from one system to another.

This thesis aims to address some of the knowledge gaps mentioned above using the tools of species distribution modelling and cost benefit analysis. A model comparison study will also be undertaken using models designed to ameliorate issues of data quality and quantity common in the marine environment. The robustness of projections will be examined, model performance will be assessed using test statistics and the usability and practical application of the approaches and their outputs will also be considered. Furthermore, the relative uncertainty contributed to model outputs by variations in input data, such as climate models and downscaling methods will be investigated. Bearing these potential uncertainties and variabilities in mind, the suite of modelling approaches will be applied to investigate the impact of climate change on marine species, with a focus on North East Atlantic regions. Specifically, this thesis aims to investigate the potential direct and indirect impacts of climate change on the distributions of threatened and commercially targeted species in the waters around the U.K. and also on the efficacy of Protected Areas. It then aims to bring together species distribution modelling and cost-benefit analysis, attempting to extrapolate some of the issues of climate change and investigate potential effects on the UK fishing industry. As this thesis explores areas of research of direct interest to fisheries managers, policy makers and conservation practitioners, it also aims for a policy-relevant output that might be understood and utilised by the non-modelling community.

Given previous studies and observations, it is hypothesized that species distributions will alter with climate change. Specifically, marine species in the North Sea and North East Atlantic are expected to experience increased environmental suitability in the northern reaches of their ranges, resulting in overall northwards movement. Changes in environmental suitability are also hypothesized to impact the suitability of protected areas for specific species, although whether this will be positive or negative will depend on their location within a species' range and environmental envelope. UK waters are thus likely to become increasingly hospitable for both more southerly distributed, such as Mediterranean, species and particular invasive species. Consequentially, the potential catch of the most common commercially targeted species in the North Sea is also predicted to change, altering the profitability of UK fisheries. However, the range of modelling methodologies, data sources, and post-model processing techniques that will be incorporated into this study are expected to contribute variation and uncertainty to model outputs and conclusions. The relative magnitude of these uncertainties remains unknown and its impact on outputs and questions posed will be an important factor in addressing the above hypotheses and applying the work of this study.

5.1. Thesis structure

The five principal thesis chapters (chapters 2 - 6) are written in the form of peer-reviewed papers. At the time of submission, chapters 2 and 3 were published, and Chapter 5 accepted for publication by *Aquatic Conservation*. Chapter 2 undertakes a model comparison study and provides the technical groundwork and model validation on which subsequent chapters are based. Chapters 3 and 4 focus on applying the models to make future projections and explore potential climate change impacts on marine species. They focus on a set of threatened and commercially targeted species respectively and species specific indicators of change. In addition to this, both chapters investigate the sensitivity of model outputs to specific variations and uncertainties in the modelling procedure. Building on findings in these chapters, Chapter 5 sought to explore how results from multi-model approaches could be presented to enhance understanding in the non-modelling community and make them most useful in a policy context. Finally, Chapter 6 explores how findings presented in previous chapters may impact the fishing industry within UK waters, and possible means of adapting to climate change.

References

Allison, E.H., Perry, A.L., Badjeck, M.-C., Adger, N.W., Brown, K., Conway, D., Halls, A.S., *et al*. (2009) Vulnerability of national economies to the impacts of climate change on fisheries. *Fish and Fisheries* **10**, 173-196.

Anderson, R.P., Gomez-Laverde, M. and Townsend Peterson, A. (2002) Geographical distributions of spiny pocket mice in South America: insights from predictive models. *Global Ecology and Biogeography* **11**, 131-141.

Archer, D. and Brovkin, V. (2008) The millennial atmospheric lifetime of anthropogenic CO2. *Climate Change* **90**, 283-297.

Arvedlund, M. (2009) First records of unusual marine fish distributions—can they predict climate changes? *Journal of the Marine Biological Association of the United Kingdom* **89**, 863-866.

Ashworth, A.C. (1996) The response of arctic Carabidae (Coleoptera) to climate change based on the fossil record of the Quaternary Period. *Ann. Zool. Fennici.* **33**, 125-131.

Austin, M. (2007) Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling* **200**, 1-19.

Austin, M.P., Nicholls, A.O. and Margules, C.R. (1990) Measurement of the realized qualitative niche: environmental niches of five eucalyptus species. *Ecological Monographs* **60**, 161-177.

Bariche, M. and Saad, M. (2009) Settlement of the lessepsian blue-barred parrotfish *Scarus ghobban* (Teleostei: Scaridae) in the eastern Mediterranean. *Marine Biodiversity Records* **1**, 7-9.

Beadman, H., Bond, Z., Campbell, D. and Thorpe, J. (2009) The UK Ocean Acidification Research Programme - Science Plan (2009-2014). *Science* **2300**, 1-19.

Beare, D., Finlay, B., Jones, E., Peach, K., Portilla, E., Greig, T., McKenzie, E., *et al*. (2004) An increase in the abundance of anchovies and sardines in the north-western North Sea since 1995. *Global Change Biology* **10**, 1209-1213.

Beaugrand, G. (2009) Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. *Deep Sea Research Part II: Topical Studies in Oceanography* **56**, 656-673.

Beaugrand, G. (2004) The North Sea regime shift: Evidence, causes, mechanisms and consequences. *Progress In Oceanography* **60**, 245-262.

Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S. and Reid, P.C. (2003) Plankton effect on cod recruitment in the North Sea. *Nature* **426**, 661-664.

Beaugrand, G. and Reid, P.C. (2003) Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology* **9**, 801-817.

Beaumont, L.J. and Hughes, L. (2002) Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. *Global Change Biology* **8**, 954-971.

Beaumont, L.J., Hughes, L. and Pitman, A.J. (2008) Why is the choice of future climate scenarios for species distribution modelling important? *Ecology*, 1135-1146.

Behrenfeld, M.J., O'Malley, R.T.O., Siegel, D.A., Mcclain, C. R., Sarmiento, J. L., Feldman, G. C., Milligan, A. J., *et al.* (2006) Climate-driven trends in contemporary ocean productivity. *Nature* **444**, 752-755.

Benestad, R.E. (2004) Empirical-Statistical Downscaling in Climate Modeling. *Eos, Transactions American Geophysical Union* **85**, 1-3.

Bernal, P.A. (1993) Global climate change in the oceans: a review. In: *Earth System Response to Global Change: Contrast between North and South America.* (eds H.A. Mooney, E.R. Fuentes and B.I. Kronberg). Academic Press, San Diego, CA, pp 1-15.

Bethoux, J.P., Gentili, B., Raunet, J. and Tailliez, D. (1990) Warming trend in the western Mediterranean deep water. *Nature* **347**, 660-662.

Bindoff, N.L. and Church, J.A. (1992) Warming of the water column in the southwest Pacific Ocean. *Nature* **357**, 59-62.

Bjornsson, B. and Steinarsson, A. (2002) The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 494-502.

Blackford, J.C. and Gilbert, F.J. (2007) pH variability and CO2 induced acidification in the North Sea. *Journal of Marine Systems* **64**, 229-241.

Blanchard, J.L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., Holt, J. *et al.* (2012) Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **367**, 2979-89.

Boeuf, G. and Payan, P. (2001) How should salinity influence fish growth? *Comparative biochemistry and physiology. Toxicology & pharmacology : CBP* **130**, 411-23.

Bollens, S.M., Frost, B.W., Schwaninger, H.R., Davis, C.S., Way, K.J. and Landsteiner, M.C. (1992) Seasonal plankton cycles in a temperate fjord and comments on the match-mismatch hypothesis. *Journal of Plankton Research* **14**, 1279-1305.

Botkin, D.B., Saxe, H., Araújo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., *et al*. (2007) Forecasting the effects of global warming on biodiversity. *BioScience* **57**, 227-236.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. and Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling* **157**, 281 - 300.

Bradshaw, W.E. and Holzapfel, C.M. (2006) Evolutionary response to rapid climate change. *Science* **312**, 1477-1478.

Brander, K. (2010) Impacts of climate change on fisheries. *Journal of Marine Systems* **79**, 389-402.

Brander, K.M. (2003) Fisheries and Climate. In: *Marine Science Frontiers For Europe*. (eds G. Wefer, F. Lamy and F. Mantoura). Springer-Verlag, Berlin, Heidelberg, New York, Tokyo, pp 29 - 38.

Brander, K.M. (2007) Global fish production and climate change. *PNAS* **104**, 19709-14.

Brander, K.M. (1995) The effect of temperature on growth of Atlantic cod. *ICES Journal of Marine Science* **52,** 1-10.

Brook, B.W., Akçakaya, H.R., Keith, D.A., Mace, G.M., Pearson, R.G. and Araújo, M.B. (2009) Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. *Biology Letters* **5**, 723-5.

Brook, B.W., Sodhi, N.S. and Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* **23**, 453-60.

Brotons, L., Thuiller, W., Araújo, M.B. and Hirzel, A.H. (2004) Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* **27**, 437-448.

Brown, J.H., Stevens, G.C. and Kaufman, D.M. (1996) The geographic range: Size, shape, boundaries and internal structure. *Annual Review of Ecology, Evolution and Systematics* **27**, 597-623.

Caldeira, K. and Wickett, M.E. (2003) Anthropogenic carbon and ocean pH. *Nature* **425**, 365.

Chassot, E., Bonhommeau, S., Dulvy, N.K., Mélin, F., Watson, R., Gascuel, D. and Le Pape, O. (2010) Global marine primary production constrains fisheries catches. *Ecology Letters* **13**, 495-505.

Chefaoui, R.M. and Lobo, J.M. (2008) Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecological Modelling* **210**, 478-486.

Cheung, W.W.L., Lam, V.W.Y. and Pauly, D. (2008) Modelling present and climate-shifted distributions of marine fishes and invertebrates. *Fisheries Centre Research Report* **16**.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R. and Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* **10**, 235-251.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., Zeller, D. and Pauly, D. (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology* **16**, 24-35.

Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T. L., Lam, V.W.Y., Palomares, D.M.L., Watson, R., *et al*. (2012) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change* **2**, 1-5.

Clarke, R.A., Fox, C.J., Viner, D. and Livermore, M. (2003) North Sea cod and climate change – modelling the effects of temperature on population dynamics. *Global Change Biology*, 1669-1680.

Close, C., Cheung, W., Hodgson, S., Lam, V., Watson, R. and Pauly, D. (2006) Distribution ranges of commercial fishes and invertebrates. *Fisheries Centre Research Report* **14**, 27-37.

COM (2006) Commission of the European Communities. Brussels, 103 final Communication from the commission to the council of the European Parliament on Improving the Economic Situation in the Fishing Industry. Available at: http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=COM:2006:0103:FIN:EN:PDF [Accessed January 4, 2013].

Connell, J.H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecological Society of America* **42**, 710-723.

Cury, P. and Pauly, D. (2000) Patterns and propensities in reproduction and growth of marine fishes. *Ecological Research* **15**, 101-106.

Cury, P., Shannon, L. and Shinm, Y. (2003) The functioning of marine ecosystems: a fisheries perspective. In: *Responsible fisheries in the marine ecosystem*. (eds M. Sinclair and G. Valdimarsson). FAO, Rome, pp 103-123.

Cushing, D.H. (1982) *Climate and Fisheries*. Academic Press, London.

Cushing, D.H. (1975) *Marine Ecology and Fisheries*. Cambridge University Press, Oxford.

Cushing, D.H. (1974) *The Natural Regulation of Fish Populations*. Elek Science, London.

Daan, N., Gislason, A., Pope, J.G. and Rice, J.C. (2005) Changes in the North Sea fish community: evidence of indirect effects of fishing. *ICES Journal of Marine Science* **62**, 177-188.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. and Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *PNAS* **105**, 6668-6672.

Dickens, G.R., O'Neil, J.R., Rea, D.K. and Owen, R.M. (1995) Dissociation of oceanic methane hydrate as a cause of the carbon isotope excursion at the end of the Paleocene. *Peleoceanography* **10**, 965-971.

van Dijk, P., Tesch, C., Hardewig, I. and Pörtner, H. (1999) Physiological disturbances at critically high temperatures: a comparison between stenothermal antarctic and eurythermal temperate eelpouts (Zoarcidae). *The Journal of Experimental Biology* **202**, 3611-21.

Drake, J.M., Randin, C. and Guisan, A. (2006) Modelling ecological niches with support vector machines. *Journal of Applied Ecology* **43**, 424-432.

Drinkwater, K.F. (2005) The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science* **62**, 1327-1337.

Drinkwater, K.F., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., Perry, R.I., Pörtner, H.-O. *et al*. (2010) On the processes linking climate to ecosystem changes. *Journal of Marine Systems* **79**, 374-388.

Dulvy, N.K., Jennings, S., Goodwin, N.B., Grant, A. and Reynolds, J.D. (2005) Comparison of threat and exploitation status in North-East Atlantic marine populations. *Journal of Applied Ecology* **42**, 883-891.

Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmller, V., Dye, S.R. and Skjoldal, H.R. (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology* **45**, 1029-1039.

Dupont, S., Havenhand, J., Thorndyke, W., Peck, L. and Thorndyke, M. (2008) Near-future level of CO2-driven ocean acidification radically affects larval survival and development in the brittlestar *Ophiothrix fragilis*. *Marine Ecology Progress Series* **373**, 285-294.

Edwards, M. and Richardson, A.J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**, 881-4.

Elith, J., Ferrier, S., Guisan, A., Graham, C.H., Anderson, R.P., Hijmans, R.J., Huettmann, F. *et al*. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129-151.

Englehard, G.H. (2008) One hundred and twenty years of change in fishing power of English North Sea trawlers. In: *Advances in Fisheries Science: 50 years on from Beverton and Holt*. (eds A. Payne, J. Cotter and T. Potter). Blackwell Publishing, Oxford, pp 1-25.

Fabricius, K.E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., *et al*. (2011) Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change* **1**, 1-5.

Failler, P. (2007) Future prospects for fish and fishery products. 4. Fish consumption in the European Union in 2015 and 2030. Part 1. European overview. P. FAO Fisheries Circular No. 972/4. 204 pp. Rome.

Feng, Y., Warner, M.E., Zhang, Y., Sun, J., Fu, F.X., Rose, J.M. and Hutchins, D.A. (2008) Interactive effects of increased pCO2, temperature and irradiance on the marine coccolithophore *Emiliania huxleyi* (Prymnesiophyceae). *European Journal of Phycology* **43**, 87-98.

Fielding, A.H. and Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/ absence models. *Environmental Conservation* **24**, 38-49.

Fortier, L. and Gagné, J.A. (1990) Larval herring (*Clupea harengus*) dispersion, growth, and survival in the St. Lawrence estuary: match/mismatch or membership/vagrancy? *Canadian Journal of Fisheries and Aquatic Science* **47**, 1898 - 1912.

Fortier, L., Ponton, D. and Gilbert, M. (1995) The match/mismatch hypothesis and the feeding success of fish larvae in ice-covered southeastern Hudson Bay. *Marine Ecology Progress Series* **120**, 11-27.

Fowler, H.J., Blenkinsop, S. and Tebaldi, C. (2007) Linking climate change modelling to impacts studies: recent advances in downscaling techniques for hydrological modelling. *International Journal of Climatology* **1578**, 1547-1578.

Frederich, M. and Pörtner, H.O. (2000) Oxygen limitation of thermal tolerance defined by cardiac and ventilatory performance in spider crab, *Maja squinado*. *American journal of physiology. Regulatory, integrative and comparative physiology* **279**, R1531-8.

Froese, R. and Pauly, D. (2011) Fishbase. Available at: www.fishbase.org, version (02/2011) [Accessed February 2, 2012].

Fukasawa, M., Freeland, H., Perkin, R., Watanabe, T., Uchida, H. and Nishina, A. (2004) Bottom water warming in the North Pacific Ocean. *Nature* **437**.

Gaylord, B. and Gaines, S. (2000) Temperature or transport? Range limits in marine species mediated solely by flow. *The American Naturalist* **155**, 769-789.

Genner, M.J., Sims, D.W., Wearmouth, V.J., Southall, E.J., Southward, A.J., Henderson, P.A. and Hawkins, S.J. (2004) Regional climatic warming drives long-term community changes of British marine fish*. Proceedings of the Royal Society B.* **271**, 655-61.

Graham, R. and Grimm, E. (1990) Effects of global climate change on the patterns of terrestrial biological communities. *Trends in Ecology & Evolution* **5**, 289-292.

Gran, H. and Braarud, T. (1935) A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine (including observations on hydrography, chemistry and turbidity). *Journal of the Biological Board of Canada* **1**, 279-467.

Grant, W.S., Clark, A.M. and Bowen, B.W. (1998) Why restriction fragment length polymorphism analysis of mitochondrial DNA failed to resolve sardine (Sardinops) biogeography: insights from mitochondrial DNA cytochrome b sequences. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 2539-2547.

Gregg, W.W. (2003) Ocean primary production and climate: Global decadal changes. *Geophysical Research Letters* **30**, 10-13.

Greve, W., Lange, U., Reiners, F. and Nast, J. (2001) Predicting the seasonality of North Sea zooplankton. In: *Burning Issues of North Sea Ecology, Proceedings of the 14th International Senck- enberg Conference North Sea 2000*. (eds I. Kroncke, M. Turkay and J. Sundermann). Senckenbergiana Maritima **31** (2), p 263e268.

Greve, W., Prinage, S., Zidowitz, H., Nast, J. and Reiners, F. (2005) On the phenology of North Sea ichthyoplankton. *ICES Journal of Marine Science* **62**, 1216-1223.

Gu, W. and Swihart, R.K. (2004) Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation* **116**, 195-203.

Guinotte, J., Bartley, J., Iqbal, A., Fautin, D. and Buddemeier, R. (2006) Modeling habitat distribution from organism occurrences and environmental data: case study using anemonefishes and their sea anemone hosts. *Marine Ecology Progress Series* **316**, 269-283.

Guisan, A. and Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**, 993-1009.

Guisan, A., Weiss, S.B. and Weiss, A.D. (1999) GLM versus CCA spatial modeling of plant distribution. *Plant Ecology* **143**, 107-122.

Guisan, A. and Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* **135**, 147-186.

Hannah, L., Midgley, G.F. and Millar, D. (2002) Climate change-integrated conservation strategies. *Global Ecology and Biogeography* **11**, 485-495.

Harborne, A.R. and Mumby, P.J. (2011) Novel ecosystems: altering fish assemblages in warming waters. *Current Biology* **21**, R822-R824.

Harris, A.H. (1993) Wisconsinan pre-pleniglacial biotic change in southeastern New Mexico. *Quaternary Research* **40**, 127 - 133.

Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S. and Samuel, M.D. (2002) Climate warming and disease risks for terrestrial and marine biota. *Science* **296**, 2158-62.

Havenhand, J.N., Buttler, F.R., Thorndyke, M.C. and Williamson, J.E. (2008) Near-future levels of ocean acidification reduce fertilization success in a sea urchin. *Current Biology* **18**, R651-R652.

Hegerl, G.C. and Bindoff, N.L. (2005) Ocean science. Warming the world's oceans. *Science* **309**, 254-5.

Heikkinen, R.K., Luoto, M., Araujo, M.B., Virkkala, R., Thuiller, W. and Sykes, M.T. (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography* **30**, 751-777.

Helfman, F.S., Collette, B.B. and Facey, D.E. (1997) *The Diversity of Fishes*. Blackwell Science, London.

Hemmingsen, A.M. (1960) Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rep. Steno Memorial Hospital Nordisk Insulinlaboratorium* **9**, 1-110.

Henderson, P. (2007) Discrete and continuous change in the fish community of the Bristol Channel in response to climate change. *Journal of the Marine Biological Association of the UK* **87**, 589-598.

Henderson, P.A. and Corps, M. (1997) The role of temperature and cannibalism in interannual recruitment variation of bass in British waters. *Journal of Fish Biology* **50**, 280-295.

Henderson, P.A. and Seaby, R.M. (2005) The role of climate in determining the temporal variation in abundance, recruitment and growth of sole *Solea solea* in the Bristol Channel. *Journal of the Marine Biological Association of the UK* **85**, 197-204.

Hernandez, P.A., Graham, C.H., Master, L.L. and Albert, D.L. (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* **29**, 773-785.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965-1978

Hijmans, R.J. and Graham, C.H. (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* **12**, 2272-2281.

Hirzel, A.H., Helfer, V., Metral, F. (2001) Assessing habitat-suitability models with a virtual species. *Ecological Modelling* **145**, 111-121.

Hirzel, A.H., Hausser, J., Chessel, D. and Perrin, N. (2002) Ecological-niche factor analysis: how to compute habitat suitability maps without absence data. *Ecology* **83**, 2027-2036.

Hjermann, D.Ø., Bogstad, B., Eikeset, A.M., Ottersen, G., Gjøsaeter, H. and Stenseth, N.C. (2007) Food web dynamics affect Northeast Arctic cod recruitment. *Proceedings of the Royal Society B.* **274**, 661-9.

Hjort, J. (1914) Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. *Rapp. P. -V. Reun. Cons. Int. Explor. Mer* **20**, 1-228.

Holt, R.A., Amandi, A., Rohovec, J.S. and Fryer, J.L. (1989) Relation of water temperature to bacterial cold-water disease in coho salmon, chinook salmon, and rainbow trout. *Journal of Aquatic Animal Health* **1**, 94-101.

Van Horn, B. (2002) Approaches to habitat modelling: the tensions between pattern and process and between specificity and generality. In: *Predicting Species Occurrences: Issues of Accuracy and Scale*. (eds J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall and F.B. Samson). Island Press, Covelo, CA, pp 63-72.

Houghton, J.T., Ding, Y., Griggs, D.J., *et al.* (2001) *Climate Change 2001: The Scientific Basis. Contributions to Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.

Hsieh, C.-H., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M. and Sugihara, G. (2006) Fishing elevates variability in the abundance of exploited species. *Nature* **443**, 859-62.

Huff, D.D., Grad, G. and Williamson, C.E. (2004) Environmental constraints on spawning depth of yellow perch: The roles of low temperature and high solar ultraviolet radiation. *Transactions of the American Fisheries Society* **133**, 718-726.

Hunt. Jr, G. and Mckinnell, S. (2006) Interplay between top-down, bottom-up, and wasp-waist control in marine ecosystems. *Progress In Oceanography* **68**, 115-124.

Huntley, B., Bartlein, P.J. and Prentice, I.C. (1989) Climatic control of the distribution and abundance of beech (Fagus L.) in Europe and North America. *Journal of Biogeography* **16**, 551-560.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Habor Symposium on Quantitative Biology* **22**, 415-457.

ICES (2004) Report of the Arctic Fisheries Working Group. ICES CM 2004/ACFM: 28.

IPCC (2007a) *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, USA.

IPCC (2007b) Summary for policymakers. In: *Climate Change 2007: The Physical Science Basis. Working Group 1 Contribution to the Fourth Assessment Report of the IPCC*. (eds S. Solomon, D. Qin, M. Manning, *et al.*). Cambridge University Press, Cambridge, UK and New York, USA.

IPCC (2010) The IPCC Data Distribution Centre. Available at: http://www.ipcc-data.org/index.html [Accessed February 3, 2010].

Ishimatsu, A., Kikkawa, T., Hayashi, M., Lee, K.S. and Kita, J. (2004) Effects of CO2 on marine fish: larvae and adults. *Journal of Oceanography* **60**, 731-741.

Jenkins, G. and Lowe, J. (2003) Handling uncertainties in the UKCIP02 scenarios of climate change. Hadley Centre technical note 44, Met Office, Exeter, UK. pp15

Jiménez-Valverde, A., Lobo, J.M. and Hortal, J. (2008) Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions* **14**, 885-890.

Jiménez-valverde, A. and Lobo, J. (2007) Threshold criteria for conversion of probability of species presence to either–or presence–absence. *Acta Oecologica* **31**, 361-369.

Kadmon, R., Farber, O. and Danin, A. (2003) A systematic analysis of factors affecting the performance of climatic envelope models. *Ecological Applications* **13**, 853-867.

Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J. Regan, H.M., *et al*. (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters.* **4**, 560-563.

King, J. (2005) Report of the study group on fisheries and ecosystem responses to recent regime shifts, PICES Scientific Report 28. 162 pp.

Kojima, I., Iwata, M. and Kurokawa, T. (1993) Development and temporal decrease in seawater adaptability during early growth in chum salmon, *Oncorhynchus keta*. *Aquaculture* **118**, 141 - 150.

Kroeker, K.J., Kordas, R.L., Crim, R.N. and Singh, G.G. (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology Letters* **13**, 1419-1434.

Kroeker, K.J., Micheli, F. and Gambi, M.C. (2012) Ocean acidification causes ecosystem shifts via altered competitive interactions. *Nature Climate Change* **2**, 1-4.

Kroeker, K.J., Michelli, F., Gambi, M.C. and Martz, T.R. (2011) Divergent ecosystem responses within a benthic marine community to ocean acidification. *PNAS* **108**, 14515-14520.

Langer, G., Geisen, M., Baumann, K.-H., Klas, J., Riebesell, U., Thoms, S. and Young, J.R. (2006) Species-specific responses of calcifying algae to changing seawater carbonate chemistry. *Geochemistry Geophysics Geosystems* **7**, Q09006.

Law, R. (2000) Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* **57**, 659-668.

Leathwick, J.R. and Austin, M.P. (2001) Competitive interactions between tree species in New Zealand's old-growth indigenous forests. *Ecology* **82**, 2560-2573.

Levitan, O., Rosenberg, G., Setlik, I., Setlikova, E., Grigel, J., Klepetar, J., Prasil, O., *et al.* (2007) Elevated CO2 enhances nitrogen fixation and growth in the marine cyanobacterium Trichodesmium. *Global Change Biology* **13**, 531-538.

Levitus, S., Antonov, J.I., Boyer, T.P. and Stephens, C. (2000) Warming of the World Ocean. *Science* **287**, 2225-2229.

Linnell, J.D.C., Strand, O. and Landa, O. (1999) Red and arctic foxes in alpine environments. Can interspecific competition explain the non-recovery of Norwegian arctic fox populations? *Wildlife Biology* **5**, 167-176.

Lobo, J.M. (2008) More complex distribution models of more representative data? *Journal of Biogeography* **82**, 14-19.

Lobo, J.M., Jiménez-valverde, A. and Real, R. (2008) AUC: A misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* **17**, 145-151.

Maes, J., Damme, P.A., Taillieu, A. and Ollevier, F. (1998) Fish communities along an oxygen-poor salinity gradient (Zeeschelde Estuary, Belgium). *Journal of Fish Biology* **52**, 534-546.

Margules, C.R. and Austin, M.P. (1991) Nature Conservation: Cost effective biological survey and data analysis. Canberra, Australia.

Martinez-Meyer, E. (2005) Climate change and biodiversity: some considerations in forecasting shifts in species' potential distributions. *Biodiversity Informatics* **2**, 42-55.

McArthur, R.H. (1972) *Patterns in the Distribution of Species*. Harper and Row, New York.

Merino, G., Barange, M., Mullon, C. and Rodwell, L. (2010) Impacts of global environmental change and aquaculture expansion on marine ecosystems. *Global Environmental Change* **20**, 586-596.

Metzger, R., Sartoris, F., Langenbuch, M. and Pörtner, H. (2007) Influence of elevated CO_2 concentrations on thermal tolerance of the edible crab *Cancer pagurus*. *Journal of Thermal Biology* **32**, 144-151.

Midgley, G.F., Hughes, G.O., Thuiller, W. and Rebelo, A.G. (2006) Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. *Biodiversity Research* **12**, 555-562.

Miles, H., Widdicombe, S., Spicer, J.I. and Hall-Spencer, J. (2007) Effects of anthropogenic seawater acidification on acid-base balance in the sea urchin *Psammechinus miliaris*. *Marine pollution bulletin* **54**, 89-96.

Minobe, S., Kuwano-Yoshida, A., Komori, N., Xie, S.-P. and Small, R.J. (2008) Influence of the Gulf Stream on the troposphere. *Nature* **452**, 206-9.

Mountain, D. and Kane, J. (2010) Major changes in the Georges Bank ecosystem, 1980s to the 1990s. *Marine Ecology Progress Series* **398**, 81-91.

Moyle, P.B. and Cech, J.J.J. (2004) *Fishes: An Introduction to Ichthyology*, 5th edn. Prentive Hall, Upper Saddle River, NJ.

Nakken, O. (1998) Past, present and future exploitation and management of marine resources in the Barents Sea and adjacent areas. *Fisheries Research* **37**, 23-35.

Nikinmaa, M. (2002) Oxygen-dependent cellular functions - why fishes and their aquatic environment are a prime choice of study. *Comp. Biochem. Physiol. A* **133**, 1-16.

Nix, H., McMahon, J. and Mackensie, D. (1977) Potential areas of production and the future of pigeon pea and other grain legumes in Australia. In: *The potential for pigeon pea in Australia. Proceedings of Pigeon Pea (Cajanus cajan (L.) Millsp.) Field Day*. (eds E. Wallis and P. Whiteman). University of Queensland, Queensland, Australia.

Orr, J.C., Fabry, V.L., Aumont, O., Bopp, L., Doney, S.C., Freely, R.A., Gnanadesikan, A., *et al.* (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* **437**, 681-686.

Ottersen, G., Kim, S., Huse, G., Polovina, J.J. and Stenseth, N.C. (2010) Major pathways by which climate may force marine fish populations. *Journal of Marine Systems* **79**, 343-360.

Ottersen, G., Stenseth, N.C. and Hurrel, J.W. (2004) Climatic fluctuations and marine systems: a general introduction to the ecological effects. In: *Marine Ecosystems and Climate Variation: The North Atlantic*. (eds N.C. Stenseth, G. Ottersen, J.W. Hurrell and A. Belgrano). Oxford University Press, Oxford, pp 3-14.

O'Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P. and Weiss, J.M. (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *PNAS* **104**, 1266-71.

Pane, E.F. and Barry, J.P. (2007) Extracellular acid–base regulation during short- term hypercapnia is effective in a shallow water crab, but ineffective in a deep- sea crab. *Marine Ecology Progress Series* **334**, 1-9.

Parmesan, C., Root, T.L. and Willig, M.R. (2000) Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meterological Society* **81**, 443-450.

Parmesan, C., Ryrholm, N., Stefanescus, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., *et al*. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**, 579-583.

Parmesan, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37-42.

Parra, J.L., Graham, C.C. and Freile, J.F. (2004) Evaluating alternative data sets for ecological niche models of birds in the Andes. *Ecography* **27**, 350-360.

Parrilla, G., Lavin, A., Bryden, H., Garcia, M. and Millard, R. (1994) Rising temperatures in the subtropical North Atlantic Ocean over the past 35 years. *Nature* **369**, 48-51.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., *et al*. (2002) Towards sustainability in world fisheries. *Nature* **418**, 689-695.

Pauly, D., Watson, R. and Alder, J. (2005) Global trends in world fisheries: impacts on marine ecosystems and food security. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **360**, 5-12.

Pearce, J. and Ferrier, S. (2000) An evaluation of alternative algorithms for fitting species distribution models using logistic regression. *Ecological Modelling* **128**, 127-147.

Pearson, R., Dawson, T.P., Berry, P.M. and Harrison, P.A. (2002) SPECIES: A Spatial Evaluation of Climate Impact on the Envelope of Species. *Ecological Modelling* **154**, 289-300.

Pearson, R.G. and Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful. *Global Ecology and Biogeography* **12**, 361-371.

Pearson, R.G., Raxworthy, C.J., Nakamura, M. and Townsend Peterson, A. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* **34**, 102-117.

Peperzak, L. (2003) Climate change and harmful algal blooms in the North Sea. *Acta Oecologica* **24**, S139-S144.

Perry, A.L., Low, P.J., Ellis, J.R. and Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. *Science* **308**, 1912-5.

Pershing, A.J., Greene, G.H., Jossi, J.W., O'Brian, L., Brodziak, J.K.T. and Bailey, B.A. (2005) Interdecadal variability in the Gulf of Maine zooplankton community, with potential impacts on fish recruitment. *ICES Journal of Marine Science* **62**, 1511 - 1523.

Peters, R.H. (1991) *A Critique for Ecology*. Cambridge University Press, Cambridge.

Pinnegar, J.K., Jennings, S., Brien, C.M.O. and Polunin, N.V.C. (2002) Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *Journal of Applied Ecology*, 377-390.

Pinnegar, J.K., Stelzenm, V., Van Der Kooij, J., Engelhard, G.H., Garrick-Maidment, N. and Righton, D.A. (2008) Occurrence of the short-snouted seahorse *Hippocampus hippocampus* in the central North Sea by. *Cybium* **32**, 343-346.

Planque, B., Fromentin, J.-M., Cury, P., Drinkwater, K.F., Jennings, S., Perry, R.I. and Kifani, S. (2010) How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems* **79**, 403-417.

Platt, T. and Frank, K.T. (2003) Spring algal bloom and larval fish survival. *Nature* **423**, 398-399.

Pörtner, H. (2001) Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Continental Shelf Research* **21**, 1975-1997.

Pörtner, H. (2008) Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. *Marine Ecology Progress Series* **373**, 203 - 217.

Pörtner, H.O., Van Dijk, P.L.M., Hardewig, I. and Sommer, A. (2000) Levels of metabolic cold adaptation: Tradeoffs in eurythermal and stenothermal ectotherms. In: *Antarctic Ecosystems: models for wider ecological understanding.* (eds W. Davison and P.B. Howard-Williams). Caxton Press, Christchurch, New Zealand, pp 109 - 122.

Pörtner, H.O. and Knust, R. (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**, 95-97.

Pounds, J.A., Fogden, M.P.L. and Campbell, J.H. (1999) Biological response to climate change on a tropical mountain. *Nature* **398**, 611-615.

Prentice, I.C. and Solomon, A.M. (1991) Vegetation models and global change. In: *Global Change of the Past*. (ed R.S. Bradley). UCAR/ Office for Interdisciplinary Earth Studies, Boulde, CO, pp 365-383.

Randall, D.A., Wood, R.A., Bony, S., Bony, S., Colman, R., Fichefet, T., Fyfe, J., *et al*. (2007) Climate models and their evaluation. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* (eds D.Q.S. Solomon, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller). Cambridge University Press, Cambridge, UK and New York, USA, pp 385-432.

Ready, J., Kaschner, K., South, A.B., Eastwood, P.D., Rees, T., Rius, J., Agbayani, E., *et al*. (2010) Predicting the distributions of marine organisms at the global scale. *Ecological Modelling* **221**, 467-478.

Ridgwell, A. and Zeebe, R.E. (2005) The role of the global carbonate cycle in the regulation and evolution of the Earth system. *Earth and Planetary Science Letters* **234**, 299-315.

Roessig, J.M., Woodley, C.M., Cech, J.J. and Hansen, L.J. (2004) Effects of global climate change on marine and estuarine fishes and fisheries. *Reviews in Fish Biology and Fisheries* **14**, 251-275.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweigk, C. and Pounds, A.J. (2003) Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57-60.

Rose, G. (2005) On distributional responses of North Atlantic fish to climate change. *ICES Journal of Marine Science* **62**, 1360-1374.

Sabine, C., Feely, R., Gruber, N., Key, R.M., Lee, K., Bullister, J.L., Wanninkhof, R., *et al*. (2004) The oceanic sink for anthropgenic CO_2. *Science* **305**, 367-371.

Sarmiento, J.L., Slater, R., Barber, R., Bopp, L., Doney, S.C., Hirst, A.C., Kleypas, J., *et al*. (2005) Response of ocean ecosystems to climate warming. *Global Biogeochemical Cycles* **18**, 1-23.

Schmidli, J., Goodess, C., Frei, C., Haylock, M., Hundecha, Y. and Ribalaygua, J. (2007) Statistical and dynamical downscaling of precipitation: an evaluation and comparison of scenarios for the European Alps. *J. Geophys. Res., 112, D04105.1-D04105.20*.

Schneider, S.H. and Root, T.L. (1998) Impacts of climate change on biological resources. In: *Status and Trends of the Nations Biological Resources, vol 1*. (eds M.J. Mac, P.A. Opler, C.E. Puckett, P. Haecker and P.D. Doran). US Geological Survey, Reston, Virginia, pp 89-116.

Scott, G.R. and Johnston, I.A. (2012) Temperature during embryonic development has persistent effects on thermal acclimation capacity in zebrafish. *PNAS* **109,** 14247-14252.

Shelford, V.E. (1931) Some concepts of bioecology. *Ecology* **12**, 455-467.

Shirayama, Y. and Thornton, H. (2005) Effect of increased atmospheric CO2 on shallow water marine benthos. *Journal of Geophysical Research* **110**, C09S08.

Simpson, S.D., Jennings, S., Johnson, M.P., Blanchard, J.L., Schön, P.-J., Sims, D.W. and Genner, M.J. (2011) Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Current Biology* **21**, 1565-1570.

Sims, D.W., Genner, M.J., Southward, a J. and Hawkins, S.J. (2001) Timing of squid migration reflects North Atlantic climate variability. *Proceedings of the Royal Society B.* **268**, 2607-11.

Sluijs, A., Bowen, G.J., Brinkhuis, H., Lourens, L.J. and Thomas, E. (2007) The Palaeocene-Eocene Thermal Maximum super greenhouse: biotic and geochemical signatures, age models and mechanisms of global change. In: *Deep time perspectives on climate change - marrying the signal from computer models and biological proxies, TMS Special Publication 2*. (eds M. Williams, A.M. Haywood, F.J. Gregory and D.N. Schmidt). The Geological Society of London, London.

Snickars, M., Sundblad, G., Sandström, A., Ljunggren, L., Bergström, U., Johansson, G. and Mattila, J. (2010) Habitat selectivity of substrate-spawning fish: modelling requirements for the Eurasian perch *Perca fluviatilis*. *Marine Ecology Progress Series* **398**, 235-243.

Southward, A.J., Hawkins, S.J. and Burrows, M.T. (1995) Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology* **20**, 127-155.

Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B. and Osman, R.W. (2002) Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *PNAS* **99**, 15497-500.

Stebbing, A.R.D., Turk, S.M.T., Wheeler, A. and Clarke, K.R. (2002) Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960-2001). *Journal of the Marine Biological Association of the United Kingdom* **82**, 177-180.

Stewart-Koster, B., Boone, E.L., Kennard, M.J., Sheldon, F., Bunn, S.E. and Olden, J.D. (2012) Incorporating ecological principles into statistical models for the prediction of species' distribution and abundance. *Ecography* **35**, 1-12.

Stockwell, D. and Peters, D. (1999) The GARP modelling system : problems and solutions to automated. *International Journal of Geographical Science* **13**, 143-158.

Stockwell, D.R. and Peterson, A.T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling* **148**, 1-13.

Sumaila, U.R., Cheung, W.W.L. and Teh, L. (2007) Rebuilding Hong Kong's marine fisheries: an evaluation of management option. Fisheries Centre Research Reports, 15 (3). 112 pp. Vancouver.

Svenning, J.-C. and Skov, F. (2004) Limited filling of the potential range in European tree species. *Ecology Letters* **7**, 565-573.

Sverdrup, H.U. (1953) On conditions for the vernal blooming of phytoplankton. *J. Cons. Int. Explor. Mer* **11**, 287-295.

Tannerfeldtm, M., Elmhagen, B. and Angerbjörn, A. (2002) Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia* **132**, 213-220.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. and Conradt, L. (2001) Ecological and evolutionary processes at expanding range margins. *Nature* **411**, 577-581.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., *et al.* (2004) Extinction risk from climate change. *Nature* **427**, 145-8.

Thornton, P., Running, S. and White, M. (1997) Generating surfaces of daily meteorological variables over large regions of complex terrain. *Journal of Hydrology* **190**, 214-251.

Thuiller, W. (2004) Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology* **10**, 2220-2227.

Thuiller, W., Albert, C., Araujo, M., Berry, P., Cabeza, M., Guisan, A., Hickler, T., *et al*. (2008) Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics* **9**, 137-152.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. and Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *PNAS* **102**, 8245-50.

Tidd, A.N., Hutton, T., Kell, L.T. and Padda, G. (2011) Exit and entry of fishing vessels: an evaluation of factors affecting investment decisions in the North Sea English beam trawl fleet. *ICES Journal of Marine Science* **68**, 961-971.

Tingley, M.W., Monahan, W.B., Beissinger, S.R. and Moritz, C. (2009) Birds track their Grinnellian niche through a century of climate change. *PNAS* **106** Suppl , 19637-43.

Tol, R.S.J (2005) Memorandum by Professor Richard S J Tol. House of Lords Economic Affairs Committee Publications, Session 2004-05. Available at: www.publications.parliament.uk/pa/ld200506/ldselect/ldeconaf/12/5020101.htm [Accessed April 7, 2013[]

Tompkins, E.L. and Adger, W.N. (2003) adaptive management of natural resources Building resilience to climate change through adaptive management of natural resources. Tyndall Centre Working Paper No. 27. UEA, Norwich.

Tsoar, A., Allouche, O., Steinitz, O., Rotem, D. and Kadmon, R. (2007) A comparative evaluation of presence-only methods for modelling species distribution. *Diversity and Distributions* **13**, 397-405.

Tuck, G., Glendining, M.J., Smith, P., House, J.I. and Wattenbach, M. (2006) The potential distribution of bioenergy crops in Europe under present and future climate. *Biomass and Bioenergy* **30**, 183-197.

Turley, C., Findlay, H.S., Mangi, S., Ridgwell, A. and Schmidt, D.N. (2009) MCCIP Ocean Acidification Review.

Turley, C.M., Roberts, J.M. and Guinotte, J.M. (2007) Corals in deep-water: Will the unseen hand of ocean acidification destroy cold-water ecosystems? *Coral Reefs* **26**, 445-448.

VanDerWal, J., Murphy, H.T., Kutt, A.S., Perkins, G.C., Bateman, B.L., Perry, J.J. and Reside, A.E. (2012) Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change* **2**, 1-5.

Verner, J., Morrison, M. and Ralph, C. (1986) *Wildlife 2000: Modelling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press, Madison, WI.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesank, C., Beebee, T.J.C., Fromentin, J.-M., *et al*. (2002) Ecological responses to recent climate change. *Nature* **416**, 389-95.

Wang, Y., Leung, L.R., McGregor, J.L., Lee, D.K., Wang, W.C., Ding, Y. and Kimura, F. (2004) Regional climate modeling: progress, challenges, and prospects. *Journal of the Meteorological Society of Japan* **82**, 1599-1628.

Ware, D.M. and Thomson, R.E. (2005) Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science* **308**, 1280-1284.

Wethey, D.S. (1984) Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus*: A field experiment. *The Biological Bulletin* **167**, 176-185.

White, C.R., Phillips, N.F. and Seymour, R.S. (2006) The scaling and temperature dependence of vertebrate metabolism. *Biology Letters* **2**, 125-7.

Widdicombe, S. and Needham, H.R. (2007) Impact of CO2 induced seawater acidification on the burrowing activity of *Nereis virens* and sediment nutrient flux. *Marine Ecology Progress Series* **341**, 111-112.

Williams, E.S., Bolitho, E.E. and Fox, S. (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. . *Proc. R. Soc. B.* **270**, 1887-1892.

Williams, S.E. and Hero, J.M. (2001) Multiple determinants of Australian tropical frog biodiversity. *Biological Conservation* **98**, 1-10.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A. T., Graham, C.H. and Guisan, A. (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions* **14**, 763-773.

Wood, H.L., Spicer, J.L. and Widdicombe, S. (2008) Ocean acidification may increase calcification rates, but at a cost. *Proceedings of the Royal Society B.* **275**, 1767-1773.

De Young, B., Harris, R., Alheit, J., Beaugrand, G., Mantua, N. and Shannon, L. (2004) Detecting regime shifts in the ocean: Data considerations. *Progress in Oceanography* **60**, 143-164.

Zaniewski, A.E., Lehmann, A. and Overton, J.M.C. (2002) Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling* **157**, 261-280.

Zsamboky, M., Fernández-Bilbao, A., Smith, D., Knight, J. and Allan, J. (2011) Impacts of climate change on disadvantaged UK coastal communities. http://www.jrf.org.uk/sites/files/jrf/disadvantage-communities-climate-change-full.pdf

Chapter 2

Modelling Commercial Fish Distributions: Predictions and Assessment Using Different Approaches

Published as:

Jones, M.C., Dye, S.R., Pinnegar, J.K., Warren, R., and Cheung, W.W.L. (2012) Modelling commercial fish distributions: Prediction and assessment using different approaches. *Ecological Modelling* **225**, 133-145.

Abstract

Species distribution models are important tools to explore the effects of future global change on biodiversity. Specifically, AquaMaps, Maxent and the *Sea Around Us* project algorithm are three approaches that have been applied to predict distributions of marine fishes and invertebrates. They were designed to cope with issues of data quality and quantity common in species distribution modelling, and especially pertinent to the marine environment. However, the characteristics of model projections for marine species from these different approaches have rarely been compared. Such comparisons provide information about the robustness and uncertainty of the projections, and are thus important for spatial planning and developing management and conservation strategies. Here I apply the three commonly used species distribution modelling methods for commercial fish in the North Sea and North Atlantic, with the aim of drawing comparisons between the approaches. The effect of different assumptions within each approach on the predicted current relative environmental suitability was assessed. Predicted current distributions were tested following data partitioning and selection of pseudoabsences from within a specified distance of occurrence data. As indicated by the test statistics, each modelling method produced plausible predictions of relative environmental suitability for each species, with subsequent incorporation of expert knowledge generally improving predictions. However, because of the differences between modelling algorithms, methodologies and patterns of relative suitability, comparing models using test statistics and selecting a 'best' model are not recommended. I propose that a multi-model approach should be preferred and a suite of possible predictions considered if biases due to uncertainty in data and model formulation are to be minimised.

1. Introduction

Many pressures are currently affecting the marine environment and driving change in species composition and distribution. Fisheries are removing fishes at a rate considered to be unsustainable (Pauly *et al.* 2002), while essential habitat is being damaged or destroyed, for example through sand and gravel extraction, or chemically altered through release of endocrine-disrupting substances. Furthermore, concern over the impact of climate change on marine ecosystems is increasing (Root *et al.* 2003), with longer-term shifts in mean environmental conditions and climatic variability moving outside the bounds within which adaptations in marine communities have previously been associated

(Beaugrand 2004; King 2005). The altered abundances and novel distributions resulting from these ocean-atmospheric changes (Southward *et al.* 1995; Stebbing *et al.* 2002; Perry *et al.* 2005; Beaugrand 2009) may severely change the biological and environmental functioning of ecosystems or food webs, the goods and services derived from them, and conservation and resource management.

Species distribution modelling is widely used to study and predict the ecological effects of climate change (Beaumont and Hughes 2002; Pearson and Dawson 2003; Hijmans and Graham 2006; Thuiller *et al.* 2008; Cheung *et al.* 2009). It uses statistically or theoretically derived response surfaces to relate observations of species occurrence or known tolerance limits to environmental predictor variables (Guisan and Zimmermann 2000), thereby predicting a species' range as the manifestation of environmental characteristics that limit or support its existence at a particular location. It is thus grounded in ecological niche theory. The environmental conditions under which a species can survive and grow and which therefore define the ecological properties of a species are described as the fundamental ecological niche (Hutchinson 1957) or a species' potential distribution. The area within a fundamental niche into which a species is restricted due to the effects of competition and other biotic interactions is described as its realized niche (Austin *et al.* 1990; Guisan and Zimmermann 2000), or distribution. To make use of the diversity of available data, a wide range of species distribution models (SDMs) have been proposed [see Guisan and Thuiller (2005) and Franklin (2009) for an overview], approaches varying widely in data requirements, mechanisms used and model performance (Guisan and Zimmermann 2000; Elith *et al.* 2006; Austin 2007; Wisz *et al.* 2008). The extent to which models are able to capture a species' realized or fundamental niche may thus vary depending on the modelling approach or data requirements.

When choosing and applying an SDM, it is therefore important to understand its performance, assumptions, characteristics and uncertainties, as well as how these might be affected by data availability and quality. Ideally, an SDM is developed from the relationship between direct or indirect environmental predictors and datasets of species presence and absence obtained by targeted surveys. Comprehensive data are, however, seldom available and instead frequently represent a restricted, patchy or biased view of species' distributions, leading to problems when data-driven modelling techniques are used to generate distribution predictions. Furthermore, it has been suggested that presence-absence data attribute superior performance, for example as measured by test statistics, to an SDM and thus a more reliable prediction (Hirzel 2001; Brotons *et al.* 2004;

Martinez-Meyer 2005; Lobo *et al.* 2008). This would not be the case, however, if absence at a particular location is caused by factors not included in the model, such as dispersal limitations, biotic interactions or incorrect assessment (Pearson and Dawson 2003; Pearson *et al.* 2007). Distributions predicted from recorded species' occurrence (presence) only may thus be more suitable for constructing models of potential environmental suitability. Several studies show that SDM model accuracy decreases and variability in predictive accuracy increases with decreasing size of the species occurrence dataset (Stockwell and Peterson 2002; Kadmon *et al.* 2003; Hernandez *et al.* 2006; Wisz *et al.* 2008). These issues of data paucity and quality are especially pertinent in the marine environment (Macleod *et al.* 2005; Kaschner *et al.* 2006).

Model complexity is another important factor affecting the performance of SDMs. Complex models are suggested to be more effective (Elith *et al.* 2006; Tsoar *et al.* 2007; Wisz *et al.* 2008) and more accurate at finer resolutions (Kimmins *et al.* 2008). However, including more parameters or fitting complex response curves may result in a model that generalizes poorly (Drake *et al.* 2006), becoming less applicable to areas at a broader scale. Greater complexity also often reduces model transparency, which is important for the effective testing and reviewing of model outputs and soliciting additional information to improve model predictions. The complexity and transparency of a selected model may therefore depend not only on its perceived robustness but also on the specific application and the community by which it is being implemented.

Maxent, AquaMaps and the *Sea Around Us* Project model are three approaches commonly used to model distributions of marine fishes and invertebrates (Close *et al.* 2006; Kaschner *et al.* 2006; Bigg *et al.* 2008; Cheung *et al.* 2009; Ready *et al.* 2010). The Maxent software package (Phillips *et al.* 2006; Phillips and Dudik 2008) was designed to overcome the problems of small sample sizes in presence-only datasets (Pearson 2007). The AquaMaps procedure, based on a Relative Suitability Model (Kaschner *et al.* 2006) and the *Sea Around Us* Project model were also designed to overcome the lack of data and knowledge for many marine species. Generative modelling approaches, such as Maxent, may, however, be more vulnerable to biases from the skewed distribution of sampling effort present in many 'opportunistically' collected datasets, especially those with limited data-points. In these instances, discriminative methods (defined here as distribution models which restrict a species distribution, from a potential extent that encompasses the entire study area, based on a set of filters determined by known parameters, environmental or habitat preferences), such that developed by the *Sea Around Us* Project (Close *et al.* 2006), might produce the more valid results. The incorporation of 'expert information' may also overcome this problem (Ready *et al.* 2010). Expert information may be defined as "habitat use information that is not directly available as raw data; published information about habitat use or preference that is based on quantitative investigations of species occurrence in relation to environmental knowledge" (Ready *et al.* 2010). It may be incorporated into a modelling procedure in various forms of knowledge such as species' behaviour, known depth range or geographic limits.

This study aims to assess the abilities of three statistical modelling approaches, representing a spectrum of theoretical frameworks and data-requirements, to predict current distributions of a range of marine species. Mentioned above, these are the correlative, presence-only modelling approaches Maxent (Phillips *et al.* 2004; http://www.cs.princeton.edu/~schapire/maxent) and AquaMaps (Kaschner *et al.*; Ready *et al.* 2010 http://www.aquamaps.org), and the discriminative approach developed for the *Sea Around Us* project (Close *et al.* 2006; http://www.seaaroundus.org). The comparison not only focuses on the perceived value of a modelling procedure as indicated by test statistics, but also considers the usability and practical application of the approaches and their results.

2. Methods

2.1. Model Construction

2.1.1. Maxent

Maxent (Phillips *et al.* 2004) uses a generative approach (Phillips *et al.* 2006) to estimate the environmental co-variates conditioning species presence and bases the final prediction on the principle of maximum entropy. This specifies that the best approximation of an unknown distribution is the probability distribution with maximum entropy, subject to the constraints imposed by the sample of species presence observations (Phillips *et al.* 2006). Maxent has been shown to compete well with alternative approaches (Phillips *et al.* 2006; Pearson 2007), perform better than classical presence-only methods (Elith *et al.* 2006) and perform well with small sample sizes (Pearson *et al.* 2007). Models were constructed using Maxent version (3.3.3e) with default parameters for a random seed, regularization parameter (1, included to reduce over-fitting), maximum iterations (500), convergence threshold (0.00001) and maximum number of background points (10000 points which have not been recorded as present). Selection of environmental features and their relative contribution to each iteration of the model was also carried out automatically.

2.1.2. AquaMaps

The AquaMaps approach to modelling species' distributions was based on a global distribution tool for marine mammals (Kaschner *et al.* 2006), and has now been applied to a large number of marine fishes (see FishBase (Froese and Pauly 2011). AquaMaps uses simple, numerical descriptors of species relationships with environmental variables to predict distributions from publically available, global occurrence databases. This methodology does not allow complex, non-linear interactions to be fit between predictors, but aims for transparency and understanding in the wider, non-modelling, community while also explicitly promoting incorporation of expert judgement.

Predicted current distributions are generated multiplicatively from a suite of 'environmental envelopes' over each cell in a study area. This produces a cell value between 0 and 1, representing the relative suitability of that cell for the specified species. The relationship between species occurrence and environmental limits is specified by a trapezoidal distribution (Fig. 2.1.).

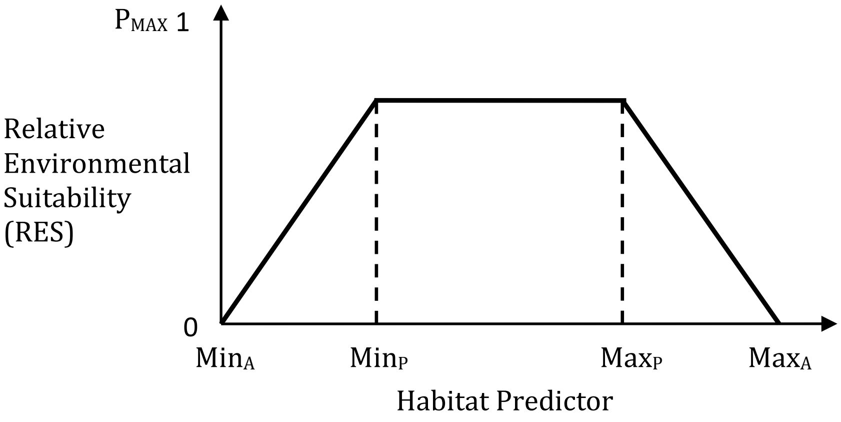


***Figure 2.1**. Trapezoidal species' response curve, showing absolute minimum (Min_A) and maximum (Max_A) and preferred minimum (Min_P) and maximum (Max_P) levels of a environmental predictor, and the Relative Environmental Suitability, the highest obtainable value being 1 (P_{Max}) (modified from Kaschner et al., 2006).*

The trapezoidal distribution represents a compromise between the likely uni-modal annual distributions exhibited by restricted range species, and the more bi-modal distribution of migratory species. To create environmental envelopes, occurrence data are associated with environmental variables to find absolute and 'preferred' preference ranges and calculated as shown in Table 2.1.

Table 2.1*. Rules used to compute environmental envelopes ($Min_{A,}$ $Min_{P,}$ $Max_{P,}$ Max_A (Fig. 2.1.)) in AquaMaps (Ready et al., 2010) and its application in calculating cell probability values for a particular environmental variable at a location (x).*

Envelope value	**Description/ Calculation**
Min_A	Absolute minimum value at which the species is observed OR the 25th percentile of the environmental values −1.5 × the interquartile range (whichever is lower)
Min_P	Preferred minimum, the 10th percentile of the environmental values
Max_P	Preferred maximum, the 90th percentile of the environmental values
Max_A	Absolute maximum value at which the species is observed OR the 25th percentile + 1.5 × the interquartile range (whichever is greater)
Condition of x	**Value/ Calculation of cell probability value**
$x \leq Min_A$	0
$Min_A < x < Min_P$	$(x - Min_A) / (Min_P - Min_A)$
$Min_P \leq x < Max_P$	1
$Max_P \leq x < Max_A$	$(Max_A - x) / (Max_A - Max_P)$
$x \geq Max_A$	0

It is therefore assumed that (relative) environmental suitability is uniformly high throughout the preferred parameter range, with a probability of 1. Those values lying outside the observed minimum or maximum (representing critical predictor limits for a species) are assigned a value of 0, while between these two thresholds, relative environmental suitability decreases linearly. Having calculated probability distributions for each predictor, overall environmental suitability can be computed by the geometric mean of all probability distributions, assuming equal influence weighting of predictors.

Expert opinion was incorporated into Maxent and AquaMaps to give refined predictions by eliminating ('clipping') areas that were currently outside known occurrence ranges, including reported occurrence/absence in large ocean basins [delineated by the United

Nations' Food and Agricultural Organisation (FAO) statistical area, www.fao.org/fishery/area/search/en] or depth limits reported in FishBase. This avoided over-prediction of relative environmental suitability in areas where species are known not to occur, or which are unsuitable due to depth.

2.1.3. The Sea Around Us Project Model

The *Sea Around Us* Project model (Close *et al.* 2006; Cheung *et al.* 2008) was specifically developed to address a need for predicting distribution ranges of commercial fish and invertebrates. The approach employs a discriminative method, applying a set of key environmental predictors, 'filters', to reduce a species' potential range. Firstly, an 'FAO filter' was applied to restrict a species on the basis of its current verified presence in the 18 FAO statistical areas. Subsequently, the distribution was refined by a filter specifying the latitudinal limits of a species' putative 'normal' distribution range. Information for both these filters is available for most fish species on FishBase. The third filter was a 'range-limiting polygon', which was applied to restrict species to a more specific level, thereby preventing occurrence in semi-enclosed seas which are located within specified FAO areas and latitudinal ranges but which are unsuitable, for example, due to low salinity values. Data for this filter was obtained from FAO publications (http://www.fao.org/fishery/species/search/en), FishBase (www.FishBase.org), SealifeBase (www.SealifeBase.org (Palomares & Pauly, 2011)) and the Sea Around Us project database (www.seaaroundus.org). A 'depth range' filter for demersal species was ascertained using the maximum and minimum depth where juvenile and adults are most often found. This range, available from FishBase may be calculated as the range within which approximately 95% of the biomass occurs. Both latitudinal and depth filters were further refined by defining a species' relative occurrence throughout the respective range, assuming a triangular distribution. The model allowed for seasonal differences in the latitudinal centroid of the distribution for migratory pelagic species (Lam *et al.* 2008). To improve a distribution prediction based on a species' association with different habitats, a habitat preference filter was applied. This assumes that the relative abundance of a taxon within a cell unit is in part determined by a fraction derived from the number of habitats (e.g. coral reefs; seamount; estuaries; see Cheung *et al*. 2008) it associates with inside that cell, and how far the association effect will extend from that habitat. Extension from a habitat is calculated as a function of a taxon's body size. Finally, an 'equatorial submergence filter' was implemented to account for the tendency for cold-water species to deepen in regions with warm surface waters (Ekman 1953; Dulvy *et al.* 2008).

2.1.4. Species Data

A set of commercially exploited fish species were chosen, reflecting a diversity of environmental preferences and life history traits. These were as follows: *Molva molva* (Ling); *Merlangius merlangus* (Whiting); *Gadus morhua* (Atlantic cod); *Melanogrammus aeglefinus* (Haddock); *Merluccius merluccius* (European Hake); *Scomber scombrus* (Atlantic mackerel); *Pleuronectes platessa* (European plaice); *Pollachius pollachius* (Pollack); *Pollachius virens* (Saithe); *Psetta maxima* (Turbot); *Solea solea* (Common Sole); *Sardina pilchardus* (European pilchard); *Sprattus sprattus* (European sprat); *Scopthalmus rhombus* (Brill). Species occurrence data were obtained from the three global online databases: the International Council for Exploration of the Sea (ICES) EcoSystemData database (http://ecosystemdata.ices.dk); the Ocean Biogeographic Information System (OBIS) (Vanden Berghe, 2007; http://www.iobis.org) and the Global Biodiversity Information Facility (GBIF) (http://data.gbif.org), all last accessed in 2010.

Occurrence records were spatially aggregated at the level of 0.5° latitude x 0.5° longitude to give a binary value of presence or absence for each cell. As these data sources are prone to error, for example, due to data being amalgamated from many sources or not being recorded with a date, data were checked and rigorously filtered using further information on species environmental preferences and geographic limits, obtained from FishBase and alternative data sources (FAO 2011; Whitehead *et al.* 1986; Ojaveer *et al.* 2003; HELCOM 2009). Points were removed if they were: 1. Located on land; 2. Located outside a verified FAO area (unless contiguous with points lying within a verified FAO area); 3. Located outside expert defined geographic range extents (obtainable as latitudinal and longitudinal limits from FishBase); 4. Located in the Baltic Sea if a species' persistence there was unverifiable (using FishBase, Whitehead *et al.*, 1986; Ojaveer *et al.*, 2003; HELCOM, 2009; FAO Fact Sheets: www. fao.org).

2.1.5. Environmental/ Oceanographic data

Environmental/ oceanographic variables were prepared on a 0.5° latitude x 0.5° longitude resolution global grid, comprising 259,200 cells of which 179,904 contain some area of ocean. Data were publically available and compiled primarily by the *Sea Around Us* Project (See Table 2.2.). The use of particular environmental variables in the SDM was based on data availability and biological relevance.

Table 2.2. *Environmental/ Oceanographic predictors input into AquaMaps and Maxent.*

Variable	Description	Source
Bathymetry	Minimum and Maximum Depth	ETOPO2 2 min resolution bathymetry dataset (NOAA 2006)
Sea Surface Temperature (SST)	Mean annual sea surface temperature (° Celsius) for the period 1982 – 1999	Climatology published by NOAA (NOAA 2007) produced following methods described by Reynolds and Smith (1995).
Sea Bottom Temperature (SBT)	Mean annual sea bottom temperature (° Celsius) for the period 1982 – 1999	*Sea Around Us* Project, unpublished data.
Salinity	Mean annual surface salinity for the period 1982 – 1999	2001 World Ocean Atlas (Conkright *et al.*)
Ice	Mean annual proportional ice cover (by area on a scale of 0.00 – 1.00, for the period 1990 – 1999. Inverse distance weighted interpolation was performed to fill missing data values in a small number of coastal cells (approximately 1000 cells).	U.S. National Snow and Ice Data Centre (Cavalieri *et al.*)
Primary Productivity	Mean annual primary production in $\mathrm{mgCm^{-2}\ day^{-1}}$ for the period 1997–2004. Generated from remotely sensed chlorophyll-*a* concentrations using an approach described in Carr *et al*. (2006).	European Joint Research Council (http://marine.jrc.ec.europa.eu/made available by Frédéric Mélin).
Distance to Coast	Nearest distance of each cell to the coast	*Sea Around Us* Project, unpublished data

2.2. Model Evaluation

Model predictions were tested using the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot test statistic. This was implemented using the ROCR package (Sing *et al.* 2007, http://rocr.bioinf.mpi-sb.mpg.de), R version 2.10.1, with the ROC curve being plotted as the true positive rate, (estimated as the number of true positives/ number of positive samples) against the false positive rate, (estimated as the number of false positives/ number of negative samples). AUC is a widely used test statistic which allows a threshold-independent measure of model performance and can be calculated using pseudoabsences from a random sample of background pixels rather than true absences. It may be interpreted as the probability that a randomly chosen presence site is ranked above a random background site, indicating the quality of site ranking according to suitability (Phillips *et al.* 2006). A random ranking has on average, AUC = 0.5 and AUC > 0.75 is suggested as providing a useful amount of discrimination between sites where a species is present and those where it is absent (Elith *et al.* 2006). Due to the lack of independent test datasets, models were assessed internally, by 4-fold cross validation (Fielding and Bell 1997). Occurrence datasets for Maxent and AquaMaps were thus split into 4 sub-sets, each containing a randomly selected 75% of points for model training, and a corresponding 25% for model testing. As no 'true' absence points were available and using randomly selected points from the entire study areas may artificially inflate the AUC statistic if the geographic area of the study is large (Lobo *et al.* 2008) or the area of suitable environmental space is small relative to the study area, pseudoabsence points were randomly selected from within specified distances of presence points using buffers (Fig. 2.2.). This allowed more valid comparisons between species if AUC values are influenced by relative predicted range area and the distance of pseudo-absence points to presence points. During selection of environmental variables, model runs were tested using global pseudoabsences and those selected from within 2000km, 1000km and 500km buffers whereas only global and 1000m pseudoabsence points were used in testing final models for all species. Maxent models were further run to perform model cross validation internally, using a random test percentage of 25%. ROC-AUC values were produced for each of 4 subsets of occurrence datapoints by plotting the ROC curve as sensitivity against 1 – specificity (the fraction of the total study area predicted present).

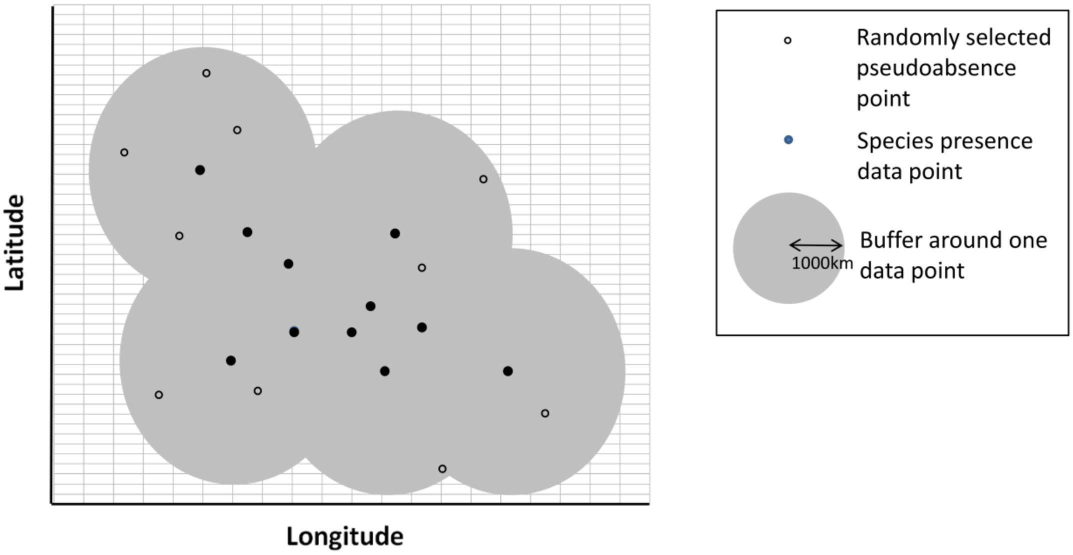


Figure 2.2*. Diagram representing the selection of pseudoabsence data points from within 1000m of species occurrence data.*

Model assessment was supplemented with the Point Biserial Coefficient (PBC) (Zheng and Agresti 2000; Elith *et al.* 2006). PBC was calculated as a Pearson's correlation coefficient between the observation in the occurrence dataset (presence (1) or pseudo-absence (O)) and the prediction and therefore takes into account how far the prediction varies from the observation. This addresses the concern that the AUC test statistic may not always reflect a model's ability to prioritise areas in terms of their environmental suitability relative to alternative models (Austin 2007; Lobo *et al.* 2008). Predictions were further inspected visually and compared to plotted occurrence data in order to assess their plausibility with respect to the known distribution and areas of environmental suitability outside known occurrence range (overprediction).

A subset of species was investigated to undertake a model selection process and determine the sensitivity of predicted species distribution to environmental variables using the Maxent and AquaMaps modelling procedures. These species include the demersal species *P. platessa* and *M. molva* and the pelagic species *S. pilchardus* and *S. scombrus.* Models were run following sequential removal of variables according to the degree of autocorrelation between them, as indicated by Pearson's correlations. They were then evaluated using AUC and PBC test statistics to enable the selection of a final set of input data.

3. Results

3.1. Model selection

Final environmental variables selected for the Maxent and AquaMaps modelling algorithms were as follows: salinity, sea surface temperature, sea bottom temperature, minimum bathymetry, ice concentration and primary productivity. Minimum bathymetry was omitted for pelagic species due to its biological irrelevance and propensity to misleadingly restrict range predictions in these species. It was, however, substituted with distance to coast to account for the fact that many pelagic species are restricted to coastal habitats at certain stages in their life cycle and may not persist in the open ocean despite its seeming environmental suitability.

The AUC values from Aquamaps predictions are above 0.75 and vary over a relatively small range of values (with the exception of *P. Pollachius*) (See Appendix, Table 2.1, for a summary of key statistics). Although test statistic values vary with the buffer used to generate pseudo-absences, with a few exceptions, the pattern of difference is similar across buffers for both AUC and PBCs. Pelagic species (*S. rhombus* and *S. pilchardus*) showed less variation in test statistics according to environmental variables included in the AquaMaps models. Maxent models also showed less variation in AUC value with different sets of environmental variables, variation instead mostly resulting from using different sets of pseudoabsences.

3.2. Model comparison

3.2.1. Maxent

Cross-validation using sub-sets of data and Maxent's automated validation test showed relatively little variation in the AUC statistic (e.g. maximum difference in AUC values of 0.01 and 0.009 in *S. rhombus* and *P. pollachius* respectively). The quality of predictions, as indicated by test statistics, was also relatively consistent across species, with the most noticeable deviation in AUC value being shown by *G.morhua* (AUC = 0.944).

Test statistic values decreased when calculated using pseudoabsences restricted to 1000m from presence points, although the extent of the difference varied between species and were generally smaller for demersal species (Fig. 2.3. a). While *M. molva*, for example, varied little in model performance (indicated by test statistics) the greatest difference was seen in *S. pilchardus*. AUC value decreased from 0.998 to 0.793 when pseudoabsences from a global and 1000km buffered distribution were used respectively. PBC values also varied little across species (Fig. 3. a), with little difference between values tested with 'global' and '1000km buffer' pseudo-negatives other than for the pelagic species *S. pilchardus* and *S. scombrus*.

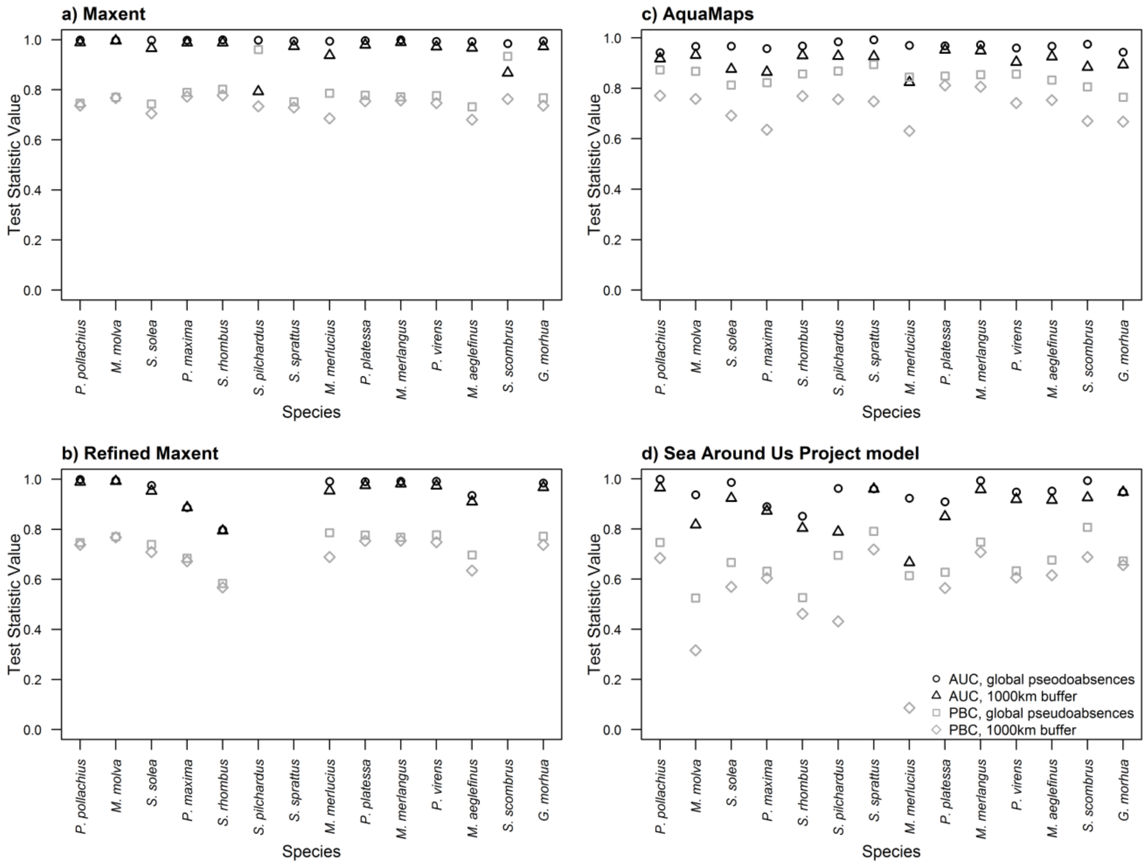


Figure 2.3*. Test statistic values for all species, calculated using pseudoabsences from within a global distribution or those restricted to within 1000km of presence points. Test statistic values are calculated as the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot test statistic, and the Point Biserial Coefficient (PBC) for each model (Maxent, Refined Maxent (following clipping of predictions by depth for all species other than pelagic species (S. pilchardus, S. sprattus, S. scombrus), AquaMaps, Sea Around Us Project model.*

With the exception of *P. pollachius* and *P. virens*, AUC values generally dropped following clipping by depth in the Maxent refined prediction, when tested using global pseudo-absences (Fig. 2.3. b). The extent of this decrease was slight, although varied between species and fell most for those species restricted to the shallowest depths. Thus while *M. molva* was clipped only to a depth of 1000m and AUC values decreased slightly by 0.004, *P. maxima* and *S. rhombus*, which were clipped to 70m and 50m decreased by 0.101 and 0.193 respectively (using 1000m buffers). The same was true for PBC values, although frequently the use of a buffer made more difference to this value than the depth clipping of the prediction, for example in *M. merluccius* and *S. solea*.

3.2.2. AquaMaps

The AquaMaps methodology showed a greater response in AUC value to the data subset used in model training and testing. With the exception of a subset of *P. pollachius* (AUC = 0.871) all subsets still obtained high values of 0.944 or greater. This modelling approach also showed greater variation between species, with the most robust, or highest performing, models, as indicated by the test statistics, being obtained for the pelagic species *S. sprattus*. Although another pelagic species (*S. pilchardus*) showed the next highest AUC values, this result was not paralleled by PBC values (Fig. 2.3. c), highlighting the difference in test statistic obtainable when binary presence/absence data are considered as opposed to actual values.

As with Maxent, refinement of predictions by depth clipping produced little difference in PBC and AUC values other than in *P. maxima* (decreases in PBC and AUC of 0.127 and 0.096, respectively) and *S. rhombus*, whereas the reduction in PBC with the 1000m buffer was more pronounced than in Maxent evaluations and showed wider variation between species. The use of the 1000m buffer has a less marked effect on test statistics in depth clipped predictions. These patterns are reflected in the high (>0.75) AUC test statistic.

There seemed to be no significant effect on the test statistic of number of occurrence points for either modelling method, although the variation in occurrence dataset size was not great (between 445 and 1323 occurrence data points). *P. pollachius*, *M. molva*, *M. merlangus* and *P. platessa* gave consistently high test statistics across AquaMaps, Maxent and their refined models, also when tested with different sets of pseudonegatives. Test statistics for *S. solea* and *M. merluccius* varied most following model clipping by depth and use of a buffer in pseudoabsence selection. Although all achieving AUC > 0.97 using global pseudoabsences, the pelagic species showed large decreases in performance relative to other species following implementation of a buffer, and this was most pronounced in Maxent.

3.2.3. Sea Around Us Project Model

The *Sea Around Us* Project methodology exhibited greater variation in test statistics than both Maxent and AquaMaps, with the AUC and PBC test statistics showing mostly parallel patterns of change across species (Fig. 2.3. d). Values decreased consistently following implementation of a buffer, with larger decreases in results for *M. merluccius* and *S. pilchardus* compared to other species (AUC decrease = 0.173 and 0.184 respectively, PBC decrease = 0.263 and 0.372 respectively). This reflects a similar pattern of results found in these two species in AquaMaps and, to a lesser extent, Maxent. Some AUC values for predictions for the *Sea Around Us* Project method compared well to AquaMaps and Maxent (such as *P. pollachius* and the pelagic species *S. sprattus, S. pilchardus* and *S. scombus*).

Variation was, however, observed in the relative performance of the three models for particular species. In almost all cases, the AquaMaps algorithm produced the least constrained prediction, and thus the greatest distribution ranges, although these were reduced following refinement by depth for demersal species. Maxent occasionally resulted in over-prediction in the Baltic Sea (e.g. *P. pollachius*; *P. virens*) with respect to verified occurrence data and other sources (see methodology). While *M. merlangus* was predicted consistently well across models, *M. molva* obtained lower test statistics in the *Sea Around Us* Project model relative to other species, failing to meet the 0.75 threshold AUC and with PBC scores below 0.333.

Overall, although the three models did not vary greatly in the area, or extent of occurrence, predicted for each species, differences lay in the detailed pattern and values of predicted suitability within this area (Figures 2.4.-2.6.). While *Sea Around Us* Project predictions were characterised by relatively low levels of suitability, they were contrasted most strongly by AquaMaps, which frequently produced uniformly high predictions across the range, only decreasing in relatively suitability around the periphery of the predicted range, as seen, for example, in *P. platessa* (Fig. 2.4.).

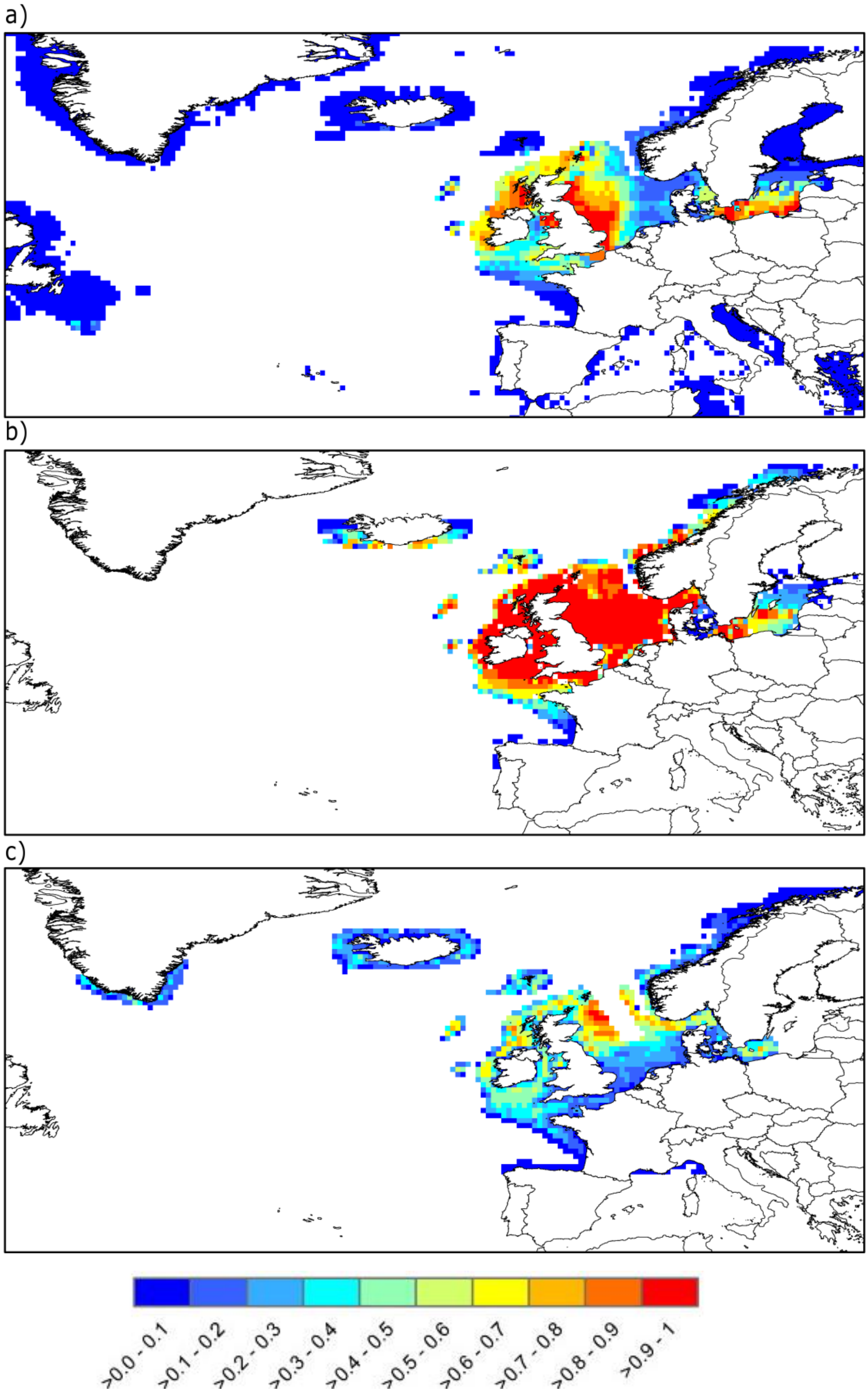


Figure 2.4. *Predicted distributions of relative environmental suitability (0 -1) for Pleuronectes platessa using a) Maxent b) AquaMaps c) Sea Around Us Project model*

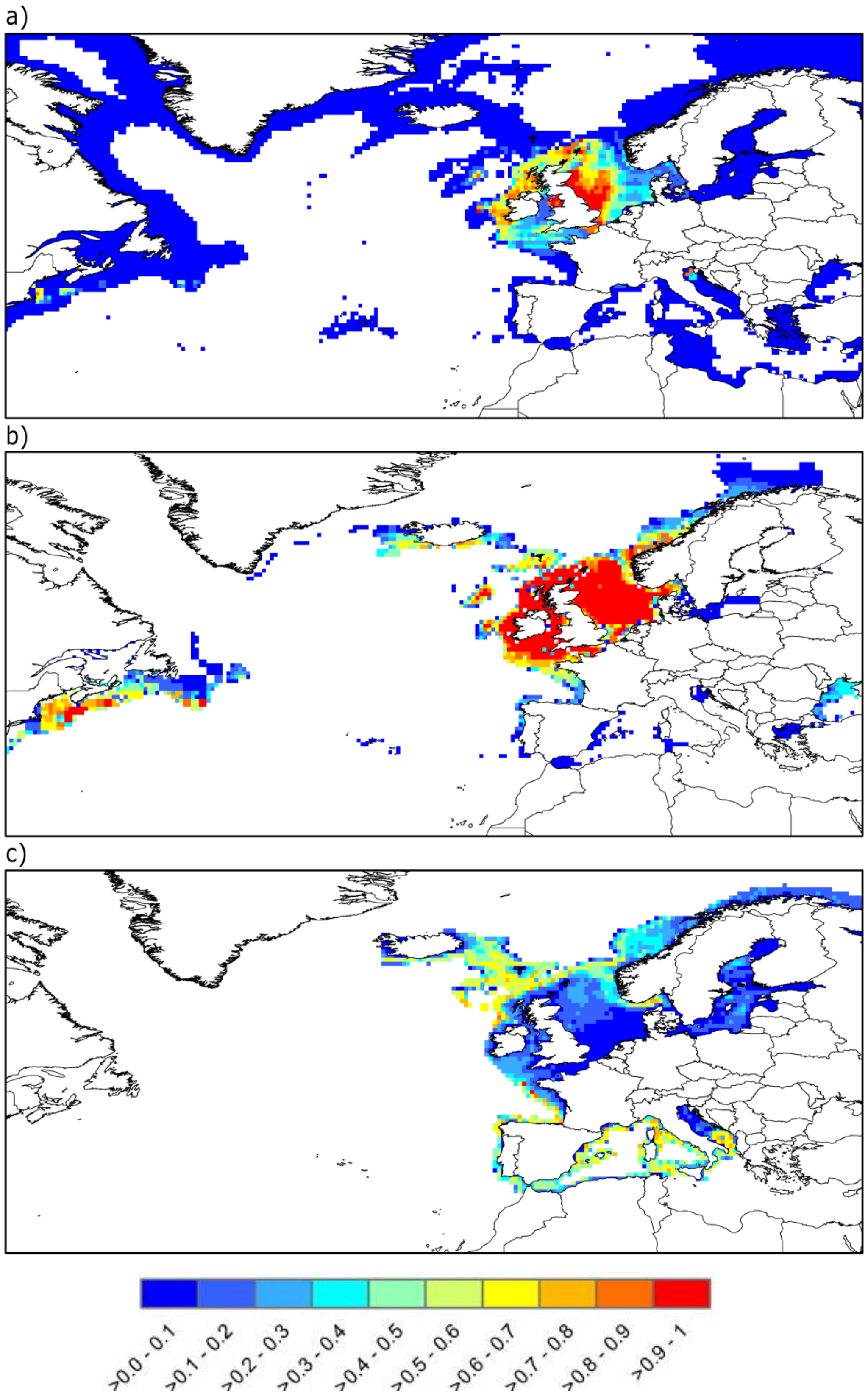


Figure 2.5. *Predicted distributions of relative environmental suitability (0 -1) for Molva molva using a) Maxent b) AquaMaps c) Sea Around Us Project model*

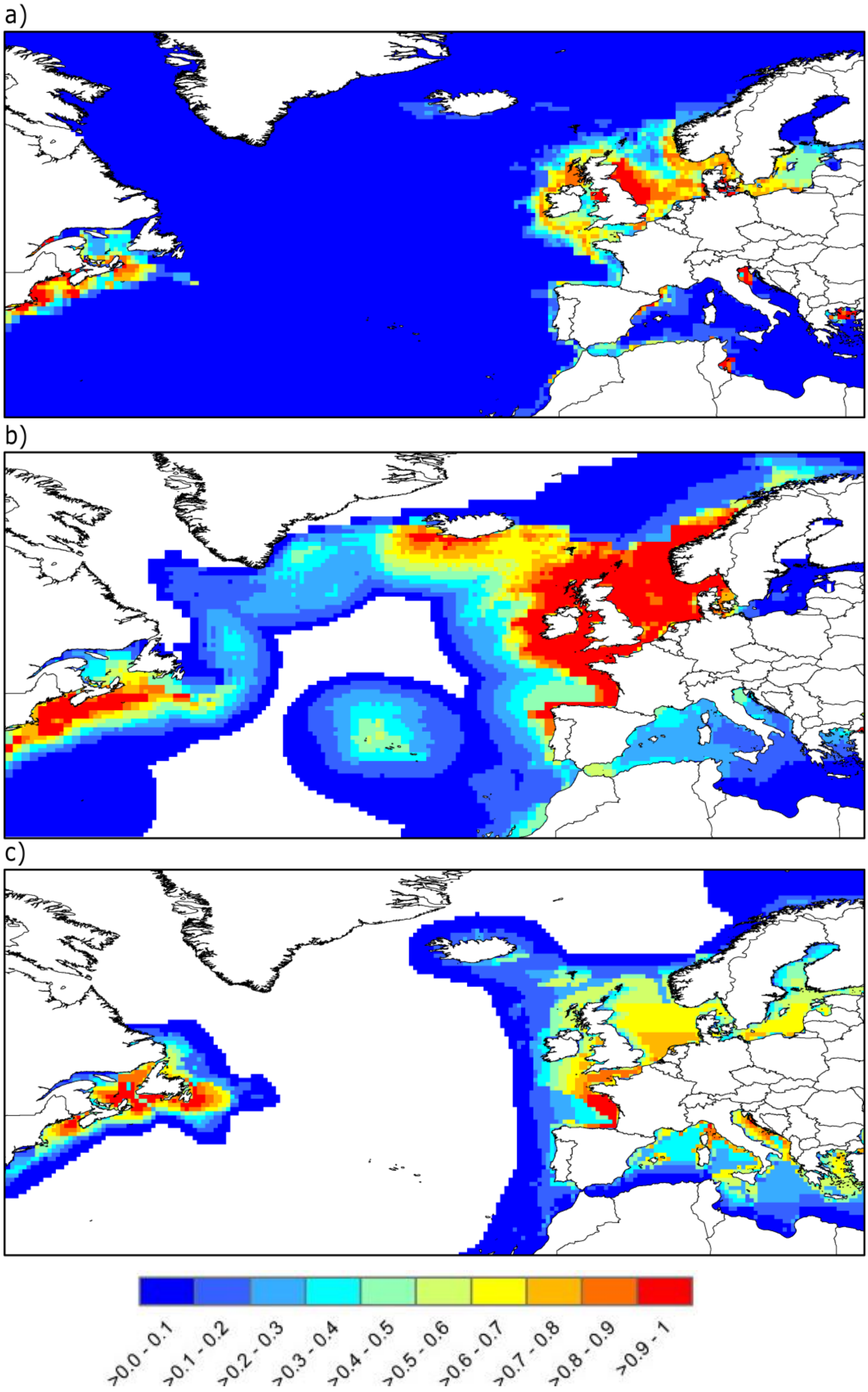


Figure 2.6*. Predicted distributions of relative environmental suitability (0 -1) for Scomber scombrus using a) Maxent b) AquaMaps c) Sea Around Us Project model*

4. Discussion

4.1. Uncertainties and assumptions

This study aimed to draw comparisons between three commonly used models for obtaining distribution predictions of marine species. Uncertainties are introduced into a multi-model procedure by differences in the data-types used, how the models are parameterized and the actual modelling mechanisms used. Confidence in species occurrence data may, for example, be lowered by sampling bias and taxonomic uncertainty, whereas data on species tolerance limits and expert judgement may be biased by limited experimental data and incomplete or out-dated knowledge. Further uncertainly is caused by inherent assumptions of any species distribution modelling procedure, such as the assumption that a species is in pseudo-equilibrium with its environment (Guisan and Thuiller 2005). Upholding this assumption ensures that the observed realized distribution used in making predictions or setting environmental filters represents the absolute environmental limits of a species' range, and that true potential range is not under-estimated by closely fitted, biased, distribution data (Svenning and Skov 2004). The assumption may not be upheld when models fail to take into account biotic interactions that prevent species occupying otherwise seemingly suitable environmental space. It has been suggested, however, that many species distributions can be assumed to be in equilibrium with current climate at the macro scale, although the finer details of the distribution may not be identified (Pearson *et al.* 2002). An attempt to counter this problem was made here by including all occurrence data available rather than restricting points to a specific time period or region. While this may introduce uncertainty as to whether current distributions fail to reflect potential movement of species population due to stock depletion in commercially exploited fisheries, it is hoped that it will contribute to capturing the species true limits of environmental tolerance. It is also assumed that there has been no adaptation towards climatic variation over the period for which data has been amalgamated. Although this might seem reasonable over a short time span, bias may be introduced if, as is frequently the case in compiled online datasets, there is no date associated with a species occurrence record. In this instance, models parameterized on known tolerance limits and expert opinion may be more suitable at depicting current distributions.

4.2. Model Characteristics

While predicted distribution ranges from AquaMaps, Maxent and the *Sea Around Us* Project model show general agreement, there are consistent differences in predictions resulting from differences in input data and model structure (Table 2.3.). Although test results from ROC-AUC and PBC values vary between species, models tested with pseudo-negatives selected from both a global and restricted (1000m buffer) distribution obtained AUC values indicating performance which is better than random [in all but one case (*M. merluccius*, *Sea Around Us* Project)], and may be considered potentially useful (> 0.75, Elith *et al*., 2006).

The generally high test statistic values obtained for Maxent predictions are consistent with its use elsewhere (Elith *et al.* 2006; Hernandez *et al.* 2006; Wisz *et al.* 2008). The lesser variation between test results for partitioned datasets in Maxent than AquaMaps also indicates a greater robustness of this procedure to the particular dataset used and thus to outliers and possibly erroneous datapoints. However, although high model performance suggests accuracy and reliability in predictions of species distribution made by Maxent, it may also be caused by the tendency of Maxent to over-fit the occurrence data of the sample, for which it has been criticised (Jiménez-Valverde *et al.* 2008). It has also been suggested that complex models, such as Maxent, are likely to be more accurate at finer resolutions (specificity), but would generalize poorly in predicting potential distributions at large spatial scale (Drake *et al.* 2006; Jiménez-Valverde *et al.* 2008) whereas simpler models, such as AquaMaps, will offer useful and parsimonious solutions at a broader scale (generality) (Thuiller *et al.* 2008). This agrees with the tendency, seen here, of Maxent to produce more constrained predictions than AquaMaps, and indicates that test statistics should not be used as definitive indicators of model performance, but should be assessed together with visual inspection of the distributions and expert knowledge.

This analysis agrees with Ready *et al*. (2010) that a 'black-box' use of complex SDM programmes such as Maxent may act as a barrier to users who are not expert, and may also hinder the potential for alteration by experts and thus perhaps their actual practical use and application. Maxent and AquaMaps models were refined by 'expert' review of a distribution map subsequent to a prediction, by 'clipping', and may thus not necessarily involve a detailed knowledge of a modelling procedure. Despite this, the ability to easily investigate and manipulate the environmental envelope for each variable in the AquaMaps approach aids the incorporation of expert judgement and checking for errors caused by potential outlying or erroneous occurrence data points.

Table 2.3. *Summary of general model characteristics for the original models of Maxent and AquaMaps and the Sea Around Us Project model, inferred from results.*

Characteristic	**Maxent**	**AquaMaps**	***Sea Around Us* Project**
Relative environmental suitability values	Relatively even allocation from high to low suitability.	Dominated by areas of uniformly high suitability following clipping by depth.	Dominated by area with low suitability values.
Extent of predicted distribution	Intermediate constraint before clipping.	Least constrained before clipping.	Most constrained.
Under-prediction with respect to occurrence data	None pre clipping, some in refined Maxent.	None pre clipping, some in refined AquaMaps.	Some e.g. *M. molva*
Variation in AUC/ PBC value in response to partitioned training/ testing data	Low	Higher	n/a
Variation in AUC/ PBC value across species	Low	Intermediate	High
Species data (minimum) requirements	Species occurrence points, presence only.	Species occurrence points, presence only.	Knowledge of general geographic range, habitat and depth preferences.
Model complexity	Complex: Statistical, generative method enabling predictor variable weighting, modelling of interactions and complex response curves.	Simple: Assumes a trapezoidal distribution and equal weighting of predictor variables.	Simple: Discriminative approach using a set of key ecological predictors.

The *Sea Around Us* Project method requires the least amount of point data, and its predicted distributions are generally more restricted relative to those predicted using the other two approaches. However, inherent differences in input data and the way environmental limits and parameters are defined under this approach further seem to prevent the valid comparison of the relative performance of these three models. Thus while the test data subset form a representative sample of the training data used to generate predictions in both Maxent and AquaMaps, a *Sea Around Us* Project prediction is generated using environmental and geographic limits and thus independently from the occurrence dataset, precluding the selection of the most accurate, reliable 'best' model by direct comparison of test statistics. Particularly, spatial auto-correlation between the presence data for distribution predictions and that for calculation of test statistics may over-estimate the performance of Maxent and AquaMaps relative to the *Sea Around Us* project method. For example, in modelling *M. molva* (Fig. 2.5.) and *M. merluccius* using the *Sea Around Us* Project approach, regions were predicted as being unsuitable despite coinciding with species occurrence data points, resulting in the models obtaining low AUC and PBC values (*M. molva*: AUC = 0.657; PBC = 0.147 with buffer, *M. merluccius*: AUC = 0.667, PBC = 0.087). This is, however, likely due to the fact that, being tested but not trained on environmental data associated with occurrence points, the minimum depth restriction imposed by the *Sea Around Us* Project filter excludes areas retained by the other models. The discrepancy presented a valid difference between the two types of data driving the approaches (species occurrence data and tolerance limits) and one that confidence in data quality did not justify eliminating. Minimum depth restrictions were therefore retained in the *Sea Around Us* Project methodology although that for *M. molva* was reduced from 100m due to the presence of immature individuals up to a depth of 15m (Whitehead *et al.* 1986). Following this adjustment, the predicted distribution for *M. molva* has an AUC that is more consistent with other species and methods. Similarly, the differences between data-types and their effect on test statistics was highlighted following incorporation of expert knowledge in Maxent and AquaMaps predictions for *P. maxima* and *S. rhombus* (Fig. 2.6.). The substantial depth restrictions of these species (of 70m and 50m respectively) encompassed areas where occurrence data are found and therefore likely result in the relatively low test statistics obtained.

Difficulty therefore lies in the relative confidence in data used for model training and testing. Although occurrence data for *S. rhombus* indicate its realized niche to be throughout the North Sea, its habit of living on sandy or mixed sea bottoms, only to a depth of 50m (FishBase), questions its long-term persistence in the deeper areas indicated by occurrence data. If the aim is to model a species' potential niche, where it can reproduce and persist and is not dependent on access to other (shallower) habitats, it may therefore be more suitable to restrict predicted distributions to the more conservative estimate, despite the wider distribution suggested as the observed, realized niche. If projecting predictions in time or space, it does, however, seem wise to take into account both range predictions as containing useful information about the species environmental requirements and tolerances.

Discrepancies between predicted relative suitability in the Baltic Sea further highlight differences in the methodologies and algorithms of the three models. The most accurate predictions for the suitability of the Baltic Sea for particular species, according to verified occurrence data and other sources (see Section 2. Methods) were produced by AquaMaps and the *Sea Around Us* Project model. This likely resulted from the equal weighting given to each environmental variable such that the effect of salinity was considered in equal proportion to other predictors in these two models. Maxent, by contrast, attributes a low contribution by salinity to the prediction, the suitability of other environmental variables in this area may compensate for an unsuitable salinity value, resulting in predicted distribution in areas a species is known not to occur. Comparing the two correlative species distribution models used here, AquaMaps is therefore more robust than Maxent to uncertainty in the relative influence of environmental predictor variable due to its simple, multiplicative approach which assigns equal weighting to each predictor.

4.3. Interpretation of test statistics and the problem of model comparison

Further to the problem, mentioned above, of comparing models based on different data sources, in reference to complex SDM techniques such as Maxent, it was suggested that model testing statistics using presence-(pseudo)absence data might produce artificially high values for more restricted distribution predictions as a greater number of absences or 'pseudo-absences' are likely to be predicted as absent. This characteristic would lead to the conclusion that complex techniques are more accurate than simpler ones, precluding any useful comparison between modelling approaches.

Furthermore, although Maxent models generally produce higher AUC values than those produced by AquaMaps, this is seldom the case using the PBC statistic. This disparity raises questions whether either value allows a useful and valid comparison across modelling procedures. Although calculation of AUC scores may be highly influenced by the total modelling area, larger areas increasing the likelihood that pseudoabsences will be more distant in environmental space and decreasing commission error (Lobo *et al.* 2008), in this case the study area remained consistent. Evaluation of perceived model performance may, however, also be affected by a species' relative occurrence. This is consistent with the observation that the test statistics for AquaMaps fell when all species were tested using pseudoabsences taken from a restricted area (within a buffer of 500 or 1000m of observed presence points). The decrease in AUC value followed by incorporation of depth limits in the distribution predictions (using Maxent and AquaMaps) do not, however, support the hypothesis that AUC values will increase with decreasing predicted extents of occurrence. This loss of model performance following depth clipping is rarely seen when test statistics are calculated using pseudoabsences restricted to particular distances from presence points, refined models then performing consistently better than the originals. The exceptions to this are shown by *P. maxima* and *S. rhombus*, whose substantial depth restrictions (of 70m and 50m respectively) encompass areas where occurrence data-points are found, likely resulting in lower test statistics if presence points from outside these restricted areas are used in their calculation. Results obtained here using global pseudoabsences therefore contrast those obtained by Ready *et al*. (2010), who found the AquaMaps approach to be generally favourable to the inclusion of expert knowledge in the form of defined depth preferences. It is thus proposed that, in this case, the perceived performance of expert reviewed, or 'refined' predictions may be subject to characteristics of model testing statistics.

As it has been suggested that the focus on predictive performance should be broadened to encompass ecological realism and model credibility to the user community (Franklin 2009), it is also important not to become over-focused on data errors and model fit. When selecting environmental variables in this study, for example, minimum bathymetry was included although it did not consistently improve test statistics as the vertical (depth) gradients of temperature and oxygen are considered important factors limiting demersal species distributions (Pauly 2010). A misunderstanding of ecological relevance may thus lead to errors in model specification despite seemingly high test statistic values. Biological relevance should therefore be considered both in model selection and when assessing the applicability of the three models used.

As undertaken here, it is suggested that a range of AUC/ PBC statistics should be calculated in order to assess the scope for variation and possibly contrasting results. Although a range of values may then only allow broad conclusions to be drawn, it is argued that the greater understanding of the model evaluation process and any differences will facilitate reasoned judgement in model evaluation. In conclusion, it is proposed that the refinement of AquaMaps and Maxent predictions by expert opinion do represent more accurate representation of species' distributions, agreeing for the most part with occurrence data and the predictions produced by the *Sea Around Us* Project model. It should be noted, however, that AUC values are useful in determining the amount of variation in predictions caused by partitioned datasets, emphasising the degree of influence of possible outlying points and the robustness of the model to the occurrence data (Lobo *et al.* 2008).

5. Conclusions

Uncertainties inherent in both specifying and testing species distribution models indicate that expert review is a vital part of the SDM process. Although the modelling approaches employed here may lose precision in assuming that species distributions are dictated by a general and restricted set of environmental variables, in modelling marine species, for which data and ecological knowledge are frequently scarce, a general approach would seem advisable. Expert review allows models to be refined and developed with increases in knowledge or data, and the ease at which this may be done, by a variety of non-specialist users, will be enhanced by a transparent and intuitive procedure.

The three modelling approaches produced predictions of relative environmental suitability which were plausible given the occurrence data of each species. This analysis does not, however, indicate whether there are differences in the capabilities of each model to portray specific features of the distribution, such as the pattern of relative environmental suitability. In conducting this comparison doubts were raised as to the validity of direct comparisons between models. Striving to find the best model, as indicated by test statistics would therefore risks substantial inaccuracies if wrong selection of alternative data sources of model design are made. Differences between modelling procedures that mask uncertainty as to true suitability values should therefore be retained and used to view the range of plausible predicted distributions for a species. It is proposed that a multi-model ensemble approach is most suitable for investigating distribution ranges, especially in the marine environment where modelling is likely to be hampered by issues of data quality.

References

Austin, M. (2007) Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling* **200**, 1-19.

Austin, M.P., Nicholls, A.O., Margules, C.R. (1990) Measurement of the realised qualitative niche: environmental niches of five Eucalyptus species. *Ecol. Monogr* **60**, 161–177.

Beaugrand, G. (2004) The North Sea regime shift: Evidence, causes, mechanisms and consequences. *Progress in Oceanography* **60**, 245-262.

Beaugrand, G. (2009) Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. *Deep Sea Research Part II: Topical Studies in Oceanography* **56**, 656-673.

Beaumont, L.J., Hughes, L. (2002) Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. *Global Change Biology* **8**, 954-971.

Bigg, G.R., Cunningham, C.W., Ottersen, G., Pogson, G.H., Wadley, M.R., Williamson, P. (2008) Ice-age survival of Atlantic cod: agreement between palaeoecological models and genetics. *Proceedings of the Royal Society B* **275**, 163-173.

Brotons, L., Thuiller, W., Araújo, M.B., Hirzel, A.H. (2004) Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* **27**, 437-448.

Cavalieri, D., Parkinson, C., Gloersen, P., Zwally, H.J. (1996) Sea Ice Concentrations from Nimbus-7 SMMR and DMSP SSM/I Passive Microwave Data [1972-2002]. Boulder, Colorado USA: National Snow and Ice Data Centre. Digital media, updated 2008.

Carr, M.-E., Friedrichs, A.M., Schmeltz, M., Aita, M.N., Antoine, D., Arrigo, K.R. *et al*. (2006) A comparison of global estimates of marine primary production from ocean color. *Deep Sea Research Part II: Topical Studies in Oceanography* **53**, 741-770.

Close, C., Cheung, W., Hodgson, S., Lam, V., Watson, R., Pauly, D. (2006) Distribution Ranges of Commercial Fishes and Invertebrates. In: Palomares, M.L.D., Stergiou, K.I., Pauly, D., editors. Fishes in Databases and Ecosystems. Fisheries Centre , University of British Columbia: *Fisheries Centre Research Reports* **14**(4), p. 27-37.

Cheung, W.W.L., Lam, V.W., Pauly, D. (2008) Dynamic Bioclimate Envelope Model to Predict Climate-Induced Changes in Distribution of Marine Fishes and Invertebrates. In: Cheung, W.W.L., Lam, V.W.Y., Pauly, D., editors. Modeling Present and Climate-shifted Distribution of Marine Fishes and Invertebrates. Fisheries Centre, University of British Columbia: *Fisheries Centre Research Reports* **16**(3) p. 5-45.

Cheung, W.W.L., Lam, V.W., Sarmiento, J.L., Kearney, K., Watson, R., Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* **10**, 235-251.

Conkright, M.E., Locarnini, R.A., Garcia, H.E., O'Brien, T.D., Boyer, T.P., Stephens, C., Antonov, J.I. (2002) World Ocean Atlas 2001: Objective analyses, Data Statistics and Figures CD-ROM documentation. U.S. National Oceanographic and Atmospheric Administration, National Oceanographic Data Centre, Silver Spring, MD.

Drake, J.M., Randin, C., Guisan, A. (2006) Modelling ecological niches with support vector machines. *Journal of Applied Ecology* **43**, 424-432.

Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmüller, V., Dye, S.R., Skjoldal, H.R. (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology* **45**, 1029-1039.

Ekman S. (1953) *Zoogeography of the Sea*. Sidgwick & Jackson, London.

Elith, J., Ferrier, S., Guisan, A., Graham, C.H., Anderson, R.P., Hijmans, R.J. *et al*. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129-151.

FAO (2011). FAO Fact Sheets. Available at: http://www.fao.org/fishery/species/search/en [Accessed March, 2011].

Fielding, A.H., Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/ absence models. *Environmental Conservation* **24** (1), 38-49.

Franklin, J. (2009) *Mapping species distributions; spatial inference and prediction*. Cambridge University Press, Cambridge.

Froese, R. and Pauly, D. (2011) Fishbase. Available at: www.fishbase.org, version (02/2011) [Accessed February 4, 2011].

GBIF (2010) Global Biodiversity Information Facility. Available at: http://data.gbif.org [Accessed November, 2010]

Guisan, A., Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**, 993-1009.

Guisan, A., Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* **135**, 147-186.

HELCOM. (2009) Biodiversity in the Baltic Sea – An integrated thematic assessment on biodiversity and nature conservation in the Baltic Sea. *Balt. Sea Environ. Proc.* 116B

Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L. (2006) The effect of sample size and species characteristics on performance of different species distribution modelling methods. *Ecography* **29**, 773 – 785.

Hijmans, R.J., Graham, C.H. (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* **12**, 2272-2281.

Hirzel, A.H., Helfer, V., Metral, F. (2001) Assessing habitat-suitability models with a virtual species. *Ecological Modelling* **145**, 111-121.

Hutchinson, G.E. (1957) Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology **22** (2), 415–427.

ICES (2011) International Council for the Exploration of the Sea Ecosystem Database. Available at: http://ecosystemdata.ices.dk [Accessed March, 2011]

Jiménez-Valverde, A., Lobo, J.M., Hortal, J. (2008) Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions* **14**, 885-890.

Kadmon, R., Farber, O., Danin, A. (2003) A systematic analysis of factors affecting the performance of climate envelope models. *Ecological Applications* **13**(3), 853-867.

Kaschner, K., Rius-Barile, J., Kesner-Reyes, K., Garilao, C., Kullander, S.O., Rees, T., Froese, R. (2010) AquaMaps: Predicted range maps for aquatic species. Version 08/2010. Available at: http://www.aquamaps.org/.

Kaschner, K., Watson, R., Trites, A.W., Pauly, D. (2006) Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. *Marine Ecology Progress Series* **316**, 285-310.

Kimmins, J.P., Blanco, J.A., Seely, B., Welham, C., Scoullar, K., (2008) Complexity in modeling forest ecosystems; how much is enough? *Forest Ecology and Management* **256**(10), 1646-1658.

King, J.R. (2005) Report of the Study Group on fisheries and ecosystem responses to recent regime shifts. *PICES Scientific Report* **28**, 162.

Lam, V.W.Y., Cheung, W.W.L., Close, C., Hodgson, S., Watson, R., Pauly, D. (2008) Modelling seasonal distribution of pelagic marine fishes and squids, p. 51-62. In: Cheung, W.W.L., Lam, V.W.Y., Pauly, D., editors. Modeling Present and Climate-shifted Distribution of Marine Fishes and Invertebrates. Fisheries Centre, University of British Columbia: *Fisheries Centre Research Reports* **16**(3) p. 51-62.

Lobo, J.M., Jiménez-valverde, A., Real, R. (2008) AUC: A misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* **17**, 145-151.

Martinez-Meyer, E. (2005) Climate change and biodiversity: some considerations in forecasting shifts in species' potential distributions. *Biodiversity Informatics* **2**, 42-55.

MacLeod, C.D., Bannon, S.M., Pierce, G.J., Schweder, C., Learmonth, J.A., Herman, J.S. *et al*. (2005) Climate change and the cetacean community of north-west Scotland. *Biological Conservation* **124**, 477-483.

NOAA (2006) ETOPO2 v" global gridded 2-minuts database. U.S. National Oceanic and Atmospheric Administration, National Environment Satellite, Data and Information Service, National Geophysical Data Centre. Available at: http://www.ngdc.noaa.gov/mgg/image/2minrelief.html [Accessed 2007]

NOAA (2007) NOAA optimum interpolation sea surface temperature analysis. U.S. National Oceanic and Atmospheric Administration, National Centre for Environ- mental Prediction. Available at: http://www.emc.ncep.noaa.gov/research/cmb/sst analysis [Accessed 2007].

Ojaveer E, Pihu E, Saat T, editors. (2003) *Fishes of Estonia*. Tallinn: Estonian Academy Publishers.

Palomares, M.L.D., Pauly, D., editors. (2011) SeaLifeBase version (10/2011). Available at: http://www.sealifebase.org/ [Accessed October, 2011].

Pauly, D. (2010) The State of Fisheries. In: *Conservation Biology for All* (eds S.N.S. Sodhi and P.R. Ehrlich). Oxford University Press, Oxford, pp. 118 – 120

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R. *et al*. (2002) Towards sustainability of world fisheries. *Nature* **418,** 689 – 695.

Pearson, R.G., Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* **12**, 361-371.

Pearson, R.G., Dawson, T., Berry, P., Harrison, P. (2002) SPECIES: A Spatial Evaluation of Climate Impact on the Envelope of Species. *Ecological Modelling* **154**, 289-300.

Pearson, R.G., Raxworthy, C.J., Nakamura, M., Townsend Peterson A. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* **34**(1), 102-117.

Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. *Science* **308**, 1912-5.

Phillips, S.J., Anderson, R.P., Schapire, R.E. (2006) Maximum entropy modelling of species geographic distributions. *Ecological Modelling* **190**, 231-259.

Phillips, S.J., Dudík, M. (2008) Modelling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**, 161-175.

Phillips, S.J., Dudík, M., Schapire, R.E. (2004) A maximum entropy approach to species distribution modelling. Proc. of the 21st International Conference on Machine Learning.

Reynolds, R.W., Smith, T.M. (1995) A high-resolution global sea surface temperature climatology. *Journal of Climate* **8,** 1571–1583.

Ready, J., Kaschner, K., South, A.B., Eastwood, P.D., Rees, T., Rius, J., Agbayani, E., Kullander, S., Froese, R. (2010) Predicting the distributions of marine organisms at the global scale. *Ecological Modelling* **221**, 467-478.

Root, T.L., Rosenzweigk, C. (2003) Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57-60.

Sea Around Us Project. Available at: http://www.seaaroundus.org/ [Accessed February 2011].

Sing, T., Sander, O., Beerenwinkel, N. and Lengauer, T. (2007) The ROCR Package. [Accessed September 20, 2011].

Southward, A.J., Hawkins, S.J., Burrows, M.T. (1995) Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English channel in relation to rising sea temperature. *Journal of Thermal Biology* **20**, 127-155.

Stebbing, A., Turk, S., Wheeler, A., Clarke, K.R. (2002) Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960-2001). *Journal of the Marine Biological Association of the United Kingdom* **82** 177-180.

Stockwell, D.R.B., Peterson, A.T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling* **148**, 1-13.

Svenning, J., Skov, F. (2004) Limited filling of the potential range in European tree species. *Ecology Letters* **7**, 565-573.

Tsoar, A., Allouche, O., Steinitz, O., Rotem, D., Kadmon, R. (2007) A comparative evaluation of presence-only methods for modelling species distribution. *Diversity and Distributions* **13**, 397-405.

Thuiller, W., Albert, C., Araujo, M., Berry, P., Cabeza, M., Guisan, A., *et al.* (2008) Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics* **9**, 137-152.

Vanden Berge E, editor. The Ocean Biogeographic Information System: web pages. Available on http://www.iobis.org. Last accessed 11/2010

Whitehead, P.J.P., Bauchot, M.L., Hureau, J.C., Nielsen, J., Tortonese, E., (eds) (1986). *Fishes of the Northeast Atlantic and Mediterranean*. UNESCO, Paris.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A. (2008) NCEAS Predicting Species Distribution Working Group. Effects of sample size on the performance of species distribution models. *Diversity and Distributions* **14**, 763-773.

Zheng, B., Agresti, A. (2000) Summarizing the predictive power of a generalized linear model. *Statistical Methods* **19**, 1771-1781.

Appendix

Table 2.1. *Test statistic values for all species, calculated using pseudoabsences from within a global distribution or those restricted to within 1000km of presence points. Test statistic values are calculated as the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot test statistic and the Point Biserial Coefficient (PBC) using Maxent, AquaMaps and the Sea Around Us Project model. Predictions made using AquaMaps and Maxent also show test statistics for Refined predictions, those following clipped by depth, for each species.*

Maxent	***P. pollachius***	***M. molva***
No of training points (75%)	**445**	**474**
AUC1	0.9760	0.9800
AUC2	0.9800	0.9820
AUC3	0.9840	0.9780
AUC4	0.9850	0.9820
Average AUC	0.9813	0.9805
AUC (calculated externally)	0.9986	0.9985
AUC 1000km buffer	0.9888	0.9962
Refined prediction, Average AUC	0.9989	0.9948
Refined prediction, AUC 1000km buffer	0.9892	0.9923
Global PBC	0.7461	0.7706
PBC 1000km buffer	0.7371	0.7672
Refined prediction, Average PBC	0.7464	0.7703
Refined prediction, PBC 1000km buffer	0.7381	0.7679
AquaMaps		
AUC 1	0.9537	0.9574
AUC 2	0.8791	0.9753
AUC 3	0.9757	0.9677
AUC 4	0.9578	0.9644
Average AUC	0.9416	0.9662
AUC, 1000km buffer	0.9175	0.9317
Refined prediction, Average AUC	0.9663	0.9707
Refined prediction AUC 1000km buffer	0.9388	0.9603
PBC 1	0.8493	0.8446
PBC 2	0.8791	0.8667
PBC 3	0.9072	0.8750
PBC 4	0.8575	0.8820
Average PBC	0.8733	0.8671
PBC, 1000km buffer	0.7709	0.7579
Average P clipped	0.8593	0.8700
PBC 1000 buffer clipped	0.8073	0.8455
***Sea Around Us* Project model**		
AUC1	0.9985	0.7202
AUC2	0.9994	0.7420
AUC3	1.0000	0.7092
AUC4	0.9960	0.7154
Average AUC	0.9985	0.7217
AUC 1000km buffer	0.9645	0.6570
PBC1	0.7282	0.2984
PBC2	0.7476	0.3009
PBC3	0.7650	0.2853
PBC4	0.7442	0.2587
Average PBC	0.7462	0.2858
PBC 1000km buffer	0.6840	0.1472

M. molva	***S. solea***	***P. maxima***	***S. rhombus***	***S. pilchardus***
(minimum depth 15m)	**496**	**504**	**519**	**522**
n/a	0.9810	0.9770	0.9790	0.9780
n/a	0.9780	0.9790	0.9810	0.9760
n/a	0.9780	0.9770	0.9790	0.9780
n/a	0.9790	0.9790	0.9710	0.9760
n/a	0.9790	0.9780	0.9775	0.9770
n/a	0.9984	0.9985	0.9999	0.9979
n/a	0.9655	0.9880	0.9878	0.7933
n/a	0.9753	0.8866	0.7977	n/a
n/a	0.9531	0.8871	0.7944	n/a
n/a	0.7431	0.7894	0.8026	0.9601
n/a	0.7054	0.7727	0.7778	0.7344
n/a	0.7396	0.6844	0.5841	n/a
n/a	0.7088	0.6727	0.5679	n/a
n/a	0.9780	0.9443	0.9795	0.9784
n/a	0.9565	0.9699	0.9449	0.9827
n/a	0.9790	0.9657	0.9766	0.9907
n/a	0.9549	0.9489	0.9705	0.9869
n/a	0.9671	0.9572	0.9679	0.9847
n/a	0.8760	0.8645	0.9297	0.9280
n/a	0.9527	0.8610	0.8091	n/a
n/a	0.9333	0.8461	0.7907	n/a
n/a	0.8266	0.7830	0.8821	0.8402
n/a	0.8218	0.8250	0.8158	0.8614
n/a	0.8028	0.8560	0.8946	0.8711
n/a	0.7987	0.8244	0.8327	0.8987
n/a	0.8125	0.8221	0.8563	0.8679
n/a	0.6919	0.6356	0.7692	0.7562
n/a	0.7990	0.6953	0.6188	n/a
n/a	0.7520	0.6523	0.5814	n/a
0.9124	0.9845	0.8892	0.8460	0.9553
0.9490	0.9792	0.8893	0.8532	0.9688
0.9431	0.9848	0.8928	0.8479	0.9765
0.9402	0.9934	0.8874	0.8570	0.9477
0.9362	0.9855	0.8897	0.8510	0.9621
0.8172	0.9231	0.8720	0.8037	0.7888
0.5337	0.6606	0.6119	0.5103	0.6705
0.5393	0.6641	0.6252	0.5364	0.6968
0.5365	0.6577	0.6470	0.5255	0.7104
0.4879	0.6841	0.6429	0.5345	0.7000
0.5244	0.6666	0.6318	0.5267	0.6944
0.3165	0.5692	0.6045	0.4620	0.4317

S. sprattus	***M. merluccius***	***P. platessa***	***M. merlangus***	***P. virens***
584	**619**	**619**	**623**	**691**
0.9760	0.9740	0.9740	0.9740	0.9770
0.9780	0.9760	0.9750	0.9760	0.9790
0.9750	0.9750	0.9760	0.9740	0.9770
0.9750	0.9710	0.9740	0.9730	0.9790
0.9760	0.9740	0.9748	0.9743	0.9780
0.9952	0.9941	0.9964	0.9998	0.9935
0.9741	0.9376	0.9794	0.9901	0.9722
n/a	0.9912	0.9900	0.9918	0.9922
n/a	0.9540	0.9755	0.9818	0.9741
0.7518	0.7859	0.7785	0.7720	0.7768
0.7294	0.6856	0.7545	0.7573	0.7465
n/a	0.7855	0.7770	0.7684	0.7773
n/a	0.6889	0.7537	0.7543	0.7485
0.9814	0.9778	0.9769	0.9782	0.9544
0.9985	0.9573	0.9648	0.9746	0.9567
0.9951	0.9669	0.9720	0.9695	0.9677
0.9943	0.9775	0.9585	0.9673	0.9601
0.9923	0.9699	0.9681	0.9724	0.9597
0.9262	0.8237	0.9521	0.9494	0.9043
n/a	0.9653	0.9664	0.9714	0.9656
n/a	0.8692	0.9605	0.9525	0.9371
0.8678	0.8702	0.8645	0.8618	0.8320
0.9006	0.7989	0.8424	0.8568	0.8615
0.9017	0.8495	0.8461	0.8649	0.8734
0.9066	0.8586	0.8404	0.8314	0.8582
0.8941	0.8443	0.8484	0.8537	0.8563
0.7477	0.6308	0.8116	0.8061	0.7415
n/a	0.8359	0.8402	0.8421	0.8527
n/a	0.6934	0.8292	0.8093	0.7905
0.9653	0.8455	0.8896	0.9879	0.9564
0.9542	0.9406	0.9125	0.9972	0.9587
0.9529	0.9563	0.9146	0.9973	0.9381
0.9682	0.9482	0.9184	0.9901	0.9383
0.9601	0.9226	0.9088	0.9931	0.9479
0.9179	0.6670	0.8496	0.9575	0.9188
0.7937	0.4204	0.6245	0.7420	0.6652
0.7756	0.6472	0.6245	0.7500	0.6247
0.7831	0.7054	0.6149	0.7691	0.6119
0.8099	0.6819	0.6447	0.7294	0.6292
0.7906	0.6137	0.6272	0.7476	0.6328
0.7186	0.0868	0.5647	0.7079	0.6058

S. scombrus	*M. aeglefinus*	*G. morhua*
926	**873**	**1323**
0.9610	0.9630	0.9460
0.9580	0.9610	0.9480
0.9610	0.9630	0.9430
0.9530	0.9610	0.9380
0.9583	0.9620	0.9438
0.9847	0.9930	0.9951
0.8679	0.9674	0.9727
n/a	0.9353	0.9847
n/a	0.9099	0.9680
0.9336	0.7321	0.7682
0.7629	0.6807	0.7366
n/a	0.6970	0.7721
n/a	0.6349	0.7376
0.9727	0.9660	0.9474
0.9700	0.9622	0.9371
0.9813	0.9635	0.9430
0.9758	0.9763	0.9461
0.9750	0.9670	0.9434
0.8845	0.9255	0.8937
n/a	0.9310	0.9644
n/a	0.9082	0.9333
0.7842	0.8207	0.7653
0.8141	0.8287	0.7635
0.8247	0.8360	0.7489
0.8006	0.8442	0.7804
0.8059	0.8324	0.7645
0.6701	0.7531	0.6678
n/a	0.7808	0.7759
n/a	0.7213	0.7262
0.9926	0.9591	0.9796
0.9932	0.9394	0.9686
0.9939	0.9532	0.9753
0.9908	0.9546	0.9644
0.9926	0.9515	0.9720
0.9256	0.9155	0.9475
0.7834	0.6755	0.7004
0.8306	0.6431	0.6432
0.8062	0.6913	0.6824
0.8053	0.6951	0.6619
0.8064	0.6762	0.6720
0.6882	0.6154	0.6561

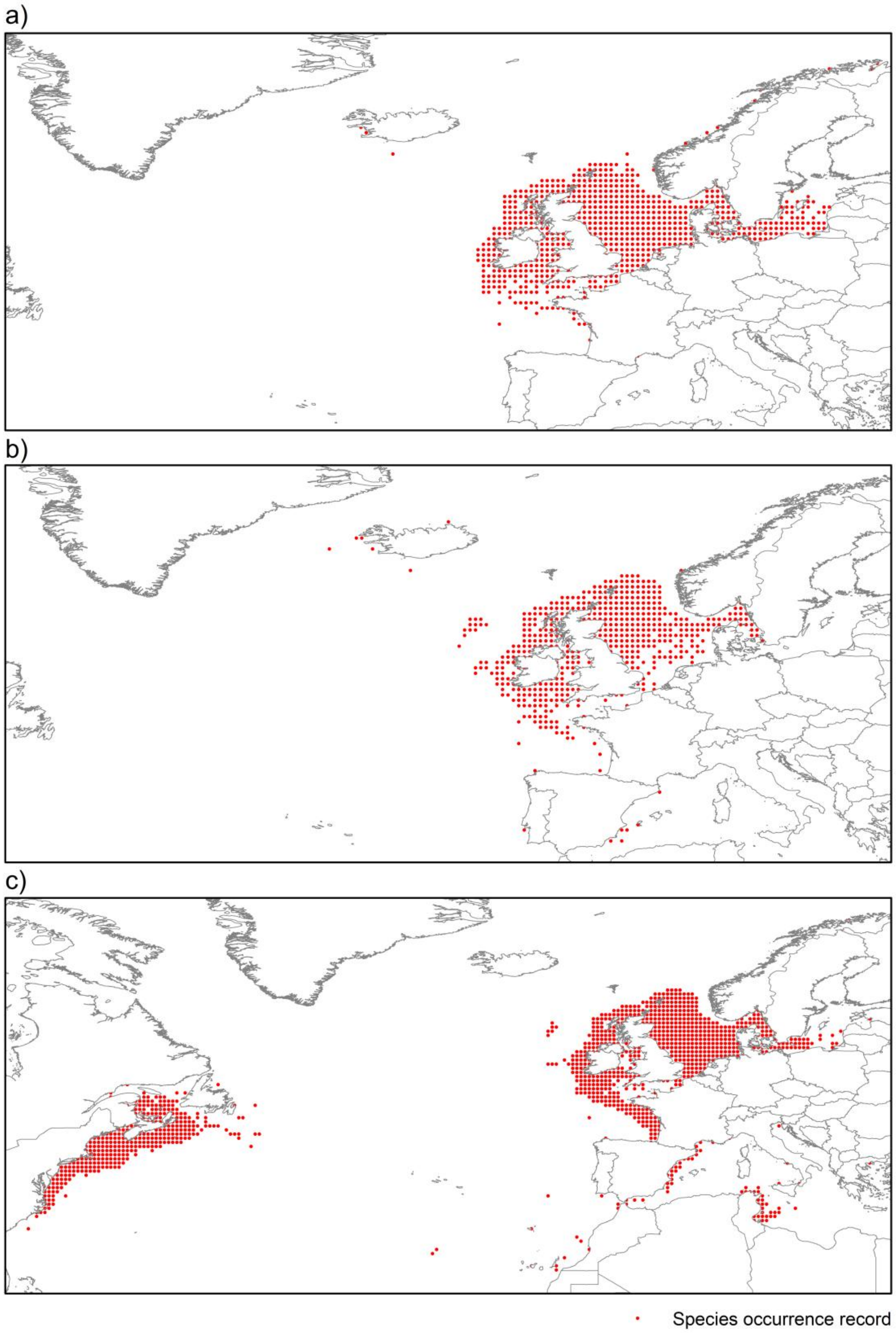


Figure 2.1. *Occurrence records for a) P. platessa b) M. molva c) S. scombrus collated from GBIF, OBIS and the ICES EcoSystemData database and cleaned according to the procedure detailed in the Methods section.*

Chapter 3

Predicting the Impact of Climate Change on Threatened Species in UK Waters

Published as:

Jones, M.C., Dye, S.R., Fernandes, J.A., Frölicher, T.L., Pinnegar, J.K., Warren, R., and Cheung, W.W.L. (2013) Predicting the impact of climate change on threatened species in UK waters. *PLoS ONE* **8**, e54216.

Abstract

Global climate change is affecting the distribution of marine species and is thought to represent a threat to biodiversity. Previous studies project expansion of species range for some species and local extinction elsewhere under climate change. Such range shifts raise concern for species whose long-term persistence is already threatened by other human disturbances such as fishing. However, few studies have attempted to assess the effects of future climate change on threatened vertebrate marine species using a multi-model approach. There has also been a recent surge of interest in climate change impacts on protected areas. This study applies three species distribution models and 2 sets of climate model projections to explore the potential impacts of climate change on marine species by 2050. A set of species in the North Sea, including seven threatened and ten major commercial species were used as a case study. Changes in environmental suitability in selected candidate protected areas around the UK under future climatic scenarios were assessed for these species. Moreover, change in the degree of overlap between commercial and threatened species ranges was calculated as a proxy of the potential threat posed by overfishing through bycatch. The ensemble projections suggest northward shifts in species at an average rate of 27 km per decade, resulting in small average changes in range overlap between threatened and commercially exploited species. Furthermore, the adverse consequences of climate change on the environmental suitability of protected areas were projected to be small. Although the models shows large variation in the predicted consequences of climate change, the multi-model approach helps identify the potential risk of increased exposure to human stressors of critically endangered species such as common skate (*Dipturus batis*) and angelshark (*Squatina squatina*).

1. Introduction

The last 100 years have seen significant changes in the global climate that are very likely to be attributed to anthropogenic greenhouse gas emissions (IPCC 2007). Mean global surface temperature has increased by approximately 0.1 °C per decade since the late 1950s and is projected to be 1.4 – 2.1 °C above pre-industrial levels by 2050 (IPCC 2007), with temperatures increasing in the Arctic at almost twice the global rate in the last century. Furthermore, the ocean is becoming more acidic and less oxygenated (IPCC 2007; Deutsch *et al.* 2011). Climate change has been observed to be having a profound effect on both marine and terrestrial biodiversity (Root *et al.* 2003; Parmesan and Yohe 2003; Hobday *et al.* 2006), and this trend is expected to continue, with associated changes in species compositions (Stralberg *et al.* 2009), distributions (Parmesan and Yohe 2003) and phenological patterns (Fitter and Fitter 2002). Concern over the impact of climate change in the marine environment is also increasing, with longer-term shifts in mean environmental conditions and climatic variability moving outside the bounds within which adaptations in marine communities have previously been associated (Beaugrand 2004). The changes in abundances and distributions that result from these ocean-atmospheric changes may severely impact the biological and environmental functioning of ecosystems or food webs (Harborne and Mumby 2011), the goods and services derived from them and conservation and resource management (Cheung *et al.* 2010; Sumaila *et al.* 2011).

The effects of climate change on threatened or endemic species (those unique to a defined geographic area) are of particular concern. These species are frequently restricted to relatively small areas and population sizes and may have highly specific environmental requirements, likely reducing their adaptive capacity to climatic change (Lawton *et al.* 1994). In addition, lack of knowledge or data concerning the abundance, dispersal and life history characteristics of threatened species is common. Recent years have thus seen an increase in studies attempting to assess how climate change might impact threatened and endemic species in terrestrial environments (Thomas *et al.* 2004; Thuiller *et al.* 2006; Hu and Jiang 2011) and how conservation goals and actions should adapt in a changing climate (Fuller *et al.* 2008; Hagerman *et al.* 2010; Cianfrani *et al.* 2011). There are far fewer studies, however, that attempt to assess the impacts of environmental and climate change on threatened marine vertebrate species. This is likely due to the issue of scarce and unreliable data available for the marine environment (Kaschner *et al.* 2006). Furthermore, there has been little attempt to assess the interactions between climate change and other anthropogenic stressors, such as fishing, on threatened marine species.

Climate and ocean changes may also affect threatened species by influencing the efficacy of measures designed to protect them. Specifically, marine protected areas are a major tool to conserve marine biodiversity (Toropova *et al.* 2010) and have been shown to enhance population resilience to climate-driven disturbance (Micheli *et al.* 2012). However, their effectiveness may itself be influenced by climate change. For example, future climate change has been predicted to reduce the amount of suitable environmental space for particular species that falls within current protected areas (Coetzee *et al.* 2009;

Cianfrani *et al.* 2011), thereby reducing its future conservation value. There is a need to increase the robustness and enhance resilience of protected areas to climate change (Conroy *et al.* 2011; Lemieux *et al.* 2011). By assessing the degree of future environmental change within proposed protected areas, conservation planning may thus be used to protect against biodiversity loss (Dockerty *et al.* 2003; Rose and Burton 2009).

Species Distribution Modelling has been widely used to predict the potential impacts of climate change on both terrestrial (Araujo *et al.* 2006; Hijmans and Graham 2006; Elith *et al.* 2010) and marine species (Cheung *et al.* 2009; Albouy *et al.* 2012; Blanchard *et al.* 2012). The bioclimatic envelope is defined here as a set of physical and biological conditions suitable for a given species (Cheung *et al.* 2008) and is frequently obtained by using statistically or theoretically derived methods to associate current climatic variables with species occurrences. By predicting a species' current range as the manifestation of environmental characteristics that limit or support its existence at a particular location, a shift in that range may be elucidated by assessing shifts of the bioclimatic envelope under climate change scenarios. Species Distribution Models (SDMs) are able to predict species' distributions with presence only data and also perform well under small sample sizes (see (Guisan and Zimmermann 2000; Guisan and Thuiller 2005; Elith *et al.* 2006) for an overview of methods). Applications of SDMs have been criticised (Botkin *et al.* 2007) and it is acknowledged that some SDMs over-simplify the mechanisms determining species' distributions. However, recently developed modelling approaches have increasingly addressed these criticisms (Kearney *et al.* 2010; Cheung *et al.* 2011). SDMs also remain useful in exploring the possible magnitude and direction of species' distribution shift under climatic change. Furthermore, key uncertainties in using SDMs to assess climate change impacts on marine biota, which stem from the differences in the structure of the SDMs and the underlying climate forcing, can be explored by comparing outputs from multiple SDMs and climate models. Using multiple SDMs with a range of complexity, data requirement and statistical mechanisms is therefore a more robust way to assess species' distributions (Jones *et al.* 2012). Climate scenarios developed from multiple models are also considered to be more robust than using a single model as climate models vary in complexity and reliability, with uncertainty being introduced by data input as well as interpolation method. There is therefore a need to compare future species' distribution predictions made using alternative SDM algorithms, Global Climate Models (GCMs) and species' occurrence/ environmental tolerance data. The uncertainties in outputs resulting from these variations help us understand the range of potential predictions, the extent of agreement between them as well as possible extremes.

This study aims to assess the potential impact of climate change on a set of threatened species [under the International Union for Conservation of Nature (IUCN) Red List of Threatened species] predominantly inhabiting the North Sea, Northeast Atlantic and Mediterranean Sea. These species are primarily threatened by overfishing through being by-catch of commercially important fisheries (Ellis 2005; Dulvy *et al.* 2006; Ellis *et al.* 2009; IUCN 2011). They are vulnerable to fishing due to particular life history characteristics which make them intrinsically sensitive to overexploitation, such as large body sizes, late maturation and consequential slow rates of population increase (Dulvy *et al.* 2003; Cheung *et al.* 2005). I express the level of impacts on these threatened species in terms of changes in range area, changes in environmental suitability throughout the species' ranges and within key protected areas around the UK, and of the possibility of bycatch. The latter is indicated by the predicted range overlap between threatened species and commercially exploited species. I hypothesize that the relative suitability of protected areas for threatened species would change as climate and ocean conditions change, thus influencing their efficacy in protecting threatened species. If both the threatened and targeted species respond similarly in direction and magnitude of distribution shift, the range overlap between species will remain similar under climate change. In contrast, if the response to climate change is species specific (Edwards and Richardson 2004; Portner and Knust 2007) and varies to a large degree, change in overlap may be expected. I examine these hypotheses by using three modelling approaches, AquaMaps, Maxent and the Dynamic Bioclimate Envelope model (DBEM) (Cheung *et al.* 2011; Jones *et al.* 2012), to project future changes in distributions of threatened and commercially exploited species in the North Sea, and their changes relative to the distributions of example protected areas. I also examine uncertainty of the projections. Finally, I discuss the implications of results found on the threat facing these species, their likely persistence and on the conservation value of protected areas.

2. Methods

2.1. Modelling Approaches

I applied three Species Distribution Models to predict the distributions of seven threatened and ten targeted fish species (Table 3.1). The SDMs are summarized here and described in greater detail in the supplementary methods, Appendix 2, and publications indicated. Two of these, Maxent (Phillips *et al.* 2006) and AquaMaps (Kaschner *et al.*

2006), apply a statistical approach to model species' distributions. These models were designed to overcome the problems of small sample sizes in presence-only datasets (Pearson *et al.* 2007) and the lack of data and knowledge for many marine species respectively. Maxent (Phillips *et al.* 2004) and AquaMaps (Kaschner *et al.* 2006) both use generative approaches to estimate the environmental co-variates conditioning species' presence from presence only occurrence data and a suite of environmental variables. Using presence only data enabled the potential of the increasing quantity of publically available, presence only datasets to be explored and was also considered more appropriate as recorded absence at a location may not reflect true absence or may not result from tolerance limits of environmental variables included in the models. While Maxent applies a complex methodology, based on the principle of maximum entropy, AquaMaps uses simple, numerical descriptors of species' relationships with environmental variables to predict distributions from occurrence databases (see supplementary information). Species' current distributions (averaged over 30 years from 1971 to 2000) were predicted by associating species' occurrence data with averaged 'current' environmental data (1971 – 2000), thereby obtaining a bioclimatic envelope for each species. Models trained on the set of current environmental data were then 'projected' by applying them to the same environmental variables representing future climate.

Expert opinion was incorporated into Maxent and AquaMaps to refine predictions by eliminating ('clipping') areas that were currently outside known occurrence ranges, including reported occurrence/absence in large ocean basins [delineated by the United Nations' Food and Agricultural Organisation (FAO) statistical area, www.fao.org/fishery/area/search/en] or depth limits (Jones *et al.* 2012). The use of large ocean-basin and wide depth limits in 'clipping' considered both the current and potential future-shifted distribution. The 'clipping' procedure avoided over-prediction of relative environmental suitability in areas of the world where species are known not to occur, or which are unsuitable due to depth. Although depth was included in each model to retain the relative environmental suitability due to depth, maximum tolerance limits may be over-estimated in Maxent and AquaMaps due to the relatively low resolution of depth and occurrence data, in particular at the edge of the continental shelf, thereby over-predicting range extent. Maximum depth limits obtained from Fishbase (Froese and Pauly 2011) were increased by 50% in predictions for both time periods. This allowed for the deepening of species with ocean warming that has been observed (Dulvy *et al.* 2008) while preventing difference in predictions between the two time periods being inflated by applying different depth cut off points.

The third model, DBEM (Cheung *et al.* 2011), combines statistical and mechanistic approaches in predicting species' distributions. It attempts to avoid the bias that might be introduced by the skewed distribution of sampling effort present in many datasets collected sporadically. Firstly, the associated *Sea Around Us Project* model (Close *et al.* 2006) is used to predict a species' current distribution based on a set of 'filters', restricting a distribution based on known parameters, geographic limits or habitat preferences. Filters were applied for FAO area, habitat, latitudinal limits and depth. The DBEM then uses the predicted current distribution to define a species' bioclimatic envelope by its 'preference profile' (the relative suitability of different environmental values) for each environmental variable. Change in a species' relative abundance following changing environmental conditions is then simulated by incorporating a population growth model (Cheung *et al.* 2008) as well as ecophysiological parameters (Cheung *et al.* 2008, 2011) (see supplementary information). Comparison between model hindcast and historical distribution changes of fishes and invertebrates from the 1970s to the 2000s in the Bering Sea and Northeast Atlantic suggest that DBEM has significant predictive skills for species distribution shifts in these regions (Barange *et al.* 2010).

2.2. Species' occurrence data

Two sets of species were selected to investigate how altered range distributions under climate change might impact species that are threatened by overfishing through bycatch. I assume that the degree of range overlap between a commercially targeted species and one classified here as 'threatened' is an indication of bycatch potential of the threatened species. Ten commercially targeted demersal species, being the top nine fish species and the top invertebrate species by value of landings that were caught by fleets in UK waters in 2006 - 2010 (Marine Management Organisation, MMO) (MMO 2011), were included (Table 3.1). Although some of these species may also be listed as endangered, for example under the IUCN Red List (IUCN 2011), they are still considered main commercial species by the fisheries. A further set of species of conservation concern, henceforth 'threatened', was chosen from the IUCN Red List of Threatened Species (IUCN 2011), the Convention for the Protection of the Marine Environment of the North-East Atlantic ('OSPAR' Convention) List of Threatened and/or Declining Species (OSPAR 2008), and the UK Biodiversity Action

Plan (UK BAP) priority marine species (BRIG 2007). These species are specifically threatened by bycatch and have ranges restricted to the North Sea, East Atlantic Ocean and Mediterranean Sea (Table 3.1).

Table 3.1. *Commercially targeted and threatened species selected for the study. (OSPAR: Convention for the Protection of the Marine Environment of the North-East Atlantic; BAP: UK Biodiversity Action Plan.)*

Commercially targeted species			
Scientific name	**Common Name**	**Landed Value 2010 (£ million)**	
Nephrops norvegicus	Norway lobster	95.3	
Lophius piscatorius	Anglerfish/Monkfish	38.5	
Melanogrammus aeglefinus	Haddock	36.2	
Gadus morhua	Atlantic cod	28.6	
Solea solea	Common Sole	14.0	
Pollachius virens	Saithe	12.4	
Merluccius merluccius	European Hake	10.2	
Lepidorhombus whiffiagonis	Megrim	10.1	
Merlangius merlangus	Whiting	9.4	
Microstomus kitt	Lemon sole	6.3	
Threatened species			
Scientific name	**Common Name**	**IUCN Red List**	**Other lists**
Dipturus batis	Common skate	Critically Endangered	OSPAR, BAP
Squatina squatina	Angelshark	Critically Endangered	OSPAR, BAP
Raja undulata	Undulate ray	Endangered	BAP
Rostroraja alba	White skate	Endangered	OSPAR, BAP
Leucoraja circularis	Sandy ray	Vulnerable	BAP
Raja clavata	Thornback ray	Near Threatened	OSPAR
Scyliorhinus stellaris	Nursehound	Near Threatened	

Species occurrence data were obtained from three global online databases: the International Council for Exploration of the Sea (ICES) EcoSystemData database (http://ecosystemdata.ices.dk); the Ocean Biogeographic Information System (OBIS)

(Vanden Berghe, 2007; http://www.iobis.org) and the Global Biodiversity Information Facility (GBIF) (http://data.gbif.org), all last accessed in 2011. Occurrence records were spatially aggregated on a 0.5° latitude x 0.5° longitude grid and rigorously filtered according to criteria detailed in Jones *et al.* (2012). This minimised recording errors due to data being compiled from many sources and gave a binary value of presence or absence of each species for each cell. Maps showing the distribution of occurrence records for each species are shown in the thesis Appendix.

2.3. Projecting distribution shifts under climate change

A range of environmental oceanographic variables for predicting species' distributions were chosen, including bathymetry, sea surface temperature (SST), sea bottom temperature (SBT), salinity, sea ice concentration, primary productivity, and distance to coast. The DBEM used additional variables mentioned previously. Ocean oceanographic variables were interpolated onto a 0.5° latitude x 0.5° longitude global grid using the nearest-neighbour method. Models were trained for each of 2 sets of average annual climatic data covering 1971 – 2000, the period corresponding as far as possible to the average climatic conditions over which occurrence data were compiled. For Maxent and Aquamap, predictions were subsequently projected into the future using a 30 year average centred on 2050. For DBEM, the model simulates changes in distribution over an annual time-step from 1971 to 2050. Environmental datasets (including physical variables as well as O_2 concentration, pH and primary productivity) were obtained from Geophysical Fluid Dynamics Laboratory's Earth System Model (GFDL ESM2.1, (Dunne *et al.* 2010)) and a further set of physical climate data (including SST, SBT, salinity and ocean advection) obtained from the World Climate Research Program (WCRP) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model dataset (http://esg.llnl.gov:8080). These data represented an ensemble of 12 different models that assessed by the fourth assessment of the Intergovernmental Panel on Climate Change (IPCC AR4), henceforth referred to as CMIP3-E. Both climatic datasets were modelled under the SRES A2 emissions scenario and are thus characterised by a heterogenous world with a continuously increasing global population and regionally orientated economic development (IPCC 2000).

The changes in range of the seven threatened species were predicted under two scenarios of dispersal: no dispersal and full dispersal. Under the no dispersal scenario, distributions of the species were restricted to their predicted current range only and the species could not colonize areas outside its current distribution. In contrast, under the full dispersal scenario, a species' distribution could shift into all potentially suitable environmental space using Maxent and AquaMaps and, in the case of DBEM, all suitable environmental space within the projected dispersal range (Cheung *et al.* 2008). The scenario of no dispersal here represents a precautionary, conservative view and, following this assessment, the scenario of full dispersal is used throughout, agreeing with the observed ability of marine aquatic organisms to disperse under environmental change (Perry *et al.* 2005; Henderson 2007).

A range of thresholds of minimum environmental suitability were applied to investigate the effect of excluding cells with lower levels of predicted environmental suitability on the analysis. Specifically, predicted environmental suitability values that are lower than the specific threshold equal 0. Thus, specific thresholds determine the extent of a species' most suitable (core) range. Thresholds are frequently used to transform the continuous predictions of relative suitability produced in species distribution modelling into predictions of presence/absence. There are several methods for selecting thresholds and their possible impacts on predicted distributions have been explored and discussed in the literature (Fielding and Bell 1997; Liu *et al.* 2005; Nenzén and Araújo 2011). However, there is currently no consensus on the most suitable and stable method for applying thresholds to species' range projections (Nenzén and Araújo 2011). As such, occurrence datasets for each species were split into 75% and 25% for model training and testing, respectively, and used to find the threshold that maximised accuracy of the model in predicting the observed occurrences/absences of a species (maximum training sensitivity plus specificity) (Liu *et al.* 2005). This was implemented using the ROCR package in R (Sing *et al.* 2007). Three fixed thresholds, of 0.05, 0.5 and 0.7, were applied to investigate the effect of increasingly restricting distributions and the implications for conclusions drawn from analysing the predicted distributions.

2.4. Latitudinal centroids

Based on the results from the full dispersal scenario for each model, the average degree of range shift was calculated for each species in 2050 (average of 2036 to 2065) relative to 1985 (average of 1971 to 2000). This was done for each SDM, climatic dataset and each of the 4 thresholds and was calculated using an equation for distribution centroids, equation (1) (Cheung *et al.* 2009):

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

where Lat_i is the latitude of the centre of the spatial cell (i), Abd is the predicted relative abundance in the cell, and n is the total number of cells (Cheung *et al.* 2009). The difference between latitudinal centroids in projected and reference years was then calculated in kilometres (km) using equation (2) (Cheung *et al.* 2011):

$$Distance\ shift\ (km) = (Lat_m - Lat_n)\frac{\pi}{180} \times 6378.2 \tag{2}$$

2.5. Range overlap analysis

I used the degree of range overlap between the threatened species and the top 10 commercially targeted species in UK waters selected above as a proxy for investigating the degree of threat by overfishing through bycatch. I measured the potential overlap between the distributions of each threatened species with that of each targeted species using the Schoener's D index (Renkonen 1938; Schoener 1968), calculated by:

$$D(p_x, p_y) = 1 - \frac{1}{2}\sum_i |p_{x,i} - p_{y,i}| \tag{3}$$

where $p_{x,i}$ *and* $p_{y,i}$ denote the probability assigned in a species distribution model computed for species *x* and *y* to grid cell *i* respectively.

This index quantifies the degree of overlap between two probability distributions or predictions of relative suitability, ranging from no overlap (0) to identical distributions (1), and is equivalent to the percent similarity index as proposed by Renkonen (1938) (Renkonen 1938). It has further been suggested as being best suited to computing niche overlaps from potential species' distributions (Rödder and Engler 2011). A value of 0.1 was added to all 1985 values (D) to avoid extremely large percentage values caused by very low overlap in 1985 relative to the difference. The final overlap value thus represented the percentage difference in overlap relative to the 1985 value.

2.6. Environmental suitability in protected areas

I calculated the changes in environmental suitability for the threatened species in candidate protected areas within and around the UK, Dutch or German waters. A set of candidate Special Areas of Conservation (cSACs) (JNCC 2011) that cover a range of habitat types and latitudinal distributions were selected (Fig 3.1.). These sites were also chosen as being of appropriate size to the resolution of predicted species' distributions. Candidate SACs have been proposed but are yet to be adopted by the European Commission and formally designated by the local governments. They are designated for habitats and species listed on the Habitats Directive and include those areas considered to be in most need of conservation at a European level (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora 1992).

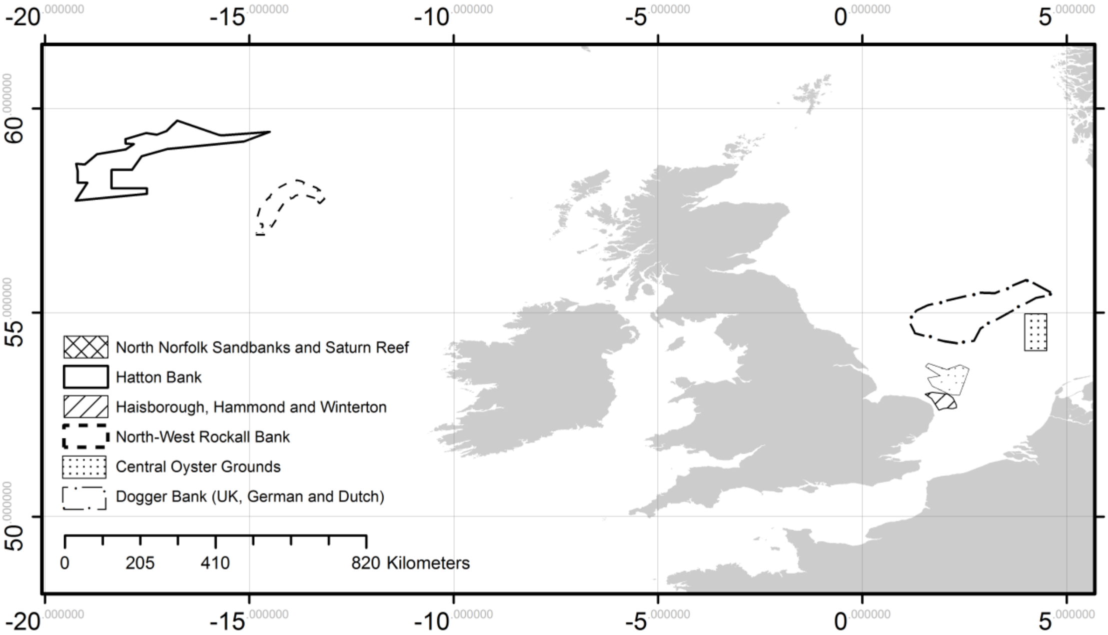


Figure 3.1. *Candidate Special Areas for Conservation included in this study.*

Under the Habitats Directive, Member States must take measures to maintain or restore natural habitats and wild species listed on the Annexes to the Directive at a favourable conservation status, introducing robust protection for habitats and species of European importance (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora 1992). These cSACs include the Dogger Bank (UK, German and Dutch), Haisborough, Hammond and Winterton, together with North Norfolk Sandbanks and Saturn Reef (HHW & NNS), the Central Oyster Grounds (COG) (Dutch), North-West Rockall Bank, and Hatton Bank (Fig. 3.1.). Relative environmental suitability values of my sample of species for all grid cells within each cSAC were obtained for 1985 and 2050. The relative suitability values for each species were standardized for each model across all cSACs, resulting in a value scale between 0 and 1. The change in relative environmental suitability between 1985 and 2050 (2050 value – 1985 value) was calculated for each 0.5° latitude x 0.5° longitude cell within a cSAC.

3. Results

Outputs from GFDL ESM2.1 suggest an average warming trend in the North Sea (Large Marine Ecosystems of the World 2012) from 1960 to 2065, with high interannual variability (Fig. 3.2.). The pattern is similar for SST and SBT, which is to be expected given that the North Sea is relatively shallow (average depth ≈ 90m). Average SST increases between 1985 and 2050 is 0.77°C and 1.27°C based on projections from GFDL ESM2.1 and CMIP3-E, respectively.

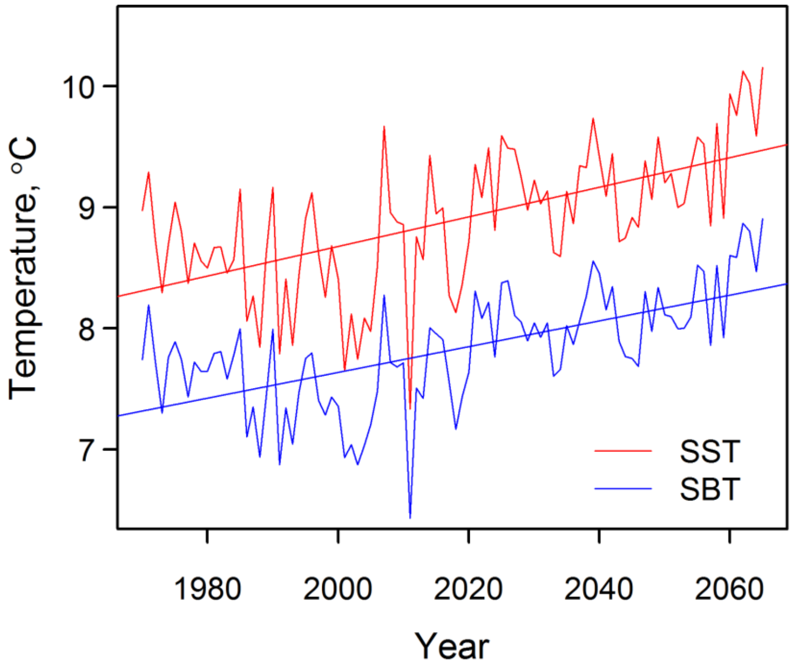


Figure 3.2. *Temperature trends from 1970-2065 in the North Sea.*
Sea Surface Temperature (SST) and Sea Bottom Temperature (SBT) trends in the North Sea were averaged over all cells at a 0.5° latitude x 0.5° longitude resolution.

3.1. Latitudinal centroids

Almost all models predicted northwards shifts in latitudinal centroid for the seven threatened species (Fig. 3.3.a) and 10 commercially exploited species (Fig. 3.3.b). Overall, my analysis projected that the distribution centroids of all species are expected to shift towards higher latitude from 1985 to 2050 under the SRES A2 scenario. The difference in poleward shift between commercially targeted and threatened species was not found to be significant when tested within each SDM model and climate dataset combination (two sample Wilcoxon test, p-value > 0.05, using species as replicates [Commercially Targetted: 10; Threatened: 6]) (Appendix 1. Fig. 3.1.). The median projected rates of poleward range shift are 167.0 and 185.6 km over 65 years, corresponding to 26 and 28 km decade^{-1} for commercially exploited and threatened species, respectively (Fig. 3.3.b). There is, however, variation within species predictions. For example, from 1985 to 2050, the predicted centroid distribution shift for *L. circularis* ranges from 8.9 km to 450km northwards while that for *R. undulata* ranges from 32 km southwards to 247 km northwards. Contrasting these projections, three out of six SDM/GCM model combinations predict a >600km northwards centroid shift for *S. stellaris* for the same period. *R. alba* was projected to shift at the fastest rate amongst the seven threatened species, reaching a maximum of 1046 km northwards by 2050 (threshold = 0.7). There is considerable variation in the predicted rate of range shift between SDMs, and to a lesser extent, between climate forcing used. However, no significant difference was found between latitudinal shifts projected using different SDM models within each of the two climate datasets, for both commercially targeted and threatened species (two sample Wilcoxon test, p-value > 0.05, using species as replicates [Commercially Targetted: 10; Threatened: 6]).

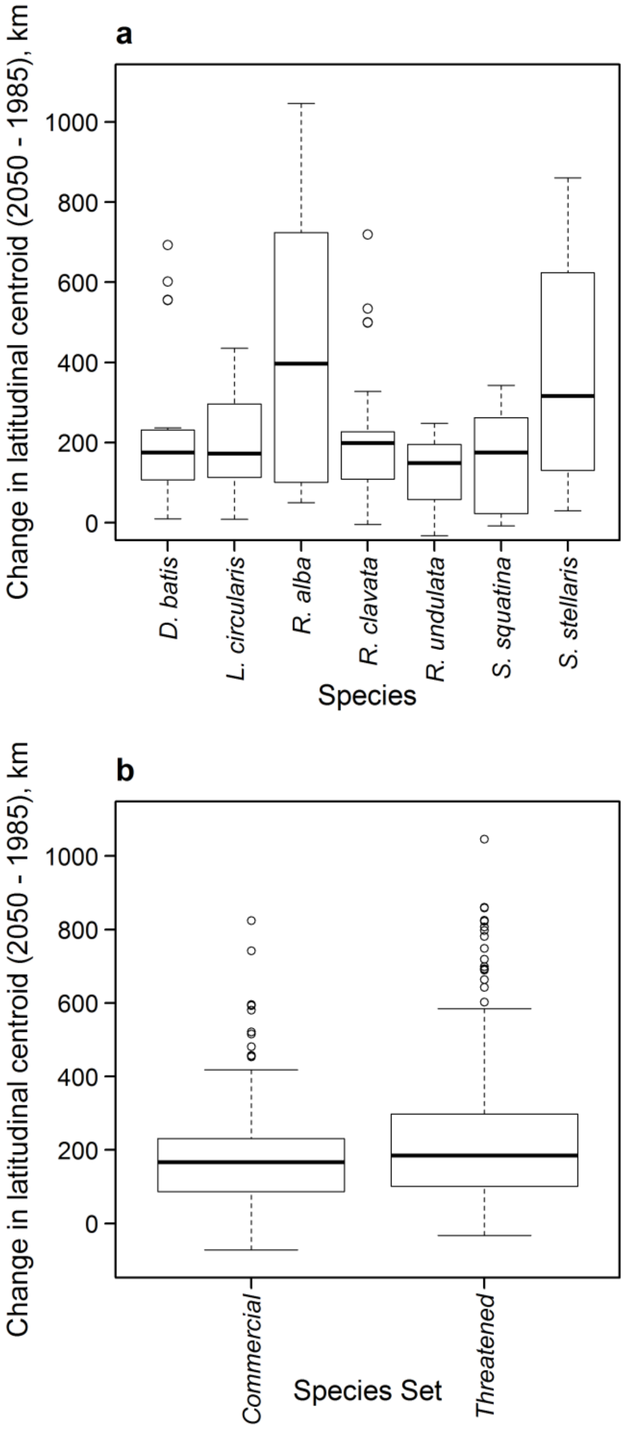


***Figure 3.3**. Shifts in latitudinal centroid for threatened and commercial species.*

Projected change (in km) in latitudinal centroid from 1985 to 2050 across the six SDM and climatic dataset combinations for a) each threatened species b) threatened and commercial species, grouped. Thick bars represent median values, the upper and lower ends of the box the upper and lower quartiles of the data, and the whiskers the most extreme datapoints no greater than 1.5 times inter-quartile range from the box. Points that are more extreme than whiskers are represented as circles.

3.2. Predicted changes in range area

Changes in area of predicted suitable environmental space between 1985 and 2050 vary considerably, both between species and models (Fig. 3.4.). Maxent and DBEM in general project net gains or no change in range area while AquaMaps frequently predicts net losses. More specifically, *L. circularis*, *R. clavata* and *S. stellaris,* were projected to have a net loss in range area by 2050 using 3 out of 6 model SDM-GCM combinations. While a net loss in range area is also seen in *R. alba* using the DBEM with CMIP3-E data, it contrasts the prediction with GFDL data that shows a net gain. The trend of predicted range area also varies between different climate forcing for *D. batis, S. squatina and R. alba*. Furthermore, the highest predicted gain (53.08%) and loss (22.44%) in area as a percentage of the 1985 range area were both predicted for *L. circularis.* The outlying points in Figure 3.4. are caused by *L. circularis* and *D. batis,* which are predicted to increase their range area by 53.08% and 42.17% respectively, using the DBEM model. These larger increases in range area are due to the DBEM- CMIP3-E model combination predicting greater range expansions to the northeast and West Atlantic than is seen for other models.

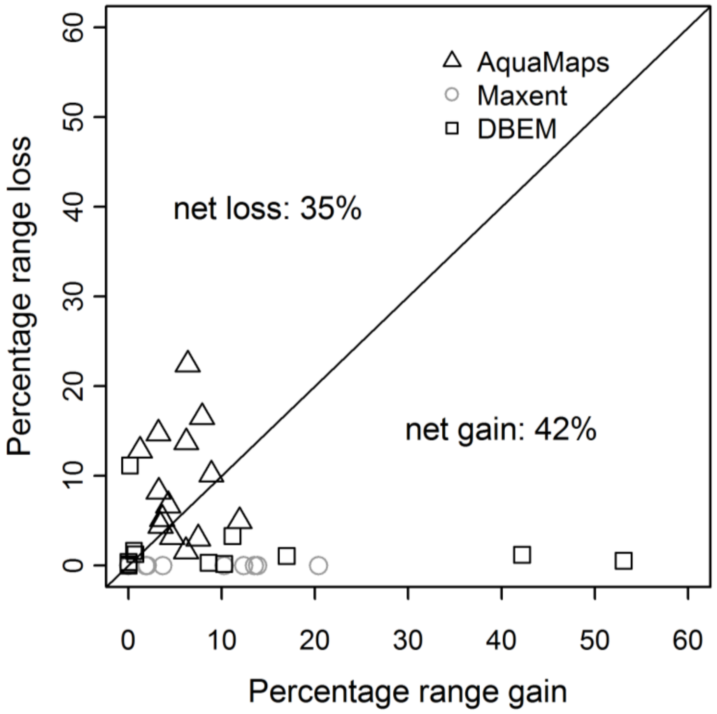


Figure 3.4. *Changes in range area.*

Range loss and gain assuming no dispersal and full dispersal, respectively, between 1985 and 2050 for each SDM using GFDL and CMIP3-E climatic datasets.

3.3. Analysis of Range Overlap

The overall median change in range overlap between threatened and commercial species (expressed as a percentage of the 1985 overlap value), across models and thresholds, is relatively small (+/- 4%). However, selected model/ threshold combinations projected large changes in overlap (exceeding +/- 50%) (Fig. 3.5.).

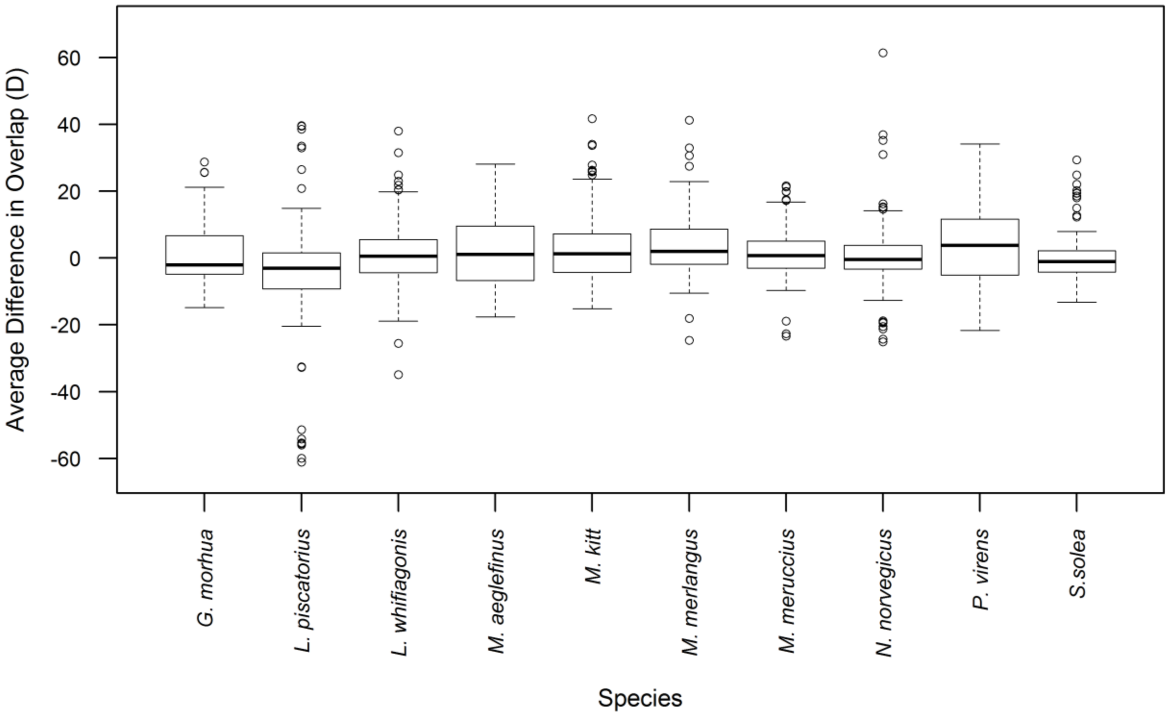


Figure 3.5. *Changes in range overlap between species. Range of predicted changes in overlap (Schoener's D) as a percentage of 1985 overlap value for each commercial species with all threatened species. Values shown include all threatened species, SDMs, climatic datasets and thresholds.*

All commercial species are predicted to decrease in overlap for at least one threatened species and modelling scenario. In contrast, all but two commercial species are, on average, projected to overlap more in predicted range with threatened species by 2050 (Supporting Information Table 3.1). The notable exception is *L. piscatorius,* which decreases in median overlap (median= -3.0%), particularly with *D. batis* (median = -0.7%, min = -61.1%) (Appendix 1. Fig. 3.2.a), *R. clavata* (median = -7.5%, min = -55.6) and *S. stellaris* (median = -5.8%, min = -51.7%). *R. alba* was projected to have the greatest increases in median range overlap across commercial species (mean = 4.9%). This species may thus be most likely to experience an increase in range overlap with the set of commercial species under climate change. *S. squatina,* on the other hand, was projected to have predominantly small, negative changes in median overlap across all commercial species (mean = -2.7%) and with only low variation between median values across species (-6% ≤ x ≤ 1%) (Appendix 1. Fig. 3.2.b). *D. batis* shows a small average change in median values (0.1%) but also varies most across all commercial species (-61.1% < x <34.2%). The commercial species showing the maximum increase in range overlap by 2050 is *N. norvegicus* (61.4%, overlap with *R. alba,* using a 0.5 threshold).

3.4. Change in relative suitability of key protected areas

The overall average change in relative environmental suitability (RES) over the protected areas is small, ranging between -0.03 and 0.09 from 1985 to 2050 (environmental suitability values lying between 0 and 1) (Fig. 3.6.a). All species except *S. stellaris* were projected to have almost no median change in overall environmental suitability across all protected area sites. However, some species and SDM-GCM combinations show larger projected change in relative environmental suitability between 1985 and 2050. The greatest mean increase in RES across all cSACs was, for example, projected for *S. stellaris* (0.08). This species, as well as *S. squatina,* with a mean increase in RES of 0.06 and minimum prediction of -0.008, is thus likely to experience an average increase in environmental suitability over all the cSACs by 2050. These proposed increases are reflected in the Dogger Bank, with relatively consistently high and increasing relative environmental suitability values for *S. squatina and S. stellaris* across climate forcing and SDMs (Appendix 1. Fig. 3.3.). In contrast, *R. clavata* shows a median decrease in relative environmental suitability across all cSACs. Although averaging a small, positive change in relative environmental suitability (0.002), *R. alba* shows a wide range of variation.

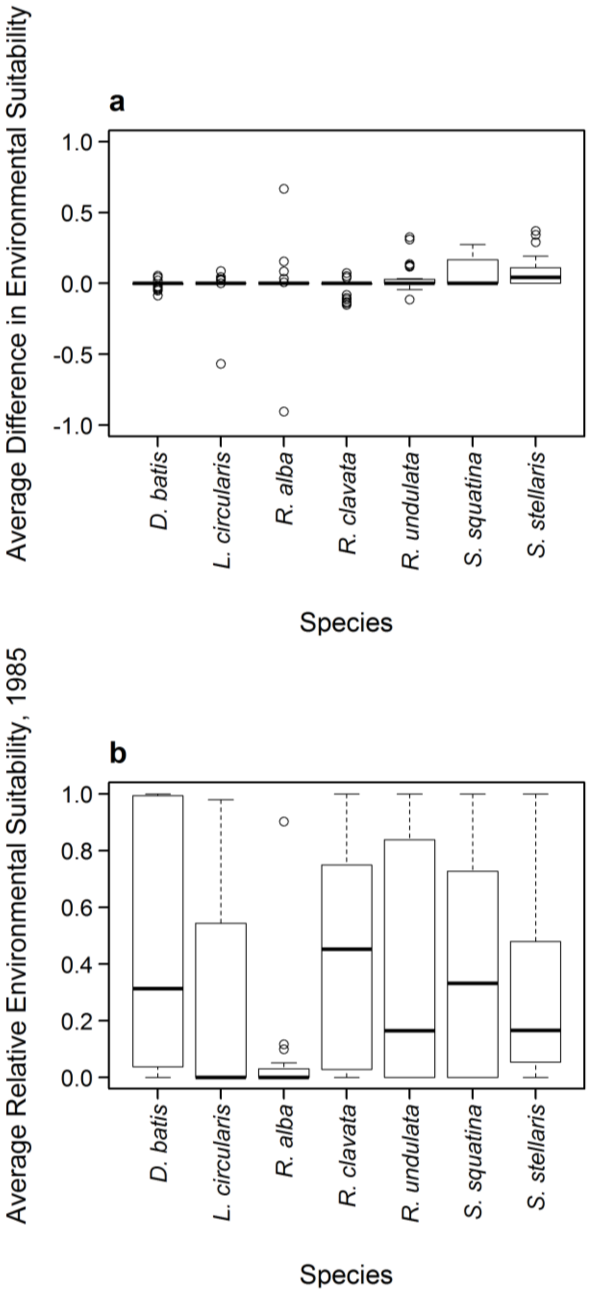


Figure 3.6. *Environmental suitability in assessed candidate Special Area of Conservation (cSAC). a) Average difference in relative suitability (2050 – 1985), b) average relative environmental suitability values in 1985 for each threatened species in all assessed cSACs.*

Comparing absolute values of predicted environmental suitability in 1985 (Fig. 3.6.b) is important as the impact of projected changes in RES will likely depend on how suitable that environmental space is currently for a particular species. For example, while the potential decrease in environmental suitability for *R. clavata* is accompanied by a mean environmental suitability in 1985 that is relatively high (0.43), the small potential increase (0.67) or decrease (-0.90) seen for *R. alba* accompanies a low average environmental suitability (0.05). A potential decrease in RES may therefore have more adverse effect on *R. alba* than *R. clavata*. The broad range of RES change observed for *R. alba* results from a strong predicted future increase in suitability of the Hatton Bank, using CMIP3-E data (Appendix 1. Fig. 3.4.), and a strong predicted decrease in suitability of the Rockall cSAC (Appendix 1. Fig. 3.5.). There are thus considerable variations in predictions between SDMs. This is highlighted in the case of *D. batis*, which shows consistencies in patterns of RES across cSACs within the modelling procedures but variation in the values of RES between models. *D. batis* is predicted to have highly suitable environmental space and no future decrease in RES in all SACs using AquaMaps (Appendix 1. Table 3.2). Although positive, predictions for *D. batis* are generally lower in Maxent, showing an average decrease in the future. Using DBEM, suitability predictions of *D. batis* in 1985 are low or decreasing, other than in Rockall. Similar patterns of variation in trends predicted by the three SDMs were projected for *S. squatina* and *S. stellaris.* In general, environmental suitability for the threatened species in most SACs was projected to improve slightly under climate change. Specifically, areas in the Rockall cSAC are projected to improve for threatened species in the future (Appendix 1. Fig. 3.5.).

3.5. Sensitivity Analysis

The projected range shifts were generally robust to different threshold values, although variations in the projections between different thresholds are high for selected species (Fig 3.7.). A notable difference in latitudinal shift caused by applying different thresholds to 1985 and 2050 distribution is seen in *R. alba and R. clavata* using the DBEM model.

For the most part there is also strong agreement in the patterns of overlap values between threshold predictions, with more variation caused by differences in SDMs and GCMs. Variation in overlap change was frequently seen using a 0.7 threshold. For example, whereas the overlap of predicted ranges for *L. circularis* and *M. kitt* was predicted to increase by 11.4% of that in 1985, using a 0.7 threshold and averaged across SDMs and GCMs, this decreases to < 2.5 % when a larger range of environmental suitability area is taken into account. Conversely, overlap for *R. alba* and *S. solea* was predicted to increase by 4% ≤ x ≤ 6% using most thresholds but decrease by 1.3% when ranges were reduced using the most restrictive threshold (0.7).

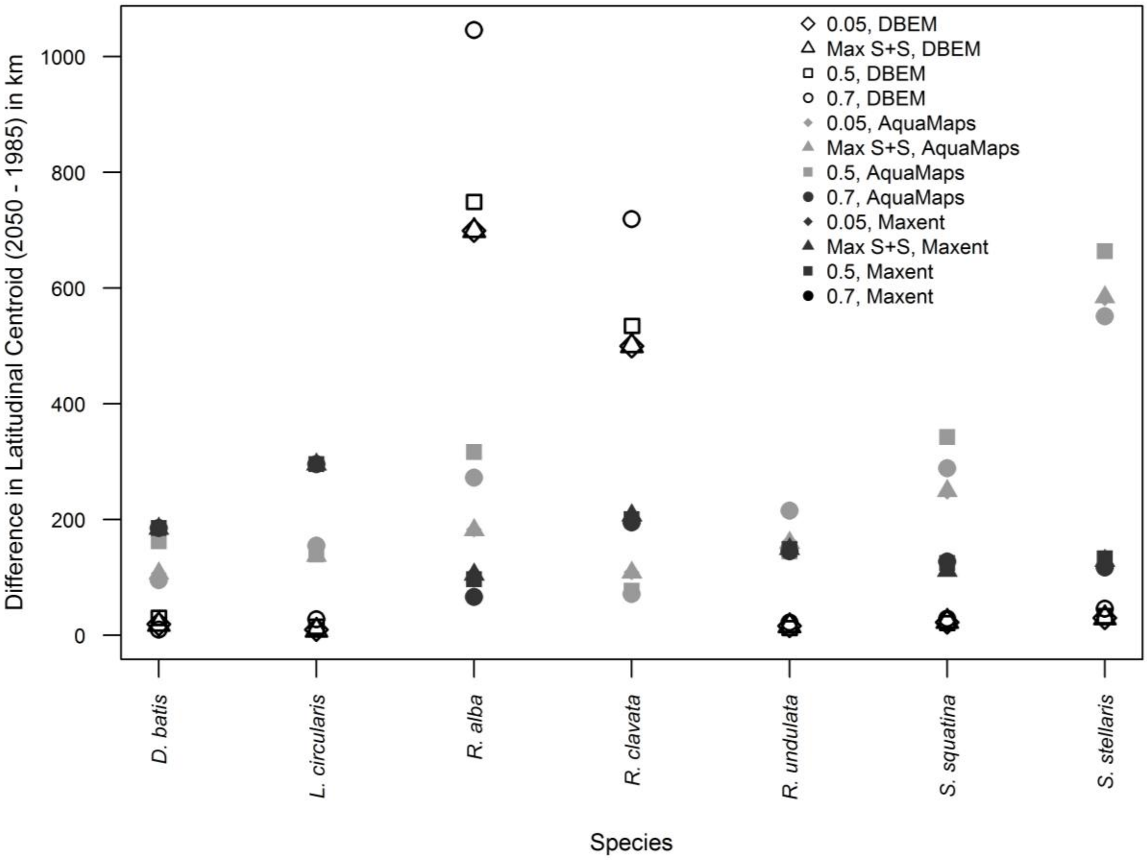


Figure 3.7. *Latitudinal centroid change with thresholds. Difference in latitudinal centroids (2050 minus 1985 values, in km) using different threshold to restrict predictions made using AquaMaps, Maxent and DBEM. Thresholds applied include the three fixed thresholds (0.05, 0.5 and 0.7) and that that of maximum training sensitivity plus specificity (Max S+S).*

4. Discussion

Analyses and results presented here highlight the variation in projections that can be obtained using different SDMs and GCMs in predicting species' distributions. For example, although differences between models in projecting northwards latitudinal shifts were not found to be significant, there are characteristic differences between predictions that reflect differences in model approaches and mechanisms. For example, the DBEM predicts a wider range of northwards movement across species, likely reflecting the incorporation of species specific values for intrinsic population growth, larval dispersal and adult migration. However, uncertainties and assumptions are inherent in any modelling procedure, in particular those projecting under novel, non-analogous climatic scenarios. It is therefore important to consider a range of plausible outcomes rather than applying only one prediction model. I thus further work for terrestrial species that proposes more robust predictions can be made by applying a multi-model or ensemble approach (Araújo and New 2007). Here, general trends from a suite of model combinations as well as individual projections or outliers are considered and discussed.

4.1. Latitudinal centroid shift

My projected northward shifts in species' distributions supported the hypothesis for poleward shifts in response to climate change. They also agree with observed changes for marine species in the last few decades (Perry *et al.* 2005; Dulvy *et al.* 2008; Simpson *et al.* 2011). In particular, my projected rate of latitudinal centroid shifts corresponds well to observations in the North Sea (Perry *et al.* 2005), where, out of 36 species examined, six species showed boundary shifts in relation to both climate and time at a rate of 22 km decade^{-1}. The projected rate of shift is smaller than that from a previous study that applies DBEM to model distribution shift of over 1000 species of marine fishes and invertebrates (Cheung *et al.* 2009). This difference is likely due to the inclusion of pelagic species by Cheung *et al.* (2009), which are modelled using higher dispersal abilities in the DBEM model while the set of threatened species included in this study were all demersal, with lower dispersal abilities. As temperature gradients are dynamic and heterogeneous across the world, predicted rates of range shift will also vary according to the regions studied. The greater shift predicted here than observed for terrestrial species (0.6 km yr^{-1} (Parmesan and Yohe 2003)) was also expected due to the lower constraints on dispersal in the sea. Furthermore, two measures of thermal shifts used by Burrows *et al*. (2011) showed that both the 'velocity' of climate change (the geographic shifts of isotherms over time) and the shift in seasonal timings of temperature to be higher in the ocean than on land at particular latitudes. The velocity of climate change was also less patchy in the sea than on land (Burrows *et al.* 2011). This disparity likely also accounts for greater observed and predicted distribution shifts seen in marine versus terrestrial species (Parmesan and Yohe 2003; Perry *et al.* 2005; Cheung *et al.* 2009; Burrows *et al.* 2011).

4.2. Changes in range area and overlap

Changes in range area under climate change may have important implications for species persistence. The association between patch area and extinction risk is one of the most ubiquitous observations in ecology (MacArthur and Wilson 1967) and has served as the basis for concepts central to conservation science, such as species area relationships, and population viability analysis. For example, one of the criteria employed by the IUCN Red List to define the level of threat (Criteria B) faced by a species is based on the extent of occurrence or area of occupancy (IUCN 2001). Although it is frequently assumed that marine species have wide geographic ranges, 55% of skate species are endemic to single zoogeographic localities (McEachran and T 1990) and 70% have ranges spanning less than 20 degrees of latitude, a proxy for geographic range size (Dulvy *et al.* 2003). Therefore, although results presented here did not show a marked climate-driven decrease in predicted range, contrary to projections for terrestrial species (Townsend Peterson *et al.* 2002; Hu and Jiang 2011), it would seem wise to take into account any potential decrease in range area and evaluate the range of predicted values rather than the median or mean.

While species are predicted to lose some of their range in at least one model prediction, the actual proportion of range being lost might also be informative, especially if more information on the dispersal capabilities and observed current distribution becomes available. While, for example, *S. squatina* is predicted by two models to reduce in overall range, given full dispersal, both values are relatively small. *D. batis,* on the other hand, is predicted to lose 11.6% of its current suitable environmental space using one SDM/GCM model combination. However, the two Critically Endangered species assessed here, *L. circularis* and *D. batis,* may also experience net gains in suitable environmental space, of 10.24% and 40.95% respectively with particular model combinations. The differing response of these two Critically Endangered species to climate change may thus likely depend on the relative dispersal ability of each species. For example, if *D. batis* is able to fully exploit new areas of potential environmental suitability it may overcome concurrent projected losses in suitable environmental space. Overall, as both threatened and commercially exploited species were projected to shift northward simultaneously, the alteration in their overlap change was low except for selected species. Particularly, this study raises concern at increased threat from bycatch for *R. alba*, which potentially increases in overlap with all commercial species for at least one SDM/GCM combination.

4.3. Protected area suitability

This study suggests that a change in climate will not result in an overall, unidirectional change in the relative environmental suitability of marine protected areas. This is generally because of the large variation in the predicted changes in relative environmental suitability between model combinations. Due to this variation across SDMs in assessing the likely protection afforded by a particular protected area to particular species, the magnitude of difference in relative environmental suitability across different SDMs and climate models seems of less importance than the actual identification of change in suitability by a model. Applying the precautionary principle, the possibility for decrease in environmental suitability of threatened species in protected areas should therefore be noted, thereby using the range of predictions to help identify the possible species and areas of concern.

Consistencies in patterns of the relative environmental suitability change between models for different SACs suggest that these inter-variations stem from characteristics of each modelling procedure, their mechanisms and algorithms. These differences might, for example, result in the majority of cells in a predicted distribution being given characteristically higher, or lower, values, explaining why predictions made using different climate forcing frequently show greater similarity than those made using the same climate forcing but different SDMs. Thus, a multi-model approach can capture structural uncertainty of projections in species distributions and suitability of candidate protected areas for particular species under climate change.

4.4. Sensitivity and uncertainty

Analyses and results presented here highlight the variation in future projections that can be obtained using different SDMs and GCMs in predicting species' distributions. For a threatened species, variations in predictions may thus present the best and worst-case scenarios for the potential range under climate change. The variations in outputs are mainly driven by the algorithm by which the SDMs predicted species' distributions. For example, while the high environmental suitability values and equal weighting of variables in AquaMaps projections make this model less sensitive to temperature change, Maxent, which weights temperature as being the dominant predictor of distribution will be more sensitive to warming. As the relative response of species to change in one or other of the environmental variables and the possible interactions between them is highly uncertain, both projected responses should be considered. Thus, a multi-model or ensemble model approach helps quantify the variability in projections. In addition, the skill of a model in predicting changes in distribution could be assessed using model hindcasts and historical distribution data, rather than relying on the assumption that the models perform equally well in making future as current species distribution predictions. For example, comparison of historical projection of rate of range shift of exploited species in the Bering Sea and North Sea by DBEM showed a significant agreement between model outputs and observed rate of range shift (Cheung *et al.* 2012). Such model assessments could be applied to compare model preferences in future studies.

The implementation of a threshold value can often have a notable impact on conclusions drawn using species distribution or bioclimatic envelope models (Fielding and Bell 1997; Pearson *et al.* 2007; Nenzén and Araújo 2011). In this case, changes in latitudinal centroids were found to be robust to a range of thresholds. Alternative SDMs or climate forcing resulted in greater variations in my projections than the use of thresholds. Thus for this set of marine species, for which data paucity and reliability are an issue, the use of thresholds is not justified. The setting of thresholds would only allow reliable conclusions to be drawn if adequate data are available and a species is known to preferentially inhabit the most environmentally suitable habitat following range contraction from its historic distribution. Without sufficient data revealing each species' actual historical distribution, all model outcomes were considered as equally valid, both in analysing latitudinal centroids and range overlaps.

A number of assumptions are made in Maxent, AquaMaps and the DBEM to deal with issues of data scarcity and quality that are especially common for marine organisms. Although data were rigorously quality controlled to ensure maximum reliability (see (Jones *et al.* 2012)), the approaches do not incorporate ecological processes or biological interactions. Although the DBEM greatly advances the capabilities of modelling marine organisms in explicitly accounting for population growth and dispersal, none of the models account for predation pressure and food availability. As is common in bioclimatic envelope models, I also assume no adaptation to projected changes in environmental conditions.

A central criticism of species distribution and bioclimatic envelope modelling lies in the assumption that a species is in pseudo-equilibrium with its environment (Guisan and

Thuiller 2005). To ensure that this assumption was upheld here, all available valid occurrence data on each species was included to obtain as near as possible the species' absolute environmental tolerance limits. However, each of the species investigated here are thought to have been recently restricted to areas which do not adequately reflect their historic distribution for reasons other than change in environmental suitability, such as fishing and other human disturbances. Predictions made using these data are therefore unlikely to represent the actual current distribution of each species, potentially biasing estimates of a species' environmental tolerance limits and environmental envelopes. However, dated occurrence data recorded between 2000 and 2011 (ICES BTS surveys, including all beam trawl surveys) show that predicted distributions are within the historic distribution. Historic data thus supports the environmental tolerance limits and envelopes obtained using data obtained from a recently recorded distribution, following range contraction. Although range contraction may have consequences for the future dispersal of these species within patterns of suitable environmental space, accurate hypotheses and conclusion could not be made due to lack of comprehensive sampling effort across the entire historic range in recent years. A beneficial addition to this work would therefore involve a wider sampling across historic ranges and the compilation of a current observed dataset for each of these species.

Applying the precautionary principle, particularly for threatened species, it is advisable to consider the ranges of predictions in addition to the means, considering, for example, best and worst case scenarios. This is especially important for the two Critically Endangered species, *D. batis* and *S. squatina,* for which the ability to respond to climatic change or novel threats is expected to be limited by their putative restriction as small populations in areas which are not optimal and from which dispersal might be limited. Species that have shifted in distribution or increased in abundance in warmer years have previously been observed to be those with faster life history traits, with smaller body sizes, faster maturation and smaller sizes at maturity (Perry *et al.* 2005; Simpson *et al.* 2011). This result would be expected if the difference in rate of movement shown by particular taxa resulted from differential rates of population turnover. The threatened species assessed here are, however, characterised by slower life history traits, with larger sizes and later maturation rates than most species in the commercially exploited group, yet their environmental envelope is shown to shift more. If dispersal and distribution shift are linked to life history traits, even though threatened species are here predicted to show a greater median northward shift than commercial species, whether they actually will be able to disperse to occupy predicted potential ranges is unknown. The study of these species and the threat to them posed by climate change would therefore benefit from an assessment of their observed shift over time and their capacity to disperse and whether or not this might be promoted by the implementation of particular protected areas. If further work were to extend the modelling of marine species beyond 2050, and a policy-relevant time-scale, it might also be beneficial to assess the variation in outputs produced by a range of SRES or RCP (Representative Concentration Pathways, developed for the IPCC 5th Assessment Report) scenarios.

5. Conclusion

Evaluating the possible effects of climatic change on species' distributions using bioclimatic envelope models is a useful tool to gain insight on how species might respond under future climatic change. In particular, the ability to make this assessment for threatened species marks an important contribution amid calls for conservation planning to take an adaptive response to enhance the resilience of protected areas and the biodiversity within them to climate change. Although all species investigated in this study are predicted to move northwards by 2050, the effect of climate change on range areas and the suitability of a set of protected areas for this set of threatened species is less detrimental than would be expected based upon studies of similar changes in the terrestrial environment. This study highlights the variation in future projections according to the SDM and GCM used. As variation stems from characteristics of the models themselves, projections from multiple models better capture model uncertainties and allow identification of a best and worst case scenario of change. For critically endangered species and those facing high levels of threat, it is particularly important to treat predictions with caution in this way. In the marine environment, there exist many unknowns and uncertainties concerning species, their habitats and the threats they face. A multi-model approach enables a precautionary approach when considering the persistence of threatened species given their uncertain responses to future climate change.

References

Albouy, C., Guilhaumon, F., Araújo, M.B., Mouillot, D. and Leprieur, F. (2012) Combining projected changes in species richness and composition reveals climate change impacts on coastal Mediterranean fish assemblages. *Global Change Biology* **18**, 2995-3003.

Araujo, M.B., Thuiller, W. and Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* **33**, 1712-1728.

Araújo, M.B. and New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution* **22**, 42-7.

BRIG (2007) Report on the Species and Habitat Review; Report by the Biodiversity Reporting and Information Group (BRIG) to the UK Standing Committee.

Barange, M., Cheung, W.W.L., Merino, G. and Perry, R.I. (2010) Modelling the potential impacts of climate change and human activities on the sustainability of marine resources. *Current Opinion in Environmental Sustainability* **2**, 326-333.

Beaugrand, G. (2004) The North Sea regime shift: Evidence, causes, mechanisms and consequences. *Progress In Oceanography* **60**, 245-262.

von Bertalanffy, L. (1951) *Theoretische Biologie. Zweiter Band, Stoffwechsel, Wachstum*. Z. Francke, Bern.

Blanchard, J.L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., Holt, J. *et al*. (2012) Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **367**, 2979-89.

Botkin, D.B., Saxe, H., Araújo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., *et al*. (2007) Forecasting the Effects of Global Warming on Biodiversity. *BioScience* **57**, 227-236.

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E. S., Brander, K. M., Brown, C., *et al*. (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334**, 652-655.

Close, C., Cheung, W., Hodgson, S., Lam, V., Watson, R. and Pauly, D. (2006) Distribution ranges of commercial fishes and invertebrates. *Fisheries Centre Research Report* **14**, 27 - 37.

Cheung, W., Pitcher, T. and Pauly, D. (2005) A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological Conservation* **124**, 97-111.

Cheung, W.W.L., Dunne, J., Sarmiento, J.L. and Pauly, D. (2011) Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. *ICES Journal of Marine Science* **68**, 1008-1018.

Cheung, W.W.L., Lam, V.W.Y. and Pauly, D. (2008) Modelling present and climate-shifted distributions of marine fishes and invertebrates. *Fisheries Centre Research Report* **16**.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R. and Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* **10**, 235-251.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., Zeller, D. and Pauly, D. (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology* **16**, 24-35.

Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T. L., Lam, V.W.Y., Palomares, D.M.L., Watson, R., *et al*. (2012) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change* **2**, 1-5.

Cianfrani, C., Lay, G.L., Maiorano, L., Satizábal, H.F., Loy, A. and Guisan, A. (2011) Adapting global conservation strategies to climate change at the European scale: The otter as a flagship species. *Biological Conservation* **144**, 2068-2080.

Close, C., Cheung, W., Hodgson, S., Lam, V., Watson, R. and Pauly, D. (2006) Distribution ranges of commercial fishes and invertebrates. *Fisheries Centre Research Report* **14**, 27 - 37.

Coetzee, B.W.T., Robertson, M.P., Erasmus, B.F.N., van Rensburg, B.J. and Thuiller, W. (2009) Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. *Global Ecology and Biogeography* **18**, 701-710.

Conroy, M.J., Runge, M.C., Nichols, J.D., Stodola, K.W. and Cooper, R.J. (2011) Conservation in the face of climate change: The roles of alternative models, monitoring, and adaptation in confronting and reducing uncertainty. *Biological Conservation* **144**, 1204-1213.

Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora (1992) Available at: http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:31992L0043:EN:HTML [Accessed November 15, 2011].

Deutsch, C., Brix, H., Ito, T., Frenzel, H. and Thompson, L. (2011) Climate-forced variability of ocean hypoxia. *Science* **333**, 336-9.

Dockerty, T., Lovett, A. and Watkinson, A. (2003) Climate change and nature reserves: examining the potential impacts, with examples from Great Britain. *Global Environmental Change* **13**, 125-135.

Dulvy, N., Notobartolo di Sciara, G., Serena, F., Tinti, F., Ungaro, N., Mancusi, C. and Ellis, J. (2006) Dipturus batis. Available at: www.iucnredlist.org [Accessed December 2, 2011].

Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmller, V., Dye, S.R. and Skjoldal, H.R. (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology* **45**, 1029-1039.

Dulvy, N.K., Sadovy, Y. and Reynolds, J.D. (2003) Extinction vulnerability in marine populations. *Fish and Fisheries* **4**, 25-64.

Dunne, J.P., Gnanadesikan, A., Sarmiento, J.L. and Slater, R.D. (2010) Technical description of the prototype version (v0) of tracers of phytoplankton with allometric zooplankton (TOPAZ) ocean biogeochemical model as used in the Princeton IFMIP model. *Biogeosciences*, 3593.

Edwards, M. and Richardson, A.J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**, 881-4.

Elith, J., Ferrier, S., Guisan, A., Graham, C.H., Anderson, R.P., Hijmans, R.J., Huettmann, F. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129-151.

Elith, J., Kearney, M. and Phillips, S. (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution* **1**, 330-342.

Ellis, J. (2005) Raja clavata. Available at: www.iucnredlist.org [Accessed December 2, 2011].

Ellis, J., Serena, F., Mancusi, C., Haka, F., Morey, G., J, G. and Schembri, T. (2009) Scyliorhinus stellaris. Available at: www.iucnredlist.org [Accessed December 2, 2011].

Fielding, A.H. and Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/ absence models. *Environmental Conservation* **24**, 38-49.

Fitter, A.H. and Fitter, R.S.R. (2002) Rapid changes in flowering time in British plants. *Science* **296**, 1689-91.

Froese, R. and Pauly, D. (2011) Fishbase. Available at: www.fishbase.org, version (02/2011) [Accessed February 2, 2012].

Fuller, T., Morton, D. and Sarkar, S. (2008) Incorporating uncertainty about species' potential distributions under climate change into the selection of conservation areas with a case study from the Arctic Coastal Plain of Alaska. *Biological Conservation* **141**, 1547-1559.

Guisan, A. and Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**, 993-1009.

Guisan, A. and Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* **135**, 147-186.

Hagerman, S., Dowlatabadi, H., Satterfield, T. and McDaniels, T. (2010) Expert views on biodiversity conservation in an era of climate change. *Global Environmental Change* **20**, 192-207.

Harborne, A.R. and Mumby, P.J. (2011) Novel ecosystems: altering fish assemblages in warming waters. *Current Biology* **21**.

Henderson, P. (2007) Discrete and continuous change in the fish community of the Bristol Channel in response to climate change. *Journal of the Marine Biological Association of the UK* **87**, 589-598.

Hijmans, R.J. and Graham, C.H. (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* **12**, 2272-2281.

Hobday, A.J., Okey, T.A., Poloczanska, E.S., Kunz, T.J. and Richardson, A.J. (2006) Impacts of climate change on Australian marine life: Part B. Technical Report. Report to the Australian Geenhouse Office, Canberra, Australia, September 2006.

Hu, J. and Jiang, Z. (2011) Climate Change Hastens the Conservation Urgency of an Endangered Ungulate. *PLoS ONE* **6**, e22873.

IPCC (2000) *Emission Scenarios, Summary for Policymakers*. Cambridge University Press, Cambridge.

IPCC (2007) Summary for policymakers. In: *Climate Change 2007: The Physical Science Basis. Working Group 1 Contribution to the Fourth Assessment Report of the IPCC*. (eds S. Solomon, D. Qin, M. Manning, *et al.*). Cambridge University Press, Cambridge, UK and New York, USA.

IUCN (2001) IUCN Red List Categories and Criteria: Version 3.1. Gland, Switzerland and Cambridge.

IUCN (2011) IUCN Red List of Threatened Species. Version 2011.2. Available at: http://www.iucnredlist.org [Accessed February 1, 2011].

JNCC (2011) Marine SACs. Available at: http://jncc.defra.gov.uk/page-1445 [Accessed November 2, 2011].

Jones, M.C., Dye, S.R., Pinnegar, J.K., Warren, R. and Cheung, W.W.L. (2012) Modelling commercial fish distributions: Prediction and assessment using different approaches. *Ecological Modelling* **225**, 133-145.

Kaschner, K., Watson, R., Trites, A. and Pauly, D. (2006) Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. *Marine Ecology Progress Series* **316**, 285-310.

Kearney, M.R., Wintle, B.A. and Porter, W.P. (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters* **3**, 203-213.

Large Marine Ecosystems of the World (2012) Available at: http://www.lme.noaa.gov/ [Accessed January 4, 2012].

Lawton, A.J.H., Daily, G. and Newton, I. (1994) Population dynamic principles. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* **344**, 61-68.

Lemieux, C.J., Beechey, T.J. and Gray, P.A. (2011) Prospects for Canada's protected areas in an era of rapid climate change. *Land Use Policy* **28**, 928-941.

Liu, C., Berry, P.M., Dawson, T.P. and Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**, 385-393.

MMO (2011) *UK Sea Fisheries Statistics 2010*.

MacArthur, R. and Wilson, E. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, USA.

McEachran, J. and T, M. (1990) Zoogeography and bathymetry of skates (Chondrichthyes, Rajoidei). In: *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries.* (eds H. Pratt, S. Gruber and T. Taniuchi). Technical report National Marine Fisheries Service, no. 90, National Oceanic and Atmospheric Administration, Washington D.C., pp 305-326.

Micheli, F., Saenz-Arroyo, A., Greenley, A., Vazquez, L., Espinoza Montes, J.A., Rossetto, M. and De Leo, G. a (2012) Evidence that marine reserves enhance resilience to climatic impacts. *PLoS ONE* **7**, e40832.

Nenzén, H.K. and Araújo, M.B. (2011) Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling* **222**, 3346-3354.

O'Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P. and Weiss, J.M. (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *PNAS* **104**, 1266-71.

OSPAR (2008) OSPAR List of Threatened and/or Declining Species and Habitats (Reference Number:2008-6).

Parmesan, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37-42.

Pearson, R.G., Raxworthy, C.J., Nakamura, M. and Townsend Peterson, A. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* **34**, 102-117.

Perry, A.L., Low, P.J., Ellis, J.R. and Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. *Science* **308**, 1912-5.

Phillips, S.J., Anderson, R.P. and Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**, 231-259.

Phillips, S.J., Dudík, M. and Schapire, R.E. (2004) A maximum entropy approach to species distribution modeling. *Proceedings of the twenty-first International Conference on Machine Learning, ACM Press, New York*, 655 - 662.

Portner, H.O. and Knust, R. (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**, 95-97.

Ready, J., Kaschner, K., South, A.B., Eastwood, P.D., Rees, T., Rius, J., Agbayani, E., *et al.* (2010) Predicting the distributions of marine organisms at the global scale. *Ecological Modelling* **221**, 467-478.

Renkonen, O. (1938) Statistisch okologische Untersuchungen uber die terrestrische Kaferwelt der finnischen Bruchmoore. *Ann. Zool. Soc. Zool. Bot. Fenn. Vanamo* **6**, 1-231.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweigk, C. and Pounds, A.J. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, 57-60.

Rose, N.-A. and Burton, P.J. (2009) Using bioclimatic envelopes to identify temporal corridors in support of conservation planning in a changing climate. *Forest Ecology and Management* **258**, S64-S74.

Rödder, D. and Engler, J.O. (2011) Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. *Global Ecology and Biogeography*, 1 - 13.

Schoener, T. (1968) The Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49**, 704-726.

Simpson, S.D., Jennings, S., Johnson, M.P., Blanchard, J.L., Schön, P.-J., Sims, D.W. and Genner, M.J. (2011) Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Current Biology* **21**, 1565-1570.

Sing, T., Sander, O., Beerenwinkel, N. and Lengauer, T. (2007) The ROCR Package.

Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A., Alexander, J.D., Wiens, J. a and Root, T.L. (2009) Re-shuffling of species with climate disruption: a no-analog future for California birds? *PLoS ONE* **4**, e6825.

Sumaila, U.R., Cheung, W.W.L., Lam, V.W.Y., Pauly, D. and Herrick, S. (2011) Climate change impacts on the biophysics and economics of world fisheries. *Nature Climate Change*, 1-8.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., *et al*. (2004) Extinction risk from climate change. *Nature* **427**, 145-8.

Thuiller, W., Midgley, G.F., Hughes, G.O., Bomhard, B., Drew, G., Rutherford, M.C. and Woodward, F.I. (2006) Endemic species and ecosystem sensitivity to climate change in Namibia. *Global Change Biology* **12**, 759-776.

Toropova, C., Meliane, I., Laffoley, D., Matthews, E. and Spalding, M. eds (2010) *Global Ocean Protection: Present Status and Future Possibilities*. Brest, France: Agence des aires marines protegees, Gland, Switzerland, Washington, DC and New York USA: IUCN WCPA, Cambridge, UK: UNEP-WCMC, Arlington, USA: TNC, Tokyo, Japan: UNU, New York, USA: WCS.

Townsend Peterson, A., Ortega-Huerta, M.A., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R.H. and Stockwell, D.R.B. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature* **416**, 626-9.

Appendix 1

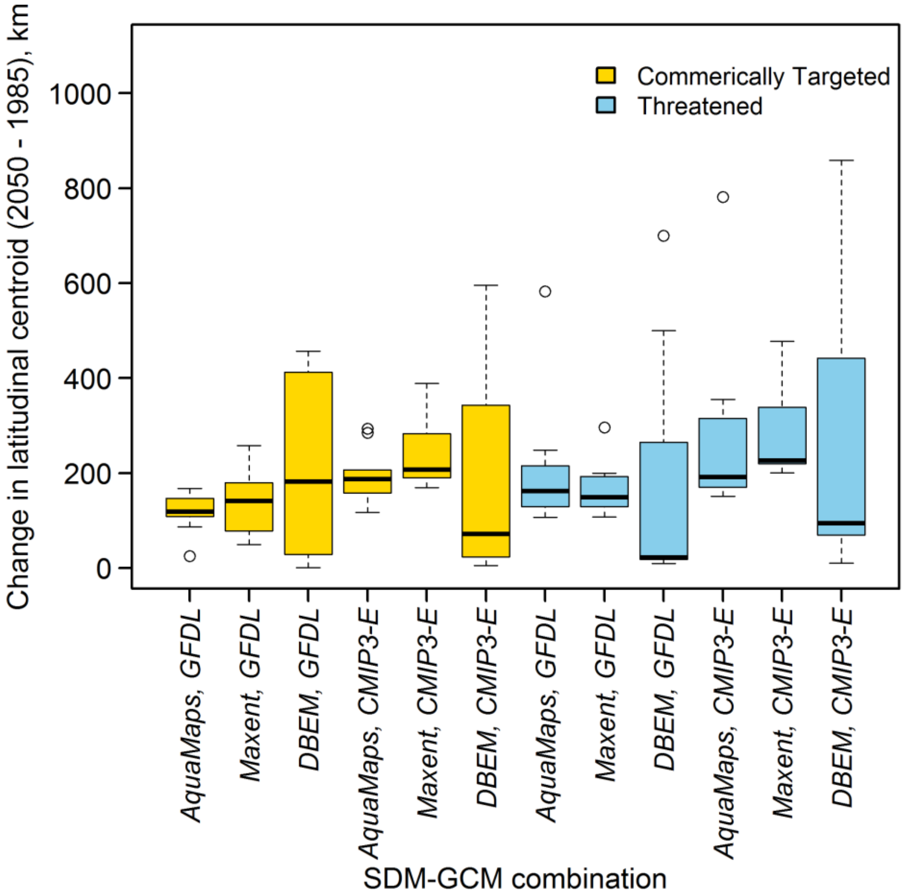


Figure 3.1. *Shifts in latitudinal centroid for threatened and commercial species. Projected change (in km) in latitudinal centroid from 1985 to 2050 using each of the six SDM and climatic dataset combinations, for both threatened species and commercial species. Thick bars represent median values, the upper and lower ends of the box the upper and lower quartiles of the data, and the whiskers the most extreme datapoints no greater than 1.5 times inter-quartile range from the box. Points that are more extreme than whiskers are represented as circles.*

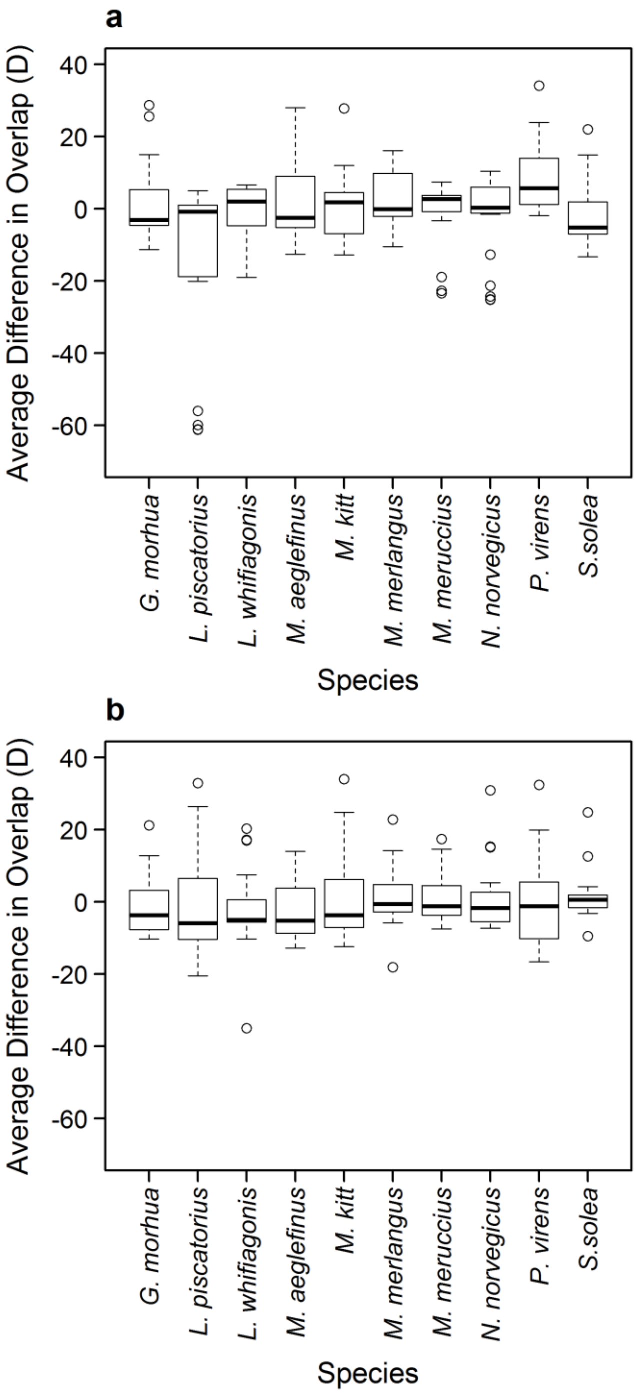


Figure 3.2. *Difference in overlap between species.*

Difference in range overlap, (Schoener's D) as a percentage of the 1985 overlap value, between commercial species and a) Dipturus batis b) Squatina squatina. Thick bars represent median values, the upper and lower ends of the box the upper and lower quartiles of the data, and the whiskers the most extreme datapoints no greater than 1.5 x inter-quartile range from the box. Points that are more extreme than whiskers are represented as circles.

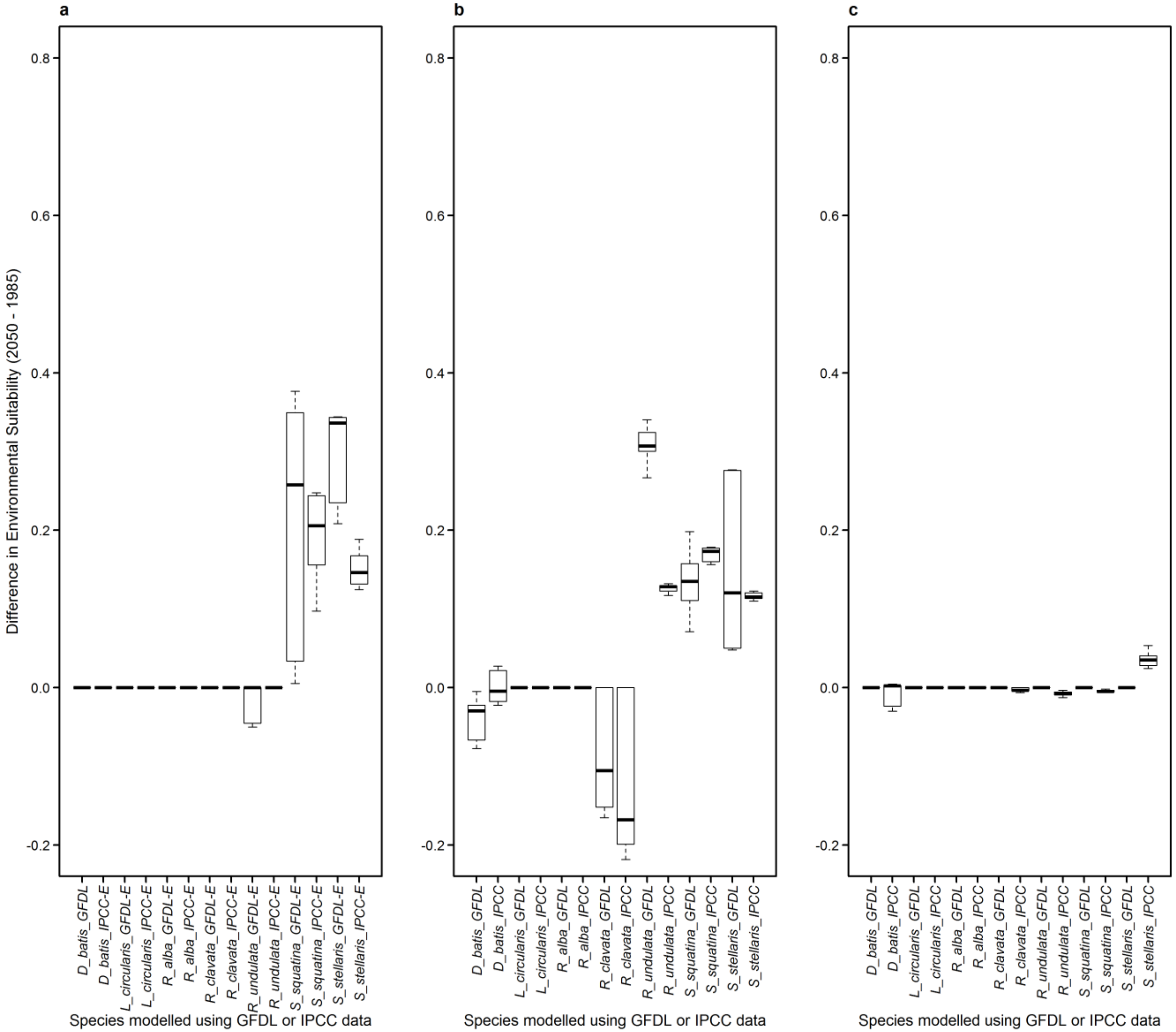


Figure3.3. *Differences in environmental suitability for threatened species in the Dogger Bank.*

Difference in environmental suitability for the each of the six SDM/GCM combinations. Difference (2050 – 1985 values) in relative environmental suitability was calculated following standardization across all cSACs for each species and model.

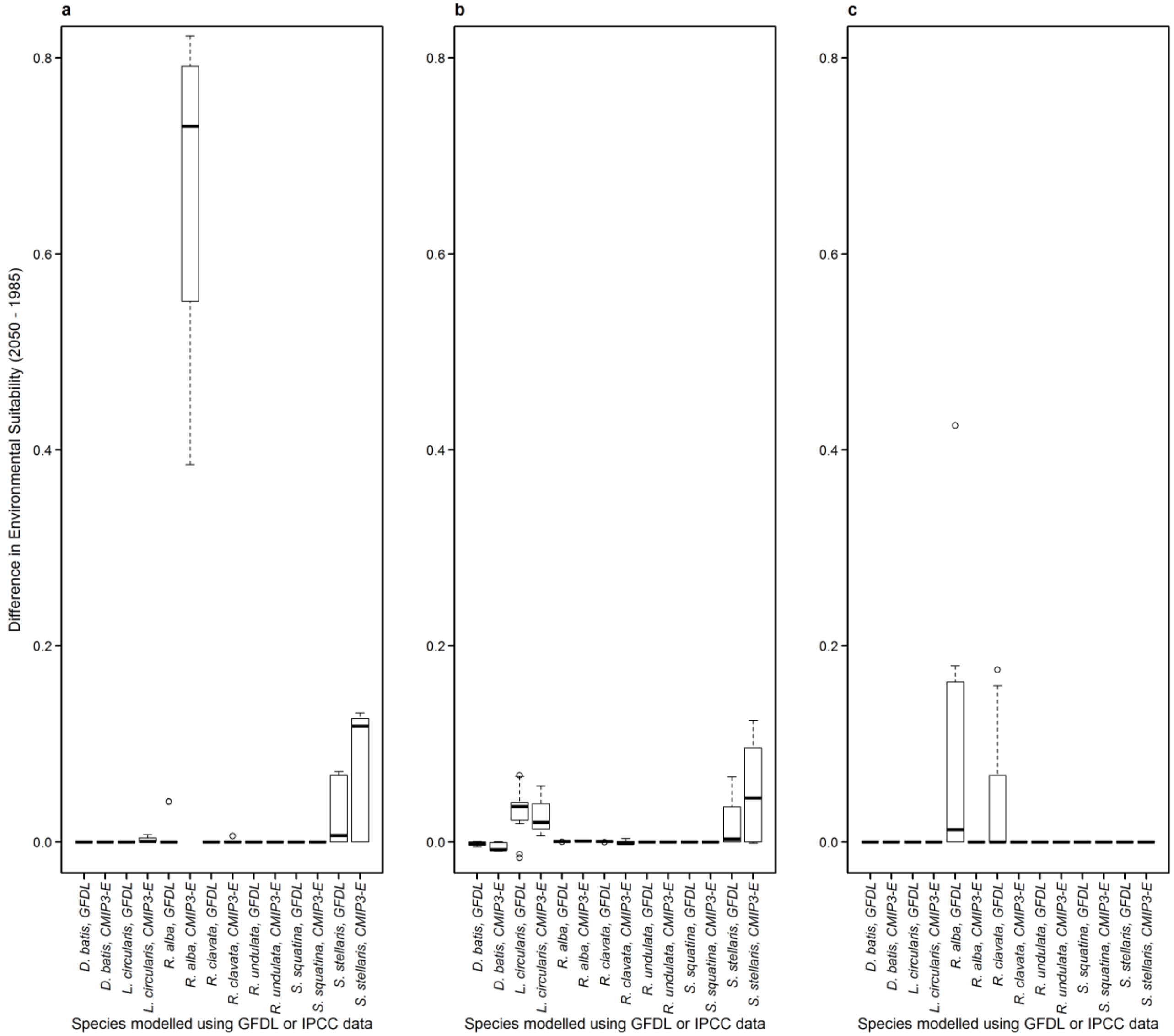


Figure 3.4. *Differences in environmental suitability for threatened species in Hatton Bank.*

Difference in environmental suitability for the each of the six SDM/GCM combinations. Difference (2050 – 1985 values) in relative environmental suitability was calculated following standardization across all cSACs for each species and model.

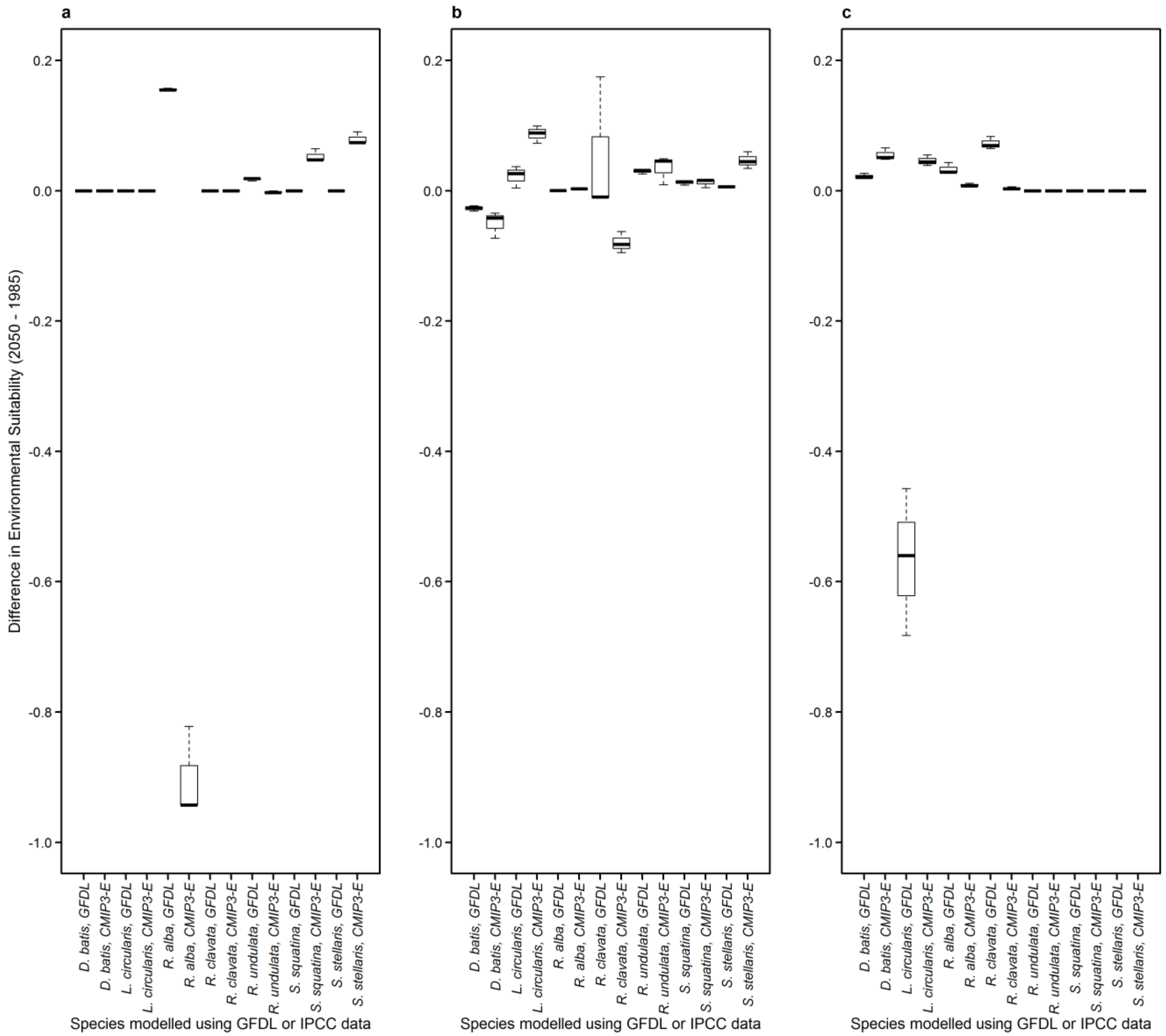


Figure 3.5. *Differences in environmental suitability for threatened species in Rockall.*

Difference in environmental suitability for the each of the six SDM/GCM combinations. Difference (2050 – 1985 values) in relative environmental suitability was calculated following standardization across all cSACs for each species and model.

Table 3.1. *Median difference in range overlap, (Schoener's D) as a percentage of the 1985 overlap value, between threatened and commercial species. Minimum, maximum and average overlap values are given for threatened species and average and overall median overlap values for commercial species.*

	G. morhua	*L. piscatorius*	*L. whiffiagonis*	*M. aeglefinus*	*M. kitt*	*M. merlangus*	*M. merluccius*	*N. norvegicus*	*P. virens*	*S. solea*	Min value	Max value	Average across species
D. batis	-3.0	-0.7	2.0	-2.5	1.8	-0.1	2.8	0.4	5.8	-5.2	-61.1	34.2	0.1
L. circularis	-2.8	-1.5	-0.6	3.9	0.8	7.5	0.7	1.1	7.5	0.3	-32.6	41.7	1.7
R. alba	8.3	-2.6	5.5	9.7	6.0	9.5	3.3	0.3	9.8	-0.8	-25.5	61.4	4.9
R. clavata	-2.2	-7.5	0.5	-1.6	1.5	1.4	-2.7	-0.9	-1.7	-1.3	-55.6	33.0	-1.4
R. undulata	-4.7	0.2	-0.7	-5.5	-4.5	-0.6	3.2	-0.9	-3.1	-2.9	-32.7	31.5	-1.9
S. Squatina	-3.7	-5.8	-5.0	-5.2	-3.6	-0.6	-1.1	-1.6	-1.2	0.7	-34.9	34.0	-2.7
S. stellaris	6.4	-5.8	-4.4	3.7	1.2	-0.1	-0.6	-1.0	7.1	1.1	-51.7	33.21	0.8
Total average	1.3	-5.5	1.1	1.8	2.7	3.8	1.3	0.8	3.7	-0.2	-34.9	34.0	1.1
Total Median	-2.03	-3.03	0.59	1.14	1.25	1.97	0.75	-0.43	3.79	-1.04			

Table 3.2. *Environmental Suitability values in 2000 and differences (2050 – 2000) for D. batis in all cSACs for each SDM/GCM combination*

SDM **GCM**	**AquaMaps** **GFDL**	**AquaMaps** **CMIP3-E**	**Maxent** **GFDL**	**Maxent** **CMIP3-E**
		1985 values		
Dogger Bank	1.000	1.000	0.414	0.230
	1.000	1.000	0.404	0.230
	1.000	1.000	0.444	0.283
	1.000	1.000	0.464	0.282
	1.000	1.000	0.416	0.230
	1.000	1.000	0.412	0.230
	1.000	1.000	0.549	0.295
	1.000	1.000	0.497	0.288
	1.000	1.000	0.493	0.289
	1.000	1.000	0.449	0.287
	1.000	1.000	0.386	0.262
	1.000	1.000	0.521	0.291
Central Oyster Grounds	1.000	1.000	0.354	0.251
	1.000	1.000	0.368	0.251
Haisborough, Hammond, Winterton and North Norfolk Sandbanks and Saturn Reef	1.000	1.000	0.492	0.231
	1.000	1.000	0.521	0.307
	1.000	1.000	0.501	0.234
	1.000	1.000	0.492	0.228
Hatton Bank	0.854	0.854	0.061	0.043
	0.871	0.871	0.062	0.043
	0.881	0.881	0.071	0.051
	0.906	0.906	0.073	0.051
	0.912	0.912	0.072	0.079
	0.915	0.915	0.073	0.079
	0.884	0.884	0.071	0.073
	0.904	0.904	0.073	0.073
	0.898	0.898	0.071	0.080
	0.871	0.871	0.070	0.073
	0.899	0.899	0.073	0.087
	0.893	0.893	0.073	0.087
Rockall	0.994	0.994	0.718	0.430
	0.997	0.997	0.715	0.523
	0.990	0.990	0.299	0.442

DBEM GFDL	**DBEM CMIP3-E**	**AquaMaps GFDL**	**AquaMaps CMIP3-E**	**Maxent GFDL**	**Maxent CMIP3-E**	**DBEM GFDL**	**DBEM CMIP3-E**
		Difference in environmental suitability (2050-1985)					
0.000	0.040	0.000	0.000	-0.014	0.027	0.000	0.003
0.000	0.034	0.000	0.000	-0.023	0.022	0.000	0.002
0.000	0.035	0.000	0.000	-0.022	0.002	0.000	0.003
0.000	0.029	0.000	0.000	-0.027	0.002	0.000	-0.029
0.000	0.030	0.000	0.000	-0.005	0.027	0.000	-0.030
0.000	0.033	0.000	0.000	-0.023	0.021	0.000	0.002
0.000	0.044	0.000	0.000	-0.058	-0.017	0.000	0.003
0.000	0.025	0.000	0.000	-0.076	-0.017	0.000	-0.025
0.000	0.000	0.000	0.000	-0.078	-0.023	0.000	0.000
0.000	0.022	0.000	0.000	-0.044	-0.022	0.000	-0.022
0.000	0.030	0.000	0.000	-0.032	-0.012	0.000	0.002
0.000	0.057	0.000	0.000	-0.077	-0.018	0.000	0.004
0.000	0.039	0.000	0.000	-0.015	-0.021	0.000	0.002
0.000	0.037	0.000	0.000	-0.025	-0.022	0.000	0.002
0.000	0.000	0.000	0.000	-0.080	-0.031	0.000	0.050
0.000	0.000	0.000	0.000	-0.083	-0.030	0.000	0.036
0.000	0.000	0.000	0.000	-0.085	-0.031	0.000	0.039
0.000	0.000	0.000	0.000	-0.089	-0.054	0.000	0.047
0.000	0.000	0.000	0.000	-0.005	-0.008	0.000	0.000
0.000	0.000	0.000	0.000	-0.005	-0.008	0.000	0.000
0.000	0.000	0.000	0.000	-0.002	0.000	0.000	0.000
0.000	0.000	0.000	0.000	-0.003	0.000	0.000	0.000
0.000	0.000	0.000	0.000	-0.003	-0.009	0.000	0.000
0.000	0.000	0.000	0.000	-0.003	-0.009	0.000	0.000
0.000	0.000	0.000	0.000	0.000	-0.008	0.000	0.000
0.000	0.000	0.000	0.000	0.000	-0.009	0.000	0.000
0.000	0.000	0.000	0.000	-0.001	-0.001	0.000	0.000
0.000	0.000	0.000	0.000	0.000	-0.008	0.000	0.000
0.000	0.000	0.000	0.000	0.000	-0.001	0.000	0.000
0.000	0.000	0.000	0.000	0.000	-0.001	0.000	0.000
0.136	0.163	0.000	0.000	-0.031	-0.042	0.019	0.048
0.154	0.183	0.000	0.000	-0.026	-0.073	0.021	0.051
0.199	0.237	0.000	0.000	-0.023	-0.034	0.027	0.066

Appendix 2

Supplementary methods

Maxent

Maxent (Phillips *et al.* 2004) uses a complex generative approach (Phillips *et al.* 2006) to estimate the environmental co-variates conditioning species' presence from presence only occurrence data and a suite of environmental variables. The final prediction is based on the principle of maximum entropy, which specifies that the best approximation of an unknown distribution is the probability distribution with maximum entropy, subject to the constraints imposed by the sample of species' presence observations (Phillips *et al.* 2006). Maxent has been shown to compete well with alternative approaches in terms of model testing statistics (Elith *et al.* 2006; Phillips *et al.* 2006) and is robust to small sample sizes (Pearson *et al.* 2007). Models were constructed using Maxent version 3.3.3e with default parameters for a random seed, regularization parameter (1, included to reduce over-fitting), maximum iterations (500), convergence threshold (0.00001) and maximum number of background points (10000 points which have not been recorded as present). The relative contribution of environmental variables to each iteration of the model was also carried out automatically. The model trained on the set of environmental variables representing the current time period was then 'projected' by its application to a set of the same environmental variables representing future climate.

AquaMaps

In contrast, the AquaMaps approach to modelling species' distributions uses simple, numerical descriptors of species' relationships with environmental variables to predict distributions from occurrence databases. Environmental envelopes for each variable are calculated by associating occurrence data with current environmental variables to find the absolute and 'preferred' preference ranges (calculated as shown in (Kaschner *et al.* 2006; Jones *et al.* 2012)), with the relationship between species' occurrence and environmental limits being specified by a trapezoidal distribution (Kaschner *et al.* 2006; Ready *et al.* 2010; Jones *et al.* 2012). While relative environmental suitability is therefore assumed to be uniformly high through the preferred parameter range (with a probabliy of 1), values lying outside the observed minimum and maximum are assigned a probability of 0. Suitability decreases linearly between the two thresholds. Predicted current distributions/ environmental suitability are generated multiplicatively from a suite of 'environmental envelopes' over each cell in a study area. Resulting cell values lie between 0 and 1 and represent the relative suitability of that cell for the specified species. The environmental envelopes obtained for a 30 year centred average on 1985 were then applied to environmental datasets representing future climatic scenarios. This methodology does not allow complex, non-linear interactions to be fit between predictors and assumes they carry equal weight in predictions. Although simple, AquaMaps allows better transparency and understanding in the wider, non-modelling, community while also explicitly promoting incorporation of expert judgement.

Expert opinion was incorporated into Maxent and AquaMaps to refine predictions by eliminating ('clipping') areas. Area eliminated were those outside known occurrence ranges, reported occurrence/absence in large ocean basins [delineated by the United Nations' Food and Agricultural Organisation (FAO) statistical area, www.fao.org/fishery/area/search/en] or beyond species specific depth limits (Jones *et al.* 2012). This avoided over-prediction of relative environmental suitability in areas of the world where species are known not to occur, or which are unsuitable due to depth, the limits of which may be over-estimated in Maxent and AquaMaps due to the relatively low resolution of depth and occurrence data, in particular at the edge of the continental shelf. Maximum depth limits obtained from Fishbase (Froese and Pauly 2011) were increased by 50% in predictions for both time periods. This allowed for the deepening of species with ocean warming that has been observed (Dulvy *et al.* 2008) while preventing difference in predictions between the two time periods being inflated and biased by applying different depth cut off points.

Dynamic Bioclimate Envelope Model (DBEM)

Contrasting the above approaches, the Dynamic Bioclimate Envelope Model (DBEM) (Cheung *et al.* 2008, 2009, 2011) combines statistical and mechanistic approaches in predicting species' distributions. Firstly, we employed the *Sea Around Us Project* (http://www.seaaroundus.org/) (SAUP) model, which was developed to address the need for distributional ranges of commercial fish and invertebrates for mapping global fisheries catches and studying the impacts of fisheries on the world's marine ecosystems. The SAUP model [55] applies a set of environmental 'filters' to delimit a species' current distribution to a realistic range from a potentially global distribution. Filters use known geographic or environmental tolerance limits to restrict a species' potential distribution and were obtained for FAO areas, latitudinal limits (with a further range-limiting filter preventing occurrence in semi-enclosed seas) and depth limits and habitat preference. For further details on the application of filters see (Close *et al.* 2006; Jones *et al.* 2012). From this distribution, the DBEM defines the species' bioclimatic envelope by its 'preference profile' (the relative suitability of different environmental values) for each environmental variable. Preference profiles were thus created by overlaying environmental data from 1971 – 2000 with maps of current relative abundance produced using the *Sea Around Us Project* model (Close *et al.* 2006; Jones *et al.* 2012). Variables incorporated into the DBEM include sea surface temperature, sea bottom temperature, coastal upwelling, salinity, distance from sea-ice and habitat types (coral reef, estuaries and sea mounts) (for full description see (Cheung *et al.* 2009, 2011)).

The DBEM differs from other Bioclimatic Envelope Models (BEMs) in simulating changes in a species' relative abundance by incorporating a logistic population growth model (Cheung *et al.* 2008) as well as ecophysiological parameters. First of all, the model simulates how changes in temperature, oxygen content (represented by O_2 concentration) and pH would affect fish and invertebrate growth, determined by the difference between anabolism and catabolism (Cheung *et al.* 2011), using an algorithm derived from the von Bertalanffy growth function (VBGF) (von Bertalanffy 1951). The VBGF parameters are subsequently used to determine change in carrying capacity in each 0.5° latitude × 0.5° longitude cell. Carrying capacity is expressed as a function of recruitment and expected biomass per recruit, the later being determined using a size-based population model. The model assumes a population's spatial and temporal dynamics to be determined by its species specific intrinsic population growth, larval dispersal and adult migration (Cheung *et al.* 2008, 2011). Larval dispersal and adult migration are assumed to follow ocean currents, with the distance and direction of movement a function of predicted pelagic larval duration (based on an empirical equation (O'Connor *et al.* 2007)). Intrinsic population growth rate is dependent on the growth rate and carrying capacity of the species, which is determined by the species' environmental preference profile and the resulted environmental suitability. Environmental suitability is expected to be positively correlated with carrying capacity for each species. Carrying capacity values for each environmental predictor are then combined multiplicatively to obtain a final value of environmental carrying capacity for a species.

Chapter 4

Predicting the Impact of Climate Change on Commercially Targeted Species in UK Waters

A paper formed from this chapter will be submitted to
Journal of Applied Ecology

Abstract

Global climate change is affecting the distribution of marine species, with both range expansions and local extinction being observed and predicted. For commercially targeted species, range shifts may alter the geographic distribution of fish and shellfish production and potential catches. This will bring increasing challenges to maintaining sustainable, long-term fisheries management, influencing the allocation of fishing rights and quotas and the efficacy of managed, or protected, areas. Few studies have assessed the effects of climate change on commercially targeted species in UK waters. Furthermore, none are known to have applied a multi-model approach to assess the range and uncertainty of potential projections. In this study, three species distribution models were used to explore the potential impacts of climate change on the distribution of commercially targeted species in the North Sea by 2050. Future changes in environmental suitability of Marine Protected Areas were also assessed. Ensemble projections suggest northward shifts in species at an average rate of 42 and 26 km per decade for pelagic and demersal species respectively. Climate change was further found to negatively affect the suitability of Marine Protected Areas for species they were designed to protect, although the extent of this change was small. Distribution shifts were robust to alternative downscaling techniques although results highlight the variation of predicted consequences of climate change between species distribution and biophysical models. The inherent uncertainty in modelling the environment and making environmental suitability predictions necessitates a multi-model approach to fully explore the potential effects of climate change on marine species.

1. Introduction

Global climate models (GCMs) predict warming around the globe to range from 1.1 to 6.4 °C by 2100 (IPCC 2007) making the Earth warmer than at any point during the past 1-40 million years (IPCC 2001). Air temperature rises are causing simultaneous warming of the world's ocean (Levitus *et al.* 2000; Fukasawa *et al.* 2004). Although the most significant warming is expected in the upper 500 – 800m (Bernal 1993), observations since 1961 have shown average temperature to be increasing to a depth of 3000m (Levitus *et al.* 2000). Species have been responding to climate change throughout evolutionary history (Harris 1993). However, there is growing concern for their ability to survive under the higher temperatures and rates of climate change currently observed and predicted

(Schneider and Root 1998; Root *et al.* 2003). In general, marine species experiencing changing environmental conditions exhibit changes in morphology (Thomas *et al.* 2004), phenology (Fitter and Fitter 2002; Root *et al.* 2003) and shifts in distribution or density (Parmesan and Yohe 2003). Evidence from Pleistocene glaciations has shown that species are more likely to show an ecological response to climate change, for example through temperature-induced changes in fitness impacting a population's density and distribution, than evolutionarily, through local adaptation. Mechanisms promoting acclimation, such as poleward or northward bio-geographical shifts (Parmesan and Yohe 2003), may thus be more likely than changes on biochemical or genetic levels (Parmesan *et al.* 2000).

In the marine environment, species distribution shifts have been observed and are predicted to occur more rapidly than their terrestrial counterparts (Parmesan and Yohe 2003; Edwards and Richardson 2004; Cheung *et al.* 2009; Burrows *et al.* 2011). This may result from fewer barriers to dispersal or the fact that ectothermic, marine animals are adapted to and depend on the maintenance of a characteristic temperature window within their natural environment (Portner 2001; Sunday *et al.* 2012). Empirical and theoretical studies have thus shown that marine fish and invertebrates tend to undergo shifts in distributions according to the changing environmental conditions, in a direction that is generally towards higher latitudes and deeper water (Stebbing *et al.* 2002; Perry *et al.* 2005; Dulvy *et al.* 2008; Cheung *et al.* 2012a).

For commercially exploited marine species, changes in primary productivity and shifts in distribution are of particular interest due to their influence on the spatial distribution of future fish and shellfish production. This will likely lead to changes in catch potential, bringing increasing challenges to the maintenance of sustainable, long-term fisheries management (Cheung *et al.* 2010; Chassot *et al.* 2010). For example, the distribution of the yellow croaker (*Larimichthys polyactis)* has been predicted to move northwards under a 2.5^{o}C temperature rise, expanding its area of occupancy out from the South China Sea into Japanese waters (Cheung *et al.* 2008a). Although fisheries productivity was predicted to remain unchanged, overall there was a marked change in the geographic distribution of potential catches. Thus North Korea and Japan experienced increases in predicted catches, rather than China and South Korea, who currently take the majority of catch (Cheung *et al.* 2008a).

In the UK shelf seas, warming has been seen to influence the distribution of species (Clarke *et al*., 2003; Dulvy *et al*., 2005), likely leading to the changes in productivity and catch potential predicted in a study by Cheung *et al.* (2010). Furthermore, the North Sea has been identified as a hotspot of societal vulnerability in coastal zones (Parry *et al.* 2007). For example, species such as haddock and mackerel have responded to increasing temperatures by moving northwards, leading to disagreements between Iceland and the EU in 2010, and protests against high Icelandic quotas for mackerel (Cheung *et al.* 2012b). However, there is also evidence that warm-water species are moving into UK and Irish waters, opening up new fishing opportunities (Cheung *et al.* 2012b). In the North Sea, species richness of the fish fauna increased from 1985 to 2006 in conjunction with large scale patterns and climate change (Hiddink and ter Hofstede 2008). Warm-adapted species such as anchovy and pilchard have also increased in abundance since 1925 (Beare *et al.* 2004). Species such as Bib (*Trisopterus luscus*) have shifted their northern range boundary by as much as 148km per decade (Perry *et al.* 2005) and UK waters have seen new or expanding fisheries for sea bass, red mullet, John Dory, anchovy and squid. Fisheries in Ireland are furthermore investing in new technologies to more effectively exploit the opportunities offered by boarfish, which is moving into the area (Pinnegar *et al*., 2002).

Shifts in distribution of commercially exploited species have the potential to compromise the effectiveness of spatial management areas, or marine protected areas (MPAs). In the North Sea, a particular type of MPAs may be established as a technical measure for management of commercial fish species under the European Union Common Fisheries Policy. Closure to fisheries can thus be set for specific time periods, vessels and gears, or to protect certain vulnerable species or habitats. For example, the North Sea 'Plaice Box' was set up to protect juveniles plaice which were typically concentrated in the shallow inshore waters and were experiencing high mortality in the beam trawl fishery, in particular from the smaller mesh sizes used for targetting sole. The Plaice Box remained open to smaller fishing vessels if they used certain gears and catch specifications. However, surveys in the Wadden Sea have shown that 1-group plaice are now completely absent from the area where they were once abundant (Engelhard *et al.* 2011), likely due to warming-related changes in productivity in the region. Although many MPAs in the North Sea have failed to reach their management objective, such as the increased abundance of adult individuals, closed areas implemented elsewhere, such as in the Georges Bank, have led to increased abundance of some species (Murawski *et al.* 2000). Although the effects of management can be difficult to extract from natural variations, warming is likely to further reduce the effectiveness of these areas for species management. Estuarine sites, in particular are likely to experience dramatic changes in temperature and river flow in the next decade, altering their suitability as protected habitat for particular species. For example, around the UK and Ireland, most fishery closures are estimated to experience a 2-3 °C temperature rise over the next 80 – 100 years (Cheung *et al.* 2012b).

This study aims to assess the potential impact of climate change on a set of commercial fish and invertebrate species in the North Sea, North East Atlantic and Mediterranean Sea. This is done using the tool of Species Distribution Modelling, and thereby assessing the shifts of a species' bioclimatic envelope under climate change scenarios. In order to make modelled outputs as robust as possible, predictions were made using three different Species Distribution Models (SDMs). These were the generative models Maxent (Phillips *et al.* 2006; Phillips and Dudik 2008) and AquaMaps (Kaschner *et al.* 2006, 2011) and the discriminative *Dynamic Bioclimate Envelope Model* (Cheung *et al.* 2011). These models have been previously described and tested (Jones *et al.* 2012) and applied to a set of threatened species in the North Sea (Chapter 3, Jones *et al*. 2013, *in press*). Although it is acknowledged that SDMs over-simplify the processes and influences governing a species' distribution, if they are used heuristically and the range of uncertainty produced by alternative SDMs is taken into account they remain useful tools in exploring the effect of climate change on species range shifts.

Further to the variation produced by different SDMs, projected changes in ocean conditions resulting from alternative climate models may also affect predicted species distribution shifts. Scenarios developed from multiple climate and earth system models are thus considered to be more robust than using a single model. Therefore, although variation in GCM used has been shown to cause less uncertainty than variation in SDM (Jones *et al.* 2013), climate data from two Global Climate Models (GCMs) were used in modelling species distributions. Furthermore, some Global Climate Models are criticised for poorly resolving the topography and dynamics of the coastal shelf sea. The process by which modelled and observational climatic data are downscaled to obtain datasets of resolution relevant to a particular study introduces a potential source of uncertainty into the modelling process. For example, the GFDL model may poorly resolve the topography and dynamics of the coastal shelf due to the relatively coarse resolution of its downscaling method. I therefore also aimed to investigate the sensitivity of the modelling procedure and outputs obtained to variation in downscaling methodology by comparing outputs derived from a statistically downscaled GCM and that from a pattern scaling regional climate model.

The impact of climate change on these species is here investigated in terms of the change in environmental suitability throughout the species range, which is used to calculate the shift in latitudinal and depth centroids for each species range. I also investigate the impact of climate change on static protected areas designed to manage specific commercial species. I hypothesise that the change in relative environmental suitability caused by climate change will result in polewards shifts in species distributions, indicated by the latitudinal centroids. A poleward shift is predicted to coincide with a deepening as species move into cooler water. I also hypothesise that the relative environmental suitability of protected areas will change with changing ocean and climate conditions, thus affecting their efficacy at managing particular species. I discuss the possible implications of these findings for fisheries.

2. Methods

2.1 Modelling Approaches

Following on from using Species Distribution models to explore the key effects of climate change on threatened species in Chapter 3, this study applies SDMs to 34 species of commercially targeted fish (Table 4.1). The models Maxent, AquaMaps and the DBEM, described in greater detail in chapters 2 and 3, Supplementary methods, are summarized here. Maxent (Phillips *et al.* 2006) and AquaMaps (Kaschner *et al.* 2006; Jones *et al.* 2012), contrasted in their relatively complexity, both use generative approaches to estimate the environmental co-variates conditioning species' presence from presence only occurrence data and a suite of environmental variables. As described in Chapter 2, expert opinion was incorporated into predictions made using Maxent and AquaMaps by 'clipping' to location within known FAO and depth limits. Maximum depth limits obtained from Fishbase (Froese and Pauly 2011) were increased by 50% in predictions for both time periods. This allowed for the deepening of species with ocean warming that has been observed (Dulvy *et al.* 2008) while preventing difference in predictions between the two time periods being inflated by applying different depth cut off points. The Dynamic Bioclimatic Envelope Model (DBEM) (Cheung *et al.* 2011), on the other hand uses the associated *Sea Around Us Project* model (Close *et al.* 2006) to predict a species' current distribution based on a set of 'filters', restricting a distribution based on known parameters, geographic limits or habitat preferences. Filters were applied for FAO area, habitat, latitudinal limits and depth. The DBEM then uses the predicted current distribution to define a species' bioclimatic envelope by its ‘preference profile’ (the relative suitability of different environmental values) for each environmental variable. Change in a species’ relative abundance following changing environmental conditions is then simulated by incorporating a population growth model (Cheung *et al.* 2008b) as well as ecophysiological parameters.

2.2 Species occurrence data

A set of 34 species of commercially exploited fish and invertebrates were selected for this study (Table 4.1). These species comprised 90% of demersal and 93% of pelagic species by weight, and 94% and 98% by value respectively, of species landed by UK vessels into the UK in 2010 (MMO 2011). *Nephrops norvegicus* was selected as representing the largest catch by value of shellfish by UK fleets into the UK, at 38% (MMO 2011). Other species were selected because of the possibility of their providing new fishing opportunities following potential shifts in their distribution (Cheung *et al.* 2012b).

Table 4.1. *Commercially targeted fish and invertebrates selected for the study.*

Species	Common Name	Value (£ million) 2010 (MMO 2012)
Clupea harengus	Atlantic Herring	10.3
Dicentrarchus labrax	European seabass	4.8
Engraulis encrasicolus	European anchovy	-
Glyptocephalus cynoglossus	Witch flounder	1.2
Gadus morhua	Atlantic cod	28.6
Hippoglossus hippoglossus	Atlantic halibut	1.3
Limanda limanda	Common dab	-
Lophius piscatorius	Angler/ Monkfish	38.5
Lepidorhombus whiffiagonis	Megrim	10.1
Melanogrammus aeglefinus	Haddock	36.2
Mullus barbatus	Red mullet	-
Microstomus kitt	Lemon sole	6.3
Merlangius merlangus	Whiting	9.4
Merluccius merluccius	European hake	10.2
Molva molva	Ling	5.7
Micromesistius poutassou	Blue Whiting	1.0

Mullus surmuletus	Surmullet	-
Nephrops norvegicus	Norway lobster/ Langoustine	95.3
Platichthys flesus	Flounder	-
Pleuronectes platessa	European plaice	3.3
Pollachius pollachius	Pollack	3.5
Pollachius virens	Saithe	12.4
Psetta maxima	Turbot	3.4
Reinhardtius hippoglossoides	Greenland halibut	-
Sardina pilchardus	European pilchard	0.6
Scophthalmus rhombus	Brill	1.6
Scomber scombrus	Atlantic mackerel	82.0
Solea solea	Common sole	14.0
Sprattus sprattus	European sprat	-
Trisopterus esmarkii	Norway pout	-
Trisopterus luscus	Pouting	-
Trisopterus minutes	Poor cod	-
Trachurus trachurus	Atlantic horse mackerel	1.8
Zeus faber	John Dory (Atlantic)	-

Species occurrence data were obtained from three global online databases: the International Council for Exploration of the Sea (ICES) EcoSystemData database (http://ecosystemdata.ices.dk); the Ocean Biogeographic Information System(OBIS) (Vanden Berghe, 2007; http://www.iobis.org) and the Global Biodiversity Information Facility (GBIF) (http://data.gbif.org), all last accessed in 2011. Occurrence records were spatially aggregated at the level of 0.5° latitude x 0.5° longitude and rigorously filtered according to criteria detailed in Jones *et al.* (2012). This minimised recording errors frequent in compiled databases due to data being compiled from many sources and gave a binary value of presence or absence of each species for each cell. Maps showing the distribution of occurrence records for each species are shown in the thesis Appendix.

2.3. Environmental predictors and climate models

A range of environmental oceanographic variables for predicting species distributions using Maxent and AquaMaps were chosen (Jones *et al.*, 2012). These variables were: bathymetry, sea surface temperature (SST), sea bottom temperature (SBT), salinity; ice;

primary productivity, and distance to coast. Two sets of oceanographic variables were obtained, from Geophysical Fluid Dynamics Laboratory's Earth System Model (GFDL ESM2.1, Dunne *et al*. 2010) and physical climate data averaged from an ensemble of 12 different CMIP3 models that are assessed by the fourth assessment of the Intergovernmental Panel on Climate Change (IPCC AR4) (CMIP3-E). The latter was obtained from the World Climate Research Program (WCRP) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model dataset (http://esg.llnl.gov:8080). This would allow the variation in predicted distributions resulting from alternative climate datasets to be assessed for this set of species. Both datasets represented the A2 climate scenario, thus being characterised by a heterogenous world with a continuously increasing global population and regionally orientated economic development (IPCC 2000). The oceanographic variables were interpolated onto a 0.5° latitude x 0.5° longitude global grid using the nearest neighbour method. Models were trained on climatic data averaged over a 30 year period centred on 1985, which corresponded as far as possible to the average climatic conditions over which species occurrence data were compiled. Environmental envelopes obtained for each climatic dataset were then projected into the future using a 30-year average centred on 2050.

In order to explore the effect of alternative climate model down-scaling techniques on distribution predictions, a high resolution dataset of GFDL 2.1 SST for each 30 year time slice was obtained using the spatial climate scenario generator ClimGen through the Community Integrated Assessment System (CIAS) model portal (Warren *et al.* 2007). The GFDL ESM2.1 data had been interpolated from its original 1° resolution (at latitudes higher than 30°N and 30°S) using a nearest neighbour method (Cheung *et al.* 2011). This avoids complicated assumptions concerning the relationship between coarse resolution model outputs and downscaled values. ClimGen contrasts this method by applying a 'pattern-scaling' approach. Taking the modelled GFDL temperature output from the reference period, ClimGen calculates the difference between this and projection period, then applying the difference to observed temperature data (HadSST2 (Rayner *et al.* 2005)) at a finer resolution than the original GFDL data. Assuming a linear increase, ClimGen may therefore produce a downscaled temperature prediction for a particular time-slice. As only SST was available using ClimGen, predictions run were compared with those run using statistically downscaled GFDL 2.1 data using both SST only and the full set of variables.

2.4. Distribution centroids

Latitudinal centroids were calculated for each species within each SDM-GCM combination using an equation for distribution centroids, equation(1) (Cheung *et al.* 2009):

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

Where Lat_i is the latitude of the centre of the spatial cell (i), Abd is the predicted relative abundance in the cell, and *n* is the total number of cells (Cheung *et al.* 2009). Similarly, the above equation was used to calculate the depth centroid for each time period, substituting latitudinal value with that for depth of the spatial cell (i). Shift in depth was then calculated as the difference between the depth in each time period (2050 – 1985), resulting in positive values indicating a deepening for that species. The difference between latitudinal centroids in projected and reference years was then calculated in kilometres (km) as (Cheung *et al.* 2011):

$$Distance\ shift = (Lat_m - Lat_n)\frac{\pi}{180} \times 6378.2 \tag{2}$$

2.5. Environmental Suitability in Fisheries Boxes

The potential effects of climate change on static areas of conservation or fisheries management was investigated using the UK Fishery Exclusion Areas, 'boxes' as a case study. Although there are a number of areas closed to fishing in the North Sea, none of these exclude all fishing activities and they were established for a range of purposes, such as protecting juveniles of a particular species, seabirds, or accidental bycatch. The relative success and failures of these boxes are contested, but although evidence is sparse for northern temperature regions, large scale studies of south European MPAs have shown instances of increased abundance of targeted individuals as well as spill over effects. However, any protection they may afford in the future is likely to further vary with changes in potential environmental suitability under climate change. The 'boxes' investigated in this study, and the species they were designed to protect are detailed in Table 4.2 and shown in Figure 4.1.

I calculated the changes in environmental suitability within the Fisheries Boxes for the species they were specifically designed to manage. Relative environmental suitability values for all grid cells in the prediction were standardized across both years to give values lying between 0 and 1, thus allowing comparison between models. The change in relative environmental suitability between 1985 and 2050 (2050 value – 1985 value) was calculated for each 0.5° latitude x 0.5° longitude cell within a Fisheries Box.

Table 4.2. *Fisheries Boxes in UK waters and their aims for management*

Fisheries Exclusion Area	Rationale
Irish Sea	To protect cod spawning areas
Trevose	To protect cod spawning areas
Norway Pout	To protect juvenile whitefish, esp haddock, whiting, cod and saithe from industrial fishing for Norway Pout as the small mesh nets used produces a bycatch of young whitefish
Mackerel	To protect juvenile mackerel from trawling and purse seining. Targeting of mackerel within the box is only permitted by handlining, and mackerel bycatch limits are set for vessels fishing for other species.
Plaice	To reduce discards of juvenile plaice and sole, protecting nursery grounds.

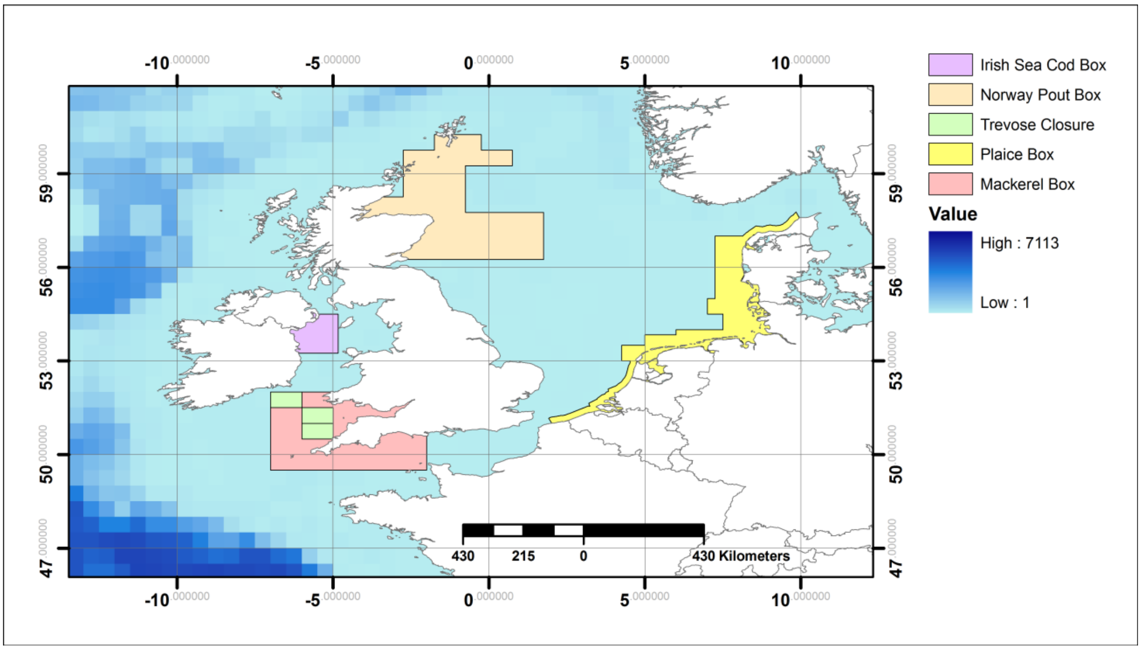


Figure 4.1. *Fisheries Boxes*

Areas closed for fishery management purposes in the UK and Ireland, including the Irish Sea Cod box, Trevose Closure, Mackerel box, Plaice box and Norway Pout box (Source: UKCP).

2.6. Model Assessment using Hindcast Data

The SDMs were further applied to GFDL data forced with historical climate data (GFDL hindcast). By comparing outputs obtained with previously observed shifts in distribution and depth, I examined the abilities of a modelling package to project environmental envelopes into alternative climatic conditions. However, any discrepancy between observations and model hindcasts could originate from uncertainties in the SDM used or the GCM. To test whether the SDM can accurately reproduce observed species shifts or occurrences would require a greater set of historically modelled, or ideally observed, climatologies. However, as hindcast data are only available for one model, and observed data were limited to SST, the methodology applied here represents an important first step in assessing the abilities of the SDMs additional to test statistics, whose limitations have been widely discussed in the literature (Lobo *et al.* 2008). GFDL hindcast SST data were first compared to observed SST data from HadISST2 (Rayner *et al.* 2005) in order to compare the modelled historic climatology. Hindcast projections were made for demersal species in order to make comparisons with available observations that largely consisted of changes in depth. As hindcast data were only available from 1959 - 2004, climatologies were averaged over 20 years to prevent overlap between time slices. Models were thus trained on a 20 year average centred on 1990 and projected on a 20 year average centred on 1970.

3. Results

3. 1. Latitudinal Centroids

My analysis projected that the distribution centroids of the 36 species investigated are expected to shift polewards from 1985 and 2050 using the SRES A2 scenario of climate change (Fig. 4.2). Overall, median projected rates of shift are significantly greater for pelagic than demersal species (Mann-Whitney U test: p-value < 0.01), at 277 and 168 km respectively over 65 years (Shapiro-Wilk tests and quantile-quantile plots were used to assess normality of data). This corresponds to a northward shift of 42 and 26 km decade^{-1}, respectively. When latitudinal shifts from each model are analysed individually, only the DBEM shows significant differences between pelagic and demersal species (Mann-Whitney U test: p-value < 0.01). For pelagic species the prediction of northward shift was found across all SDM-GCM combinations, with variation being shown in the magnitude of predicted shift within species. In particular, although *S. scombus* has a predicted median poleward shift similar to *S. sprattus,* the magnitude of variation around this median is about three times greater (range = 1849 and 604 respectively) (Fig. 4.3a). In general, DBEM predicts the greatest polewards shifts for pelagic species (S Fig. 4.1).

Although all demersal species were predicted to show a median northward shift, there were variations within species using different SDMs, and, to a lesser extent, GCMs. In particular, although Maxent and Aquamaps consistently predicted positive (northwards) shifts, some demersal species were predicted to move south using the DBEM, most frequently using CMIP3-E data (Fig. 4.3b). For example, the greatest southwards shift was projected for *S. Rhombus* (-215), despite having a median projected shift of 117 km northwards. The greatest variation in range shift is predicted for *Z. Faber,* (153 km southward – 428 km northward). For several species, such as *M. kitt and D. labrax,* there is good consensus in both the direction and magnitude of range shift between models. Contrasting pelagic species, the DBEM in general predicts smaller polewards shifts for demersal species (S Fig. 4.2), with greater variation than Maxent and AquaMaps, which again show good consensus using both climatic datasets.

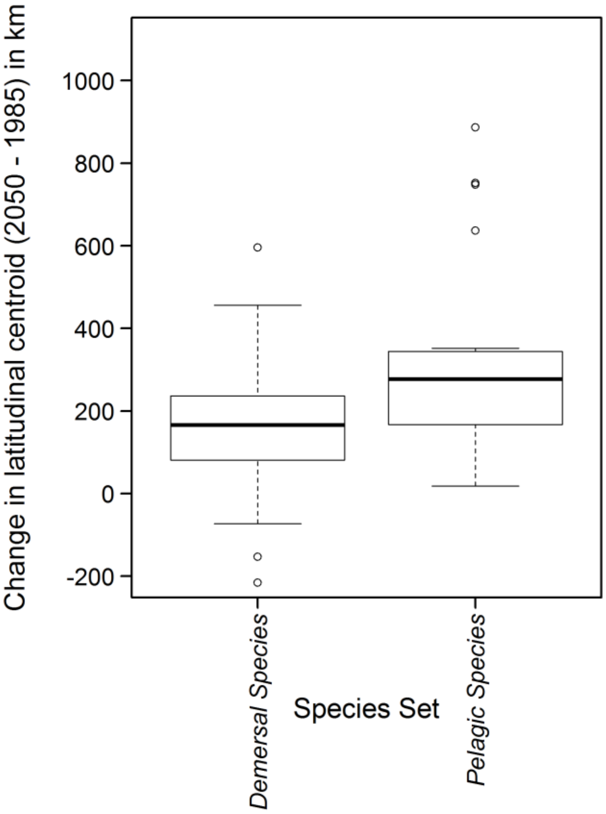


Figure 4.2. *Shifts in latitudinal centroid for grouped demersal and pelagic species. Projected change (in km) in latitudinal centroid from 1985 to 2050 across SDMs and climatic datasets for species grouped as demersal and pelagic. Thick bars represent median values, the upper and lower ends of the box represent the upper and lower quartiles of the data, and the whiskers represent the most extreme data points no greater than 1.5 times the inter-quartile range from the box. Points that are more extreme than whiskers are represented as circles.*

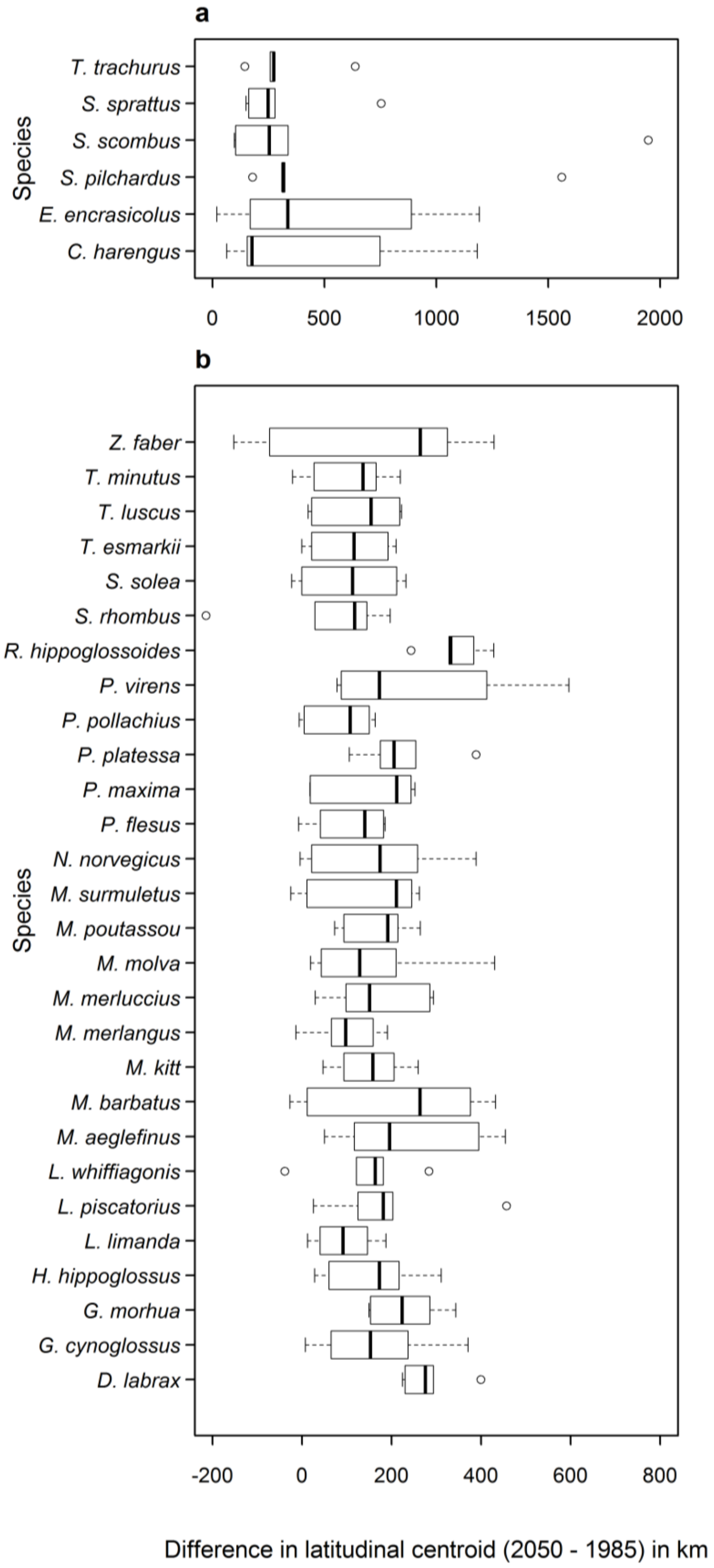


Figure 4.3. *Shifts in latitudinal centroids*

Projected change (in km) in latitudinal centroids from 1985 to 2050 across SDMs and climatic datasets for a) pelagic species and b) demeral species.

3.2. Depth

The median change in depth centroids over all demersal species and model combinations was predicted to be positive, implying a deepening of species, although small (0.12 m per decade) (Fig. 4.4). However, this value masks a large variation between species that is seen across model combinations. Although most species are predicted to show a median deepening between 1985 and 2050 under the SRES A2 scenario, changes in depth centroids show fewer consensuses in direction than predicted latitudinal shifts. Specifically, each species is predicted to shallow and deepen when different model combinations are applied (S Table 4.1). Of the four species predicted to experience the greatest shallowing, three of these, *M. Poutassou, R. hipoglopssoides* and *H. hippoglossus* had the greatest depth of centroids in 1985 using all six model combinations, with *L. piscatorius* appearing in 10 deepest centroids. No relationship was found between the prediction rate of shallowing and the latitudinal centroids value in 1985 or the degree of poleward movement.

3.3. Fisheries Boxes

The median change in Relative Environmental Suitability (RES) values (lying between 0 and 1) across all SDM-GCM model combinations for the specific species analysed in each Fisheries Box was small (Fig. 4.5). Median values indicate a general decrease in relative environmental suitability by 2050, ranging between -0.08 and 0. Median values of relative environmental suitability for each SDM-GCM combination in 1985 and 2050, the differences between time periods and the range of difference across each Fisheries Box, are given in Supplementary Table 4.2. The largest median decrease in relative environmental suitability (ΔRES) across all models is shown by Cod in the Trevose Box (ΔRES = -0.12), with a median decreases in RES throughout the Trevose Closure being predicted using all model combinations (S Table 4.2). Likewise, Cod is predicted to experience a decrease in environmental suitability in the Irish Cod Box, with agreement in the direction of change across all models except using AquaMaps and Maxent with GFDL data. Although these decreases in RES are accompanied by high median initial (1985) RES values in the Trevose Box, 1985 RES values in the Irish Sea Cod Box are predicted to be lower. In particular, AquaMaps and Maxent-GFDL do not show the high suitability values they characteristically achieve in other Fishery Boxes. However, these predicted suitabilities are contrasted by the DBEM, which although characteristically predicts low values of environmental suitability in other Fishery Boxes, predicts suitability values more consistent with the other modelling procedures in the Irish Sea Box.

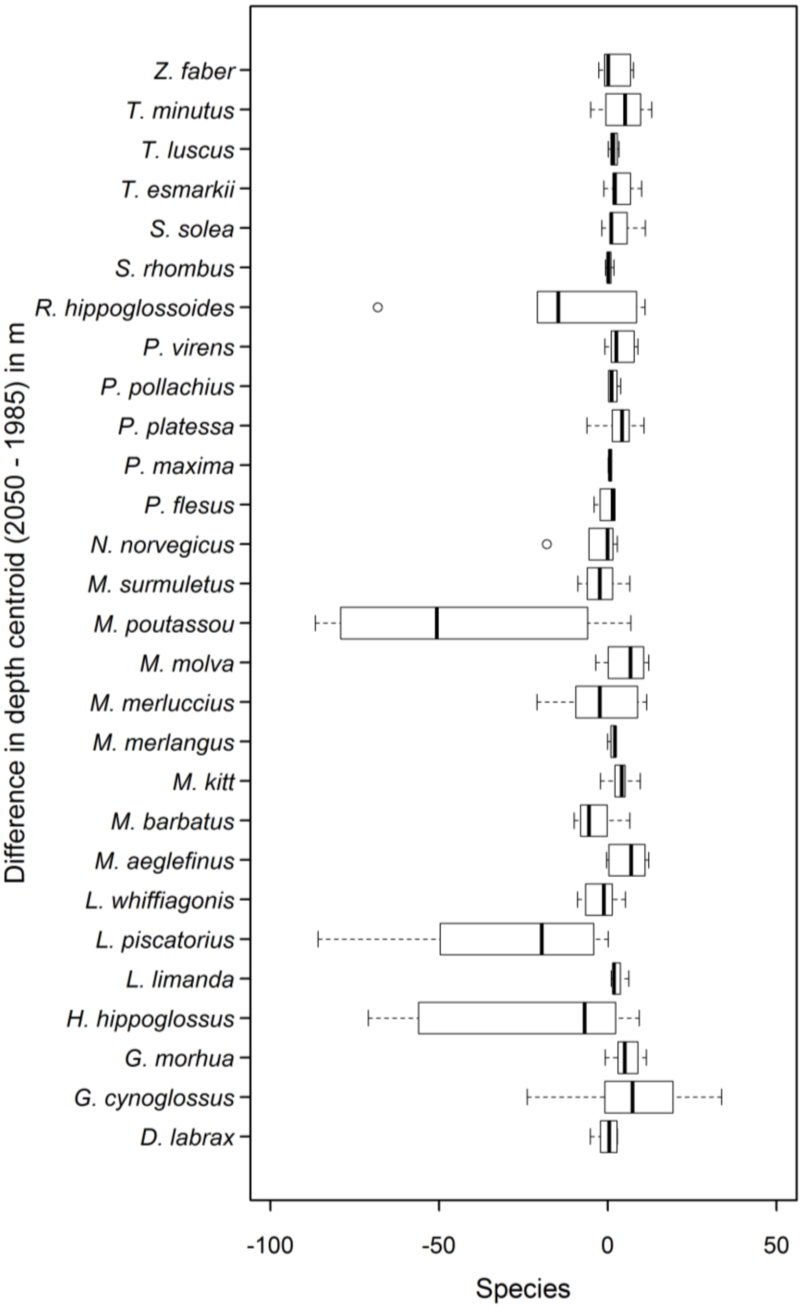


Figure 4.4. *Shifts in depth centroid for demersal species.*

Projected change (in m) in depth centroids from 1985 to 2050 across SDMs and climatic datasets for demersal species. Thick bars represent median values, the upper and lower ends of the box represent the upper and lower quartiles of the data, and the whiskers represent the most extreme data points no greater than 1.5 times inter-quartile range from the box. Points that are more extreme than whiskers are represented as circles.

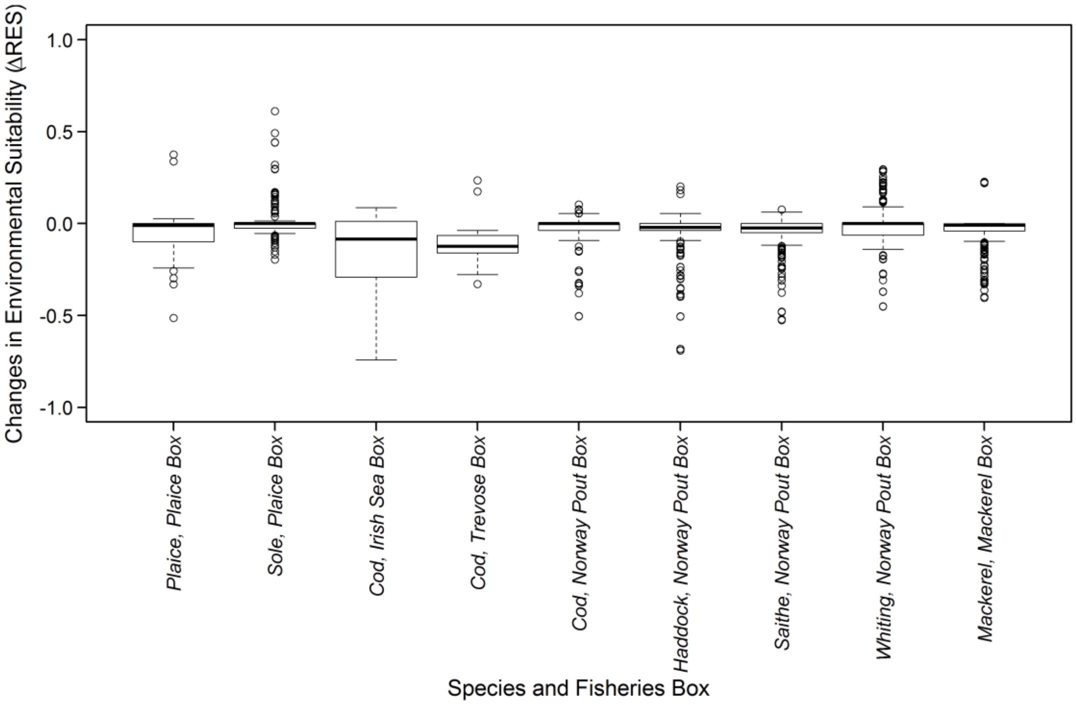


Figure 4.5. *Environmental suitability in Fisheries Boxes.*
Average difference in relative environmental suitability (2050 – 1985) for specified species in the assessed Fisheries Boxes.

Greater variation in the direction of change in relative environmental suitability under climate change is predicted for Sole in the Plaice Box. Sole shows the most positive predicted change in RES, although variations are seen between Maxent, which predicts the area to, in general, increase in RES, and the DBEM, which predicts a decrease. A similar pattern is seen in predictions for Plaice in the Plaice Box. However, although predictions of change for Plaice and Sole show a spread of similar magnitude to Cod in the Irish Box (0.88, 0.81 and 0.82 respectively), while greatest variations for Cod are produced between predictions using different models, both Plaice and Sole show wide variations across the cells of the Plaice Box using one model combination, such as Maxent - CMIP3-E (Plaice's ΔRES = 0.7) and AquaMaps - GFDL (Sole's ΔRES = 0.61) (S Table 4.2).

In the Norway Pout Box, all four whitebait species which the Box was set up to protect, as well as Norway pout itself are predicted to experience similar changes in environmental suitability, with the greatest spread of change across the fisheries box being predicted using Maxent. For example, Maxent with GFDL data predicted a median increase in environmental suitability across the fisheries box for Whiting (ΔRES = 0.02) and Cod (ΔRES = 0.01). Aside from this variation in environmental suitability change across the Norway Pout Box seen for Maxent, there is good agreement between SDM-GCM combinations in the degree of environmental suitability change (median values between -0.13 and 0.02 for all species). The SDM models show characteristics patterns of RES magnitude across the species (S Figure 4.3).

The only pelagic species to have been investigated in relation to its environmental suitability in protected areas shows similar patterns of change and characteristic RES values across models. Specifically, the area is in general predicted to decrease by a small amount (median ΔRES = -0.008), with strong agreement in the direction of change between models and relatively low variation in predicted change across the Mackerel Box.

3.4. Sensitivity Analysis

Sea surface temperature values obtained using the spatial climate scenario generator ClimGen were characteristically higher across the study area (average 13.0 °C) than those output by the GFDL model (average 12.0°C) (Fig. 4.6, a and b). As models were independently trained and projected for each SST dataset, this disparity should not affect a comparison of the effect of the two datasets on model output parameters. There were also regional variations in the rate of warming between the two models (Fig. 4.6, c-d), with GFDL showing greater average warming than ClimGen (0.85°C and 0.65°C respectively). The most striking difference between the climatologies is seen in the North Sea and Norwegian Sea. In the finer scale predictions produced by ClimGen, the Eastern and Northern North Sea, Celtic-Biscay shelf and Norwegian Sea show a similar temperature increase of 0.4 - 0.8°C between the two time periods. This is contrasted in the GFDL climatology, which shows greater temperature increases in these areas, in particular, areas of the Norwegian Sea increasing by 1.2 – 1.6°C.

Overall, the Species Distribution Models were found to be sensitive to differences in the downscaling technique applied to climate data, with latitudinal centroids being predicted to show smaller median northwards shifts between 1985 and 2050 using ClimGen than GFDL SST data, for all SDMs (Fig. 4.7), thus agreeing with the slower rates of warming predicted in the former. This difference was found to be significant for AquaMaps (Mann

Whitney p-value < 0.01), Maxent (Mann Whitney p-value < 0.01) and DBEM (two sample t-test p-value < 0.01). Latitudinal shifts predicted using only SST and bathymetry data have median values greater than those using all environmental variables, although the latter show a greater range of predictions across species, in particular using Maxent and DBEM.

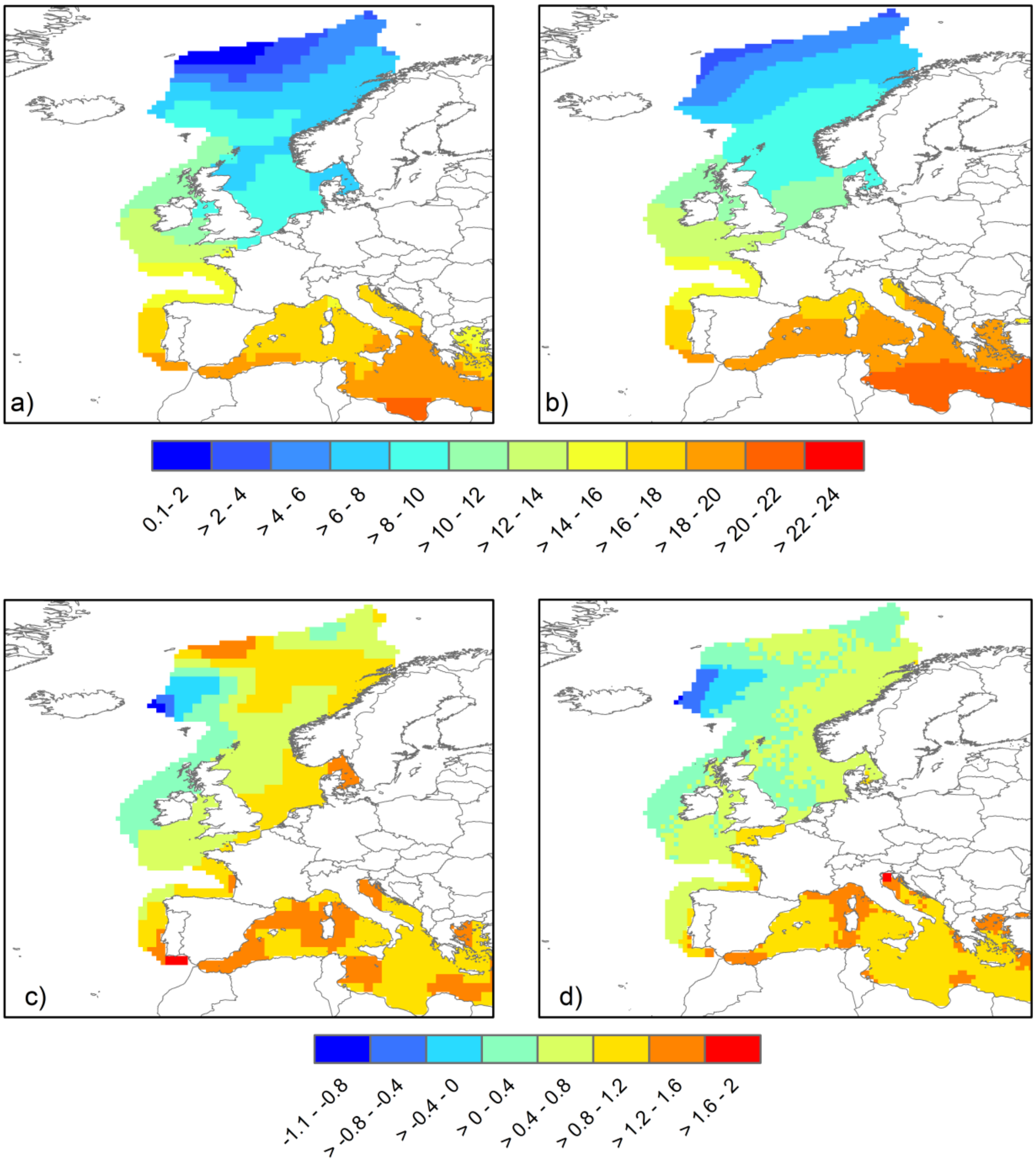


Figure 4.6. *Comparison of Sea Surface Temperature*

Sea surface temperature in 1985 a) modelled data from GFDL ESM2.1 b) observed data from HadSST2, and the difference in SST across the study areas between 1985 and 2050 using data from c) GFDL ESM2.1 d) ClimGen

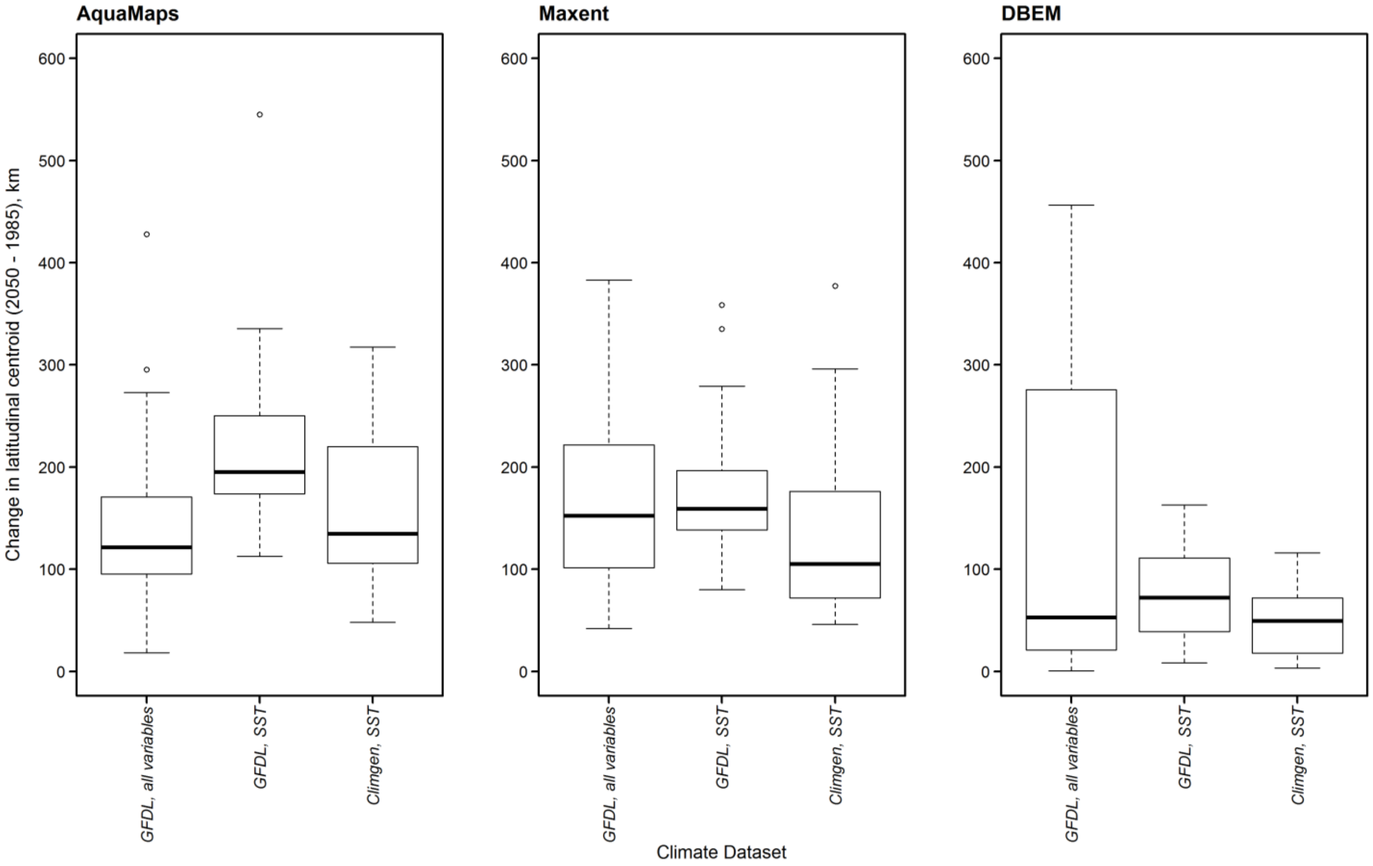


Figure 4.7. *Shifts in latitudinal centroid for demersal species.*

Projected change (in km) in latitudinal centroids from 1985 to 2050 for all demersal species using all GFDL ESM2.1 environmental variables, GFDL ESM2.1 SST and depth only and ClimGen SST and depth only, for a) AquaMaps b) Maxent c) DBEM.

3.5. Model Assessment using Hindcast Data

A time series of GFDL hindcast modelled SST data and HadISST observed SST shows strong agreement in the inter-annual variability between the two data sources (Fig. 4.8). There is, however, a mismatch in the overall temperature values, with HadISST observed data typically having a value ~ 1.5 degrees higher than those of the GFDL hindcast data between 1959 and 2004 (Fig. 4.8). As when creating projections using GFDL and ClimGen SST data, because SDMs will be both trained on and projected using GFDL hindcast, this difference is thought to be of less importance than the replication of temperature variation between years and the identification of a temperature trend. GFDL hindcast data thus indicated a decrease in water temperature in the North Sea between 1970 and 1990 for both SST (-0.13 °C) and SBT (-0.2 °C). Although this accompanied a concurrent decrease in temperature in the more northerly Norwegian Sea (SST: -0.18 °C, SBT: -0.56 °C), temperatures in the Celtic-Biscay shelf increased slightly (SST: 0.56 °C, SBT: 0.59 °C). Furthermore, the direction of temperature change varied for different cells in the study area between 1970 and 1990 (S Figure 4.4).

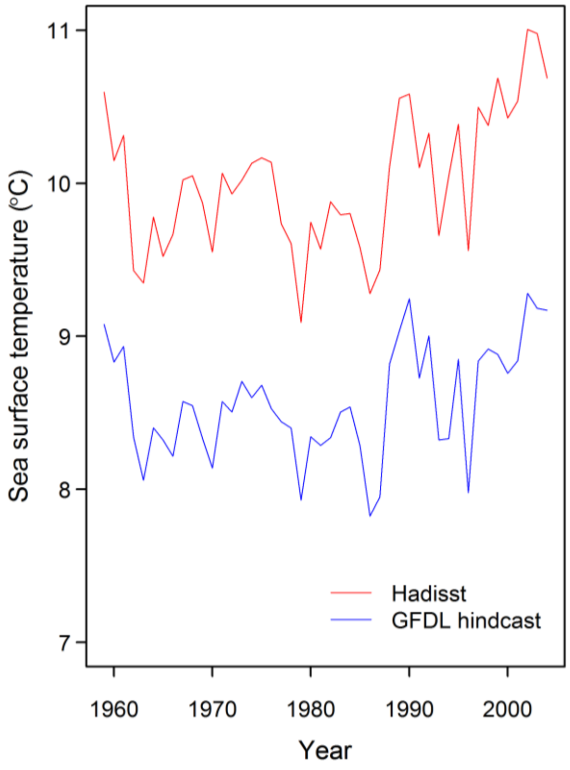


Figure 4.8. *Temperature trends from 1959-2005 in the North Sea.*

Sea Surface Temperature (SST) trends in the North Sea averaged over all cells at a 0.5° latitude x 0.5° longitude resolution from GFDL hindcast and HadISST observed data.

The mean deepening response of the set of demersal species to modelled climate change from 1970 to 1990 was 3.6 m decade $^{-1}$, averaged over all three SDMs. Individually, the mean deepening was 4.6 m, 5.0 m and 1.3 m for AquaMaps, Maxent and the DBEM respectively. Median values, however, were lower, at 0.09, -0.73 and 1.2 m respectively, and some species show a tendency to move into shallower water from 1970 to 1990 (Fig. 4.9a). In particular, all models predict a slight shallowing of *D. labrax* (median = -1.4 m) and plaice is predicted to shallow by 27 m using Maxent over this period. The median values for Maxent also indicates a general shallowing of the species assemblage (-0.73 m). There are also discrepancies between models in the direction of change for individual species, with DBEM predicting the opposite shift to Maxent and AquaMaps, for example for *P. maxima, P. platessa, M. Merluccius* and *M. aeglefinus* (S Table 4.3).

The latitudinal shift of the demersal species assemblage is in general predicted to be negative (mean = -49km decade^{-1}) (Fig. 4.9b), indicating a general southwards shift of the species assemblage between 1970 and 1990. Although this value reflects very large southward movement in a couple of species, in particular *P. platessa* and *M. merlangus* using Maxent, the median change in latitudinal centroid across all species and model combinations also indicates a southward shift (-6.5 km decade^{-1}). The discrepancies between the three SDMs are reflected in the individual median values, at 12.22 km decade^{-1} and 0.78 km decade^{-1} southward, and 0.41 km decade^{-1} northward for AquaMaps, Maxent and the DBEM respectively, between 1970 and 1990. As with the deepening response, there is much variation in the direction and magnitude of latitudinal shift between species and models, with the largest southward movement being projected with Maxent. However, while no relationship was found between initial latitudinal centroids and the degree of latitudinal shift in AquaMaps and DBEM, in Maxent, the species showing the greatest southwards shift are those with the most northerly distributions (S Figure 4.5). For example, while more northerly species such as *P. virens, P. platessa* and *G. morhua* show southwards shifts of 1921, 1694 and 913 km from 1970 to 1990 respectively, those with more southerly latitudinal centroids or a more geographically spread distribution show lesser shifts. For example, *Z. faber* is predicted to move south by 196 km while *S. rhombus* is predicted to move northwards by 167km. No relationship was found between the magnitude of depth shift and latitudinal shift. Further investigation of the response of the species assemblage to each variable of the hindcast data individually showed the southward shift to be exhibited across all variables, although most strongly in sea bottom temperature and primary productivity.

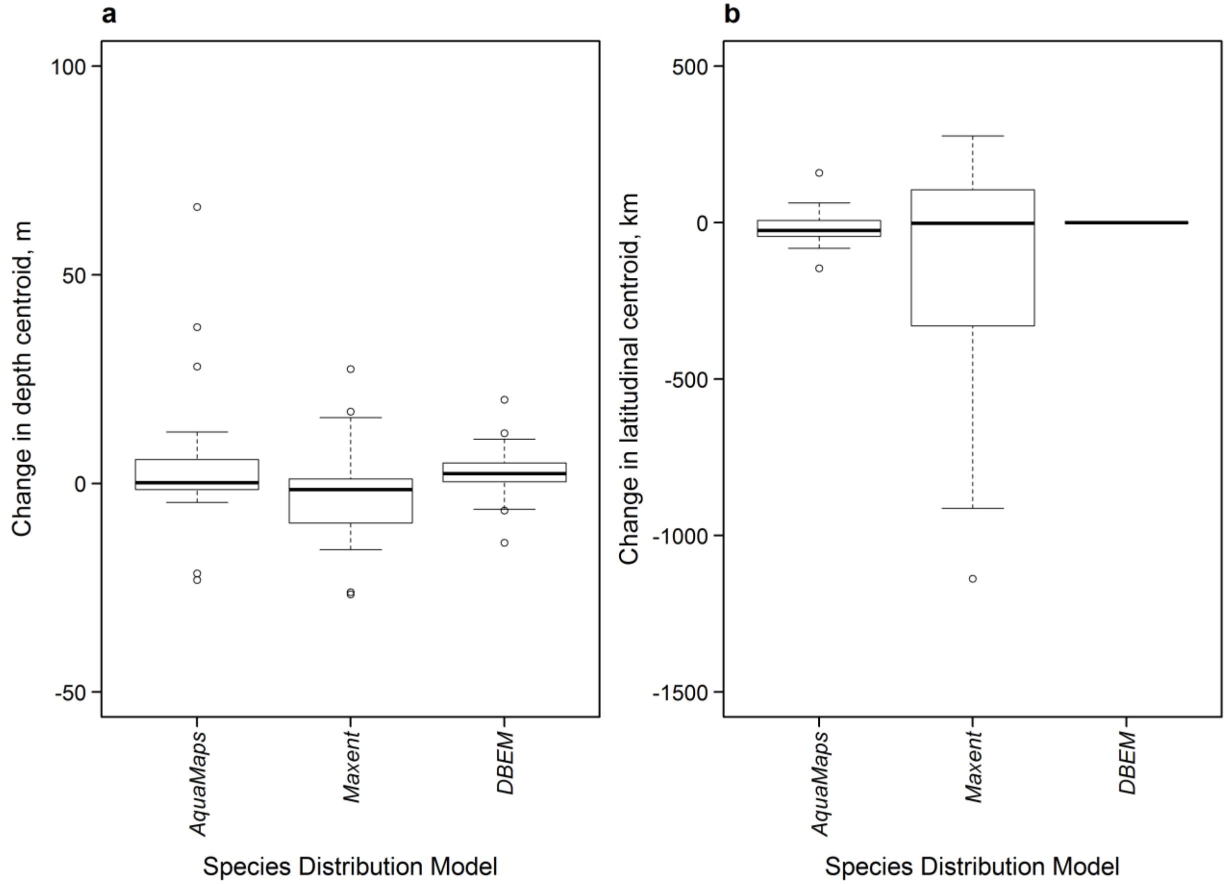


Figure 4.9. *Shifts in depth and latitudinal centroids for demersal species with hindcast data.*

Projected change in a) depth centroids (m, negative values indicating shallowing) and b) latitudinal centroids (km, negative values indicating southwards shift) from 1985 to 2050 using AquaMaps, Maxent and DBEM and GFDL hindcast environmental data for all demersal species.

4. Discussion

This study represents the second application of a set of species distribution and global climate models to marine vertebrate species. It highlights the sensitivity of commercially exploited fish species in the North Sea to climate change. As found in a previous application to threatened marine vertebrates (Chapter 3), this work emphasizes the variation in distribution predictions and output parameters achievable using a range of equally valid distribution models, climatic datasets and downscaling techniques. In assessing the future distributions of a set of commercial species, predictions such as these provide the foresight to inform management plans and measures that might contribute to enhancing the resilience and adaptability of fisheries in UK waters by allowing consideration of future scenarios of change. Given the importance of fishery adaptability and the potential expense of management measures in terms of implementation and lost revenue from fisheries, the variability in predictions and their sensitivity to different input datasets is important. If uncertainty in assumptions, datasets and modelling approaches is ignored in favour of tractability and uni-directional predictions, the utility of species distribution modelling in making decisions for lasting or future results may be lost and decisions made risk being misplaced. I therefore assess the range of predictions made, looking at the consequences for application in terms of general trend from the suite of models as well as potential outliers.

4.1. Distribution centroids of Future Climate

Predictions of northward shifts in distribution made here support the hypotheses for poleward movements in response to climate change that are frequently made for both terrestrial and marine species. My results further agree with the distribution shifts for marine species observed in the last few decades (Stebbing *et al.* 2002; Perry *et al.* 2005; Macleod *et al.* 2005; Dulvy *et al.* 2008; Simpson *et al.* 2011). In particular, results are similar to findings observed in the North Sea between 1978 and 2001 (Perry *et al.* 2005), where, out of 36 demersal species examined, six species showed boundary shifts in relation to both climate and time at a rate of 22 km decade^{-1}, thus corresponding well to the 26 km decade^{-1} projected range shift for demersal species found here. The greater range shift found here for pelagic species agrees with their greater motility and ability to span a wider range of locations and temperature ranges due to the ability to migrate. Pelagic species are also expected to show greater range shifts due to the faster rate of warming near the sea surface, where these species are found, than near the sea bed. This disparity in rate of shift agrees with Cheung *et al*. (2009), where range limits for pelagic and demersal species were projected to shift poleward by a median of 127 km for pelagic species (n = 209) and 47 km for demersal species (n = 857). The difference in magnitude of shift between this study and Cheung *et al*. (2009) likely reflects the greater number of species, covering a global range, the measurement of rate of shift at the range margin and the use of a different high range SRES scenario of climate change (A1B) in Cheung *et al.* (2009). AquaMaps and Maxent individually did not, however, predict significantly different range shifts for pelagic and demersal species. This differences in result is unlikely to be caused by the addition of dispersal in the DBEM, as any area suitable in terms of environmental parameters is predicted as present by AquaMaps and Maxent whether dispersal was thought to be achieved or not. Instead, the disparity is likely due to the incorporation of seasonal change in distributions of pelagic species by the DBEM while AquaMaps and Maxent predictions were based on annual average conditions only. By modelling a summer and winter distribution, the extremes of the thermal tolerance limits of these species, for example brought about for different environmental requirements in summer and winter due to breeding, would not be lost by annual averaging and the overall environmental tolerances are likely to be broader. By failing to account for the ability to span a wider range of climates in different season, Maxent and AquaMaps as applied here have likely led to an underestimation of potential range shift. It is recommended that future work should model pelagic, migratory species in both seasons, combining these predictions to obtain a distribution map over an entire year. This would prevent information on the true environmental envelope being lost when forming an annual value for environmental variables.

The greater range of predictions resulting from the DBEM for both pelagic and demersal species may reflect the greater sensitivity of this model to inter-annual fluctuations in the climate data. Specifically, while Maxent and AquaMaps train and project the environmental envelope on a 30 year average of each environmental variable, the DBEM creates a time series of projections, which are then averaged over the same 30 years. It is likely, that in applying an environmental envelope or preference profile to each year individually, outputs such as latitudinal shifts are more affected by inter-annual fluctuations in the DBEM. The southward shifts predicted for example for *S. rhombus* may thus reflect periods of cooling that have resulted in strong southward shifts and are translated more directly into the average shift value than in Maxent and AquaMaps, whose prior averaging evens out periods of cooling.

4.2. Fisheries Boxes

Whether the establishment of MPAs can lead to increase in abundance, age, size and fecundity of depleted stocks will depend on a number of factors, in particular the role of natural mortality and recruitment relative to scales of exploitation, as well as the nature of the target species concerned, the size of the MPA and enforcement issues. Further to these issues, a future change in climate over time may severely impact the suitability of a protected area for specific species, rendering them ineffective for protection and management purposes. Data analysed here support the hypothesis that a change in climate will result in a change in the relative environmental suitability of marine protected areas for particular species. Median values of change in relative environmental suitability for each Fisheries Box are zero or negative, indicating a decline in the environmental suitability for each species looked at. Assuming there are no changes in alternative management strategies for the species investigated, this implies a potential decrease in abundance of each species within the PA due to environmental change and a decline in the benefits of this management strategy. However, change in environmental suitability of species being commercially targeted in a Fisheries Box may also influence their future utility as a management tool. For example, although the Norway Pout is predicted to experience 0 median change in RES in the Norway Pout Box, the range of predictions encompass both predicted increases and decreases. If fisheries were to follow movement of Norway Pout stocks, the efficacy of the Fisheries Box in protecting particular species from the effects of industrial fishing for Norway Pout may be further reduced.

However, despite negative median values, there is variation in the change in environmental suitability across each protected area and according to the SDM and GCM used. Thus it is also possible that Fisheries Boxes might offer some resilience to climate change, providing a degree of protection to particular species. This is especially likely to be the case if the pressures of environmental change and fishing combine synergistically to negatively impact a species, its growth and reproduction. The degree of protection afforded will thus depend on the relative pressures attributable to both climate change and fishing outside and within the protected area. For example, if the climatic change within a Fisheries Box is relatively low compared to elsewhere in a species’ range, and fishing pressure is reduced, the Box might provide valuable buffering and spill-over effects. For the species investigated here, this buffering capacity may be most likely provided by the Plaice Box for Sole. Although the relative environmental suitability for this species varies according to the SDM used, with DBEM and AquaMaps predicting low and high RES respectively, increases in RES at certain locations within the Fisheries Box are predicted for both climatic datasets using Maxent and AquaMaps. In the case of Cod, more precaution should be taken in assessing the protection afforded by the Irish and Trevose Boxes in the future. In these cases, there is a more consistent prediction for decreasing environmental suitability. This might be due to their position nearer the edge of Cod's range, contrasted by the Norway Pout Box, which, lying to the east of UK, show a greater initial environmental suitability in 1985 and lesser tendency to decrease in suitability, using Maxent and AquaMaps.

4.3. Sensitivity Analysis

The disparity between median latitudinal shift modelled using only GFDL SST and bathymetry and those using the whole suite of environmental variables is likely due to the more restrictive effect of using a greater number of variables on the range shift, as well as the greater rate of change for SST than, for example, SBT and salinity. For example, locations that become suitable in 2050 due to warming SST may still be rendered unsuitable by other environmental variables. The extent of restrictions by variables other than SST varies between species distribution models. For example, distributions predicted using AquaMaps shows lower rate of latitudinal shifts because not all environmental variables, which were equally weighted in AquaMaps, were projected to become suitable for the species. Conversely, the greater range of latitudinal shift across species projected by Maxent may reflect the less restricted distribution constructed by variable weighting of different environmental factors. As the DBEM required all environmental variables to be input in order for a model output to be produced, variables other than SST were maintained at a constant level. In assessing outputs produced, it seems likely that this may have had the effect of restricting the prediction.

The differences in latitudinal centroids shift seen using all models with GFDL SST and ClimGen SST are likely due to variations in the amount and spatial distribution of warming seen over the study region between the two climatologies. For example, the greater warming in the northern extent of many species ranges (such as the Norwegian Sea) seen using GFDL ESM2.1 SST data is likely to increase the environmental suitability for many species in this area. As the calculation of latitudinal centroids reflects the magnitude of environmental suitability, this greater warming would drive a stronger poleward shift. It is thus hypothesised that inputting a full dataset downscaled using the ClimGen methodology would produce more conservative projections of median latitudinal shift across this set of demersal species. The most resilient model to this change in SST climatology is the DBEM. These results highlight the variation in outputs obtainable using alternative downscaling techniques on the same climate dataset.

4.4. Model Assessment using Hindcast Data

The average deepening response of 3.6 m decade^{-1} for this set of demersal species between 1970 and 1990 corresponds well to results previously observed. Dulvy *et al.* (2008), for example, found the demersal fish assemblage of the North Sea, composed of 28 species, to deepen significantly at a rate of ~3.6 m decade^{-1} between 1980 and 2004. These observed depth shifts were seen to vary from year to year (species being shallowest in the cool mid 1980s and deepest in the peak warming in the mid-1990s) whilst corresponding to temperature change over a longer time scale (Dulvy *et al.* 2008). However, the average value that indicates deepening masks variation between species, with all models projecting shallowing for some species. Although this could be due to the difference in species set used here and in Dulvy *et al.* (2008), this likely also results from the difference in temperature change between the two studies. Thus while between 1970 and 1990, GFDL hindcast data predicted a slight decrease in temperature through much of the study area, there was a 1.6 ^{o}C increase in SBT over the 25 years (1980 – 2004) reported in Dulvy *et al.* (2008).

Other studies report observed northwards shifts in species distribution in response to warming. Perry *et al*. (2005), for example, found demersal species in the North Sea to move between 48 and 403 km from 1977 to 2001, with 13 out of 15 of these shifts being northward. However, this time period coincided with an observed temperature increase of 1.05°C (Perry *et al.* (2005), using data from the ICES Oceanographic Database). The overall cooling predicted by the GFDL hindcast data may thus explain the unexpected predicted southward movement of species between 1970 and 1990. This is supported by the largest southwards shifts being observed for the most northern distributed species in Maxent, for which temperatures at the northern boundaries of their range are most likely to become unsuitable on cooling, forcing a southward shift. The predicted trend of distribution shifts are therefore consistent with modelled temperatures that suggest partial cooling in the North Sea as well as the Norwegian Sea, while the heterogeneous nature of this temperature change is also reflected in the variation in species responses.

Although a deepening response has been found, it is difficult to tell whether this reflects local warming of shallow waters or results as a product of the latitudinal shift, especially due to the shallow and variable topography of the North Sea which might prevent a relationship between depth shift and latitudinal shift being found.

In order to undertake a more rigorous testing and obtain empirical support indicating the ability of these modelling procedures to re-create observed results, hindcast climatic data from a greater number of climate models would be useful. Also, hindcast data covering a greater time period would enable datasets for model training and testing to be obtained covering a greater time span. This might result in more consistent, unidirectional changes in temperature between the two time periods used for model projections as well as allowing modelled results to coincide more precisely with the time frame of observed species shifts. A datasets of historic and current observed temperature change would also allow comparison to observations of distribution and abundance shifts obtained from research surveys. This would be beneficial in testing the abilities of the whole modelling procedure to historic species movements or the changes in the centroid of their distributions. Results could also be compared to those obtained by Englehard *et al.* (2008) and Simpson *et al.* (2011).

5. Conclusions

This study demonstrates the importance of considering sources of variation in modelling approaches and data inputs when projecting species distributions under climate change. Comparing results from multiple models and data sets increases our understanding of the relationship between distribution shifts and changes in different environmental conditions. Specifically, this study suggests distributions of pelagic species to be most sensitive to climate change, potentially having a larger impact on their fisheries, for example, through disputes in quotas of transboundary stocks. The possible movement of demersal species to deeper waters may also affect their catchability. If catches are then reduced, fishermen may have to develop alternative strategies to maximise fishing output, such as targeting species that might be moving to shallower or more accessible waters, employing different gears, or altering fishing location. Results from this study provide information for government and industry to develop scenarios of such impacts and identify adaptation options. Such application is illustrated by the analysis of the UK Fisheries Boxes. Particularly, the changing environmental suitability of these Fisheries

Boxes is important due to the potential for synergistic impacts of fishing and climate change on fish stocks. The positioning of these Boxes within a particular species' range likely influences how its relative habit suitability might alter with climate change and thus its continued efficacy as a management tool. This study provides useful information to formulate and apply management strategies such that the efficacy of each Box for the particular species they are designed to protect is enhanced both currently and in the future.

References

Beare, D., Finlay, B., Jones, E., Peach, K., Portilla, E., Greig, T., McKenzie, E., *et al*. (2004) An increase in the abundance of anchovies and sardines in the north-western North Sea since 1995. *Global Change Biology* **10**, 1209–1213.

Bernal, P.A. (1993) Global climate change in the oceans: a review. In: *Earth System Response to Global Change: Contrast between North and South America.* (eds H.A. Mooney, E.R. Fuentes and B.I. Kronberg). Academic Press, San Diego, CA, pp 1–15.

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E. S., Brander, K. M., Brown, C., *et al*. (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334**, 652–655.

Chassot, E., Bonhommeau, S., Dulvy, N.K., Mélin, F., Watson, R., Gascuel, D. and Le Pape, O. (2010) Global marine primary production constrains fisheries catches. *Ecology Letters* **13**, 495–505.

Cheung, W.W.L., Close, C., Lam, V., Watson, R. and Pauly, D. (2008a) Application of macroecological theory to predict effects of climate change on global fisheries potential. *Marine Ecology Progress Series* **365**, 187–197.

Cheung, W.W.L., Dunne, J., Sarmiento, J.L. and Pauly, D. (2011) Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. *ICES Journal of Marine Science* **68**, 1008–1018.

Cheung, W.W.L., Lam, V.W.Y. and Pauly, D. (2008b) Modelling present and climate-shifted distributions of marine fishes and invertebrates. *Fisheries Centre Research Report* **16**.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R. and Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* **10**, 235–251.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., Zeller, D. and Pauly, D. (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology* **16**, 24–35.

Cheung, W.W.L., Meeuwig, J.J., Feng, M., Harvey, E., Lam, V.W.Y., Langlois, T., Slawinski, D., *et al*. (2012a) Climate-change induced tropicalisation of marine communities in Western Australia. *Marine and Freshwater Research* **63**, 415 – 427.

Cheung, W.W.L., Pinnegar, J., Merino, G., Jones, M.C. and Barange, M. (2012b) Review of climate change impacts on marine fisheries in the UK and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **22**, 368–388.

Clarke, R.A., Fox, C.J., Viner, D. and Livermore, M. (2003) North Sea cod and climate change – modelling the effects of temperature on population dynamics. *Global Change Biology*, **9**, 1669–1680.

Close, C., Cheung, W., Hodgson, S., Lam, V., Watson, R. and Pauly, D. (2006) Distribution ranges of commercial fishes and invertebrates. *Fisheries Centre Research Report* **14**, 27 – 37.

Dulvy, N.K., Jennings, S., Goodwin, N.B., Grant, A. and Reynolds, J.D. (2005) Comparison of threat and exploitation status in North-East Atlantic marine populations. *Journal of Applied Ecology* **42**, 883–891.

Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmller, V., Dye, S.R. and Skjoldal, H.R. (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology* **45**, 1029–1039.

Edwards, M. and Richardson, A.J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**, 881–4.

Engelhard, G.H., Pinnegar, J.K., Kell, L.T. and Rijnsdorp, A. D. (2011) Nine decades of North Sea sole and plaice distribution. *ICES Journal of Marine Science* **68**, 1090–1104.

Fitter, A.H. and Fitter, R.S.R. (2002) Rapid changes in flowering time in British plants. *Science* **296**, 1689–91.

Froese, R. and Pauly, D. (2011) Fishbase. Available at: www.fishbase.org, version (02/2011) [Accessed February 2, 2012].

Fukasawa, M., Freeland, H., Perkin, R., Watanabe, T., Uchida, H. and Nishina, A. (2004) Bottom water warming in the North Pacific Ocean. *Nature* **437,** 825–827.

Harris, A.H. (1993) Wisconsinan pre-pleniglacial biotic change in southeastern New Mexico. *Quaternary Research* **40**, 127–133.

Hiddink, J.G. and ter Hofstede, R. (2008) Climate induced increases in species richness of marine fishes. *Global Change Biology* **14**, 453–460.

IPCC, 2001: *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* [eds J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, *et al.*]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 881pp.

IPCC (2007) Summary for policymakers. In: *Climate Change 2007: The Physical Science Basis. Working Group 1 Contribution to the Fourth Assessment Report of the IPCC*. (eds S. Solomon, D. Qin, M. Manning, *et al.*). Cambridge University Press, Cambridge, UK and New York, USA. 996pp

Jones, M.C., Dye, S.R., Pinnegar, J.K., Warren, R. and Cheung, W.W.L. (2012) Modelling commercial fish distributions: Prediction and assessment using different approaches. *Ecological Modelling* **225**, 133–145.

Kaschner, K., Tittensor, D.P., Ready, J., Gerrodette, T. and Worm, B. (2011) Current and future patterns of global marine mammal biodiversity. *PLoS ONE* **6**, e19653.

Kaschner, K., Watson, R., Trites, A. and Pauly, D. (2006) Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. *Marine Ecology Progress Series* **316**, 285–310.

Levitus, S., Antonov, J.I., Boyer, T.P. and Stephens, C. (2000) Warming of the world ocean. *Science* **287**, 2225–2229.

Lobo, J.M., Jiménez-valverde, A. and Real, R. (2008) AUC: A misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* **17**, 145–151.

MMO (2011) *UK Sea Fisheries Statistics 2010*.

Macleod, C., Bannon, S., Pierce, G., Schweder, C., Learmonth, J., Herman, J. and Reid, R. (2005) Climate change and the cetacean community of north-west Scotland. *Biological Conservation* **124**, 477–483.

Murawski, S.A., Brown, R., Lai, H.L., Rago, P.J. and Hendrickson, L. (2000) Large-scale closed areas as a fishery-management tool in temperate marine systems: the Georges Bank experience. *Bulletin of Marine Science* **66**, 775–798.

Parmesan, C., Root, T.L. and Willig, M.R. (2000) Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meterological Society* **81**, 443–450.

Parmesan, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.

Parry, M.L., Canziani, O.F., Palutikof, J.P., Linden, van der, P.J. and Hanson, C.E. (2007) Climate Change 2007: Impacts, Adaptation and Vulnerability. In: *Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel of Climate Change*. Cambridge University Press, Cambridge, UK, pp 976.

Perry, A.L., Low, P.J., Ellis, J.R. and Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–5.

Phillips, S.J., Anderson, R.P. and Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**, 231–259.

Phillips, S.J. and Dudik, M. (2008) Modeling of species distributions with Maxent : new extensions and a comprehensive evaluation. *Ecography* **31**, 161–175.

Pinnegar, J.K., Jennings, S., Brien, C.M.O. and Polunin, N.V.C. (2002) Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *Journal of Applied Ecology* **39**, 377–390.

Portner, H. (2001) Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Continental Shelf Research* **21**, 1975–1997.

Rayner, N.A., Brohan, P., Parker, D.E., Folland, C.K., Kennedy, M., Vanicek, M. and Ansell, T.J. (2005) Improved analyses of changes and uncertainties in sea surface temperature measured in situ since the mid-nineteenth century : The HadSST2 Dataset. *Journal of Climate* **19**, 446–469.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweigk, C. and Pounds, A.J. (2003) Fingerprints of global warming on wild animals and plants. *Nature* **42**, 57–60.

Schneider, S.H. and Root, T.L. (1998) Impacts of climate change on biological resources. In: *Status and Trends of the Nations Biological Resources, vol 1*. (eds M.J. Mac, P.A. Opler, C.E. Puckett, P. Haecker and P.D. Doran). US Geological Survey, Reston, Virginia, pp 89–116.

Simpson, S.D., Jennings, S., Johnson, M.P., Blanchard, J.L., Schön, P.-J., Sims, D.W. and Genner, M.J. (2011) Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Current Biology* **21**, 1565–1570.

Stebbing, A.R.D., Turk, S.M.T., Wheeler, A. and Clarke, K.R. (2002) Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960-2001). *Journal of the Marine Biological Association of the United Kingdom* **82**, 177–180.

Sunday, J.M., Bates, A.E. and Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change* **2**, 1–5.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B.F.N., *et al*. (2004) Extinction risk from climate change. *Nature* **427**, 145–8.

Warren, R., Delanavasantos, S., Arnell, N., Bane, M., Baker, T., Barton, C., Ford, R., *et al*. (2007) Development and illustrative outputs of the Community Integrated

Assessment System (CIAS), a multi-institutional modular integrated assessment approach for modelling climate change. *Environmental Modelling & Software* **23:** 592–610.

Appendix

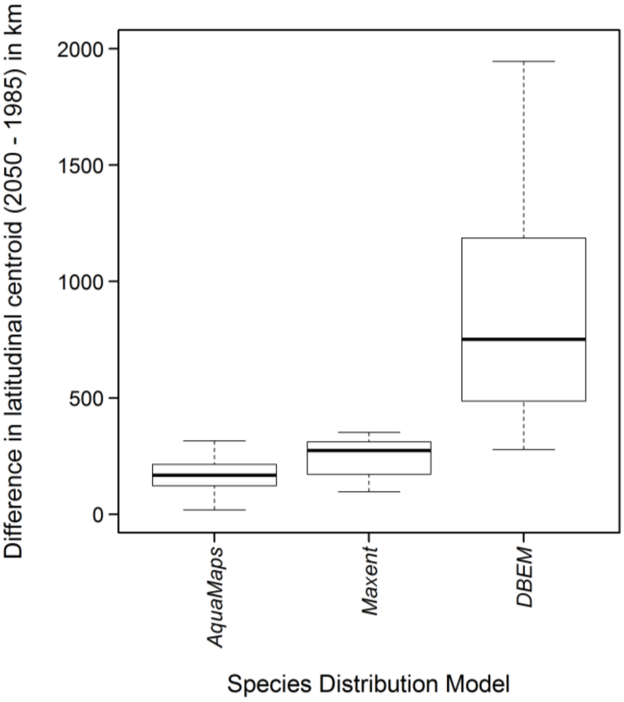


Figure 4.1. *Change in latitudinal centroids (2050 – 1985) for pelagic species across both climate datasets (GFDL and CMIP3-E) using AquaMaps, Maxent and DBEM*

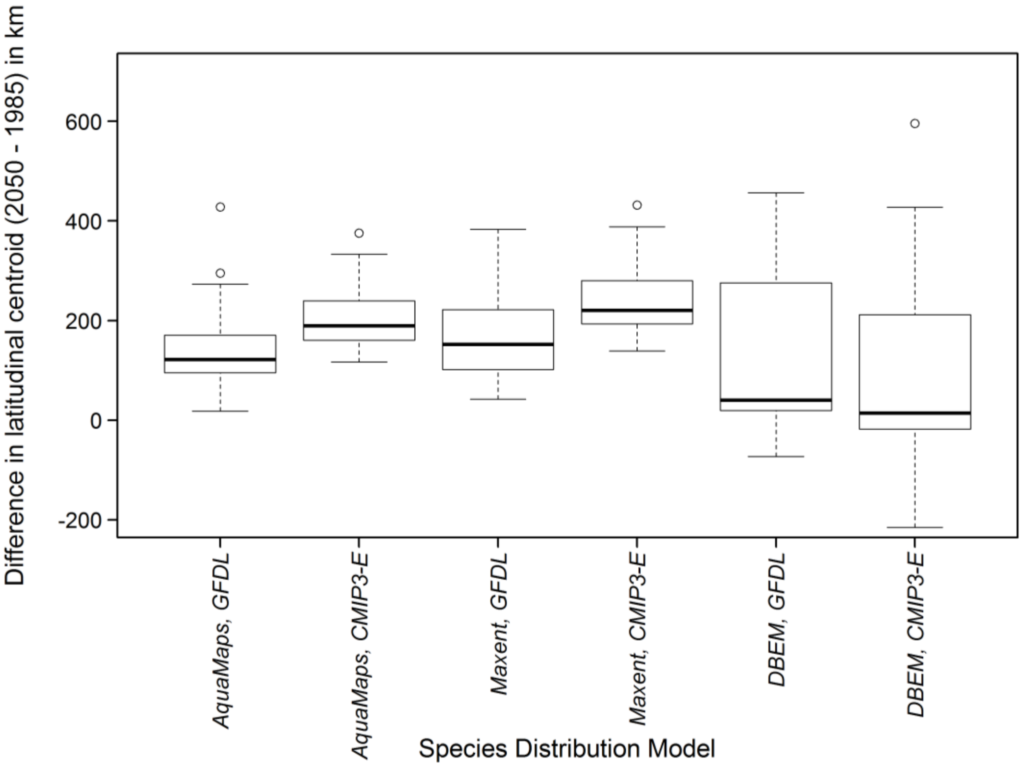


Figure 4.2. *Change in latitudinal centroids (2050 – 1985) for demersal species using AquaMaps, Maxent and DBEM with GFDL and CMIP3-E climate datasets.*

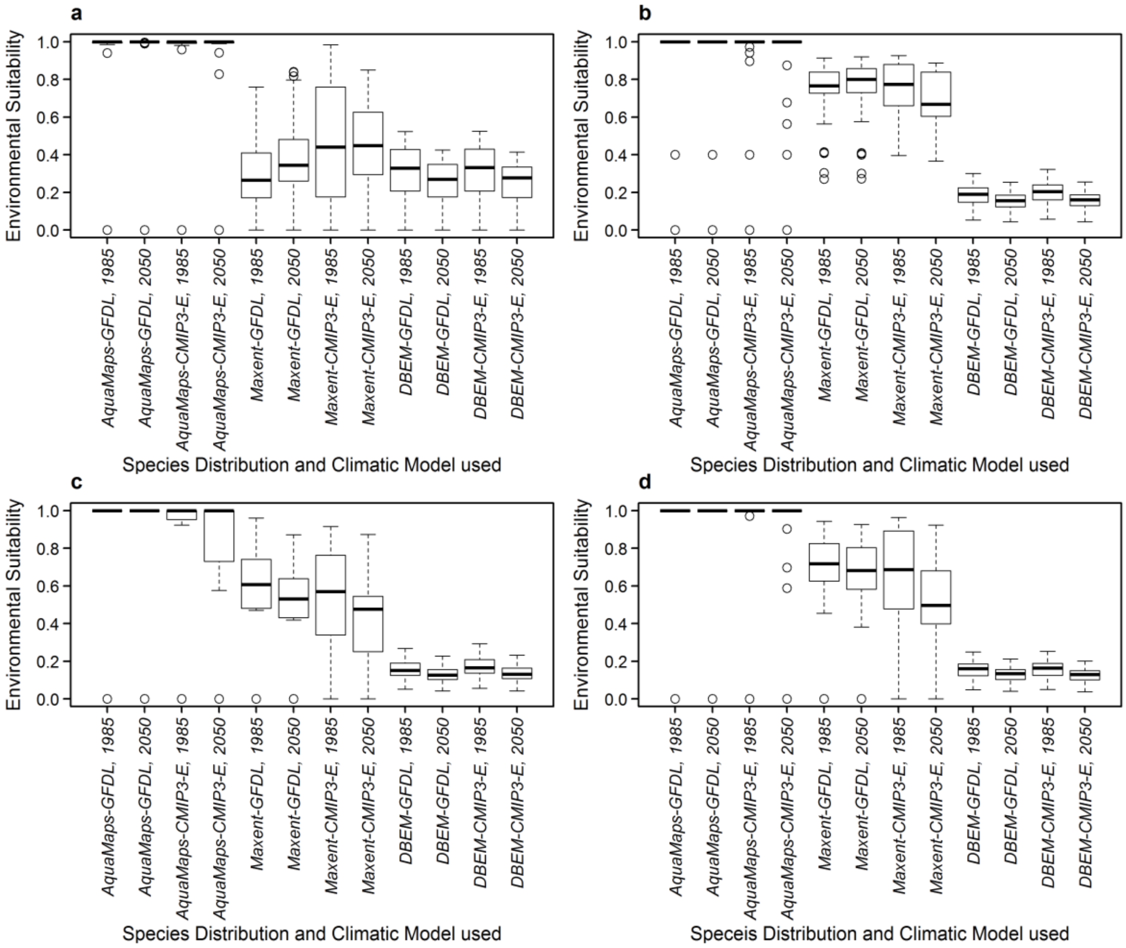


Figure 4.3. *Environmental suitability in the Norway Pout Box.*

Environmental suitabilities predicted in 1985 and 2050 for the Norway Pout Box for a) Whiting b) Cod c) Saithe d) Haddock, using AquaMaps, Maxent and the DBEM, with GFDL and CMIP-E data.

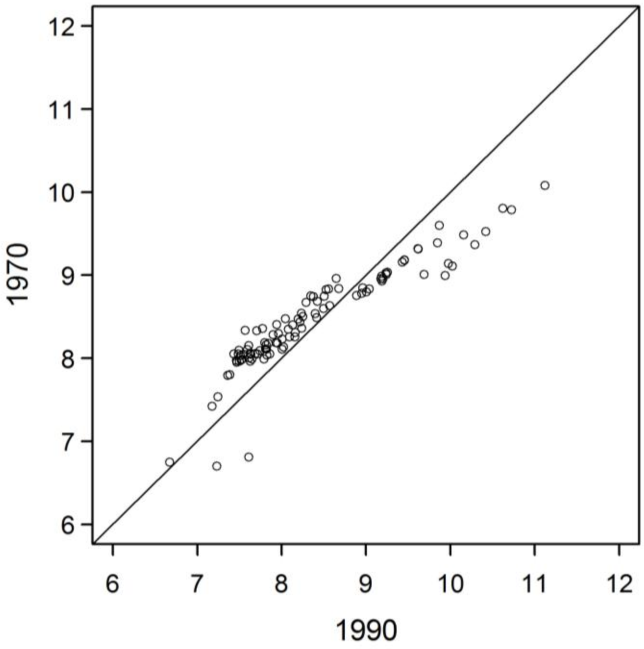


Figure 4.4. *GFDL Hindcast SST data for each 0.5° latitude x 0.5° longitude cell in the North Sea, averaged over 20 years centred on 1970 and 1990.*

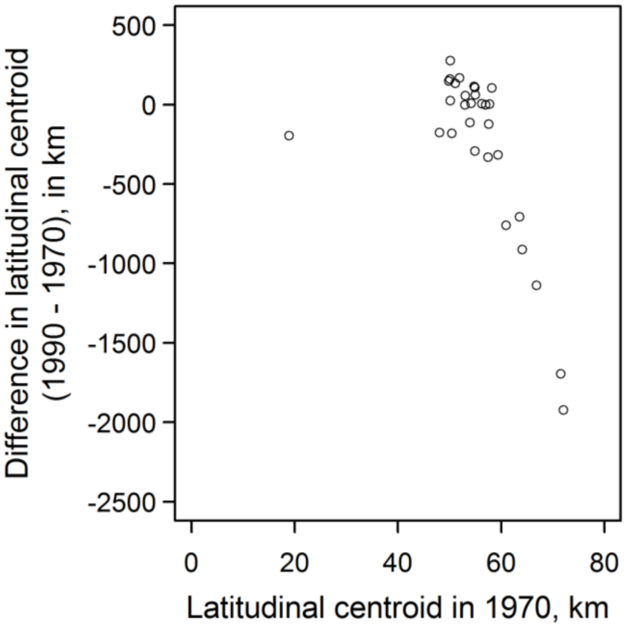


Figure 4.5. *Change in Latitudinal shift between 1970 and 1990 plotted against initial latitudinal centroids in 1970, modelled using Maxent*

Table 4.1.

Changes in latitudinal centroid shift, in kilometres, using each species distribution model with both GFDL and CMIP3-E climate data.

Species	**AquaMaps, GFDL (km)**	**AquaMaps, CMIP3-E (km)**	**Maxent, GFDL (km)**	**Maxent, CMIP3-E (km)**	**DBEM, GFDL (km)**	**DBEM, CMIP3-E (km)**	**Median**
D. labrax	2.73	2.60	0.78	-0.10	-5.26	-2.22	0.34
G. cynoglossus	-23.98	-0.91	0.48	19.20	33.67	14.05	7.27
G. morhua	-0.82	8.84	3.00	11.35	3.97	5.91	4.94
H. hippoglossus	-10.85	-71.06	2.21	9.22	-3.05	-56.14	-6.95
L. limanda	0.91	6.11	1.72	3.64	1.37	1.76	1.74
L. piscatorius	-28.24	-4.22	-11.13	0.07	-49.75	-85.91	-19.69
L. whiffiagonis	-9.10	0.52	-2.93	5.12	1.21	-6.69	-1.21
M. aeglefinus	2.73	10.98	0.24	10.98	-0.41	12.05	6.85
M. barbatus	-5.37	-5.96	-10.01	-8.17	-0.22	6.44	-5.67
M. kitt	5.09	9.60	-2.29	4.60	3.56	2.07	4.08
M. merlangus	-0.15	2.07	0.83	2.38	1.96	2.33	2.01
M. merluccius	-21.01	-9.51	-3.86	8.79	-1.03	11.47	-2.45
M. molva	-3.63	7.95	0.03	12.04	5.45	10.57	6.70
M. poutassou	-86.79	-72.62	-79.22	-28.80	-6.06	6.73	-50.71
M. surmuletus	-8.93	-4.66	-6.16	1.40	-0.18	6.41	-2.42
N. norvegicus	-18.19	2.71	-5.64	0.89	-1.15	1.49	-0.13
P. flesus	2.04	1.28	-4.14	-2.36	1.35	2.06	1.32
P. maxima	0.48	1.06	0.23	1.04	0.04	0.67	0.57
P. platessa	6.30	10.67	-6.21	1.20	4.21	3.99	4.10
P. pollachius	0.14	2.64	0.99	3.75	0.11	1.07	1.03
P. virens	2.28	7.79	2.63	8.84	-0.98	1.00	2.45
R. hippoglossoides	-20.93	-68.28	-15.52	-13.98	10.95	8.46	-14.75

Species	AquaMaps, GFDL (km)	AquaMaps, CMIP3-E (km)	Maxent, GFDL (km)	Maxent, CMIP3-E (km)	DBEM, GFDL (km)	DBEM, CMIP3-E (km)	Median
S. rhombus	0.30	0.82	-0.79	-0.25	-0.12	1.71	0.09
S. solea	0.56	1.01	-1.89	0.82	5.66	11.04	0.92
T. esmarkii	-1.22	6.63	1.42	9.93	2.18	1.98	2.08
T. luscus	0.94	2.09	0.88	3.28	0.05	2.78	1.52
T. minutus	-5.20	9.65	5.43	12.94	-0.65	4.70	5.06
Z. faber	-2.78	-0.41	-1.09	0.60	6.67	7.54	0.09

Table 4.2.

Median values of relative environmental suitability for each SDM-GCM combination in 1985 and 2050, the median differences between time periods and the range of difference across each Fisheries Box.

Species/ Fisheries Box		**AquaMaps, GFDL**	**AquaMaps, CMIP3-E**	**Maxent, GFDL**	**Maxent, CMIP3-E**	**DBEM, GFDL**	**DBEM, CMIP3-E**
Cod, Trevose Box	Median difference in RES	-0.06	-0.14	-0.04	-0.19	-0.15	-0.14
	Range of difference in RES	0.02	0.20	0.32	0.17	0.08	0.07
	Median standardized RES, 1985	0.98	1.00	0.48	0.56	0.84	0.84
	Median standardized RES, 2050	0.91	0.86	0.43	0.36	0.70	0.70
Cod, Irish Sea Box	Median difference in RES	0.08	-0.29	0.01	-0.41	-0.12	-0.09
	Range of difference in RES	0.09	0.32	0.01	0.41	0.19	0.14
	Median standardized RES, 1985	0.64	0.66	0.08	0.72	0.60	0.60
	Median standardized RES, 2050	0.72	0.36	0.10	0.33	0.48	0.51
Mackerel, Mackerel Box	Median difference in RES	0.00	-0.03	-0.02	-0.21	-0.01	0.00
	Range of difference in RES	0.00	0.19	0.27	0.41	0.02	0.00
	Median standardized RES, 1985	1.00	1.00	0.34	0.64	0.09	0.00
	Median standardized RES, 2050	1.00	0.90	0.32	0.33	0.08	0.00
Sole, Plaice Box	Median difference in RES	0.00	0.00	0.12	-0.04	-0.02	-0.02
	Range of difference in RES	0.61	0.30	0.49	0.64	0.03	0.04
	Median standardized RES, 1985	1.00	1.00	0.60	0.37	0.09	0.09
	Median standardized RES, 2050	1.00	1.00	0.77	0.38	0.07	0.07
Plaice, Plaice Box	Median difference in RES	0.00	0.00	-0.13	-0.12	0.01	-0.01
	Range of difference in RES	0.00	0.51	0.15	0.71	0.04	0.02
	Median standardized RES, 1985	1.00	1.00	0.76	0.34	0.18	0.17
	Median standardized RES, 2050	1.00	1.00	0.66	0.22	0.19	0.16
Cod, Norway Pout Box	Median difference in RES	0.00	0.00	0.02	-0.04	-0.03	-0.04

	Range of difference in RES	0.00	0.48	0.05	0.58	0.04	0.06
	Median standardized RES, 1985	1.00	1.00	0.77	0.77	0.19	0.20
	Median standardized RES, 2050	1.00	1.00	0.80	0.67	0.16	0.16
Haddock, Norway Pout Box	Median difference in RES	0.00	0.00	-0.02	-0.13	-0.03	-0.03
	Range of difference in RES	0.00	0.38	0.09	0.89	0.04	0.04
	Median standardized RES, 1985	1.00	1.00	0.72	0.69	0.16	0.16
	Median standardized RES, 2050	1.00	1.00	0.68	0.50	0.13	0.13
Norway Pout, Norway Pout Box	Median difference in RES	0.00	0.00	0.00	-0.08	-0.03	-0.03
	Range of difference in RES	0.11	0.91	0.26	0.73	0.05	0.06
	Median standardized RES, 1985	0.92	1.00	0.34	0.50	0.17	0.18
	Median standardized RES, 2050	1.00	1.00	0.42	0.32	0.14	0.14
Saithe, Norway Pout Box	Median difference in RES	0.00	0.00	-0.09	-0.07	-0.03	-0.04
	Range of difference in RES	0.00	0.45	0.16	0.59	0.04	0.05
	Median standardized RES, 1985	1.00	1.00	0.61	0.57	0.15	0.17
	Median standardized RES, 2050	1.00	1.00	0.53	0.48	0.13	0.13
Whiting, Norway Pout Box	Median difference in RES	0.00	0.00	0.03	-0.05	-0.06	-0.06
	Range of difference in RES	0.06	0.21	0.36	0.75	0.10	0.11
	Median standardized RES, 1985	1.00	1.00	0.27	0.44	0.33	0.33
	Median standardized RES, 2050	1.00	1.00	0.34	0.45	0.27	0.28

Table 4.3.

Deepening responses of demersal species, in meters, between 1970 and 1990 using Aquamaps, Maxent and the DBEM with GFDL hindcast data.

TaxonName	**AquaMap (m)**	**Maxent (m)**	**DBEM (m)**	**Mean (m)**
D. labrax	-1.44	-2.92	-0.78	-1.71
G. cynoglossus	-23.11	-1.46	-1.79	-8.79
G. morhua	0.69	-26.03	1.34	-8.00
H. hippoglossus	-21.52	-9.50	5.68	-8.45
L. limanda	-1.19	-6.19	2.88	-1.50
L. piscatorius	28.01	17.26	-6.16	13.04
L. whiffiagonis	3.55	4.92	1.87	3.44
M. aeglefinus	-4.53	-13.75	12.04	-2.08
M. kitt	-3.68	-14.62	4.19	-4.70
M. merlangus	-0.55	-10.19	2.42	-2.77
M. merluccius	37.52	15.84	-6.49	15.62
M. molva	5.79	0.97	10.60	5.79
M. poutassou	131.60	332.07	20.06	161.25
N. norvegicus	12.33	0.76	2.39	5.16
P. flesus	-1.35	1.12	2.08	0.62
P. maxima	-1.46	-6.38	0.50	-2.44
P. platessa	-3.84	-26.55	4.96	-8.48
P. pollachius	0.31	-1.10	4.11	1.11
P. virens	-3.11	-15.84	2.51	-5.48
R. hippoglossoides	66.32	27.44	-14.21	26.52
S. rhombus	0.08	-0.64	0.90	0.11
S. solea	-0.20	-2.20	-1.28	-1.23
T. esmarkii	2.90	2.45	9.12	4.83
T. luscus	0.32	-1.44	4.99	1.29
T. minutus	2.57	-1.48	3.19	1.43
Z. faber	10.86	-3.27	0.47	2.69
median	0.20	-1.47	2.41	0.37
mean	9.11	9.97	2.52	7.20
max	131.60	332.07	20.06	161.25
min	-23.11	-26.55	-14.21	-8.79
Decadal change				
median	0.10	-0.73	1.20	0.18
mean	4.56	4.99	1.26	3.60
max	65.80	166.04	10.03	80.62
min	-11.56	-13.28	-7.10	-4.39

Chapter 5

Applying Distribution Model Projections for an Uncertain Future: the case of the Pacific Oyster in UK waters

In press at *Aquatic Conservation* as:
Jones, M.C., Dye, S.R., Pinnegar, J.K., Warren, R. and Cheung, W.W.L. Applying distribution model projections for an uncertain future: the case of the Pacific Oyster in UK waters.

Abstract

The inherent complexity of the environment is such that attempts to model it must operate under simplifications and assumptions. Considering predictions from alternative models, with a range of assumptions and data requirements, therefore provides a more robust approach. The intractability and uncertainty resulting from a suite of predictions may hinder the application of science in policy, where a single prediction with little ambiguity or uncertainty would be most desirable. Few studies modelling species' distributions attempt to present multi-model outputs in a format most useful to the non-modelling community, and none of these have done so for the marine environment. The problem of uncertainty is particularly prevalent in predicting the distribution of invasive alien species under climate change. As invasive alien species are one of the main drivers of biodiversity loss and may incur significant economic costs, the benefit of applying predictions to highlight areas of possible establishment and inform policy and management may be large. We apply an ensemble prediction to assess the distribution of suitable environmental space for the Pacific oyster, *Crassostrea gigas*, in UK waters both currently and in the future. The ensemble incorporates predictions from three species distribution models, using data from two global climate models. We develop a method highlighting the agreement of the ensemble, further applying threshold values to retain information from constituent predictions in the final map of agreement. Ensemble predictions made here suggest that Pacific oyster will experience an opening of suitable environmental space in northern UK waters, reaching the Faroe Islands and the eastern Norwegian Sea by 2050. Environmental suitability will increase with warming temperatures in the English Channel and Central North Sea for this species. The approaches applied here can be incorporated into risk assessment frameworks for invasive species, as stipulated in the Convention on Biological Diversity.

1. Introduction

Science is often relied upon to help inform environmental policy-making and to provide answers in the face of political controversies. From the decision-maker's perspective, the most desirable form of advice would constitute a single prediction or projection with little ambiguity or uncertainty. Currently there is a tendency to expect that the introduction of better and more complete data will necessarily facilitate better and more effective policy-making. This is exemplified by calls for more research following politically sensitive or environmentally controversial decisions. However, while I do not dismiss the need for environmental policy to be founded on sound evidence, I stress that there is sometimes a limit to what science can realistically offer and it is often unwise to delay decisions while awaiting better, or more accurate data. The complexity of the natural world is such that modelling must, by necessity, be reductionist. Unambiguous answers are rarely achieved and for pragmatic reasons modellers must make assumptions and simplifications, with even the most complex models being approximations of a real system (Collins *et al*., 2012). Different modellers may also favour particular modelling frameworks/formulations with their inherent biases and peculiarities. Furthermore, rarely are a suite of equally-plausible models tested and compared.

The wealth of methodologies for dealing with ecological complexity or uncertainty may not only lead to confusion, but also to criticism and scepticism among the non-modelling community. For example, model comparison studies have demonstrated the variation in outputs achievable using different Species Distribution Models (SDMs) (Araújo *et al*., 2005; Araújo and New, 2007, Pearson *et al*., 2006) and with inputs from alternative global climate projections (Jones *et al*., 2013). A multi-model procedure (an 'ensemble' of models) is advocated in Jones *et al*. (2012) rather than assuming that any one model gives a 'true' picture of the ecosystem. For biological or ecosystem projections, the best possible policy outcome will often be achieved not by limiting outlook to a perceived 'best' model. Instead, a range of available projections from a variety of validated methodologies and sources should be taken into account.

If variability in predictions is great enough to cause confusion or misunderstanding, the utility of a multi-model approach in guiding policy will be limited and may even hinder the decision making process. In such instances, the use of techniques to summarise the discrepancies and concordances within an 'ensemble' framework would seem desirable for presenting the maximum amount of information in a single figure. The statistical 'ensemble' approach' was pioneered by J Willard Gibbs in 1878 as an idealisation consisting of a large number of copies of a system, considered all at once, each of which represents a possible state that the real system might be in at some specified time. Ensemble methods aim to obtain better predictive performance than could be obtained from any of the constituent models runs, and the approach has become particularly prevalent among physical and meteorological modellers that participate in the Intergovernmental Panel on Climate Change (IPCC 2007). It has been argued that significant improvements in the robustness of a forecast can be achieved if an ensemble approach is used and the results are analysed appropriately (Araújo and New 2007). A non-ecological study has further shown that as long as individual forecasts contain some independent information, combined forecasts would yield lower mean error than any of the constituent forecasts (Bates and Granger 2012). There are several methodologies for constructing ensemble forecasts (Araujo *et al.* 2006; Araújo and New 2007; Marmion *et al.* 2009; Coetzee *et al.* 2009; Diniz-Filho *et al.* 2009) and these have been widely explored in species distribution modelling (Araujo *et al.* 2006; Pearson *et al.* 2006; Prasad *et al.* 2006; Carvalho *et al.* 2011). Several of these methods attempt to find the central tendency of forecasts through measures such as the mean or median (Araújo *et al.* 2005; Marmion *et al.* 2009). They attempt to distinguish the 'signal' of the combined predictions from the 'noise' surrounding it that might be associated with individual model error and uncertainty. Alternatively, an ensemble of predictions can be used to define the bounding box (Araújo and New 2007). This method identifies the range in forecasts from the ensemble members and the maximum area of predicted distribution, without quantifying the probability distribution or conditional probabilities. No ensemble average or confidence limits around the average are calculated.

Here I demonstrate the application and utility of a non-statistical ensemble approach considering the example of the Pacific oyster, *Crassostrea gigas.* The Pacific oyster is native to Japan and east Asia but has been introduced intentionally to countries such as Australia, France, United States and the United Kingdom for aquaculture, and is now the most widely farmed and commercially important oyster in the world. Within the UK, 1400 tonnes of Pacific oyster were grown in aquaculture facilities in 2006 (GB Non-Native Species Secretariat (NNSS), 2012). Pacific oyster was deliberately introduced for commercial purposes after Ministry of Agriculture, Fisheries and Food (MAFF) trials in the 1960s and early 1970s had indicated that the species required temperatures clearly in excess of those in British waters for successful reproduction in the wild (Mann 1979; Utting and Spencer 1992). Accordingly, hatchery-produced seed were produced in large numbers for commercial rearing. However, natural recruitment has since occurred within the British Isles, although with regional differences. Some local recruitment occurred in estuaries of south-west England and north Wales following unusually warm summers in 1989 and 1990 (Spencer *et al.* 1994) and there are now well established 'wild' adult populations. To date, there have been no substantiated records of spatfall in Scottish waters although maturation of the gonad and gamete release have been noted occasionally during atypically warm weather and in shallow, sheltered sea lochs (Maggs *et al.* 2010). However, in 2005, temperatures in Strangford Lough, Northern Ireland, reached those sufficient to allow spat development and settlement, and were reflected by high frequencies of ages classes recruited in 2005 (Guy and Roberts 2010).

Despite the economic benefits, wild establishment of Pacific oyster may cause significant economic losses by outcompeting native species of bivalves, especially native oysters *Ostrea edulis,* as well as mussels and cockles. In the Wadden Sea, for example, Pacific oyster has been seen to displace mussel fisheries in some areas (Nehls *et al.* 2006) and it has been suggested that their reefs may cause major shifts in the community of benthic filter feeders, with subsequent negative effects on bird populations (Smaal *et al.* 2005). Furthermore, the presence of their sharp shells on the intertidal zone and mudflats may deter human leisure activities, thus negatively affecting tourism.

There are several terms used for describing species persisting outside their native range. Non-native refers to all species that have been deliberately or accidentally introduced to an area from their native range (Kolar and Lodge, 2001). While non-native species that establish themselves in a new range but do not cause negative impacts are referred to as naturalised or non-invasive (Kolar and Lodge, 2001), the term 'invasive alien species' is used to describe those that cause, or have the potential to cause, harm to the environment, economies, or human health (Global Invasive Species Programme, 1999). Invasive alien species are identified as one of the main drivers of biodiversity loss and ecosystem malfunction (Mcneely 2001; Underwood *et al.* 2003; Molnar *et al.* 2008). With good evidence that climate change favours the spread of some non-native species (Stachowicz *et al.* 2002; Sax *et al.* 2007), the interaction between invasive alien species and climate change is thus becoming a pressing issue for conservation and fisheries economics. Although the extent to which the non-native Pacific oyster may affect UK native species and habitats is poorly understood, the increasingly favourable conditions caused by warming seawater temperatures are likely to benefit this species and promote its further spread. The UK is bound by international agreements such as the Convention on Biological Diversity, the United Nations Convention on the Law of the Sea, The Convention on the Conservation of Migratory Species of Wild Animals (Bonn, 1979), The Convention on the Conservation of European Wildlife and Natural Habitat (Bern, 1979), the EC Habitats and Species Directives, as well as the EU Water Framework Directive and Marine Strategy Framework Directive. All of these aim to protect biodiversity and most include provisions aimed at preventing the further introduction of, or control of, non-native species, especially those that pose a risk to native or protected species (JNCC 2012).

Furthermore, the total cost of invasive alien and non-native species to the UK economy (both terrestrial and aquatic) is estimated at £1.7 billion per annum (Williams *et al.* 2010). Aquatic molluscs alone are thought to cause damages of $1 billion per year in the US (Pimentel 2005). Therefore early warning systems to highlight potentially invadable areas by species could be a useful first step in any proposed management, monitoring or prevention plan. This would seem especially useful in the case of Pacific oyster, for which no management plan exists and thus the most desirable route to preventing spread would be enhanced bio-security and vigilance against further deliberate and accidental introductions. The first UK Climate Change Risk Assessment (CCRA) published in January 2012 (a requirement under the UK Climate Change Act 2008) specifically argued that a more statistically rigorous and defensible study was needed of projection techniques for non-native aquatic species, as this report could only manage a very crude attempt at predicting future distribution. Species Distribution Models (SDMs) have been used to predict the distribution of environmental suitability for other non-native marine species in Europe (e.g. Chinese mitten crab, *Eriocheir sinensis* (Herborg 2007)) and have further been used to inform management efforts aimed at identifying areas at risk of zebra mussel (*Dreissena polymorpha*) invasion in the western United States (Drake and Bossenbroek 2004). Here I aim to explore the application of an ensemble model approach and its utility in assessing the potential threat by an invasive species. Concurrently, I attempt to provide predictions of projected environmental suitability for the Pacific oyster in a format useable by policy makers and the non-modelling community.

2. Methods

Predictions of relative environmental suitability in UK for both current and future time periods were generated for the Pacific oyster using three different Species Distribution Models (SDMs) and outputs from two distinct Global Climate Models (GCMs). The Species Distribution Models were AquaMaps (Kaschner *et al.* 2006; Ready *et al.* 2010), Maxent (Phillips *et al.* 2006), and the Dynamic Bioclimate Envelope Model (DBEM) (Cheung *et al.* 2011). These models (described in detail in Chapter 3, Appendix 2) have been shown to produce plausible predictions of species' current distributions given occurrence data, which are used in model testing (Jones *et al.* 2012). Furthermore, comparisons between model hindcast and historical distribution changes of fishes and invertebrates from the 1970s to the 2000s in the Bering Sea and Northeast Atlantic suggest that DBEM has significant skill in predicting distribution shifts in these regions (Cheung *et al.* 2012).

AquaMaps and Maxent are statistical models, which differ in complexity but which both generate predictions of a species' relative environmental suitability by associating presence-only data on a species' occurrence with a set of environmental variables. Species' occurrence data were obtained from two global online databases: the Ocean Biogeographic Information System (OBIS) (http://www.iobis.org) and the Global Biodiversity Information Facility (GBIF) (http://data.gbif.org), all last accessed in 2011. Occurrence records were rigorously filtered to minimise the recording error likely in using data compiled from many sources. Thus, additional information on species' environmental preferences and geographic limits (Fishbase, Froese and Pauly, 2011; FAO fact sheets: http://www.fao.org/fishery/species/3514/en; The Marine Life Information Network (MarLIN) www.marlin.ac.uk) was used to remove occurrence points located on land or outside expert-defined geographic ranges (obtained as latitudinal and longitudinal limits from FishBase) or FAO areas'. Occurrence data were spatially aggregated at the level of 0.5° latitude x 0.5° longitude, giving a binary value of presence or absence for each cell. Occurrence records following cleaning are shown in the Appendix, Figure 5.1.

Environmental datasets were obtained at 0.5 latitude x 0.5 longitude resolution from the Geophysical Fluid Dynamics Laboratory's Earth System Model (GFDL ESM2.1, (Dunne *et al.* 2010)). These included sea surface temperature, sea bottom temperature, salinity, primary productivity and depth. A further set of physical climate data were obtained from an ensemble of 12 different CMIP3 models that were assembled under the auspices of the fourth assessment of the Intergovernmental Panel on Climate Change (IPCC AR4). These were obtained from the World Climate Research Program (WCRP) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model dataset (http://esg.llnl.gov:8080). Both climatic datasets were modelled under the SRES A2 emissions scenario and are thus characterized by a heterogenous world with a continuously increasing global population and regionally orientated economic development (IPCC 2000). Environmental envelopes generated by each model were used to predict the distribution of Pacific oyster, using a 30 year average of environmental data centred on 1985 (1970 – 2000), representing the current time period. This was then applied to a 30 year average centred on 2050 (2035 – 2065), representing the future, under climate change.

The DBEM, and associated *Sea Around Us Project* model contrast the above approaches by firstly defining a species current distribution based on the following geographic and environmental tolerance limits: FAO area, latitudinal and depth ranges and habitat preferences (Close *et al.* 2006; Jones *et al.* 2012). This distribution is then used to define the species' bioclimatic envelope by its 'preference profile', formed by overlaying current 1970 – 2000 averaged environmental data over the maps of current relative suitability. In projecting the bioclimatic envelope under scenarios of climate change, the DBEM incorporates the effects of oxygen level and acidification on species growth through incorporation of ecophysiological model components and a logistic population growth model (Cheung *et al.* 2011). As diffusion and advection are important factors determining the dispersal of pelagic larvae (Gaylord and Gaines 2000; Bradbury and Snelgrove 2001) the DBEM also explicitly represents larval dispersal using an advection-diffusion-reaction model (Cheung *et al.* 2008). This determines change in relative larvae abundance over time by passive diffusion and current-driven movements based on pelagic larval duration (PLD) and ocean current velocity data. PLD, expressed in days, is calculated from an empirical equation established from a meta-analysis of PLD from 72 species of fish and invertebrates (O'Connor *et al.* 2007) which takes into account, for example, temperature and larval development type (Cheung *et al*. 2008). Diffusion is characterized by a diffusion parameter, while advection is characterized by the two current velocity parameters which describe the east-west and north-south current movement. A detailed description of this methodology and the algorithms and parameters used are given in Cheung *et al*. (2008). Annual average current fields were obtained from the NOAA/GFDL Coupled Model 2.1.

Predictions from each model and time period were standardized to give values lying between 0 and 1 and representing the relative environmental suitability of each cell of the study area for Pacific oyster.

The centroid of the distribution predicted for each time period (Latitudinal centroids) was calculated for predictions made using each SDM-GCM combination and threshold using the equation (1) (Cheung *et al.* 2009):

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

Where Lat_i is the latitude of the centre of the spatial cell (i), Abd is the predicted relative environmental suitability in the cell, and n is the total number of cells (Cheung *et al.,* 2012). The difference between latitudinal centroids in projected and reference years was then calculated in kilometres (km) (Cheung *et al.* 2011):

$$Distance\ shift\ (km) = (Lat_m - Lat_n)\frac{\pi}{180} \times 6378.2 \tag{2}$$

Where Lat_m and Lat_m are the latitudinal centroids in 2050 and 1985 respectively, and 6478.2 km is the approximated equatorial radius of the Earth.

Further to predicting shifts in latitudinal centroid of a distribution, potential changes in range area between reference and projected years was calculated as the difference in the number of cells with environmental suitability > 0 (number in 2050 – number in 1985).

Model predictions were combined using a 'bounding box' method, retaining the information from each prediction using an index of model agreement. When applying species distribution models to an environmental problem there may be an element of perceived risk and cost. For example, the cost of acting on a forecast that gave a restricted estimate of invasion potential might be high if a non-native species had particularly damaging environmental effects. This idea was introduced into the ensemble forecasting process by applying thresholds. Thresholds may be used to transform the continuous predictions of relative suitability produced by SDMs into predictions of presence/absence. There are several methods for selecting threshold values, although there is currently no consensus on the most suitable method for applying thresholds to species' range projections (Liu *et al.* 2005; Nenzén and Araújo 2011). For example, if a low threshold is set, low values of environmental suitability will be converted into potential 'presence' areas. When investigating the spread of the Pacific oyster, such a technique could be beneficial in making a precautionary prediction of potentially invadable areas and assessing the species that might suffer the negative impact of invasion. However, if the main focus is to implement a strategy of prevention or mitigation, areas of incorrect prediction might incur considerable and unnecessary costs that might be better deployed elsewhere. Here, each of the six predictions in an ensemble was converted from a probability distribution to a binary prediction of presence or absence using one of three threshold cut off values, providing a range of invasion outcomes.

The first threshold chosen was one that maximizes the accuracy of the model in predicting the observed occurrences/ absences (maximum training sensitivity plus specificity (MaxSS)), as indicated in model testing. To find this value, occurrence data were split in two, with 75% being used to train and 25% to test the model. Model testing was implemented using the ROCR package in R (Sing *et al.* 2007), a package designed for evaluating and visualising classifier performance using R. Two fixed thresholds, of 0.5 and 0.7 were also chosen. These would produce more constrained predictions by retaining only cells with predicted relative environmental suitability values higher than the 50th and 70th percentile respectively of the relative environmental suitability distribution. Predicted environmental suitability that is lower than the specified threshold value was thus allocated a value of 0, while values higher were allocated a value of 1. Having obtained a set of occurrence predictions across all model combinations for each threshold, projections within each set were summed to produce an index of agreement ranging between 0 and 6. This would result in a map that not only displays the maximum agreed areas of prediction but also the extent of agreement across 0.5° lat. x 0.5° long. cells in the study area. Similarly, thresholds were used to retain information on the magnitude of change in presenting ensemble maps of the difference in relative environmental suitability (ΔRES) values between projection and reference time periods (2050 – 1985, values ranging between -1 and 1). Having calculated ΔRES for each SDM-GCM combination, cut offs of ±0.1, ±0.2 and ±0.4 were applied to create binary predictions as described above. These cut off values reflected the range of ΔRESs found while also allowing information on the degree of change to be portrayed in the map of agreement. These were summed across all SDM-GCM combinations to produce an index of agreement potentially ranging from -6 (maximum agreement of a decrease in environmental suitability across models) to 6 (maximum agreement of an increase in environmental suitability). As the index aimed to portray agreement of change, cells predicted to show no change remained at 0.

3. Results

Sea surface temperature in UK waters is predicted to rise by an average of 0.49°C (5%) using GFDL ESM 2.1 data and by 0.99°C (10%) using CMIP3 data from 1985 to 2050. Almost all model combinations predict a northward range shift for Pacific oyster across its range between 1985 and 2050 (median = 467km). The threshold applied to predictions makes little difference to the median prediction of range shift across SDM and climate datasets (Figure 5.1a), although variation in predictions is seen across thresholds within SDM and climate dataset, in particular using AquaMaps (Table 5.1). The median latitudinal shift is also predicted to vary across SDMs, with Maxent predicting the most conservative median value and the smallest range (Figure 5.1b). However, the extent of difference between predictions of latitudinal shift using alternative SDMs is dependent on both the climate dataset and threshold used (Table 5.1). Thus while results within SDM are relatively consistent using IPCC data at different threshold levels, the greatest differences in latitudinal shift are caused by alternative species distribution models. Using

GFDL data, the difference between SDM predictions increase with more restrictive (higher) threshold values.

Within UK waters (represented by the UK Exclusive Economic Zone (EEZ)) only AquaMaps and the DBEM, applied to GFDL climate data predicted an increase in the number of 0.5° latitude x 0.5° longitude cells containing suitable environmental space (the range area) between 1985 and 2050, and thus range expansion across thresholds (Table 5.2). Using CMIP3-E data, a slight decrease in range area was predicted in some cases, while predictions from Maxent do not show change in range area within the UK EEZ.

Table 5.1. *Predicted latitudinal shifts in km using AquaMaps, Maxent and the DBEM with each threshold (Maximum Sensitivity + Specificity (MaxSS), 0.5 and 0.7 fixed thresholds) and climate dataset (GFDL and CMIP3-E)*

	AquaMaps	**Maxent**	**DBEM**	**Maximum Difference**
GFDL, MaxSS	644.09	451.78	431.94	212.15
GFDL, 0.5	859.95	466.99	465.98	393.97
GFDL, 0.7	1067.07	444.39	445.71	622.68
Maximum difference (GFDL)	422.98	22.60	34.05	
CMIP3-E, MaxSS	290.50	487.55	667.81	487.23
CMIP3-E, 0.5	308.26	488.78	688.52	488.20
CMIP3-E, 0.7	433.42	466.31	594.11	466.44
Maximum difference (CMIP3-E)	142.92	22.47	94.40	

An example of the change in environmental suitability that contributes to the predicted northward shifts in latitudinal centroid is shown for all SDMs with GFDL data and using the MaxSS threshold in Figure 5.2. Here, in particular using AquaMaps and Maxent, an increase in environmental suitability in seen in the central North Sea, and around the northern coast of Norway and Scotland, while a slight decrease in environmental suitability is seen south of the UK and towards the Mediterranean.

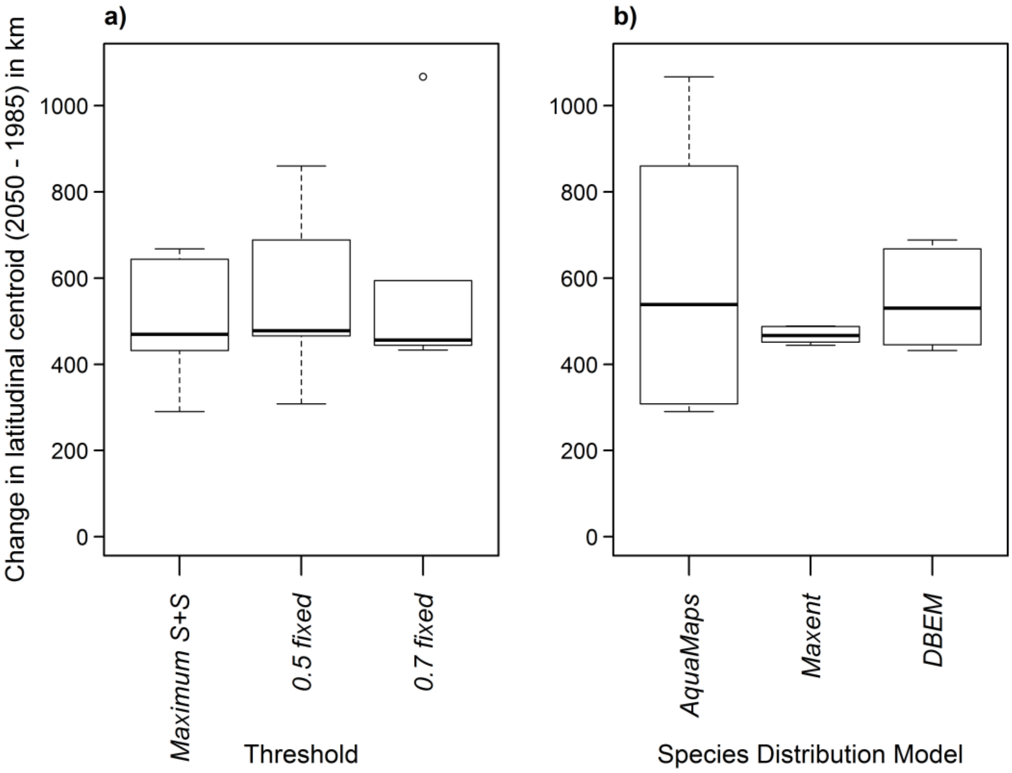


Figure 5.1. *Shift in latitudinal centroids for Pacific Oyster. Change in latitudinal centroid (2050-1985) in km a) across different thresholds for all SDM-GCM combinations b) across different SDM models for both GCM datasets and all thresholds.*

Maps of agreement of Pacific oyster presence amongst the six combinations of SDM-GCMs in 2050 are shown in Figure 5.3, panels 1a, 2a, 3a. Here royal blue (0) denotes areas with no prediction of occurrence using any model, rather than no agreement between models. These projections also show the difference in maximum agreement when applying different thresholds. Thus, in applying a relatively low threshold, maximum sensitivity plus specificity, the outputs show high agreement in predicted environmental suitability throughout the southern North Sea and English Channel as well as coastal waters around the UK and the west coast of France. This area of maximum agreement decreases as the thresholds become more restrictive (i.e. panels 2a and 3a), with the highest agreement under the 0.7 threshold being predominantly restricted the south-west, south and south-east coasts of England and Wales. Larger areas of agreement were obtained for outputs in 2050 than 1985, indicating the increased suitability of the North Sea, Norwegian coast and waters around Scotland and Northern Island to Pacific oyster under climatic change. This is highlighted in Figure 5.3, panels 1b, 2b, 3b, which show the agreement of change in environmental suitability (2050-1985) across threshold cut off values of 0.1, 0.2, and 0.4, respectively. There is a prevalence of positive differences in RES, with decreases in RES values predominantly being restricted to the English Channel and southern European waters. Although maximum agreement (-6 or 6) in ΔRES was not achieved in UK waters, there is relatively high model agreement in > 0.1 ΔRES (RES values lying between 0 and 1), in particular three or four models predicting positive change around the west and north coasts of Scotland and west coast of Norway. Three models also predict increasing environmental suitability change of > 0.4 ΔRES in the north-east Irish Sea. There was relatively poor agreement between models predictions in the Skagerrak, Kattegat, Baltic and coastal waters of the Mediterranean seas.

Table 5.2. *Potential change in area, calculated as the number of 0.5° latitude x 0.5° longitude cells predicted as suitable in 1985 and 2050 in the UK EEZ using each threshold: Maximum Sensitivity + Specificity (MaxSS), 0.5 and 0.7 fixed thresholds.*

	MaxSS threshold		**0.5 threshold**		**0.7 threshold**	
	1985	**2050**	**1985**	**2050**	**1985**	**2050**
AquaMaps, GFDL	277	307	246	298	210	235
AquaMaps , CMIP3-E	307	307	303	298	289	280
Maxent, GFDL	320	320	320	320	320	320
Maxent, CMIP3-E	320	320	320	320	320	320
DBEM, GFDL	175	221	122	136	93	109
DBEM, CMIP3-E	230	230	201	186	148	150

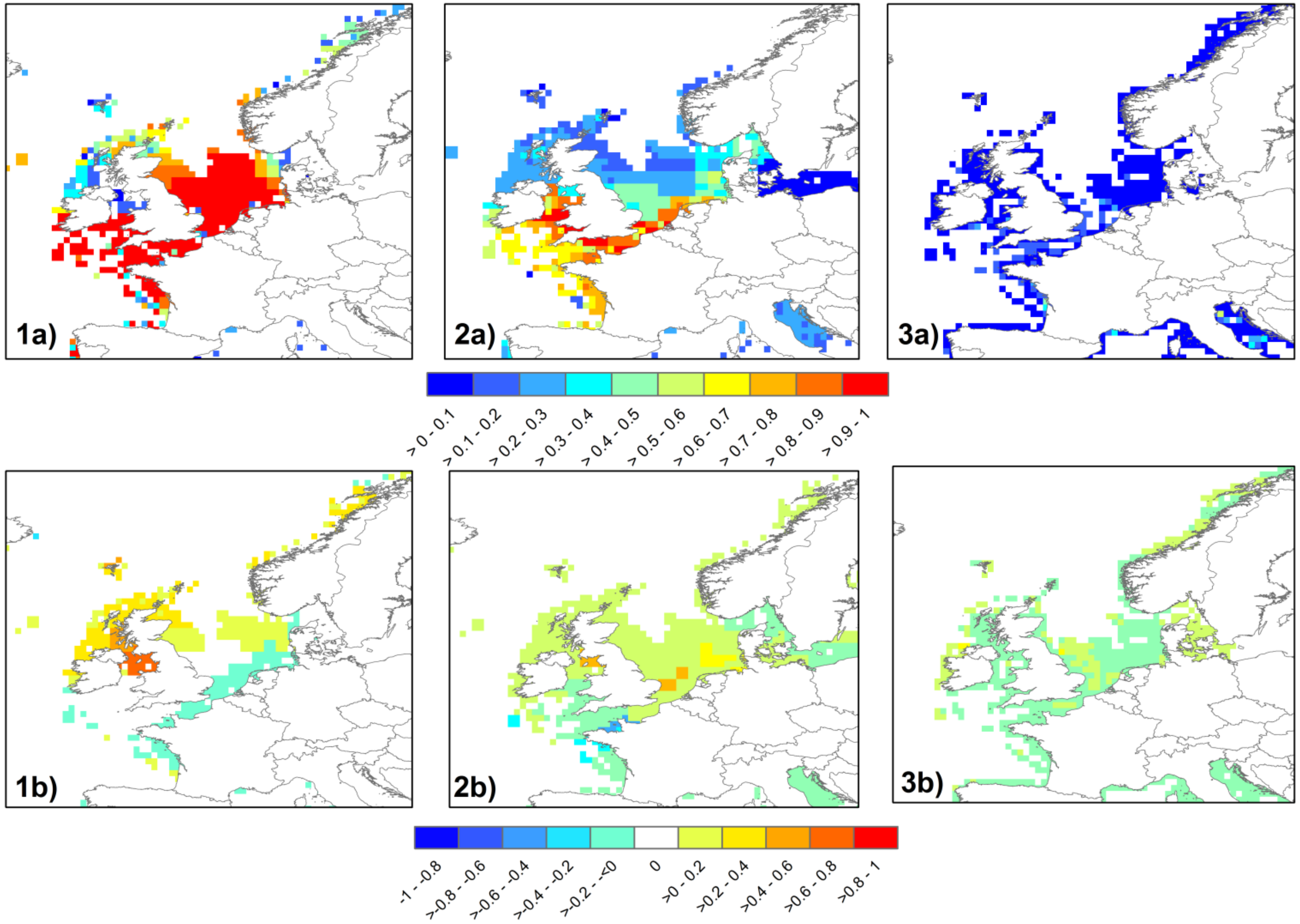


Figure 5.2. *Predicted distributions of relative environmental suitability for Pacific Oyster. Predictions made for the Pacific oyster using GFDL Topaz ESM2.1 data and species distribution models 1) AquaMaps 2) Maxent C) DBEM with the maximum sensitivity + specificity threshold and depicting a) relative environmental suitability (0-1) in 1985 and b) difference in relative environmental suitability (2050 – 1985 values).*

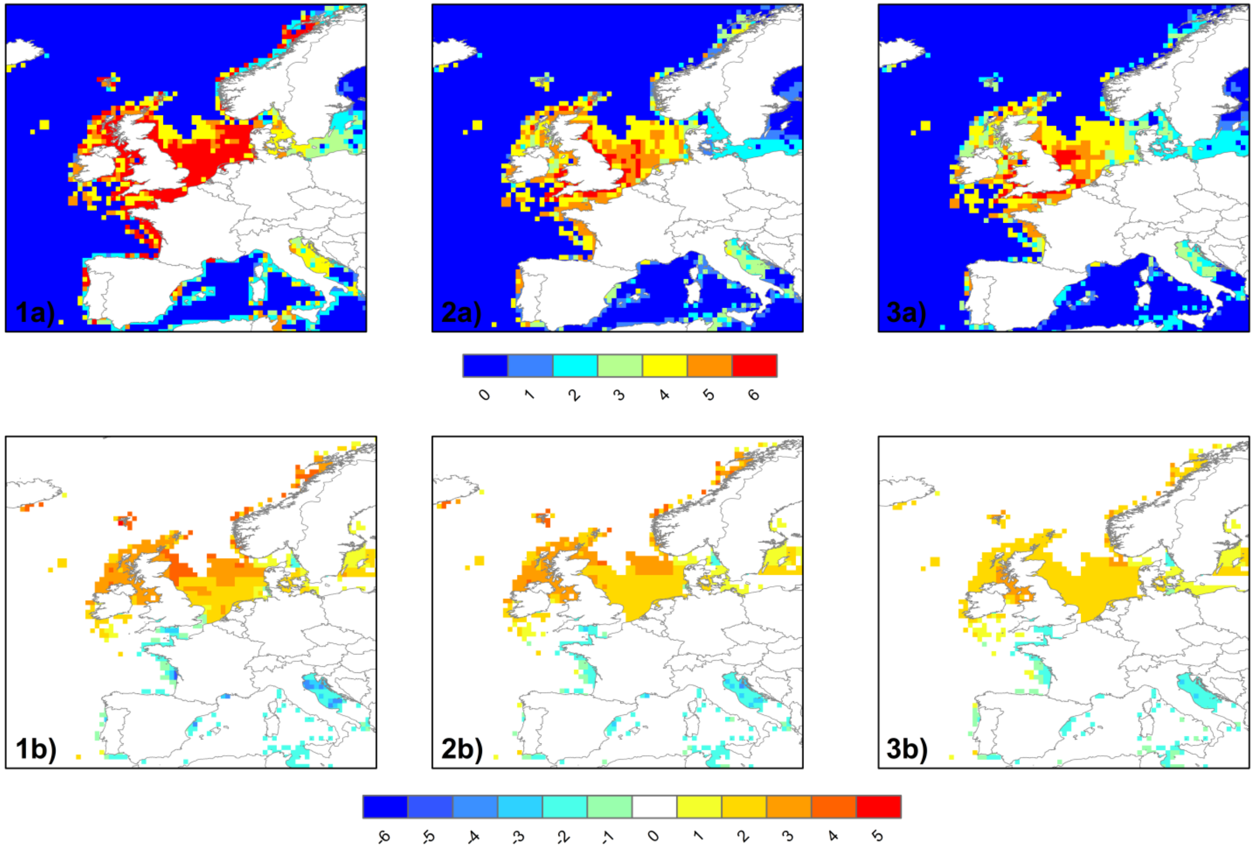


Figure 5.3. *Ensemble predictions for Pacific oyster using AquaMaps, Maxent and DBEM and environmental data from GFDL ESM 2.1 and CMIP3-E. a) Agreement in relative environmental suitability predicted for 2050 and threshold cut off values set at 1) maximum sensitivity + specificity 2) 0.5 3) 0.7. Cells with no prediction using any models remain at 0 (blue). b) Agreement in change in relative environmental suitability values between projection (2050) and reference (1985) time periods, with threshold cut off values set at 1) ±0.1 2) ±0.2 3) ±0.4. Within each threshold, cells predicted to show no change across all models remain at 0 (white).*

4. Discussion

Overall, my findings suggest that UK waters are projected to become more suitable for Pacific oyster population, potentially allowing further expansion of oyster distribution. Although an increase in suitable environmental space for the Pacific oyster is predicted within the UK Exclusive Economic Zone for some model combinations, range expansion may also occur through colonization of currently suitable but un-occupied areas. Also consistent with hypotheses of potential range expansion for Pacific oyster are the predictions of increased environmental suitability within the range, in particular reflected in the calculation of latitudinal centroids.

Prior to applying the ensemble approach, results presented here highlight the variability in projections obtainable using different SDM and GCM combinations. Although predictions contrast previous studies that found the DBEM to predict the greatest distributional shifts (Jones *et al.* 2013), results are consistent with the inclusion of dispersal, the influence of which depends on species specific parameters of dispersal. As the Pacific oyster is sedentary, no adult movement is included. Variation between SDMs agrees with previous studies suggesting differences to be predominantly influenced by the specific model characteristics and techniques applied (Jones *et al.* 2012). However, projections from AquaMaps and the DBEM show a larger amount of variation to be caused by the climate dataset used (GFDL or CMIP3-E). This may result from the varying ability of the GCMs to model the shelf sea and coastal regions where the Pacific oyster is predominantly found. In this case, Maxent is more robust to variations in the climate data. However, as many uncertainties exist in predicting environmental and oceanographic change in shelf seas, considering impacts from different predictions is important. This work may thus benefit from the inclusion of datasets from additional climate models, discussed below.

Applying predictions from Species Distribution Models to assess invasive alien species or develop management plans would benefit from systematic ground-truthing and continued monitoring to assess the rate of spread of a species into predicted suitable areas. Although using occurrence data following previous range expansion into UK waters more accurately portrays locations that Pacific oyster might currently inhabit, some of these areas may not be currently inhabited due to dispersal limitation in the time period this area has become suitable. For example, no records of occurrence were obtained for the East Coast of

Scotland, although the environmental envelopes generated here predicted suitable environmental space for both the current and future time period. For this reason also, absence data would not contribute valid information on the environmental preferences of an invasive alien species. Although absence data might contribute useful information for species occupying their entire environmental niche space, these data would be misleading if absence at a location were caused by factors not used in constructing an environmental envelope, such as dispersal. These maps therefore provide information on sites of likely invasion both currently and under climate change. This information may be subsequently informed and refined using spatially explicit information on suitable substrate for the Pacific oyster. For example, although Pacific oyster can be found on mud and sand-mud substrate, settlement and invasion may be more likely in areas of hard or rocky substrates, on which they preferentially attach (FAO 2013). Although the benefits of applying Species Distribution Models to invasive alien species and the foresight obtainable are highlighted here, this application also demonstrates one of the difficulties in modelling species for which no systematic sampling has been undertaken, or for which locations of occurrence may be rapidly changing.

Given the variability in both model algorithms and output characteristics (Jones *et al.* 2012), a consensus approach to ensemble forecasting was not considered appropriate in this case, and unlikely to match the truth (Thuiller *et al.* 2004; Araújo and New 2007). A method of compiling predictions more analogous to the bounding box method was therefore applied. The ensemble maps compiled provide a useful method of conveying the uncertainty and variation in species distributions resulting from a multi model approach.

However, it is important to note that the set of Species Distribution Models and Global Climate Model projections applied here does not provide comprehensive coverage of model characteristics and possible sources of variability. Variation and uncertainty may result from SDMs according to their complexity, data requirements and algorithms. Similarly, uncertainty is introduced into GCMs due to the current climate, downscaling method, greenhouse gas emission scenario, and the climate model itself. Thus while an ensemble allows variability according to differences in component models to be captured, certain model similarities cause other variability to be excluded. For example, although the ensemble compiled here takes into account differences in species environmental envelopes, the data and mechanisms used to construct them, none of the SDMs consider inter-specific interactions or evolutionary adaptation, all relying on the assumption that a species is in pseudo-equilibrium with its environment. This assumption may not be upheld if models fail to take into account biotic interactions that prevent species occupying otherwise suitable environmental space, or in the case of modelling a species for which there is little, or outdated, data, as discussed above. Furthermore, both climate models from which data were obtained are global and may be criticized for poor resolution of the topography and dynamics of the coastal shelf sea. The utility of spatial projections that do not incorporate the full ranges of uncertainty has been cautioned against (Planque *et al.* 2011). However, this ensemble technique presents information as a range of possibilities, thereby providing a useful method to project climate-shifted distributions that can be updated and refined as alternative techniques and data become available. Further exploration of this example in the UK shelf sea may thus benefit from incorporation of a down-scaled regional climate model, ground-truthing of input data and incorporation of further predictors such as substrate, as suggested above. Although climate data may also incorporate systematic bias (Stock *et al.* 2011), no bias correction was undertaken for this study due to insufficient observation data for all environmental variables incorporated in this study. However, both building and projecting species distribution models using modelled climate data, ensured a consistency that minimised the effect of this source of bias on conclusions drawn.

With the exception of Maxent, which was found to be insensitive to changes in predicted range size using this set of thresholds, the use of thresholds enables some of the information contained in the prediction (the probability distribution) to be maintained while being converted into a simpler, more easily communicated, policy-relevant format. An application may be informed by a threshold selected according to the costs and risks involved in addressing a particular environmental problem. For an invasive alien species, this would involve weighing up the costs involved with preventing establishment compared to economic losses following establishment and costs of management or eradication. Eradication programmes can be very expensive. For example, the cost of eradication of the current (very small) UK population of carpet sea squirt (*Didemnum vexillum*) from marinas was estimated at £2.4 million in a recent study for the UK Department for Environment Food and Rural Affairs (Pinnegar, 2012). If the carpet sea squirt were to spread over the whole of the UK, then the overall cost of eradication could rise to £72 million (Williams *et al.*, 2010). Eradication of Pacific oyster would be even more costly. On the other hand, range expansion of Pacific oyster may favour the development of highly profitable oyster farming. The risk of ecological impacts from invasion of Pacific oyster and the economic benefits from oyster farming needs to be properly assessed; approaches employed here would be useful for such an assessment.

A set of thresholds may also be treated as a range of scenarios on extent of spread of a particular species. It is here emphasized that decision-making may be aided and policy enhanced through consideration of a range of the available science and the extent of agreement between alternative model formulations, rather than the use of a perceived 'best' model. Ensemble models may provide a useful solution for policy making for the future when there is uncertainty concerning the reliability and accuracy of data and model outputs or disparity in the assumptions of particular models. However, the ensemble approach should not be viewed as an alternative to improving and developing models and collecting better data. In modelling a changing environment, data may be continually updated and models refined. Whilst this is occurring, ensemble forecasts can go some way to providing confidence and thereby prevent inaction due to uncertainty and barriers in understanding between modellers and environmental policy makers.

5. Conclusions

Ensemble predictions made here suggest that Pacific oyster will experience suitable environmental space as far north as the Faroe Islands and the eastern Norwegian Sea by 2050. In the worst case scenario, there is substantial agreement in this prediction between Species Distribution Models and alternative climatic datasets. A potential northward movement will also coincide with a decrease in environmental suitability in the English Channel and an increase in the southern and central North Sea. However, whether the species will be able to fully exploit this potential environmental niche will depend on its ability to disperse and settle. A more optimistic possibility is suggested by limiting areas of potential environmental suitability to only the most suitable environmental space. In this case, although areas around the North of Scotland, Shetland and Faroe Islands are still predicted as suitable both currently and in the future, there is less agreement between models. Predictions such as these may thus be combined with analyses of the perceived costs and risk of establishment and eradication to target management plans most efficiently. They would further facilitate application of the precautionary approach to non-native species that is emphasised in the Convention on Biological Diversity (CBD) when there is lack of firm scientific evidence. This technique may be usefully incorporated into frameworks such as the 'GB risk analysis mechanism', developed to promote risk assessment and the precautionary approach, as stipulated in the CBD.

References

Araújo, M.B., and New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution* **22,** 42–7.

Araújo, M.B., Whittaker, R.J., Ladle, R.J. and Erhard, M. (2005) Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography* **14,** 529–538.

Araújo, M.B., Thuiller, W. and Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* **33,** 1712–1728.

Bates, J.M. and Granger, C.W.J. (2012) The Combination of Forecasts. *Operational Research Quarterly* **20,** 451–468.

Bradbury, I.R. and Snelgrove, P.V.R. (2001) Contrasting larval transport in demersal fish and benthic invertebrates: the role of behaviour and advective processes in determining spatial pattern. *Canadian Journal of Fisheries and Aquatic Science* **55**, 1890-1892.

Carvalho, S.B., Brito, J.C., Crespo, E.G., Watts, M.E. and Possingham, H.P. (2011) Conservation planning under climate change: Toward accounting for uncertainty in predicted species distributions to increase confidence in conservation investments in space and time. *Biological Conservation* **144,** 2020–2030 .

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R. and Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* **10**, 235-251.

Cheung, W.W.L., Dunne, J., Sarmiento, J.L. and Pauly, D. (2011) Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. *ICES Journal of Marine Science* **68**, 1008–1018.

Cheung, W.W.L., Lam, V.W.Y. and Pauly, D. (2008) Modelling present and climate-shifted distributions of marine fishes and invertebrates. *Fisheries Centre Research Report* **16**.

Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T. L., Lam, V.W.Y., Palomares, D.M.L., Watson, R., *et al*. (2012) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change* **2**, 1-5.

Coetzee, B.W.T., Robertson, M.P., Erasmus, B.F.N., van Rensburg, B.J. and Thuiller, W. (2009) Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. *Global Ecology and Biogeography* **18,** 701–710.

Collins, M., Chandler, R., Cox, P.M., Huthnance, J.M., Rougier, J. and Stephenson, D.B. (2012) Quantifying future climate change. *Nature Climate Change* **2,** 403-409.

Diniz-Filho, J.A.F., Bini, L.M., Rangel, T.F., Loyola, R.D., Hof, C., Nogués-Bravo, D. and Araújo, M.B. (2009) Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. *Ecography* **32,** 897–906.

Drake, J.M. and Bossenbroek, J.M. (2004) The Potential Distribution of Zebra Mussels in the United States. *BioScience* **54,** 931-941.

Dunne, J.P., Gnanadesikan, A., Sarmiento, J.L. and Slater, R.D. (2010) Technical description of the prototype version (v0) of tracers of phytoplankton with allometric zooplankton (TOPAZ) ocean biogeochemical model as used in the Princeton IFMIP model. *Biogeosciences*, 3593.

FAO, http://www.fao.org/fishery/species/search/en [Accessed March, 2011].

FAO (2013). *Crassostrea gigas,* FAO factsheet. Fisheries and Aquaculture Department, FAO. Available at: http://www.fao.org/fishery/culturedspecies/Crassostrea_gigas/en Accessed [June, 2012].

Froese, R. and Pauly, D. (2011) Fishbase. Available at: www.fishbase.org, version (02/2011) [Accessed December, 2011].

Gaylord, B. and Gaines, S.D. (2000) Temperature or transport? Range limits in marine species mediated solely by flow. *The American Naturalist* **155**, 769-789.

Global Invasive Species Programme. 1999. Available at: www.gisp.org/about/IAS.asp [Accessed July, 2012]

Guy, C. and Roberts, D. (2010) Can the spread of non-native oysters (*Crassostrea gigas*) at the early stages of population expansion be managed? *Marine Pollution Bulletin* **60,** 1059–1064.

Herborg, L.M. (2007) Predicting the range of Chinese Mitten Crabs in Europe. *Conservation Biology* **21,** 1316 – 1323.

IPCC (2000) *Emission Scenarios, Summary for Policymakers*. (eds N. Nakicenovic and R. Swart). Cambridge University Press: Cambridge.

IPCC (2007) *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. Averyt, M. Tignor and, H. Miller). Cambridge University Press: Cambridge, UK and New York, USA.

JNCC Marine Advice: Non-Native Species. 2012. Available at: http://jncc.defra.gov.uk/page-1528 [Accessed June, 2012]

Jones, M.C., Dye, S.R., Pinnegar, J.K., Warren, R. and Cheung, W.W.L. (2012) Modelling commercial fish distributions: Prediction and assessment using different approaches. *Ecological Modelling* **225**, 133-145.

Jones, M.C., Dye, S.R., Fernandes, J.A., Frölicher, T.L., Pinnegar, J.K., Warren, R. and Cheung, W.W.L. (2013) Predicting the impact of climate change on threatened species in UK waters. *PLoS ONE* **8**(1),e54216.

Kaschner, K., Watson, R., Trites, A. and Pauly, D. (2006) Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. *Marine Ecology Progress Series* **316**, 285-310.

Kolar, C.S. and Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* **16**, 199-204.

Liu, C., Berry, P.M., Dawson, T.P. and Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**, 385-393.

Marine Life Information Network (MarLIN). Available at: www.marlin.ac.uk. [Accessed March, 2011]

Maggs, C., Mineur, F., Bishop, J. and McCollin, T. (2010) Non-natives. In: *MCCIP Annual Report Card 2010-11, MCCIP Science Review*, pp. 1–11.

Mann, R. (1979) Some biochemical and physiological aspects of growth and gametogenesis in *Crassostrea gigas* and *Ostrea edulis* grown at sustained elevated temperatures. *Journal of the Marine Biological Asociation. U.K.* **59,** 95–110.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. and Thuiller, W. (2009) Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions* **15,** 59–69.

Mcneely, J. (2001) Invasive species : a costly catastrophe for native biodiversity. *Land Use and Water Resources Research* **1,** 1–10.

Molnar, J.L., Gamboa, R.L., Revenga, C. and Spalding, M.D. (2008) Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* **6,** 485–492.

NNSS (2010) Pacific oyster, *Crassostrea gigas*. Available at: https://secure.fera.defra.gov.uk/nonnativespecies/factsheet/factsheet.cfm?speciesId=1013 [Accessed June, 2012].

Nehls, G., Diederich, S., Thieltges, D. and Stasser, M. (2006) Waden Sea mussel beds invaded by oysters and slipper limpets: competition or climate control? *Hegoland Marine Research* **60,** 135–143.

Nenzén, H.K. and Araújo, M.B. (2011) Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling* **222**, 3346–3354.

O'Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P. and Weiss, J.M. (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *PNAS* **104**, 1266-71.

Pearson, R.G., Thuiller, W., Araújo, M.B., Martinez-Meyer, E., Brotons, L., McClean, C. and Miles, L. *et al.* (2006). Model-based uncertainty in species range prediction. *Journal of Biogeography* **33,** 1704–1711.

Phillips, S.J., Anderson, R.P. and Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**, 231-259.

Pimentel, D. (2005) Aquatic Nuisance Species in the New York State Canal and Hudson River Systems and the Great Lakes Basin: An Economic and Environmental Assessment. *Environmental Management* **35,** 692–702.

Pinnegar, J., Watt, T. and Kennedy, K. (2012) Climate Change Risk Assessment for the Marine and Fisheries Sector, UK Climate Change Risk Assessment 2012. Available at: www.defra.gov.uk/environment/climate/government/risk-assessment/#sectors [Accessed January, 2013].

Prasad, A.M., Iverson, L.R. and Liaw, A. (2006) Newer Classification and Regression Tree Techniques: Bagging and Random Forests for Ecological Prediction. *Ecosystems* **9,** 181–199.

Ready, J., Kaschner, K., South, A.B., Eastwood, P.D., Rees, T., Rius, J., Agbayani, E. *et al.* (2010) Predicting the distributions of marine organisms at the global scale. *Ecological Modelling* **221,** 467–478.

Sax, D., Stachowicz, J., Brown, J., Bruno, J., Dawson, M., Gaines, S. and Grosberg, R. *et al.* (2007) Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution* **22,** 465–471.

Sing, T., Sander, O., Beerenwinkel, N. and Lengauer, T. (2007) The ROCR Package. Available at: http://rocr.bioinf.mpi-sb.mpg.de/

Smaal, A., van Stralen, M. and Craeymeersch, J. (2005). Does the introduction of the Pacific Oyster *Crassostrea gigas* lead to speceis shifts in the Wadden Sea? In: *The Comparitive Roles of Suspension Feeders in Ecosystems. NATO Searies IV - Earth and Environmental Sciences*, (eds R. Dame, S. Olenin). Springer Dordrecht: Netherlands.

Spencer, B.E., Edwards, D.B., Kaiser, M.J. and Richardson, C.A. (1994). Spatfalls of the non-native Pacific oyster, *Crassostrea gigas*, in British waters. *Aquatic Conservation: Marine and Freshwater Ecosystems* **4,** 203–217.

Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B. and Osman, R.W. (2002) Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *PNAS* **99,** 15497–15500.

Thuiller, W., Araújo, M.B., Pearson, R.G., Whittaker, R.J., Brotons, L. and Lavorel, S. (2004) Biodiversity conservation: Uncertainty in predictions of extinction risk. *Nature* **430,** 145–148.

Underwood, E., Ustin, S. and DiPietro, D. (2003) Mapping non-native plants using hyperspectral imagery. *Remote Sensing of Environment* ***86*****,** 150–161.

Utting, S. and Spencer, B. (1992) Introductions of bivalve molluscs into the United Kingdom for commercial culture - case histories. *ICES Marine Science Symposium* **194,** 84 – 91.

Williams, F., Eschen, R., Harris, A., Djeddour, D., Pratt, C., Shaw, R., Varia, S., Lamontagne-Godwin, J., Thomas, S. and Murphy, S. (2010) *The Economic Cost of Invasive Non-Native Species on Great Britain*. CABI Europe, UK

Appendix

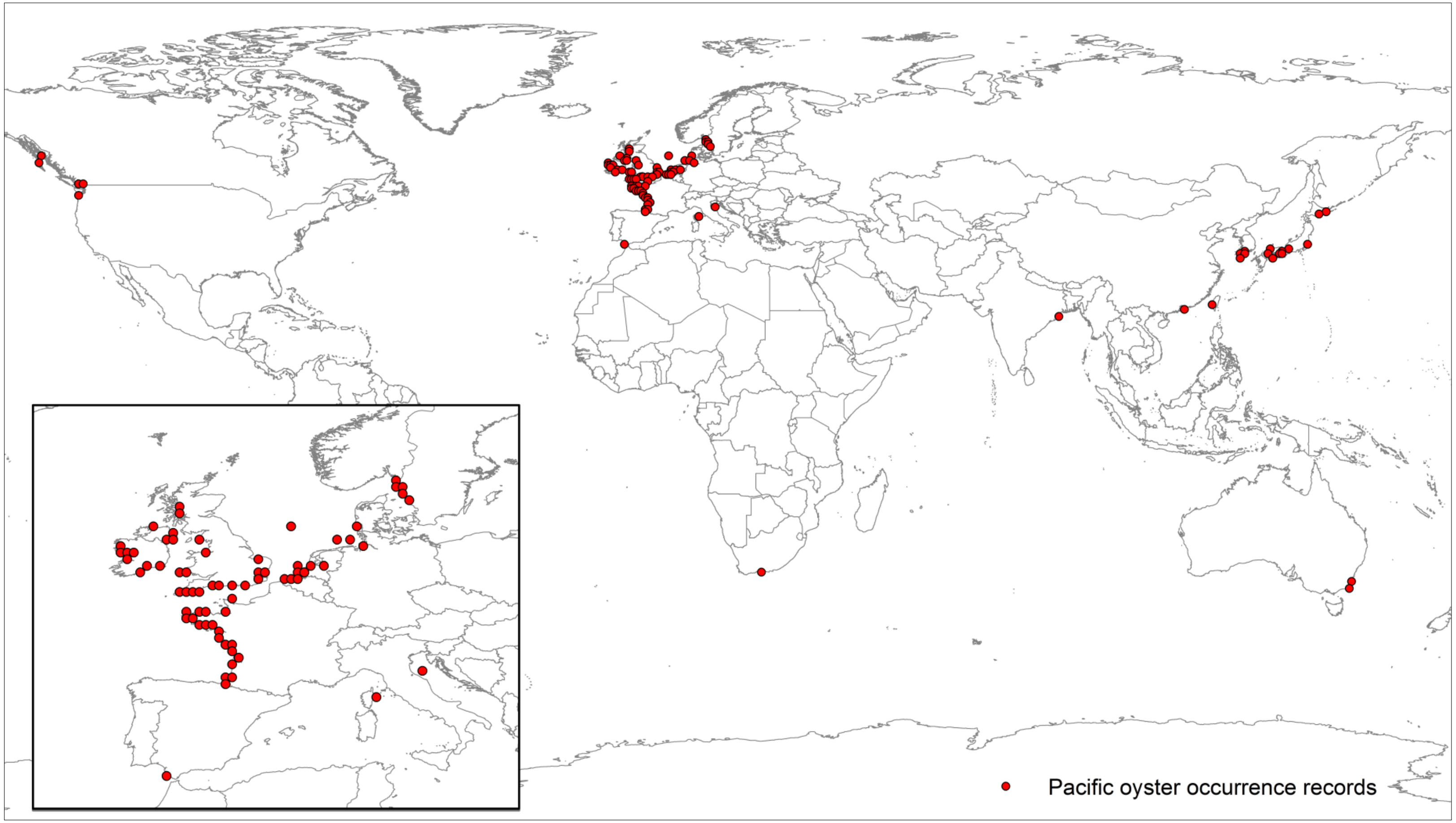


Figure 5.1. *Occurrence records for Pacific oyster, collated from GBIF and OBIS.*

Chapter 6

Modelling the Profitability of UK Fisheries Under Climate Change

Abstract

Over-exploitation and economic underperformance are widespread in the world's fisheries, exacerbated by problems such as over-capacity and fuel price fluctuations. Global climate change is further affecting the distribution of marine species, presenting additional challenges to fisheries management. Projected species' range shifts thus raise concern for both the persistence of biodiversity and the fisheries that target them. However, despite the recent surge in species distribution modelling, few studies have attempted to extrapolate bioclimatic projections to assess the impact of climate change on the socio-economic sphere. This study thus investigates the potential implications of climate-induced changes in relative environmental suitability and fisheries catch potential on UK fisheries by linking species distribution modelling with cost-benefit analyses, using a set of key species in UK waters as a case study. Furthermore, we develop a set of scenarios and apply a multi-model approach to explore the economic sensitivity of UK fisheries, as well as key sources of uncertainty in the modelling procedure. This study applies three species distribution models and two sets of climate data in modelling species' relative environmental suitability. It further uses two alternative algorithms and sets of primary productivity data to calculate projected maximum catch potential. Scenarios applied here thus include alternative predictions of change in maximum catch potential as well as the altered responses in terms of net present value over a 45 year period depending on fuel price, discount rate and government subsidies. Results suggest that the total maximum catch potential will decrease within the UK EEZ by 2050 using all model combinations. Extending these predictions into the cost benefit analysis results in a median decrease in net present value of 10%. Net present value over the study period decreases further when trends of fuel price change are extrapolated into the future, becoming negative when capacity-enhancing subsidies are removed. Despite the variation in predictions resulting from alternative models and data input, the direction of changes in net present value according to each scenario is robust. This study highlights key factors influencing future profitability of UK fisheries and the importance of enhancing adaptive capacity in UK fisheries and their resilience to climate change.

1. Introduction

Fishing is an important socio-economic activity throughout the world. The global fishery sector employs almost half a billion people (FAO 2010) and contributes US$230 billion to the global economy (Dyck and Sumaila 2010). Furthermore, fishing provides over 20% of the per capita animal protein to 1.5 billion people (FAO, 2009). In the UK and Ireland, commercial fishing continues to be an important socio-economic activity. The fishing sector in the UK directly employ approximately 12 000 people, some coastal communities having a job dependency of over 20% on this sector. However, many commercially important fish species have been over-exploited, and while total landings into the UK peaked at 1.1 million tonnes in 1930, by 2010 they had decreased to 600 000 tonnes (Cheung *et al*. 2012a). This fall occurred despite a concurrent fishery expansion and increase in fishing power by an order of magnitude (Englehard 2008).

The problem of over-exploitation has been compounded by pollution, habitat degradation and over-capacity in many fishing fleets. Over-capacity has encouraged the development of sub-optimal fishing, marginal profitability (Hentrich and Salomon 2006) and the economic underperformance of global fisheries (Sumaila *et al.* 2011), with estimated annual losses on the order of $50 billion in the world's fishers (WorldBank and FAO 2008). Many EU fleets have been facing economic problems since 1995 – 2000, exacerbated by decreasing availability of resources and almost constant fish prices (Abernethy *et al.* 2010). Recent increases in fuel prices have further reduced the economic benefits, with some fleets operating at a loss (COM, 2006).

The decline in profitability of global fisheries is masked by technological creep and fishery subsidies, allowing vessels to exploit new fishing grounds in areas progressively deeper and further from shore (Sumaila 2003; Morato *et al.* 2006; WorldBank and FAO 2008). Fishery subsidies may be defined as financial transfers, direct or indirect, from public entities to the fishing sector, enabling the sector to make more profit than would otherwise be feasible and significantly enhancing the decline of fishery resources due to overfishing (Sumaila *et al.* 2010). Global fishing subsidies have been estimated at US$ 25 – 29 billion, 15- 30% of which are fuel subsidies (Sumaila *et al.* 2010). Europe provides US$ 4.7 billion in subsidies, second only to Asia (Heymas *et al.* 2011, Sumaila *et al.* 2010). However, subsidies that promote fishing resource conservation and management may be regarded as beneficial and necessary (Milazzo 1998). Fishery subsidies have thus been categorized by treating fishery resources as renewable natural capital (Munro and

Sumaila 2002). One can therefore ‘invest’ in it by refraining from fishing and allowing resources to rebuild to sustainable, profitable levels. Overfishing, on the other hand, would represent ‘disinvestment’ in the natural capital resource. The three categories of subsidy identified are 1) beneficial 2) capacity enhancing and 3) ambiguous. Beneficial subsidies lead to increased fish stocks through programs that invest in natural capital assets, while the impact of subsidies defined as ambiguous are unknown (Sumaila *et al.* 2010). Capacity enhancing subsidies artificially increase profits, allowing the development of fishing capacity and promotion of effort to a point where resources are over-exploited and long term maximum sustainable benefits are unachievable (Milazzo 1998). These subsidies include capital inputs from public sources that reduce costs or enhance revenues, such as subsidies on fuel, boat construction and modernization, fishing port construction and renovation programs, and price and marketing support (Sumaila *et al.* 2010)**.**

Added to the challenges of over-capacity and marginal profitability in the world’s fisheries, marine fisheries productivity will be affected by the changing ocean conditions associated with climate change (Bakun 1990; IPCC 2007a; Sumaila *et al.* 2011). For example, changes in water temperature, biogeochemistry and primary productivity are expected to affect the productivity and distribution of marine fisheries (Brander 2007; Cheung *et al.* 2010). Theoretical and empirical studies have shown that life history, productivity and distributions of marine ectotherms to be strongly dependent on oceanic variables, such as temperature (Pauly 1980; Drinkwater 2005; Perry *et al.* 2005; Portner 2008; Cheung *et al.* 2012b) with a shift in stock distribution being the most commonly reported ecological response of marine species to climate change. In the North Sea, marine species have been observed to have been moving polewards by 22km decade^{-1} in relation to climate (Perry *et al.* 2005) and also deepening by 3.6 m decade $^{-1}$ (Dulvy et al., 2008). Distribution shifts such as these have been observed to have influenced community structure (Fodrie *et al.* 2010) and are predicted to result in local extinctions and invasions worldwide (Cheung *et al.* 2009).

In addition to wider ecological effects, distribution shifts will likely have important consequences for the livelihoods of the world’s 36 million fisherfolk (Dulvy *et al.* 2010) as well as food security and national economies (Sumaila *et al.* 2011). The effects of El Niño Southern Oscillation (ENSO) events on fisheries may provide insights into the possible effects of climate change on fisheries. For example, during the 1997-8 El Niño event, landings in Chilean and Peruvian pelagic fisheries declined by around 50%, resulting in a drop in fishmeal exports by approximately US$ 8.2 billion, negative economic effects and hardship due to lost jobs and income (Caviedes and Fik 1992). The potential for large-scale shifts in marine species' distributions due to climate change has thus been predicted to result in the redistribution of global catch potential, a proxy for potential fisheries productivity which takes into account primary productivity and species distributions (Cheung *et al.* 2010). Despite a projected increase in global primary productivity of 0.7 – 8.1% by 2050 (Sarmiento *et al*. 2004), large regional differences will lead to wide variation in potential fisheries catch. Thus while ocean warming and retreating sea ice may cause maximum catch potential to increase by 30 – 70% in high latitudes countries, such as Norway and Greenland, tropical nations such as Indonesia, the US and Chile might experience declines of up to 40% (Cheung *et al.* 2010). Changes such as these will bring increased challenges to long-term fisheries management. As fish stocks shift their distributions across jurisdictional boundaries, management policies and quota allocations may become out-dated or contested (Miller and Munro 2004). Disagreements resulting from species shifts and quota allocations have already been seen for North Sea mackerel (Cheung *et al.* 2012a). Furthermore, the economic consequences of climate change for fisheries may manifest themselves through changes in the price and value of catches, fishing costs, fisher's incomes, earnings to fishing companies, discount rates and economic rents.

It is clear that there will be winners and losers with respect to fisheries and climate change. For example, while climate change is predicted to have a positive effect on the fisheries of Iceland and Greenland (Arnason 2007), earnings to the European sardine fishery are estimated to decrease by up to 1.4% on average per year with rising temperatures (Garza-Gil *et al.* 2010). Whether a fishery 'wins' or 'loses' will depend not only on the location of the country or region, but also on their vulnerability and ability to adapt, for example by switching target species, gear types or moving to more marginally productive areas or even leaving to find employment in other sectors (Sumaila *et al.* 2011).

Here we investigate the potential implications of climate-induced shifts in species' distributions and fisheries catch potential on UK fisheries by linking species distribution modelling with cost-benefit analyses. Specifically, we focus on a set of likely consequences for the profitability of fisheries. It is difficult to predict the complex interaction of changes in fishers' behaviour (decision-making), fisheries governance, and the broader social-economic development. Therefore, we explore alternative scenarios of how the UK fisheries would respond to climate change and examine their economic sensitivity (Haynie *et al*. 2012). A scenario is described as a narrative or storyline which provides a powerful tool in developing an understanding of a range of options or plausible alternative futures (Haward *et al.* 2012). Rather than focusing on accurate prediction, they enable a variety of futures to be considered, thereby allowing uncertainties to be explored (Peterson *et al.* 2003). Due to imperfect knowledge of the consequences of climate change in many contexts, scenarios aid decision making and strategic formulation of policy under social and environmental change. Qualitative scenarios have been applied for example, to examine the impacts of climate change, or different conservation/ management strategies (Pinnegar *et al.* 2006; IPCC 2007a; Carlson *et al.* 2011). The scenarios applied here include a range of alternative responses to shifts in species' potential catch in terms of fishing costs, fuel price, discount rates and government subsidies. The sensitivity of results to changes in discount rates and predictions of change in primary production is also investigated. Investigation of potential consequences might thus provide the foresight necessary for adapting and coping with some of the effects of climate change on fisheries.

2. Methods

2.1. Prediction of species' relative environmental suitabilities

Maps of species' Relative Environmental Suitabilities (RES) were generated using the approaches detailed and analysed in Jones *et al.* (2013), Jones *et al.* (2012) and Chapter 4 of this thesis: the three Species Distribution Models (SDMs) AquaMaps (Kaschner *et al*. 2006; Ready *et al*. 2010), Maxent (Philips *et al*. 2006) and the Dynamics Bioclimate Envelope Model (DBEM). The generative models Maxent (Phillips *et al.* 2006) and AquaMaps (Kaschner *et al.* 2006; Ready *et al.* 2010) apply a statistical approach to modelling species' distributions. They predict species' current distributions (averaged over 30 years from 1971 to 2000) by associating species' occurrence data with averaged 'current' environmental data (1971 – 2000), thereby obtaining a bioclimatic envelope for each species. The Dynamic Bioclimatic Envelope Model (DBEM) (Cheung *et al.* 2011) and associated *Sea Around Us Project* model (Close *et al*. 2006) instead uses a discriminative approach (Jones *et al.* 2012), applying a set of 'filters' of known geographical or tolerance limits to delimit a species' current distribution (Close *et al.* 2006; Jones *et al*. 2012). The DBEM further simulates changes in species relative abundance spatially and temporally by incorporating population dynamic models with ecophysiological parameters (Cheung *et al.*

2011). Cell values for the predicted distributions from each model represent the relative suitability of each cell for a species.

2.2. Species' occurrence data

A set of 31 species of commercially exploited fish and invertebrates were selected for distribution modelling (Table 6.1). As described in Chapter 4, these species comprised 90% of demersal and 93% of pelagic species by weight, and 94% and 98% by value respectively, of species landed by UK vessels into the UK in 2010, as reported by the Marine Management Organisation (MMO 2011). *Nephrops norvegicus* was selected as representing the largest catch by value of shellfish by UK fleets into the UK, at 38% (MMO 2011). Additional species were selected because of the possibility of their providing new fishing opportunities following potential shifts in distribution in response to climate change (Cheung *et al.* 2012a). Species occurrence data were obtained from global online databases: the International Council for Exploration of the Sea (ICES) EcoSystemData database (http://ecosystemdata.ices.dk); the Ocean Biogeographic Information System (OBIS) (Vanden Berghe, 2007; http://www.iobis.org) and the Global Biodiversity Information Facility (GBIF) (http://data.gbif.org), accessed in 2011. Occurrence records were spatially aggregated at the level of 0.5° latitude x 0.5° longitude and rigorously filtered according to criteria detailed in Jones *et al.* (2012), resulting in a binary value of presence or absence of each species for each cell.

2.3 Environmental predictors and climate models

A range of oceanographic variables for predicting species distributions using Maxent and AquaMaps were chosen as in previous chapters. These variables were: bathymetry, sea surface temperature (SST), sea bottom temperature (SBT), salinity; ice; primary productivity, and distance to coast. Two sets of oceanographic variables were obtained, from Geophysical Fluid Dynamics Laboratory's Earth System Model (GFDL ESM2.1, Dunne *et al*. 2010) and physical climate data from an ensemble of 12 different models obtained from the World Climate Research Program (WCRP) Coupled Model Intercomparison Project phase 3 multi-model dataset (http://esg.llnl.gov:8080) (CMIP3).

Table 6.1. *Commercially targeted fish and invertebrates selected for the study and their landed value in 2010.*

Species	**Common Name**	**Value (£ million) 2010 (MMO 2011)**
Clupea harengus	Atlantic Herring	10.3
Dicentrarchus labrax	European seabass	4.8
Engraulis encrasicolus	European anchovy	-
Glyptocephalus cynoglossus	Witch flounder	1.2
Gadus morhua	Atlantic cod	28.6
Hippoglossus hippoglossus	Atlantic halibut	1.3
Limanda limanda	Common dab	-
Lophius piscatorius	Angler/ Monkfish	38.5
Lepidorhombus whiffiagonis	Megrim	10.1
Melanogrammus aeglefinus	Haddock	36.2
Microstomus kitt	Lemon sole	6.3
Merlangius merlangus	Whiting	9.4
Merluccius merluccius	European hake	10.2
Molva molva	Ling	5.7
Micromesistius poutassou	Blue Whiting	1.0
Mullus surmuletus	Surmullet	-
Nephrops norvegicus	Norway lobster	95.3
Platichthys flesus	Flounder	-
Pleuronectes platessa	European plaice	3.3
Pollachius pollachius	Pollack	3.5
Pollachius virens	Saithe	12.4
Psetta maxima	Turbot	3.4
Sardina pilchardus	European pilchard	0.6
Scophthalmus rhombus	Brill	1.6
Scomber scombrus	Atlantic mackerel	82.0
Solea solea	Common sole	14.0
Sprattus sprattus	European sprat	-
Trisopterus esmarkii	Norway pout	-
Trisopterus luscus	Pouting	-
Trachurus trachurus	Atlantic horse mackerel	1.8
Zeus faber	John Dory (Atlantic)	-

As no primary productivity data were available for CMIP3, that from GFDL ESM2.1 was used in calculating maximum catch potential for both climate datasets. Both datasets represented the A2 climate scenario, thus being characterised by a heterogenous world with a continuously increasing global population and regionally orientated economic development (IPCC 2000). This scenario estimates a high best estimate of 3.4°C increase by 2090-2099 relative to 1980-1999, which, from the six alternatives, is only lower than the A1F1 scenario (IPCC 2007b). The oceanographic variables were interpolated onto a 0.5° latitude x 0.5° longitude global grid using the nearest-neighbour method. Models were trained on climatic data averaged over a 30 year period centred on 1985, which corresponded as far as possible to the average climatic conditions over which species occurrence data were compiled. Environmental envelopes obtained for each climatic dataset were then projected into the future using a 30-year average centred on 2050. The results of these species distribution projections have been presented in Chapter 4.

2.4. Calculating Maximum Catch Potential

Maximum Catch Potential (MCP) was calculated in the following two ways:

Maximum Catch Potential 1

Firstly, Maximum Catch Potential was calculated for each species in both the reference and projection time periods as a function of the area of a study site and the primary productivity within that area. As data on marine species abundance is seldom available, the maximum catch of the time-series was used as a proxy for maximum sustainable yield (Srinivasan *et al.* 2010; Froese *et al.* 2012). Current maximum annual catch of each species in UK waters was derived from two data sources. Firstly ICES Catch Statistics (1950 – 2010) were used to calculate the mean maximum catch for the highest 10 years, thus accounting for some inter-annual variation. Secondly, maximum catch data for the UK EEZ was extracted from a database collated by the *Sea Around Us Project* (SAUP). This database presents a time series landings data at a range of spatial scales formed by applying a rule-based approach to spatially distribute global landings statistics to a grid of 30 minutes latitude x 30 minutes longitude (Watson *et al.* 2004). The 10 years of highest catch within the UK EEZ were again averaged for the available years (1950 – 2006). The value of maximum annual catch, calculated using each dataset for the initial time period *t0*, and the change in primary productivity between initial and future (t) time periods (1985

– 2050) were then used to estimate the Maximum Catch Potential (MCP) in the future (equation 1). This methodology is supported by both modelled and empirical work which show potential marine fisheries production to be primarily governed by available primary productivity (Ware and Thomson 2005; Cheung *et al.* 2008a; Chassot *et al.* 2010; Blanchard *et al.* 2012). We used an algorithm derived from an empirical equation between observed maximum catch potential, net primary production and range area to project future catch potential (Cheung *et al.* 2008b):

$$\text{Maximum Catch}_t = \text{Maximum Catch}_{t0} \times \frac{\sum(P)_{i,t} \times A_{i,t}}{\sum(P)_{i,t0} \times A_{i,t0}} \tag{1}$$

where P is the total primary productivity in each 0.5° lat. x 0.5° long. cell (i) of a species' exploitable range and A is the area of each cell within that range.

The total future maximum catch estimated for each species was re-distributed over the study area using predictions of relative environmental suitability from each SDM model using each set of climate data. During this process, values from the DBEM were normalised across time periods relative to the maximum relative abundance for the initial time period, thereby subsequent changes in the overall relative abundance would be reflected in the catch potential. The percentage difference between Maximum Catch Potential in 1985 and 2050 for each cell of a species' distribution was calculated for each species. These values were then associated with a location-specific dataset of catch weight and value for UK fishing fleets in the UK EEZ to undertake a cost-benefit analysis.

Maximum Catch Potential 2

Secondly, an alternative method of calculating Maximum Catch Potential was implemented. This algorithm (MCP 2) incorporated predicted relative environmental suitability for each species within the EEZ as follows:

$$\text{Maximum Catch}_t = \text{Maximum Catch}_{t0} \times \frac{\sum(P \times RES)_{i,t}}{\sum(P \times RES)_{i,t0}} \tag{2}$$

where RES is the relative environmental suitability in cell i of the study area.

This method does not re-distribute values over all cells in the study area according to their relative environmental suitability value, instead retaining aggregate values. Aggregate values of future maximum catch potential for each species within the UK EEZ were subsequently incorporated into the cost-benefit analysis.

As there are large uncertainties in the response of primary productivity to climate change and variations between alternative model simulations (for example, Sarmiento *et al.* 2005; Steinacher *et al.* 2010), the sensitivity of the maximum catch potential algorithm to variation in projections of primary productivity was explored using equation 2 (MCP2). An additional dataset of primary productivity was thus obtained from the Medusa model (Yool *et al.* 2011), which differs from the GFDL ESM2.1 in terms of model structure, such as the number of phytoplankton groups incorporated, intial parameter values, resolution and physical model coupling. Annual estimates from the Medusa model were averaged as above to obtain average predictions in 1985 and 2050.

2.5. Scenario Development

A set of socio-economic scenarios was developed to assess the potential financial implications of climate change-induced changes in catch potential for UK fleets fishing in UK's Exclusive Economic Zone. Three scenarios were designed based on narratives from the Alternative Future Scenarios for Marine Ecosystems (AFMEC) scenarios (Pinnegar *et al.* 2006), from which alternative trajectories of changes in total catch, potential catch, fishing cost, and effort were developed.

Scenario1. Increased costs for industry (Baseline)

This scenario depicts a future in which the costs of fishing will increase according to historical trends. Specifically, fuel costs will increase while annual levels of catch value and weight remain constant at 2005 levels for every year between 2005 and 2050, therefore giving a baseline estimate of profitability. The effect of removing capacity enhancing subsidies (Sumaila *et al.* 2010) on profitability is then investigated. Capacity enhancing subsidies have been estimated at £8,331,694 per year for the UK (Sumaila *et al*. 2010).

Two assumptions of fuel-price change were calculated to reflect average long-term and short-term rates of increase. To obtain possible projections of future fuel price increase, a time series of retail prices of diesel was obtained from the UK Department of Energy and Climate Change (DECC) (www.decc.gov.uk/en/content/cms/statistics/energy_stats/prices/prices.aspx). To extrapolate the historical trend, we corrected for inflation using a Consumer Price Index (CPI) obtained from the Office for National Statistics (www.ons.gov.uk/ons/rel/cpi/consumer-price-indices/july-2011/tsd-june-2011.html), thereby obtaining the real price of diesel in each year between 1988 and 2011. Having been converted to base year 2011, real values thus expressed the value of diesel in each year in prices of 2011. The annual CPI for all items was used to avoid variations in fuel price being lost due to change already being captured in a fuel specific CPI.

Linear regressions were carried out to estimate the price of fuel as a function of year. In order to obtain trends of fuel price increase in the long-term and short-term, linear models were run for two time periods. The first of these was 1988 – 2011 and the second 2005 – 2011. Model fit was selected according to R-squared and adjusted R-squared values, resulting in a linear fit being chosen for each model ($R^2 = 0.92$ and 0.65 for the long term and short term trend respectively) (Fig. 6.1). The equations obtained to increase fuel costs annually in the required scenarios were as follows.

Long-term trend: Fuel cost = 0.27 * (Year – 1988) + 0.58
Short-term trend: Fuel cost = 0.41 * (Year – 2005) + 1.01

For particular scenarios, total cost of fuel was therefore increased in each year according to the long-term and short-term fuel trends. To do this, the unit price of fuel was used to calculate the total number of fuel units (U) consumed. Fuel cost was then calculated for each year (yr) using equation (3), for example for the long-term:

$$Fuel\ cost_{yr} = Annual\ average\ fuel\ cost + U \times (yr \ \times 2.73) \tag{3}$$

As we assume that fishing locations do not change under altered distribution of MCP, average annual fuel costs calculated for 2005 were assumed to remain constant for all scenarios.

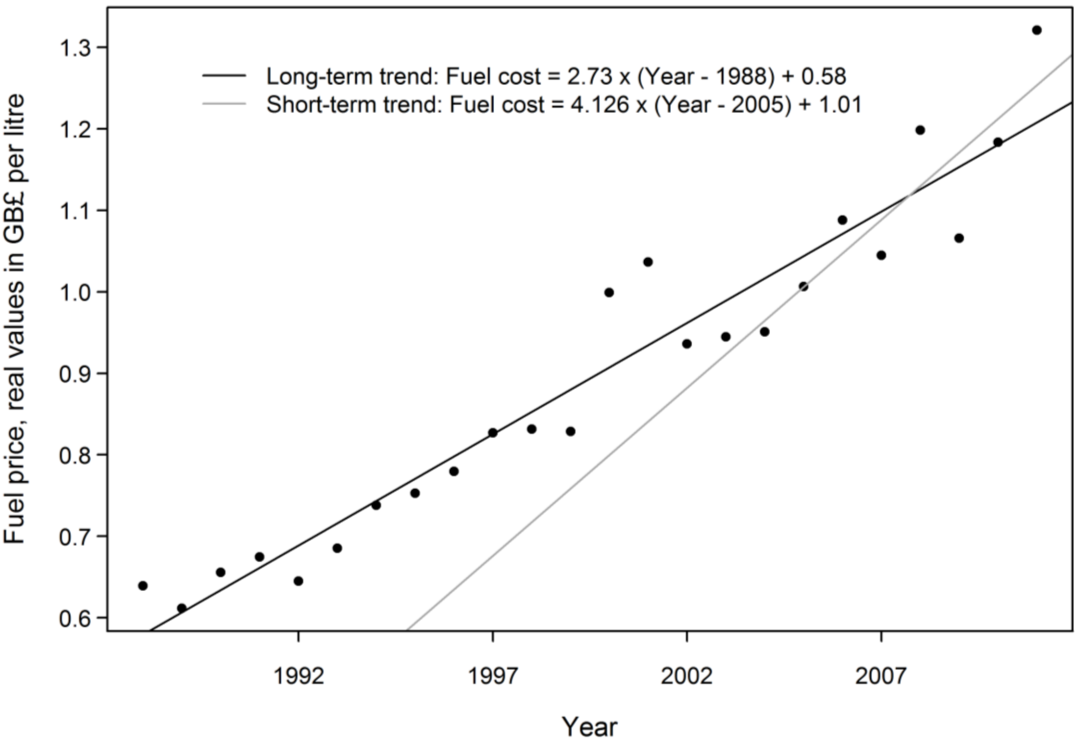


Figure 6.1. *Changes in retail price of diesel between 1988 and 2011 (DECC) with long-term and short-term trends fit using linear models according to time values from 1988 – 2011 and 2005 – 2011 respectively. Fuel price is given in real values, in GB£ per litre, having been converted to base year 2011.*

Scenario 2. Climate change impacts catch

In this scenario, climate change affects the catch value of each species as a result of changes in its maximum catch potential, and thereby influenced by changes in marine primary production. It assumes that catch changes proportionally to projected future maximum catch potential, while total fishing effort remains constant. An increase in costs resulting from a rise in fuel cost will be compensated by a proportional increase in government subsidies, thus ensuring that fuel costs to the fisher remain constant. In other words, the UK's public will pay for the cost of increasing fuel price.

Scenario 3. Sustainable future

This scenario reflects the introduction of management measures to ensure that stocks can continue to be exploited with current levels of fishing effort and furthermore, that stocks have been rebuilt to levels approximating their Maximum Sustainable Yield (MSY). MSY is defined as the maximum use that a renewable resource can sustain without impairing its renewability through natural growth or replenishment (OECD 2001). As MSY has not been estimated for many species in the UK EEZ, the maximum catch for each species, calculated as described above using ICES Catch Statistics, was again used as a proxy. The percentage difference between maximum catch and catch averaged for 2005 was calculated and used to adjust predicted future catch for each species, thereby reflecting the rebuilding of stocks. We therefore assume that catch will be proportional to fish abundance (as demonstrated by Fernandes *et al*. submitted), the latter indicated by the calculated maximum catch potential which was projected using the algorithm described above (eq. 1). Summing these adjusted catches for each species allowed an estimation of the future potential catch if current stocks were allowed to rebuild to MSY levels. The scenario was also run using the baseline catch rates of *Increased costs for Industry* to estimate the implications of rebuilt stocks on current catches.

Because fishing effort remains constant, this scenario assumes that fishing costs will not change in the future. However, as this might over-estimate the additional economic benefits obtained from increased fish abundance, the scenario was also run allowing fuel costs to increase according to the additional weight of catch.

Both the *Climate Change Impacts Catch* and *Sustainable Future* scenarios were run for each of the SDM-GCM model combinations and variation between projected NPVs were compared.

2.6. Cost Benefit Analysis

Cost-benefit analyses were conducted to assess the financial implications of climate change-induced changes in catches on the UK fisheries fishing in the UK EEZ between 2005 and 2050 under the three economic scenarios. Ex-vessel price of fish was assumed to be constant because of the difficulty in predicting its changes. Net potential catch values for each year were calculated as the catch values predicted for each year minus total costs. Conventional and Intergenerational discounting was then applied to calculate the Net Present Value of benefits from 2005 and 2050.

Catches in weight and ex-vessel price by year, gear and species from 2000 to 2010 were obtained from the Fisheries Activity Database of Defra/Cefas. Catches were recorded by

11 gear types: Bottom trawl, mid-water trawl, bottom seine, mid-water seine, drift nets, fixed nets, pots, lines, picking, dredge, and other nets. Total value of catch was calculated as the weight x price, summed across all species being investigated and averaged over the 10 years to account for inter-annual variability. Species-specific percentage changes in maximum catch potential were re-projected from the original 0.5° latitude x 0.5° longitude onto the ICES statistical rectangles (0.5° latitude x 1.0° longitude) by averaging the catch from subset of 0.5 x 0.5 degree cells within each ICES statistical rectangle. The percentage change in maximum catch potential was then used to calculate the annual change in catch weight and value by species at each ICES rectangle. We therefore assumed the percentage change in MCP between 1985 and 2050 changed in equal increments for each of the 65 years, that all gears would remain constant in their catchability of each species in the future and that vessels would not alter their fishing grounds during this time.

Costs of fishing were extracted from a global cost of fishing database (Lam *et al*. 2011) for the UK, which recorded the annual costs by gear types. This database comprised of costs for fuel, repair, labour, depreciation, interest and running costs. Values were converted from US dollars to Great Britain pounds sterling, using the 2005 average exchange rate, 0.55 (World Bank, 2012 (http://data.worldbank.org/indicator/PA.NUS.FCRF), thereby corresponding to the time period for which the data had been converted to real values (Lam *et al*. 2011). Fishing costs were expressed per unit weight of catch. All costs except fuel costs were summed to be included in the cost benefit model. Fuel costs were multiplied by weight at the gear level, obtaining the total costs expended for all fish caught using each gear. These were summed across years and averaged as for catch value to account for inter-annual variability.

2.7. Discounting

2.7.1. Conventional Discounting

Conventional discounting was applied to account for the difference attributed to value of catch currently and in the future to give a Net Present Value (NPV). The NPV over the study period was calculated using equation (4):

$$NPV = \sum_{t=0}^{T} V_t W_t \qquad (4)$$

(Sumaila and Walters 2005)

Where V_t is the net benefit in period t, and W_t is the weight used to discount V_t to the net present value (Sumaila and Walters 2005). The conventional weight, W_c, in year t is calculated as:

$$W_{c_t} = d^t \tag{5}$$

Where d is the conventional discount factor, calculated from the conventional discount rate, r, as

$$d = \frac{1}{(1+r)} \tag{6}$$

2.7.2. Intergenerational Discounting

Under intergenerational discounting (Sumaila and Walters 2005) the Net Present Value (NPV) considers the value of benefits from a resource that are received by the current generation as well as those received by an annual influx of 1/ (generation time) new stakeholders (Sumaila and Walters 2005), who renew the valuation of future earnings, partially resetting the discounting clock. NPV was calculated using equation (4), but replacing W_c with an intergeneration weight W_i, calculated as in equation (7).

$$W_{i_t} = d^t + \frac{d_{fg} d^{t-1}}{G}\left[\frac{1-\Delta^t}{1-\Delta}\right] \tag{7}$$

(Sumaila and Walters 2005)

Where $\Delta = d_{fg}/ d$, the ratio between the intergenerational and the conventional discount factor and where the conventional, or standard, discount factor (d) was given by equation (8).

$$d = \frac{1}{(1+r)} \tag{8}$$

and the future generation discount rate (d_{fg}) by equation (9).

$$d_{fg} = \frac{1}{(1+r_{fg})} \tag{9}$$

Where r is the conventional discount rate and r_{fg} is the future discount rate. In cases where $d_{fg} = d$, this reduces eq. (7) to the formula shown in equation (10).

$$W_{i,t} = d^t + \frac{d_{fg}d^{t-1}\, t}{G} \tag{10}$$

(Sumaila and Walters 2005)

2.7.3. Choice of Discount Rate

The choice of discount rate may have considerable effect on the NPV of a project or assessment. An infinite discount rate attributes no value to profits made in the future, with the primary concern being the maximising of current annual profits. Conversely, a discount rate of 0 gives net revenue equal value irrespective of the time period (year) it is earned in. As 0.03 (3%) is that recommended by the HM Treasury for appraisal and evaluation for longer term discount rates (projects between 31-75 years long) (HM Treasury, 2011 (http://www.hm-treasury.gov.uk/data_greenbook_index.htm, accessed 05/10/12)) while 0.05 represents the average discount rate for 2012 (http://www.bankofengland.co.uk/boeapps/iadb/) as well as the current official Bank Rate of the Bank of England (http://www.bankofengland.co.uk/boeapps/iadb/Repo.asp?Travel=NIxIRx, accessed 05/10/12). These rates were applied as $r = 0.03$ and $r^{fg} = 0.05$ under intergenerational discounting method.

In order to investigate the effect of varying discount rates on NPV, a sensitivity analysis was carried out using a lower and upper extreme value of discount rates of 1% and 10%. Variation will also exist between applying conventional and intergenerational discounting. When applying intergenerational discounting, it must be decided how to allocate the value of the future generation discount rate, relative to the standard discount rate. A larger future discount rate, for example, might represent a greater value placed on benefits accrued in the present, than by future generations. This might result from uncertainty in future access to a resource and would result in over-exploitation, such as is seen in many fish stocks around the world (FAO, 2012)

3. Results

3.1. Relative Environmental Suitability and Maximum Catch Potential

The majority of species investigated in this study are predicted to experience a decrease in median relative environmental suitability by 2050 within the UK EEZ (median = -4.66%) (Fig. 6.2). However, environmental suitability is predicted to increase for a few species under some SDM-GCM combinations. In particular, European Sea Bass (*D. labrax*) is predicted to experience a median increase in RES of 24%, while those for John Dory (*Z. faber*), Sardine (*S. pilchardus*) and Monkfish (*L. piscatorius*) are predicted to increase by 8.01%, 9.32% and 5.73% respectively.

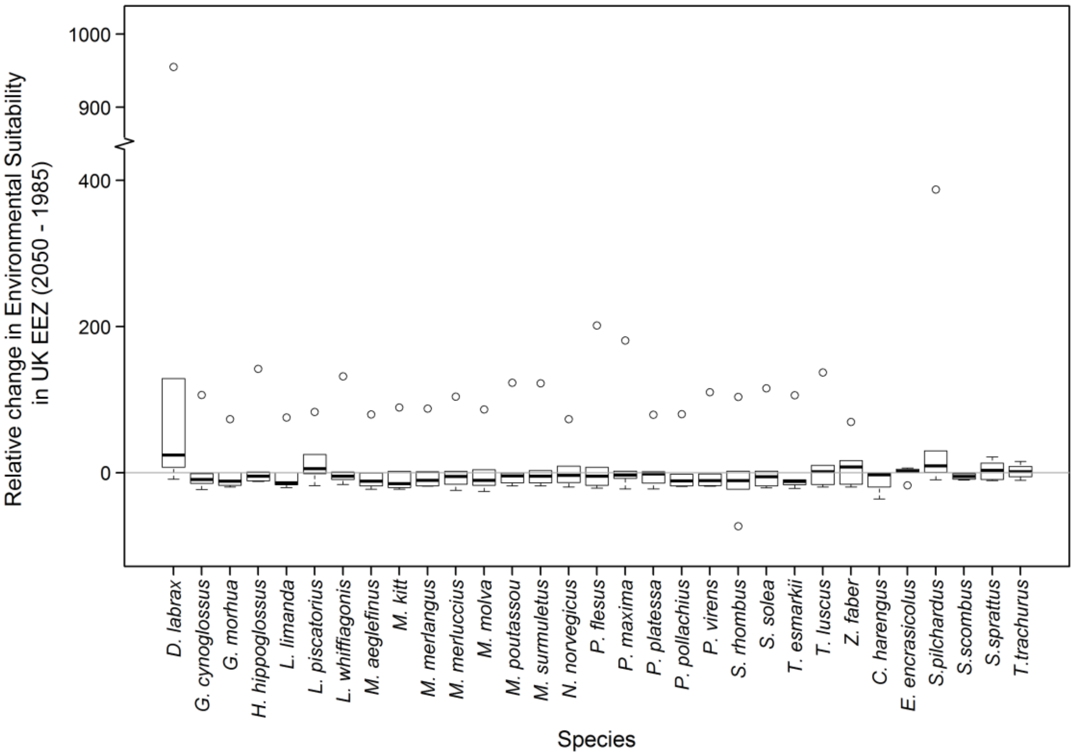


Figure 6.2. *Predicted change in Environmental Suitability.*

The percentage difference in total relative environmental suitability within the UK EEZ, for each species across GCMs and SDMs. Thick bars represent median values, the upper and lower ends of the box the upper and lower quartiles of the data, and the whiskers the most extreme datapoints no greater than 1.5 times inter-quartile range from the box. Points that are more extreme than whiskers are represented as circles.

Between 2000 and the 2050, primary productivity across all 0.5 latitude x 0.5 longitude grid cells of the UK EEZ is estimated to decrease by a median of 5% and a mean of 6% (range: 20% decrease - 7% increase) using the Geophysical Fluid Dynamics Laboratory's Earth System Model (GFDL ESM2.1, (Dunne *et al*. 2010). Using the Medusa model (Yool *et al.* 2011) primary productivity across the UK EEZ is predicted to decrease by a median of 44% and a mean of 39% (range: 70% decrease – 0.4% increase).

3.2. Maximum Catch Potential

Overall, the annual maximum catch potential for this set of species is predicted to decrease between 1985 and 2050 in the UK EEZ using eq. (1) (mean total decrease = 8.3%) (Fig. 6.3).

3.3. Cost-Benefit Analysis

3.3.1. The Scenarios

Scenario 1. Increased Costs for Industry

The total Net Present Value of benefits from the UK fishing fleet over 46 years (2005 – 2050), assuming constant fuel prices, no change in fishing location and catch, and intergenerational discounting with a conventional discount rate of 0.3% and a future discount rate of 0.05% is estimated at £2.6 billion. This value decreases to £1.5 billion, using a discount rate of 0.3% under conventional discounting methods (Appendix, Table 6.1). This represents an overall profitability of 36.2% and 21.2% using intergenerational and conventional discounting respectively, for the baseline scenario. Increasing fuel prices according to a long term (1988 – 2011) and short term (2005 – 2011) trend causes the net profitability of annual catch value to fall by 1.2% and 1.8% respectively between 2005 and 2050. It further increases the cost of fuel as a proportion of the total costs over the 45 year period (assuming no change in the latter) from 13.8% to 14.7% and 15.1% for long term and short term trends respectively. In 2050, fuel price increases result in annual fuel accounting for 15.8% and 16.8% respectively of total costs. These increases are also reflected in the percentage fuel cost as a proportion of total value. Higher fuel prices reduce overall profitability, using intergenerational discounting, over 46 years to 35.65% for the long term fuel price trend and 35.38% for the short term one. The substantial

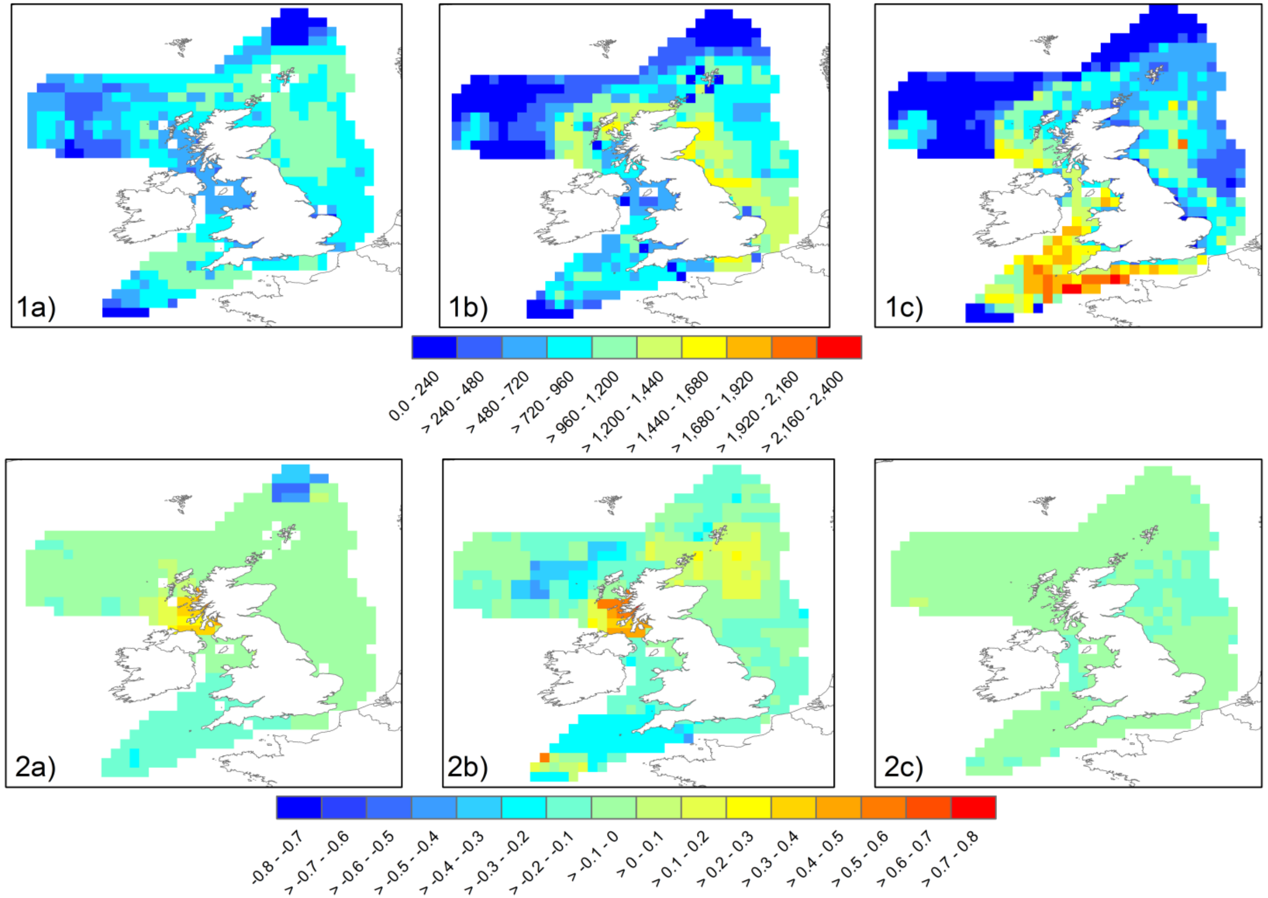


Figure 6.3. *Predicted total maximum catch potential in the UK EEZ.*

1) Maximum Catch Potential in tonnes in 1985, summed for all species and 2) difference in total MCP (2050 – 1985 values) using GFDL Topaz ESM2.1 data and species distribution models a) Maxent b) AquaMaps c) DBEM.

contribution of subsidies to the profitability of the fishing industry is shown when the contribution of capacity enhancing subsidies is removed from the cost benefit analysis, causing profitability to become negative, at -13.09%.

Scenario 2. Climate Change Impacts Catch

This scenario predicts climate change to have a negative impact on catch value, assuming fishing location remains constant (Fig. 6.4). Although the direction of change in NPV of benefits is consistent across predictions using different SDMs and climate datasets, the magnitude of this decrease varies. The majority of variation is spread evenly around a central tendency (e.g. median decrease in profitability for Scenario 2 = 10%), with outlying predictions from AquaMaps-GFDL presenting a best case scenario (3% decrease) and those from DBEM-GFDL present a worst case scenario (19% decrease).

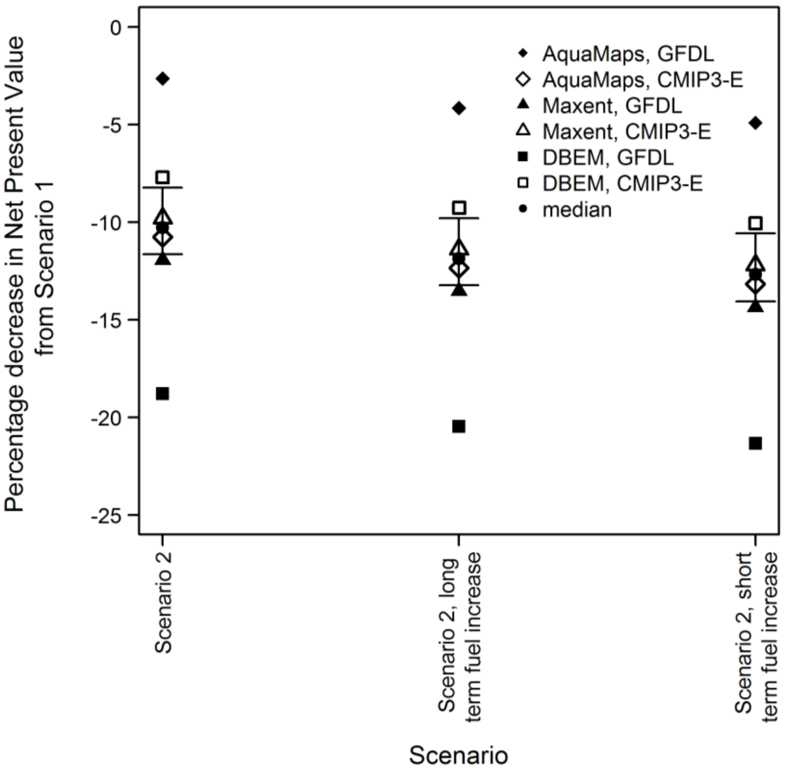


Figure 6.4. *Percentage decrease in Net Present Value of Scenario 2 from Scenario 1 current catch values (baseline). Results are shown with no increase in fuel price and with fuel price increasing according to long-term and short-term trends.*

This decrease in profitability results in a proportional increase in fuel costs relative to total profits, from 8.5% at the baseline scenario to a projected median of 9.1% under climate change across model combinations. Fuel cost would further increase to 9.8% and 10.1% of profits if fuel price were to increase by the long-term and short-term trends, respectively. To prevent this further decrease in profitability, subsidies were assumed to increase, representing a societal cost of climate change impacts on the fishing industry. In this scenario, by 2050, subsidies must increase by an additional £1.9 million per year for long term trends, and £2.9 million per year for short term trends, or at a rate of 2% and 3% per year, respectively.

Scenario 3. Sustainable Future

When all costs are assumed to remain constant and catches reflect the rebuilding of stocks to their maximum levels, a large increase in profitability is observed. Using $d = 0.03$ and $d_{fg} = 0.05$, the NPV over 45 years, assuming catch levels don't change due to climate change (at *Increased costs for Industry* levels), is estimated at 61.7% and 25.5% higher than that currently. Applying this to NPV calculations made under the *Climate Impacts Catch* predictions results in a comparable increase in profitability (median = 59.4%). Taking into account the additional fuel costs required in obtaining a larger catch likely provides a more realistic prediction of the profitability of sustainably harvested fish stocks in the UK EEZ. Thus, median profitability of the NPV assuming the cost of fuel increases according to catch weight, whereas total costs remain constant, is estimated at 54.1% (range: 51.47 – 55.30).

3.4. Sensitivity Analysis

3.4.1. Maximum Catch Potential

The choice of maximum catch dataset (ICES or SAUP) used to calculate maximum catch makes no difference to the percentage change in MCP (Fig. 6.5a), although there is variation in the decrease predicted using CMIP3-E and GFDL climatic data, with the former predicting a slightly larger decrease (median decrease = -8.02 and -7.73 with GFDL and CMIP3-E datasets respectively). Although using SAUP data to calculate the actual MCP values gives a greater spread of results, when tested within SDM and GCM, the differences between the two maximum catch datasets were also found not to be significant (Fig. 6.5b) (Kruskal-Wallis test, $p = > 0.01$, using species as replicates [n=31]).

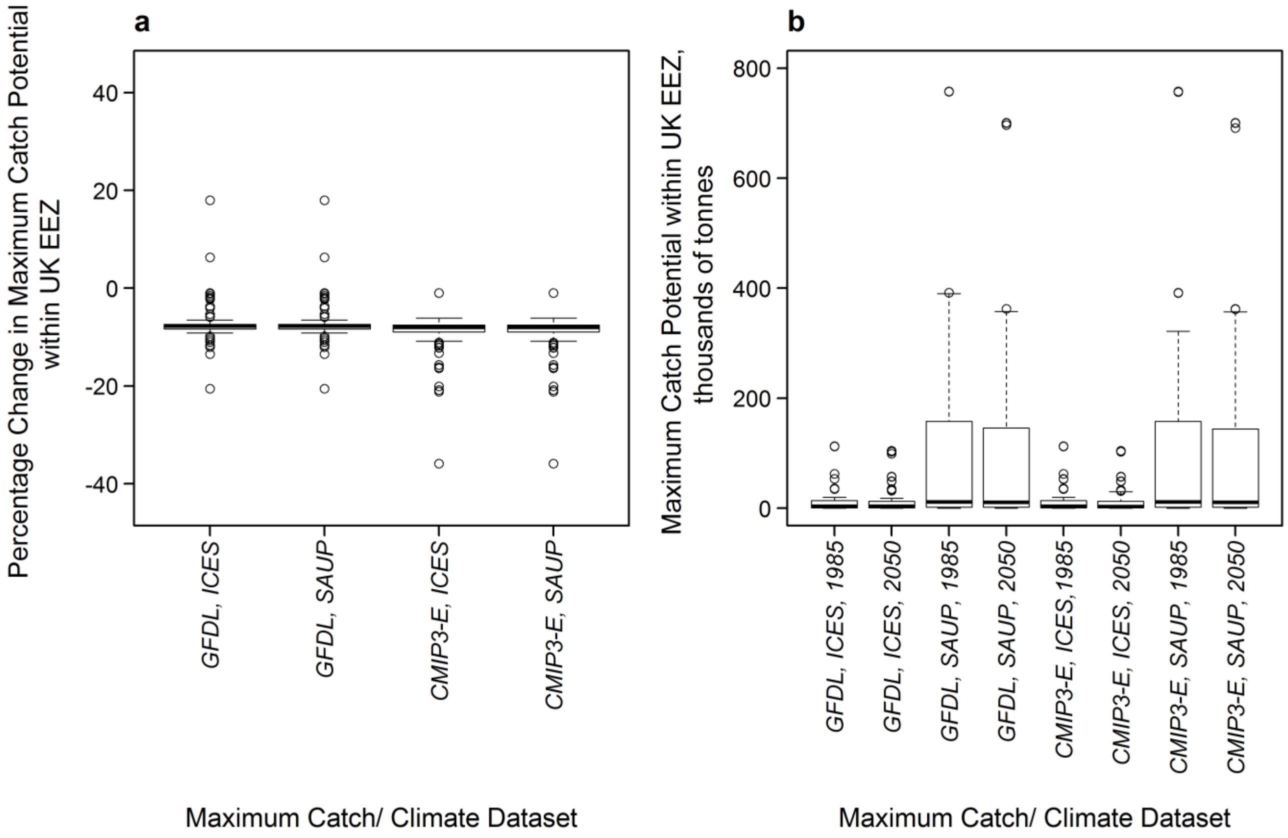


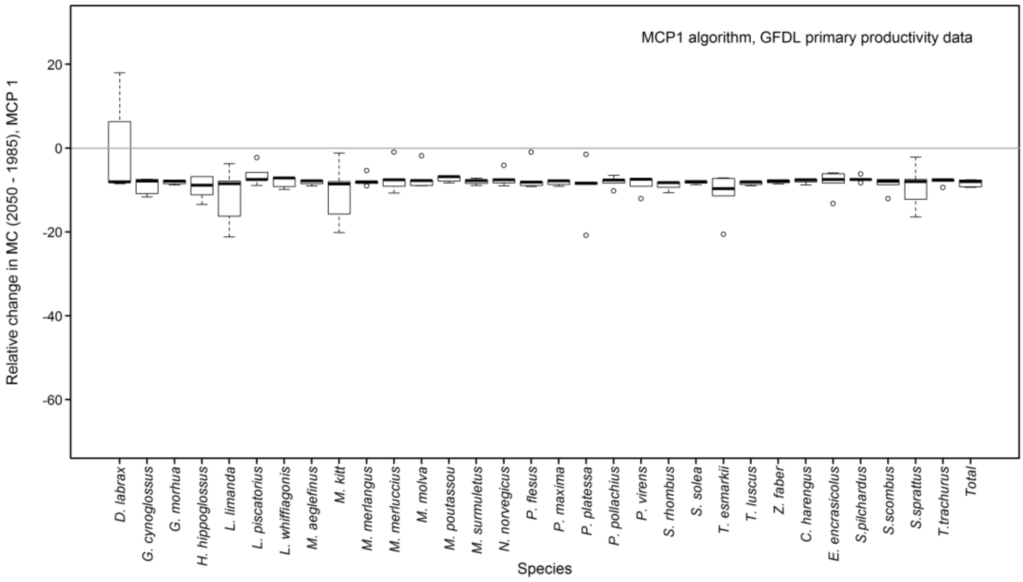
Figure 6.5. *Change in Maximum Catch Potential using MCP1. a) Percentage Change in maximum catch potential between 1985 and 2050 and b) MCP values in the UK EEZ for each time period across all species, using GFDL and CMIP3-E data and maximum catch values obtained from ICES and SAUP.*

The Species Distribution Model used did not have a significant effect on either the difference or value of MCP using both sources of maximum catch data, tested within each climate dataset (Kruskal-Wallis test, p = > 0.01, using species as replicates [n=31]). Although all species reflect the decreasing trend in total MCP in the UK EEZ (Fig. 6.6a), there is variation within species across SDM-GCM model combinations. In particular, sea bass (*D. labrax*) is predicted to increase in MCP by 18% using the DBEM with GFDL data while Dab (*L. limanda*) is predicted to decrease by 21% using AquaMaps and IPCC data.

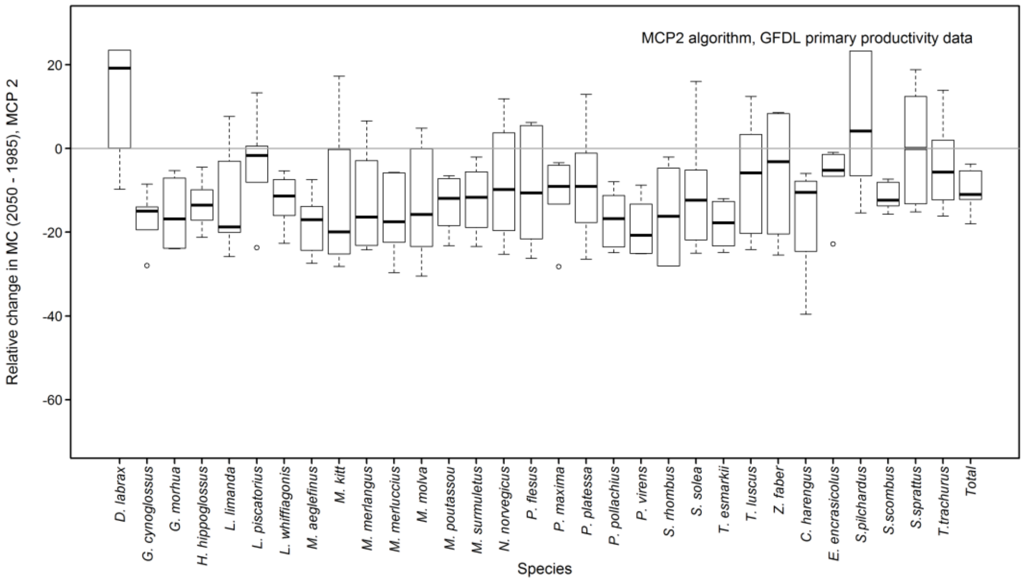
The decrease in total maximum catch potential predicted using MCP1 (eq. 1) is mirrored using the alternative algorithm, MCP2 (eq. 2), which predicts a mean total decrease of 10.2% across model combinations. More variation between the algorithms is seen for individual species. For example, MCP1 predicts a median decreases in MCP for all species. Introducing environmental suitability into the maximum catch algorithm (MCP2), however, produces a wider range of predictions across the six model combinations, with several species showing predicted increases using at least one model combination (Fig. 6.6b). Specifically, sea bass and sardine are predicted to show median increases in maximum catch potential of 19.2% and 4.2% respectively.

Figure 6.6. *(Following page) Change in maximum catch potential in the UK EEZ. Percentage change in maximum catch potential for each species in the UK EEZ between 1985 and 2050 using a) MCP1 (eq. 1) b) MCP2 (eq. 2) c) MCP2 using Medusa primary productivity data. Results are shown for all SDM and GFDL combinations, with thick bars representing median values, the upper and lower ends of the box the upper and lower quartiles of the data, and the whiskers the most extreme datapoints no greater than 1.5 times inter-quartile range from the box. Points that are more extreme than whiskers are represented as circles.*

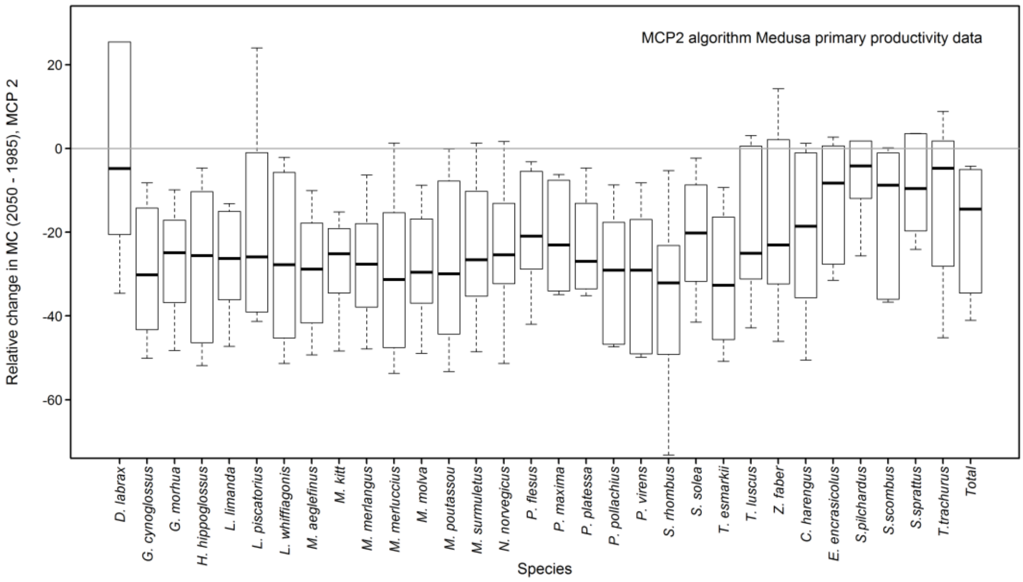
a


MCP1 algorithm, GFDL primary productivity data
Relative change in MC (2050 - 1985), MCP 1
20
0
-20
-40
-60
D. labrax
G. cynoglossus
G. morhua
H. hippoglossus
L. limanda
L. piscatorius
L. whiffiagonis
M. aeglefinus
M. kitt
M. merlangus
M. merluccius
M. molva
M. poutassou
M. surmuletus
N. norvegicus
P. flesus
P. maxima
P. platessa
P. pollachius
P. virens
S. rhombus
S. solea
T. esmarkii
T. luscus
Z. faber
C. harengus
E. encrasicolus
S.pilchardus
S.scombus
S.sprattus
T.trachurus
Total
Species

b


MCP2 algorithm, GFDL primary productivity data
Relative change in MC (2050 - 1985), MCP 2
20
0
-20
-40
-60
D. labrax
G. cynoglossus
G. morhua
H. hippoglossus
L. limanda
L. piscatorius
L. whiffiagonis
M. aeglefinus
M. kitt
M. merlangus
M. merluccius
M. molva
M. poutassou
M. surmuletus
N. norvegicus
P. flesus
P. maxima
P. platessa
P. pollachius
P. virens
S. rhombus
S. solea
T. esmarkii
T. luscus
Z. faber
C. harengus
E. encrasicolus
S.pilchardus
S.scombus
S.sprattus
T.trachurus
Total
Species

c


MCP2 algorithm Medusa primary productivity data
Relative change in MC (2050 - 1985), MCP 2
20
0
-20
-40
-60
D. labrax
G. cynoglossus
G. morhua
H. hippoglossus
L. limanda
L. piscatorius
L. whiffiagonis
M. aeglefinus
M. kitt
M. merlangus
M. merluccius
M. molva
M. poutassou
M. surmuletus
N. norvegicus
P. flesus
P. maxima
P. platessa
P. pollachius
P. virens
S. rhombus
S. solea
T. esmarkii
T. luscus
Z. faber
C. harengus
E. encrasicolus
S.pilchardus
S.scombus
S.sprattus
T.trachurus
Total
Species

The effect of variation in the MCP algorithm on Net Present Value is shown in Figure 6.7**.** In general, incorporating environmental suitability into the maximum catch potential algorithm (MCP2) results in higher values of percentage profitability. When the effect of different model combinations has been accounted for, this difference is significant ($p < 0.05$, df = 5). Furthermore, the variation resulting from different scenarios is strongly significant ($p < 0.01$, df = 5). However, despite variation between MCP algorithms, both predict decreases in NPV from the baseline scenario for Scenario 2 and increases for Scenario 3 (Table 6.2).

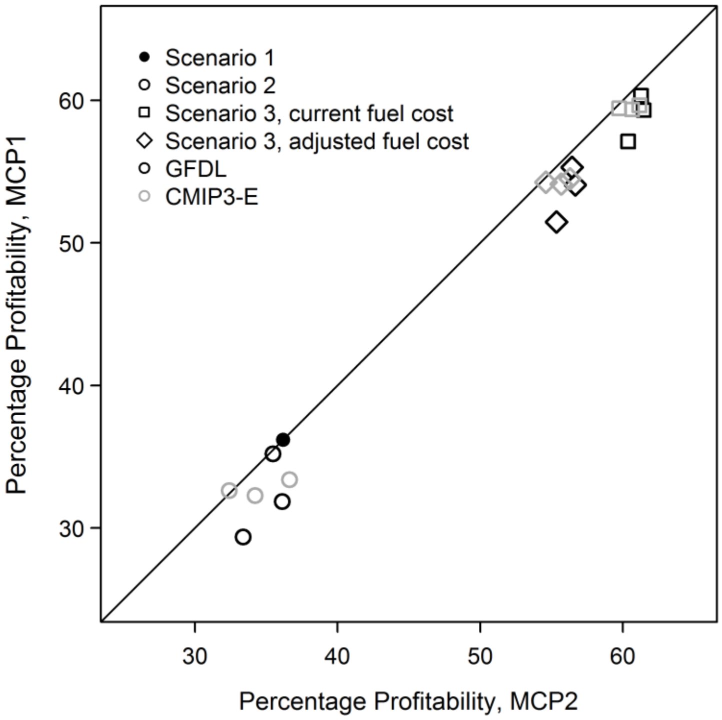


Figure 6.7. *Percent profitability of Net Present Values for each SDM-GCM combination using the two algorithms for calculating Maximum Catch Potential (MCP1 and MCP2) and Scenario 1: Increased Costs for Industry, Scenario 2: Climate Change Impacts Catch, and Scenario 3: Sustainable Future.*

able 6.2. *Median Net Present Values across model combinations using MCP1 (equation 1) and MCP2 (equation 2) algorithms.*

	Scenario 1: *Increased Costs for Industry*	**Scenario 2: *Climate Change Impacts Catch***	**Scenario 3: *Sustainable future,* current fuel**	**Scenario 3: *Sustainable future,* future fuel**
MCP1	36.18	32.46	59.39	54.19
MCP2, GFDL data	n/a	34.84	60.89	55.98
MCP2, Medusa data	n/a	32.03	59.72	54.58

3.4.2. Alternative Primary Productivity Dataset

In UK waters, primary productivity is predicted to decrease by an average of 39% using data from the Medusa model, compared to 5% using data from GFDL ESM2.1. The greater decrease in primary productivity shown by Medusa data is reflected in predictions of MCP for each species using the MCP2 algorithm. Thus, all species are predicted to show a median decrease in MCP (Fig. 6.6.c). However, using Medusa primary productivity data in calculating maximum catch potential using MCP2 showed that although median predictions of MCP were consistently lower, this was not always the case for predictions using each model combination. For example, while the total median percentage changes in MCP using GFDL and Medusa data are predicted at -5.3% and -34.5% respectively, using CMIP3-E data, median total decreases are greater using GFDL PP (-11.3%) than Medusa (-5%) data. This pattern is consistent across MCP predictions for individual species (Appendix, Table 6.2). Furthermore, the direction of difference is not consistent across model combinations (Fig. 6.8).

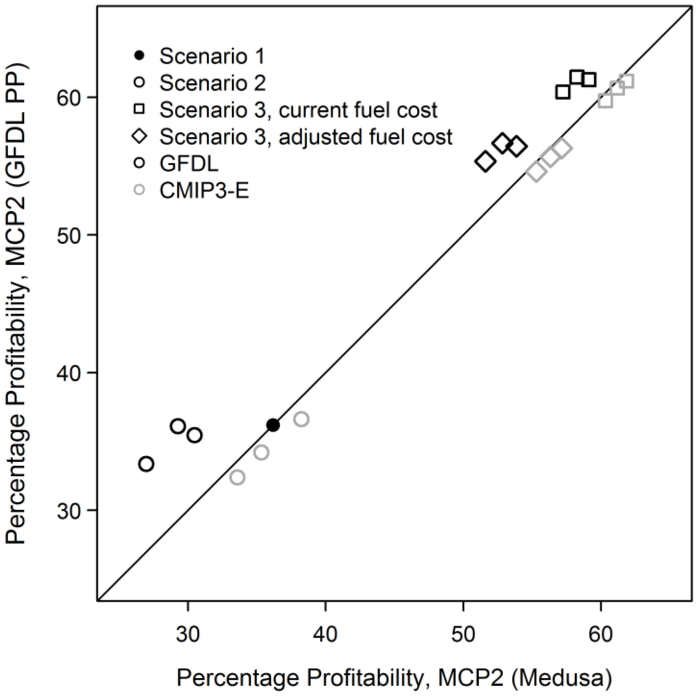


Figure 6.8. *Percent profitability of Net Present Values for each SDM-GCM combination using the MCP2 algorithm with primary productivity data from GFDL and Medusa for Scenario 1: Increased Costs for Industry, Scenario 2: Climate Change Impacts Catch, and Scenario 3: Sustainable Future. Model combinations using GFDL climate data to predict relative environmental suitability are depicted in black, those using CMIP3-E data in grey.*

3.4.3. Discount rate (using MCP1)

As expected, applying higher discount rates decreases the annual net profits obtained using both conventional and intergenerational discounting (Fig. 6.9), resulting in lower NPVs calculated over the whole period. Applying intergenerational discounting results in a lesser drop in annual net benefits over time compared to conventional discounting, with an increase being observed when low values (e.g. 0.01) of both conventional (r) and future (r^{fg}) discount rates are applied. Likewise, increasing the conventional discount rate has a greater effect on NPV than a comparable change in the future discount rate (r^{fg}) (Fig. 6.10). In general, this variation between NPV using different discount rates within a given model is greater that between both *Increased Costs for Industry* and *Climate Change Impacts Catch* scenarios and *Increased Costs for Industry* run with different SDM-GCM model combinations.

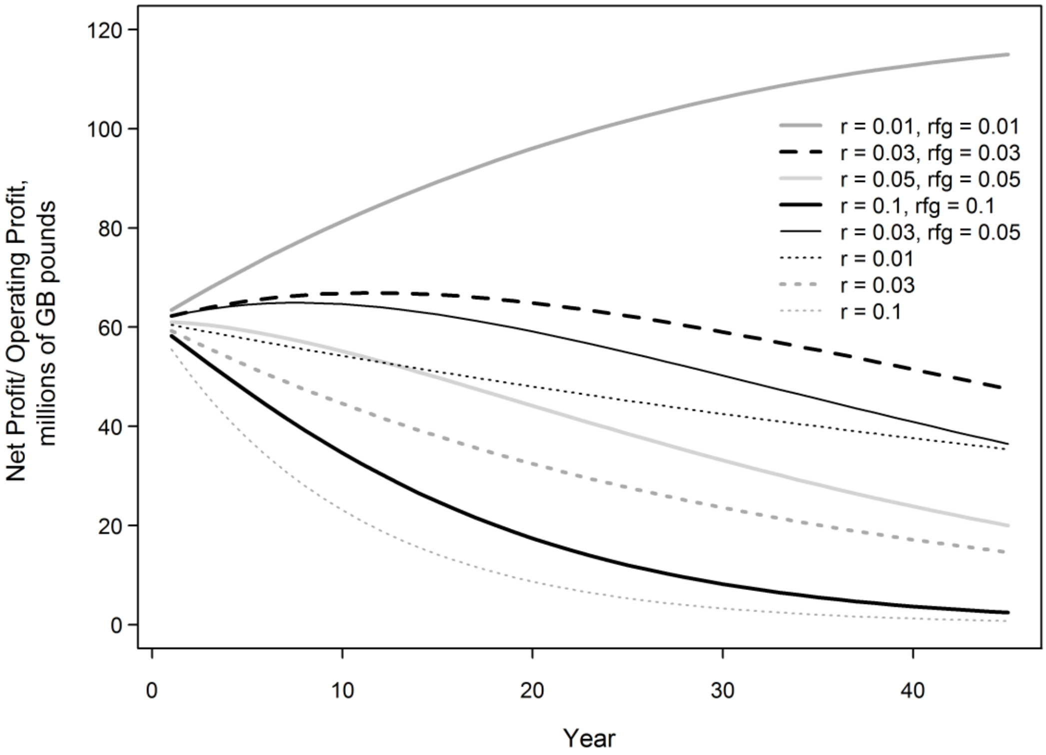


Figure 6.9. *Change in annual net profits between 2005 and 2050 using different conventional and intergenerational discount rates. Annual net profits are modelled using the Climate Change Impacts Catch scenario with change in maximum catch potential predicted using the MCP1 algorithm.*

However, although profitability values for different scenarios vary widely depending on discount rates used, variation is more consistent across scenarios or model combinations within a chosen discount rate. For example, using Scenario 3, the NPV of AquaMaps-GFDL varies between 105.7% and 14.78% when different discount rates are applied (intergenerational: r=0.01, r^{fg} = 0.01 and conventional: r=0.1 respectively). Within each discount rate, however, the difference between Scenario 1 (AquaMaps-GFDL) NPV and Scenario 3 NPV only ranges between 6.3% and 41.3%. Therefore although the actual magnitude of NPV varies widely according to the conventional and future discount rate applied, the pattern of profitability across scenarios and model combination within particular discount rates is relatively robust.

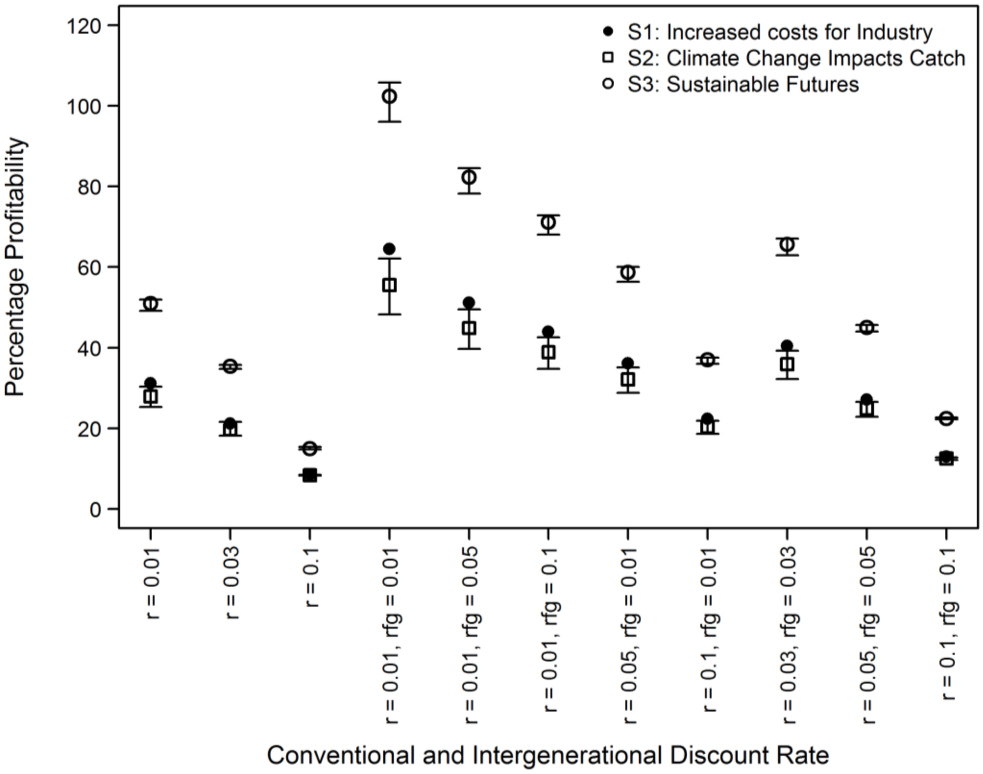


Figure 6.10. *Mean changes in percentage profitability of the Net Present Value over a 45 year period using different conventional (r) and future (r^{fg}) discount rates for Scenario 1, 2 and 3. Error bars show the range of predictions within each scenario across the six model combinations. (Scenario 2 has only one profitability calculation).*

4. Discussion

Projected changes in maximum catch potential using MCP1 are driven by the predicted decrease in primary productivity across UK waters, using GFDL data. Change in MCP is determined by area and primary productivity, thus presenting the biomass production sustainable by predicted levels of lower trophic level production. This reflects previous findings that indicate primary productivity to be the key driver of production at higher trophic levels (Ottersen *et al.* 2010; Chassot *et al.* 2010; Blanchard *et al.* 2012). Explicitly considering primary productivity when making predictions under climate change is thus crucial if a study aims to predict changes in relative abundance in addition to environmental suitability. Although primary productivity was included as an environmental predictor in projections of environmental suitability, its effect may be diluted by the inclusion of other variables, or, in the case of models that weight variables, such as Maxent, down-weighted in its impact on distribution in favour of key variables influencing distribution, such as temperature.

The influence of variation in maximum catch value and climatic dataset on the percentage change in MCP across the UK EEZ agrees with what would be expected given the modelling procedure. Thus as maximum catch potential values calculated using ICES and SAUP estimates of maximum catch were re-distributed for both time periods across a consistent area (the UK EEZ), no variation in percentage change was found. However, the alternative patterns of distribution of relative environmental suitability created using CMIP3-E or GFDL climate data cause variation in the re-distributions of the total Maximum Catch Potential over the EEZ.

4.1. Cost-Benefit Analysis

4.1.1. The Scenarios

Scenario 1. Increased costs for Industry

The calculation of profitability here aimed to present a realistic estimate to explore the potential effects of fuel price and changes in distribution and catch potential of key targeted species, rather than provide accurate absolute values of NPV. The operating profit for 2005, as an average of catch between 2000 and 2010 is estimated at 38.9%. This is higher than the operating profit of the UK fleet calculated by Seafish in 2009, at 25% of total fleet earnings (Curtis & Brodie, 2011). However, the result lies within the wider range calculated for different fleet segments, which varied between 3% for the West of Scotland nephrops over 250kW fleet segment, and 41% for vessels less than 10m (Curtis and Brodie 2011), although these profits decreased in 2010 (Curtis and Anderson 2012). Variability between operating profit estimated here and that calculated by Seafish could be due to a range of factors. For example, as this study aimed to make future projections specific to particular species, it focussed on a set of key species, rather than calculating total profitability. If this set of species represented greater value by weight, estimated profitability would be higher. Opportunity costs are also not accounted for here and labour costs do not include those of the skipper, which can account for a high proportion of costs.

The substantial impact of removing capacity enhancing subsidies, resulting in negative profitability (-13.1%), agrees with findings and predictions for fisheries worldwide. For example, in 2004, global fisheries were estimated to have a profitability deficit of $5 billion, compared to the operating profit of $5.5 billion before subsidies were subtracted (WorldBank and FAO 2008).

Fuel price is estimated to account for 13.8% of the total costs calculated here in 2005. Although fuel costs can represent up to 60% of the cost of fishing in the commercial fisheries of Hong Kong (Sumaila *et al.* 2007a) and purse seiners in NW Africa (FAO 1995; Sumaila *et al.* 2008), this result compares well to values for the SE Australian fishery, calculated at 10-25% of total operating costs (Sumaila *et al.* 2008). However, despite this relatively low percentage, fisheries such as the SE Australian fishery and European fisheries are still experiencing difficulties in the face of increasing fuel costs (COM, 2006). The influence of fuel cost on profitability is highlighted by the trend of fuel price increase, which with a more conservative long term price trend, will decrease overall annual profitability by 1.2% for the year 2050 relative to 2005. Although this study does not take into account potential change in fish price, predictions by the International Energy Agency suggest continued rising fuel prices over the next three decades (IEA 2010) and relatively little or no significant increase at the first point of sale for catches (Abernethy *et al.* 2010), thus contributing to the decline in profitability of capture fisheries, as seen here. For example, although fuel prices for fishers in Cornwall, UK increased by 359% from 1998 to 2008, fish prices remained relatively stable and failed to balance this increased cost (Abernethy *et al.* 2010). It should also be noted that growth in aquaculture production in the last few decades has increased the consumption of species from this source which were once wild-caught, thereby further reducing prices relative to the cost of fuel inputs (Sumaila *et al.* 2007b). The price fluctuations of aquaculture production as well as supply and demand are thus likely to impact the price of fish in the future and its value at first point of sale (FAO 2012).

Scenario 2. Climate Change Impacts Catch

Future predictions of Maximum Catch Potential are estimated to decrease the profitability of UK fisheries irrespective of the modelling procedure or discount rate used. If fishers are to maintain profitability, they must be able to adapt and cope with this change, increasing the value of their catch relative to the costs of obtaining it. The simplest method of doing this would be to increase catch value by improving fish prices at the first point of sale.

However, as mentioned above, stagnancy of the price of fish has not only prevented fishers from passing on the increased costs of fishing down the market chain but has also stopped them benefitting from times of reduced fish supply, when retail prices have not risen as would be expected (Abernethy *et al.* 2010). In this event, fishers must act to prevent decreases in marine production resulting in a drop in profitability. This may be done in one of several ways.

Fishers may attempt to increase their catch by increasing fishing effort. They may thus explore new fishing grounds at greater distances from port or fish for longer. However, the low profitability resulting from altered marine production presented here is further enhanced by rising fuel prices. As the cost of fuel increases with steaming time, both distance and time will be limited by costs, with fuel price likely reducing the effort applied to more distant fishing grounds. For example, Abernethy *et al*. (Abernethy *et al.* 2010) found rapidly increasing fuel price influenced how skippers fished and the amount they caught in 2008. They employed methods that would reduce fuel consumption, for example fishing closer to port or only in fine weather. Furthermore, 21% of skippers said they no longer explored new fishing grounds as they couldn't take the risk of not catching anything (Abernethy *et al.* 2010). Anticipated travel costs due to increased sea surface temperature and consequential changes in squid distribution have also been observed to decrease the number of boats targeting squid in fisheries off Monterey Bay, California (Dalton 2001).

Thus although results here predict the decrease in profitability caused by lower maximum catch potential to be greater than that caused by fuel, findings elsewhere suggest that fishers respond directly to increased fuel costs (Dalton 2001; Abernethy *et al.* 2010; Tidd *et al.* 2011). This is likely because the change in profits calculated here reflects 45 years of change in Maximum Catch Potential. Predicted changes in MCP and distribution may therefore not change enough to impact fisher behaviour over that caused by fuel in a shorter time frame, such as one year. In the future, there may be more marked responses in fisher location. For example, as well as average trip length, catch rate has been found to be significant in influencing fishing location choice in the subsequent year (Hutton *et al.* 2004). However, if the profit margins are tight enough for fishers to show behavioural responses to increasing fuel prices, any further decrease in profitability is likely to have severe consequences on fleet/ fishery persistence. If profit margins are more flexible, future changes in maximum catch potential may overcome the effect of fuel price in the future and fishermen might fish for longer and further away.

An alternative strategy for an individual skipper or fishing vessel to address both rising fuel costs and altered fishing patterns of marine production would be to change fishing gears. Gears/segments vary considerably in the amount of fuel consumed by a vessel, with towed gears being more consumptive. For example, of the 11 gear types looked at here (bottom trawl, mid-water trawl, bottom seine, mid-water seine, drift nets, fixed nets, pots, lines, picking, dredge, and other nets), the total annual spending in 2009 ranged from 6% of income for 10m vessels using hooks, to 57% of income for North Sea beam trawlers under 300kw. In segment differentiations used here, dredging was most expensive in terms of fuel use, while fixed nets were the least expensive. Choice of gear will thus depend on its relative fuel consumption as well as the relative value, abundance and catchability of target species. However, as results here suggest that overall maximum catch potential within the UK EEZ will decrease, a complete shift in species targeted may not sufficiently reverse falling profitability. Diversifying in terms of gears and species targeted would thus seem an optimal adaptation strategy. To improving resilience to uncertain changes in marine production and input costs, vessels thus need to be efficient, adaptable in terms of gears deployed and species targeted and resilient to weather and increasing costs.

Scenario 3. Sustainable futures

Fishing has affected the population size and structure of many commercially targeted species in the UK EEZ. Results presented here show that although climate change will still have a negative effect on profit following the rebuilding of fish stocks to sustainable levels, this profit remains higher than that estimated for current catch levels. The impact of climate change on future fish populations will therefore depend on how other anthropogenic threats have been managed and mitigated.

Although results here show the impact of climate change additional to that of current fishing pressure, they do not account for potential interactions between these factors. A population with lowered growth rates, weight-at-age and reproductive outputs due to living in sub-optimal environmental conditions is likely to be less resilient to unfavourable environmental conditions or provide the surplus production necessary to sustain fishing pressure, resulting in declining biomass (Reynolds *et al.* 2001; Cheung *et al.* 2005). Sustainably harvested populations will therefore not only be beneficial in terms of biomass and surplus production, but also in terms of resilience to future climate change and potentially sub-optimal environmental conditions.

Therefore despite predictions of decreasing profitability for the UK fishing fleet within its EEZ, analyses undertaken here suggest that the realised impacts of climate change on the UK fishing industry will depend on the capacity to adapt. Results presented here highlight that the key to ensuring adaptation and resilience to climate change in marine fisheries is to ensure adaptive capacity at all levels. Adaptation to climate change has been defined as involving an adjustment in ecological, social or economic systems in response to observed or expected changes in climate stimuli and their effects, in order to alleviate adverse impacts of change or take advantage of new opportunities (IPCC, 2001).

Households within the EU have been found to have higher than average levels of social and economic flexibility (Stead 2005; MacNeil *et al.* 2010), thereby allowing some North Sea fishing societies to persist through periods of low catches and reduced quotas. However, the substantial cost to society of artificially maintaining profits through subsidies, thereby buffering the effects of changing economic and ecological conditions and encouraging entry into the fishing industry has been highlighted here. If efforts are made to support the fishing industry by absorbing rising costs through increased subsidies, this cost to society will increase and the incentive to adapt decrease. The challenge under climate change is therefore to achieve adaptive capacity without increasing societal cost or subsidies. Reducing subsidies would encourage energy efficiency and contribute towards reducing overcapacity, for example through reducing vessel number or fishing effort. Reduced overcapacity may in turn encourage the rebuilding of fish stocks and biological resilience (Pauly *et al.* 2002; Sumaila *et al.* 2008), with the potential to improve Catch Per Unit Effort (CPUE). This is corroborated by Arnason (Arnason 2007), who predicted that a long term reduction in fishing effort could lead to increased sustainable yield and less chance of stock collapse. However, reducing overcapacity in this way has significant social implications, in particular for smaller fishing vessels with few adaptation options, and brings challenges in providing appropriate alternative livelihood strategies in coastal communities which have high dependencies on the fishing sector. Allowing the price of fish to fluctuate according to supply and demand would transfer some costs from society to the consumer and would allow market forces to realistically reflect changing costs to the industry. However, this also faces challenges if increased price of fish affects demand or causes fish caught by UK vessels to become more expensive than those imported from elsewhere. Markets or trade arrangements would also need to be developed or expanded for fish species new to UK waters, maximising the opportunities from changes in species distributions and climate.

4.2. Sensitivity Analysis

The cost-benefit analysis presents an initial attempt at combining predictions made using species distribution models with economic data and spatially explicit records of catch weight and value. Although the approach developed here is simplistic, it allows an exploration of how key factors will impact fishery profitability. Further sensitivity analysis allowed an exploration of the uncertainties associated with predictions and highlighted how results may vary with changes in data inputs and model algorithms.

Applying the algorithm MCP1 to predict future changes in maximum catch potential depends on the assumption that the dominant influence on marine productivity is bottom up, determined by primary productivity. This assumption may not hold if, for example, presence of one species in an area prevents another increasing in abundance, or if overfishing has caused a species to be sufficiently low in abundance in a particular area that primary production is not limiting and a density dependent response is precluded. Whether marine production will follow predictions made using MCP1 or MCP2 will thus depend on this assumption. However, although incorporating relative environmental suitability in the calculation of maximum catch potential (MCP2) results in greater variation in predictions from alternative SDM-GCM combinations, median predictions of change for the majority of species remain negative. This similarity is reflected in calculations of net present values for different scenarios. Thus although results show that predictions of NPV are sensitive to the MCP algorithm used, the direction of change for each scenario is robust.

Further to uncertainties introduced into predictions of relative environmental suitability by alternative climate models, as mentioned above, here prediction of maximum catch potential is predominantly determined by primary productivity. Models projecting the biological response to climate change are less well developed than their physical counterparts, and there is much uncertainty surrounding how primary productivity will respond (Hinder *et al.* 2012). For example, although the temperature sensitivity of primary productivity for a given chlorophyll content may be the most critical factor determining oceanic response of PP to climate, there are further large differences between the AOGCM simulations and thus uncertainties in the predicted biological response (Sarmiento 2004).

Here we compared outputs using primary productivity data from two sources to calculate MCP. Within the UK EEZ, primary productivity was predicted to decrease on average eight times more using the Medusa model than GFDL. However, comparing outputs using alterative primary productivity datasets showed that predictions using CMIP3-E data to calculate relative environmental suitability resulted in higher maximum catch potential values when combined with Medusa than GFDL primary productivity. Conversely, those MCP values incorporating the GFDL climate dataset and Medusa primary productivity data were lower than those using primary productivity from GFDL. As this pattern is not seen when comparing output from MCP1 (only incorporating primary productivity) and MCP2 (incorporating both primary productivity and relative environmental suitability), it is unlikely due to the fact that primary productivity is not included in the CMIP3-E predictions of relative environmental suitability. It may therefore be the spatial pattern of change in Medusa primary productivity that interacts with predictions of relative environmental suitability to lessen predicted decreases in maximum catch potential, and thus net present value. This result highlights the importance of considering a range of model outputs to assess the uncertainty attributed to different factors in the modelling procedure. Further work may thus benefit from a more in-depth study of variations in projected primary productivity, in particular as high resolution projections for continental shelf seas become available.

4.2.1. Discount rate

Results show that the choice of discount rate can have a substantial effect on conclusions made if the actual NPV and profitability values are assessed. However, their impact is minimised when comparing results across scenarios, for the same discount rate. General conclusions regarding the impact of specific scenarios are therefore robust to the discount rate chosen. However, it should be noted that the magnitude of variation across models and thus the differences between prediction of profitability using different scenarios increases with lower discount rates. Applying a set of conventional and future discount rates provides a useful way of exploring the effect of possible changes in discount rate on the Net Present Value of a resource. For example, it has been suggested that low discount rates favour environmentally sustainable behaviour (Cline 1992; Hasselmann *et al.* 1997), but also that uncertainty might increase discount rates, increasing the preference for money now rather than in an uncertain future. If the added uncertainty imposed by climate change on resource use and stock persistence increase discount rates, any tendency to fish sustainably might be reduced, with implications for management.

4.3. Assumptions in cost-benefit analysis

The cost benefit analysis undertaken here aimed to explore the effect of specific factors on profitability and was limited in its scope to estimate factors such as when profitability might decrease below minimum viable levels or how fishers might respond. An important factor influencing this is opportunity cost. If profits reduce below those to be made in alternative employment, fishers may leave the fishery. For share fishermen, whose salary is determined as a proportion of profits, opportunity costs are particularly important in influencing individual decisions on whether to leave the fishery. However, adaptation strategies might also involve temporality switching to alternative occupations when fishing becomes less profitable, such as during winter and bad weather.

Furthermore, ‘other costs’ included in this analysis (including repair costs and labour costs) were assumed not to change by 2050. Although this is unlikely, predicting their change is difficult and unlikely to have as much influence on profitability as fuel price. Added to these uncertainties are those caused by changing environmental phenomena, which may incur substantial capital costs. For example, the growing frequency of natural disasters such as floods and storms will increase the vulnerability of fishing communities through damage to gear and infrastructure and threat to human health (Alison *et al.* 2009). Increased risk of accidents and damage will push up insurance and likely cause more fishing days at sea to be lost to bad weather (Lane 2010). Furthermore, this analysis fails to account for any strategies aimed at decarbonising the fishing industry in line with commitments to climate change mitigation for increases in marine areas where sulphur-oxide emission levels are controlled. These factors are likely to further add to the cost of fuel of influence fishing location.

5. Conclusions

Climate change may influence the profitability of UK fisheries either directly, by altering the availability of fish to fishers, or indirectly, by altering the costs of inputs to a fishery, such as fuel and gear maintenance, or the time spent fishing. The decrease in marine productivity due to climate change projected here will likely lead to future decreases in total catch value and weight. Thus although environmental suitability within the UK EEZ may decrease for some species and increase for others, this is not translated to fishery productivity. The degree to which fishery profitability will decrease will further depend on changes in factors such as fuel price and subsidies. Furthermore, it will depend on the price paid for fish, as well as human behaviour and the opportunity costs of fishing. To minimise projected decreases in profitability, fisheries need to build adaptive capacity and diversify, ideally without incurring additional societal costs.

References

Abernethy, K.E., Trebilcock, P., Kebede, B., Allison, E.H. and Dulvy, N.K. (2010) Fuelling the decline in UK fishing communities? *ICES Journal of Marine Science* **65**, 1076–1085.

Arnason, R. (2007) The economics of rising fuel costs and European fisheries. *EuroChoices* **6**, 22–29.

Bakun, A. (1990) Coastal ocean upwelling. *Science* **247**, 198–201.

Blanchard, J.L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J.I., Holt, J. *et al*. (2012) Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philosophical transactions of the Royal Society of London Series B.* **367**, 2979–89.

Brander, K.M. (2007) Global fish production and climate change. *PNAS* **104**, 19709–14.

Carlson, M.J., Mitchell, R. and Rodriguez, L. (2011) Scenario Analysis to Identify Viable Conservation Strategies in Paraguay' s Imperiled Atlantic Forest. *Ecology and Society* **16** (3), 8.

Caviedes, C.N. and Fik, T.J. (1992) In: *Climate Variability, Climate Change and Fisheries*. (ed M. Glantz). Cambridge University Press, Cambridge.

Chassot, E., Bonhommeau, S., Dulvy, N.K., Mélin, F., Watson, R., Gascuel, D. and Le Pape, O. (2010) Global marine primary production constrains fisheries catches. *Ecology Letters* **13**, 495–505.

Cheung, W., Pitcher, T. and Pauly, D. (2005) A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological Conservation* **124**, 97–111.

Cheung, W.W.L., Close, C., Lam, V., Watson, R. and Pauly, D. (2008a) Application of macroecological theory to predict effects of climate change on global fisheries potential. *Marine Ecology Progress Series* **365**, 187–197.

Cheung, W.W.L., Dunne, J., Sarmiento, J.L. and Pauly, D. (2011) Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. *ICES Journal of Marine Science* **68**, 1008–1018.

Cheung, W.W.L., Lam, V.W.Y. and Pauly, D. (2008b) Modelling present and climate-shifted distributions of marine fishes and invertebrates. *Fisheries Centre Research Report* **16**.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R. and Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* **10**, 235–251.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., Zeller, D. and Pauly, D. (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology* **16**, 24–35.

Cheung, W.W.L., Pinnegar, J., Merino, G., Jones, M.C. and Barange, M. (2012a) Review of climate change impacts on marine fisheries in the UK and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **22**, 368-388.

Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W.Y., Deng P.M.L., Watson, R. *et al*. (2012b) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change* **2**, 1–5.

Cline, W.R. (1992) *The Economics of Global Warming*. Institute for International Economics, Washington D.C.

COM (2006) Commission of the European Communities. Brussels, 09.03.2006, 103 final communication form the commission to the council and the European Parliament on improving the economic situation in the fishing industry. Available at: http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=COM:2006:0103:FIN:EN:PDF [Accessed January 4, 2013].

Curtis, H. and Anderson, J. (2012) 2010 Economic Survey of the UK Fishing Fleet Short Report.

Curtis, H. and Brodie, C. (2011) 2009 Economic Survey of the UK Fishing Fleet Short Report.

Dalton, M.G. (2001) El Niño, Expectations, and Fishing Effort in Monterey Bay, California. *Journal of Environmental Economics and Management* **42**, 336–359.

Drinkwater, K.F. (2005) The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science* **62**, 1327–1337.

Dulvy, N.K., Reynolds, J.D., Pilling, G.M., Pinnegar, J.K., Phillips, J.S., Allison, E.H. and Badjeck, M. (2010) Chapter 1 Fisheries management and governance challenges in a climate change. In: *The Economics of Adapting Fisheries to Climate Change*. OECD, pp 31–89.

Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmller, V., Dye, S.R. and Skjoldal, H.R. (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology* **45**, 1029–1039.

Dyck, A.J. and Sumaila, U.R. (2010) Economic impact of ocean fish populations in the global fishery. *Journal of Bioeconomics* **12**, 227–243.

Englehard, G.H. (2008) One hundred and twenty years of change in fishing power of English North Sea trawlers. In: *Advances in Fisheries Science: 50 years on from Beverton and Holt*. (eds A. Payne, J. Cotter and T. Potter). Blackwell Publishing, Oxford, pp 1–25.

FAO (2009) Climate change implications for fisheries and aquaculture (eds. K. Cochrane, C. DeYoung, D. Soto, and T. Bahri). FAO Fisheries and Aquaculture Technical Paper 530, FAO, Rome.

FAO (1995) Summary report of the CRODT/FAO CECAF ad hoc technical meeting on economic aspects of the exploitation of sardinellas and other small pelagic species of the Northwest African coast, CRODT, Dakar 1-3 December, 1993. Rome.

FAO (2010) The State of World Fisheries and Aquaculture. FAO Rome. Available at: http://www.fao.org/docrep/013/i1820e/i1820e00.htm.

FAO (2012) The State of World Fisheries and Aquaculture. FAO, Rome. Available at http://www.fao.org/docrep/016/i2727e/i2727e00.htm.

Fodrie, F.J., Heck, K.L., Powers, S.P., Graham, W.M. and Robinson, K.L. (2010) Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico. *Global Change Biology* **16**, 48–59.

Froese, R., Zeller, D., Kleisner, K. and Pauly, D. (2012) What catch data can tell us about the status of global fisheries. *Marine Biology* **159**, 1283–1292.

Garza-Gil, M.D., Torralba-Cano, J. and Varela-Lafuente, M.M. (2010) Evaluating the economic effects of climate change on the European sardine fishery. *Regional Environmental Change* **11**, 87–95.

Hasselmann, K., Hasselmann, S., Giering, R., Ocana, V. and Sorch, H.V. (1997) Sensitivity study of optimal CO_2 emission paths using a simplified structural integrated assessment model (SIAM). *Climate Change* **37**, 335–343.

Haward, M., Davidson, J., Lockwood, M., Hockings, M., Kriwoken, L. and Allchin, R. (2012) Climate change, scenarios and marine biodiversity conservation. *Marine Policy* **38**, 438-446.

Hentrich, S. and Salomon, M. (2006) Flexible management of fishing rights and a sustainable fisheries industry in Europe. *Marine Policy* **30**, 712–720.

Heymans, J.J., Mackinson, S., Sumaila, U.R., Dyck, A. and Little, A. (2011) The impact of subsidies on the ecological sustainability and future profits from North Sea fisheries. *PLoS ONE* **6**(5) e20239.

Hinder, S.L., Hays, G.C., Edwards, M., Roberts, E.C., Walne, A.W. and Gravenor, M.B. (2012) Changes in marine dinoflagellate and diatom abundance under climate change. *Nature Climate Change* **2**, 271–275.

Hutton, T., Mardle, S., Pascoe, S. and Clark, R. (2004) Modelling fishing location choice within mixed fisheries: English North Sea beam trawlers in 2000 and 2001. *ICES Journal of Marine Science* **61**, 1443–1452.

IEA (2010) Word Energy Outlook 2010. Paris. Available at www.iea.org/publications/freepublications/publication/weo2010.pdf [Accessed January, 2013].

IPCC (2007a) *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, USA.

IPCC (2007b) Summary for policymakers. In: *Climate Change 2007: The Physical Science Basis. Working Group 1 Contribution to the Fourth Assessment Report of the IPCC*. (eds S. Solomon, D. Qin, M. Manning, *et al.*). Cambridge University Press, Cambridge, UK and New York, USA.

Jones, M.C., Dye, S.R., Fernandes, J.A., Frölicher, T.L., Pinnegar, J.K., Warren, R. and Cheung, W.W.L. (2013) Predicting the Impact of Climate Change on Threatened Species in UK Waters. *PLoS ONE* **8**, e54216.

Jones, M.C., Dye, S.R., Pinnegar, J.K., Warren, R. and Cheung, W.W.L. (2012) Modelling commercial fish distributions: Prediction and assessment using different approaches. *Ecological Modelling* **225**, 133–145.

Kaschner, K., Watson, R., Trites, A. and Pauly, D. (2006) Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. *Marine Ecology Progress Series* **316**, 285–310.

Lane, D.E. (2010) Is the current fisheries management toolbox sufficient to address climate change? In: *The Economics of Adapting Fisheries to Climate Change*. OECD Publishing.

MMO (2011) *UK Sea Fisheries Statistics 2010*. Almond S, Thomas B, editors. Available at: http://www.marinemanagement.org.uk/fisheries/statistics/annual.htm.

MacNeil, M.A., Graham, N.A.J., Cinner, J.E., Dulvy, N.K., Loring, P.A., Jennings, S., Polunin, N.V.C. *et al*. (2010) Transitional states in marine fisheries: adapting to predicted global change. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **365**, 3753–63.

Milazzo, M. (1998) Subsidies in world fisheries: A re-examination. World Bank technical paper no 406. Fisheries series. Washington D.C.

Miller, K.A. and Munro, G.R. (2004) Climate and Cooperation: a new perspective on the management of shared fish stocks. *Marine Resource Economics* **19**, 367–393.

Morato, T., Watson, R., Pitcher, T.J. and Pauly, D. (2006) Fishing down the deep. *Fish and Fisheries* **7**, 24–34.

Munro, G. and Sumaila, U.R. (2002) The impact of subsidies upon fisheries management and sustainability: the case of the North Atlantic. *Fish and Fisheries* **3**, 233–250.

OECD (2001) The Organisation for Economic Co-operation and Development (OCED) website, Glossary of Statsitcial Terms. Available at: http://stats.oecd.org/glossary/index.htm [Accessed January 25, 2013].

Ottersen, G., Kim, S., Huse, G., Polovina, J.J. and Stenseth, N.C. (2010) Major pathways by which climate may force marine fish populations. *Journal of Marine Systems* **79**, 343–360.

Pauly, D. (1980) On the iterrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal de Conseil International pour l'Exploration de la Mer* **39**, 175–192.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R. *et al*. (2002) Towards sustainability in world fisheries. *Nature* **418**, 689–695.

Perry, A.L., Low, P.J., Ellis, J.R. and Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–5.

Peterson, G.D., Cumming, G.S. and Carpenter, S.R. (2003) Scenario Planning: a Tool for Conservation in an Uncertain World. *Conservation Biology* **17**, 358–366.

Phillips, S.J., Anderson, R.P. and Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**, 231–259.

Pinnegar, J.K., Jennings, S., Brien, C.M.O. and Polunin, N.V.C. (2002) Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *Journal of Applied Ecology* **39**, 377–390.

Pinnegar, J.K., Viner, D., Hadley, D., Dye, S., Harris, M., Berkhout, F. and Simpson, M. (2006) Alternative futures for marine ecosystems; tecnical report. 109 pp. Lowestoft.

Portner, H. (2008) Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. *Marine Ecology Progress Series* **373**, 203 – 217.

Ready, J., Kaschner, K., South, A.B., Eastwood, P.D., Rees, T., Rius, J., Agbayani, E. *et al*. (2010) Predicting the distributions of marine organisms at the global scale. *Ecological Modelling* **221**, 467–478.

Reynolds, J.D., Jennings, S. and Dulvy, N.K. (2001) Life histories of fishes and population responses to exploitation. In: *Conservation of Exploited Species*. (eds J.D. Reynolds, G.M. Mace, K.H. Redford and J.G. Robinson). Cambridge University Press, Cambridge, pp 147–169.

Sarmiento, J.L. Slater, R., Barber, R., Bopp, L., Doney, S.C., Hirst, A.C., Kleypas, J. *et al*. (2004) Response of ocean ecosystems to climate warming. *Global Biogeochemical Cycles* **18**. GB3003, doi: 10.1029/2003GB002134.

Srinivasan, U.T., Cheung, W.W.L., Watson, R. and Sumaila, U.R. (2010) Food security implications of global marine catch losses due to overfishing. *Journal of Bioeconomics* **12**, 183–200.

Stead, S. (2005) Changes in Scottish coastal fishing communities—Understanding socio-economic dynamics to aid management, planning and policy. *Ocean & Coastal Management* **48**, 670–692.

Sumaila, U. and Walters, C. (2005) Intergenerational discounting: a new intuitive approach. *Ecological Economics* **52**, 135–142.

Sumaila, U.R. (2003) A fish called Subsidy. *Science and the Environment* **12**.

Sumaila, U.R., Cheung, W.W.L., Lam, V.W.Y., Pauly, D. and Herrick, S. (2011) Climate change impacts on the biophysics and economics of world fisheries. *Nature Climate Change* **1**, 449-456.

Sumaila, U.R., Cheung, W.W.L. and Teh, L. (2007a) Rebuilding Hong Kong's marine fisheries: an evaluation of management option. Fisheries Centre Research Reports, **15** (3). 112 pp. Vancouver.

Sumaila, U.R., Khan, A.S., Dyck, A.J., Watson, R., Munro, G., Tydemers, P. and Pauly, D. (2010) A bottom-up re-estimation of global fisheries subsidies. *Journal of Bioeconomics* **12**, 201–225.

Sumaila, U.R., Teh, L., Watson, R., Tyedmers, P. and Pauly, D. (2008) Fuel price increase, subsidies, overcapacity, and resource sustainability. *ICES Journal of Marine Science* **65**, 832–840.

Sumaila, U.R., Volpe, J. and Liu, Y. (2007b) Potential economic benefits from sablefish farming in British Columbia. *Marine Policy* **31**, 81–84.

Tidd, A.N., Hutton, T., Kell, L.T. and Padda, G. (2011) Exit and entry of fishing vessels: an evaluation of factors affecting investment decisions in the North Sea English beam trawl fleet. *ICES Journal of Marine Science* **68**, 961–971.

Ware, D.M. and Thomson, R.E. (2005) Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science* **308**, 1280–1284.

Watson, R., Kitchingman, A., Gelchu, A. and Pauly, D. (2004) Mapping global fisheries: sharpening our focus. *Fish and Fisheries* **5**: 168-177.

WorldBank and FAO (2008) *The Sunken Billions. The economic justification for fisheries reform.* Washington, D.C. Rome.

Yool, A., Popova, E.E. and Anderson, T.R. (2011) Medusa-1.0: a new intermediate complexity plankton ecosystem model for the global domain. *Geoscientific Model Development* **4**, 381–417.

Appendix

Table 6.1. *Table showing the Net Present Value (NPV) and profitability of catch value over a 45 year period (2005 – 2050) under different scenarios and using standard discount rate 0.03 and future discount rate 0.05. Values in millions of GB £s.*

Scenario	Total NPV (d = 0.03, dfg = 0.05) (GB £, millions)	Sum Total Value	Fuel 2000	Fuel 2050	Other Costs	Overall Profitability	Fuel as a percentage of total value
Scenario 1	2562.85	7083.39	13.31	13.31	82.91	36.18	8.46
S1 (standard discounting, d = 0.03)	1500.21	7083.39	13.31	13.31	82.91	21.18	8.46
S1 + subsidies	-926.97	7083.39	13.31	13.31	82.91	-13.09	8.46
S1 fuel increase, long term trend	2525.11	7083.39	13.36	15.23	82.91	35.65	9.08
S1 fuel increase, short term trend	2505.81	7083.39	13.38	16.20	82.91	35.38	9.40
MCP1							
Scenario 2							
AqM_GFDL	2447.80	6949.33	13.31	13.31	82.91	35.22	8.62
AqM_IPCC	2120.90	6568.40	13.31	13.31	82.91	32.29	9.19
Max_GFDL	2076.56	6516.74	13.31	13.31	82.91	31.87	9.62
Max_IPCC	2157.30	6610.82	13.31	13.31	82.91	32.63	9.12
DBEM_GFDL	1830.72	6230.26	13.31	13.31	82.91	29.38	9.06
DBEM_IPCC	2239.62	6706.74	13.31	13.31	82.91	33.39	8.93
Scenario 2, fuel increase, long term					**median**	**32.46**	**9.09**
AqM_GFDL	2410.06	6949.33	13.36	15.23	82.91	34.68	9.25
AqM_IPCC	2083.16	6568.40	13.36	15.23	82.91	31.71	9.79
Max_GFDL	2038.82	6516.74	13.36	15.23	82.91	31.29	9.87

Max_IPCC	2119.56	6610.82	13.36	15.23	82.91	32.06	9.73
DBEM_GFDL	1792.98	6230.26	13.36	15.23	82.91	28.78	10.32
DBEM_IPCC	2201.88	6706.74	13.36	15.23	82.91	32.83	9.59
Scenario 2, fuel increase, short term					**median**	**31.89**	**9.76**
AqM_GFDL	2390.76	6949.33	13.38	16.20	82.91	34.40	9.58
AqM_IPCC	2063.86	6568.40	13.38	16.20	82.91	31.42	10.13
Max_GFDL	2019.52	6516.74	13.38	16.20	82.91	30.99	10.21
Max_IPCC	2100.26	6610.82	13.38	16.20	82.91	31.77	10.07
DBEM_GFDL	1773.68	6230.26	13.38	16.20	82.91	28.47	10.68
DBEM_IPCC	2182.58	6706.74	13.36	15.23	82.91	32.54	9.92
Scenario 3, current fuel					**median**	**31.60**	**10.10**
AqM_GFDL	7330.01	12151.70	13.31	13.31	82.91	60.32	4.93
AqM_IPCC	6943.13	11700.87	13.31	13.31	82.91	59.34	5.12
Max_GFDL	6925.56	11680.40	13.31	13.31	82.91	59.29	5.13
Max_IPCC	6982.68	11746.97	13.31	13.31	82.91	59.44	5.10
DBEM_GFDL	6166.46	10795.86	13.31	13.31	82.91	57.12	5.55
DBEM_IPCC	7062.51	11839.98	13.31	13.31	82.91	59.65	5.06
Scenario 3, corrected fuel					**median**	**59.39**	**5.11**
AqM_GFDL	6719.99	12151.70	27.88	27.88	82.91	55.30	10.32
AqM_IPCC	6333.10	11700.87	27.88	27.88	82.91	54.12	10.72
Max_GFDL	6315.53	11680.40	27.88	27.88	82.91	54.07	10.74
Max_IPCC	6372.65	11746.97	27.88	27.88	82.91	54.25	10.68
DBEM_GFDL	5556.43	10795.86	27.88	27.88	82.91	51.47	11.62
DBEM_IPCC	6452.48	11839.98	27.88	27.88	82.91	54.50	10.60
MCP2					**median**	**54.19**	**10.70**
Scenario 2							
AqM_GFDL	2475.89	6982.06	13.31	13.31	82.91	35.46	

AqM_IPCC	2332.15	6814.57	13.31	13.31	82.91	34.22
Max_GFDL	2555.97	7075.37	13.31	13.31	82.91	36.12
Max_IPCC	2132.00	6581.34	13.31	13.31	82.91	32.39
DBEM_GFDL	2238.53	6705.47	13.31	13.31	82.91	33.38
DBEM_IPCC	2618.65	7148.41	13.31	13.31	82.91	36.63
Scenario 3, current fuel					**median**	**34.84**
AqM_GFDL	7734.74	12623.31	13.31	13.31	82.91	61.27
AqM_IPCC	7460.65	12303.93	13.31	13.31	82.91	60.64
Max_GFDL	7816.34	12718.40	13.31	13.31	82.91	61.46
Max_IPCC	7097.47	11880.73	13.31	13.31	82.91	59.74
DBEM_GFDL	7343.83	12167.79	13.31	13.31	82.91	60.35
DBEM_IPCC	7679.45	12558.88	13.31	13.31	82.91	61.15
Scenario 3, corrected fuel					**median**	**60.89**
AqM_GFDL	7124.71	12623.31	27.88	27.88	82.91	56.44
AqM_IPCC	6850.63	12303.93	27.88	27.88	82.91	55.68
Max_GFDL	7206.31	12718.40	27.88	27.88	82.91	56.66
Max_IPCC	6487.44	11880.73	27.88	27.88	82.91	54.60
DBEM_GFDL	6733.80	12167.79	27.88	27.88	82.91	55.34
DBEM_IPCC	7069.42	12558.88	27.88	27.88	82.91	56.29
MCP2 Medusa					**median**	**55.98**
Scenario 2						
AqM_GFDL	1936.73	6353.80	13.31	13.31	82.91	30.48
Max_GFDL	1819.87	6217.62	13.31	13.31	82.91	29.27
DBEM_GFDL	1610.16	5973.26	13.31	13.31	82.91	26.96
AqM_IPCC	2461.16	6964.89	13.31	13.31	82.91	35.34
Max_IPCC	2259.73	6730.18	13.31	13.31	82.91	33.58
DBEM_IPCC	2823.78	7387.44	13.31	13.31	82.91	38.22

Scenario 3, current fuel						**median**	**32.03**
AqM_GFDL	6858.51		11602.27	13.31	13.31	82.91	59.11
AqM_IPCC	7695.42		12577.50	13.31	13.31	82.91	61.18
Max_GFDL	6548.48		11241.00	13.31	13.31	82.91	58.26
Max_IPCC	7328.40		12149.82	13.31	13.31	82.91	60.32
DBEM_GFDL	6201.67		10836.88	13.31	13.31	82.91	57.23
DBEM_IPCC	7997.84		12929.89	13.31	13.31	82.91	61.86
Scenario 3, corrected fuel						**median**	**59.72**
AqM_GFDL	6248.48		11602.27	27.88	27.88	82.91	53.86
AqM_IPCC	7085.39		12577.50	27.88	27.88	82.91	56.33
Max_GFDL	5938.45		11241.00	27.88	27.88	82.91	52.83
Max_IPCC	6718.38		12149.82	27.88	27.88	82.91	55.30
DBEM_GFDL	5591.64		10836.88	27.88	27.88	82.91	51.60
DBEM_IPCC	7387.81		12929.89	27.88	27.88	82.91	57.14

Table 6.2. *Change in maximum catch potential (2050-1985) using GFDL ESM2.1 and CMIP3-E climatic datasets, GFDL ESM2.1 and Medusa projections of primary productivity and 2 algorithms for maximum catch potential.*

	Medusa, MCP2		**GFDL, MCP2**		**GFDL, MCP1**	
	GFDL	**IPCC**	**GFDL**	**IPCC**	**GFDL**	**IPCC**
D.labrax	-20.56	25.47	20.28	18.11	6.32	-8.01
G. cynoglossus	-43.29	-14.20	-13.92	-19.42	-7.44	-8.25
G. morhua	-36.81	-17.14	-7.08	-23.80	-7.84	-7.88
H. hippoglossus	-46.36	-10.31	-9.87	-16.30	-7.86	-9.83
L. limanda	-36.15	-15.03	-3.03	-19.34	-7.90	-16.19
L. piscatorius	-39.04	-0.99	-0.99	-8.06	-5.79	-7.48
L. whiffiagonis	-45.25	-5.72	-11.72	-10.96	-7.07	-7.10
M. aeglefinus	-41.65	-17.82	-13.84	-24.31	-7.75	-7.80
M. kitt	-34.52	-19.12	-0.24	-25.21	-7.97	-15.72
M. merlangus	-37.89	-17.95	-2.92	-23.13	-7.95	-8.02
M. merluccius	-47.55	-15.36	-17.37	-22.39	-7.51	-7.51
M. molva	-36.95	-16.83	-0.11	-23.38	-7.74	-7.74
M. poutassou	-44.31	-7.74	-10.76	-12.98	-6.81	-7.84
M. surmuletus	-35.25	-10.23	-5.56	-17.71	-7.74	-7.74
N. norvegicus	-32.26	-13.08	3.73	-19.57	-7.49	-8.30
P. flesus	-28.78	-5.45	5.49	-11.65	-8.12	-8.11
P. maxima	-34.04	-7.56	-4.01	-13.27	-7.74	-7.81
P. platessa	-33.52	-13.10	-1.11	-17.70	-8.08	-8.50
P. pollachius	-46.75	-17.60	-11.19	-23.48	-7.50	-7.63
P. virens	-49.07	-16.96	-18.59	-22.85	-7.38	-7.39
S. rhombus	-32.91	-23.16	-4.68	-28.01	-8.17	-8.20
S. solea	-31.75	-8.67	-5.14	-15.67	-7.97	-7.98
T. esmarkii	-45.61	-16.38	-15.02	-23.28	-8.66	-10.57
T. luscus	-31.15	0.52	3.38	-7.11	-8.00	-8.02
Z. faber	-32.37	2.12	-0.74	-5.61	-7.76	-7.77
C. harengus	-34.04	-3.10	-10.91	-10.08	-7.53	-7.50
E. encrasicolus	-27.66	0.40	-1.41	-6.61	-7.48	-7.48
S. pilchardus	-11.90	0.69	14.06	-6.51	-7.61	-7.38
S. scombus	-36.02	-7.62	-11.72	-13.71	-8.32	-7.50
S .sprattus	-19.65	-8.27	12.43	-13.17	-7.48	-12.19
T. trachurus	-28.12	0.75	-5.22	-6.09	-7.48	-7.58
Total	-34.50	-5.05	-5.30	-11.27	-7.61	-9.23

Chapter 7

Key Findings and Discussion

Recent decades have seen the wide-spread development and application of species distribution models to investigate the distribution of biodiversity, the spread of invasive species and the ecological impacts of climate change. Whether due to challenges of data quality and quantity that are particularly prevalent in the marine environment or the lesser quantity of research in this area, due to limitations imposed by cost and logistics, species distribution modelling in the marine environment has previously lagged behind that for terrestrial species. However, the pressing nature of threats imposed on marine biodiversity and the additional uncertainty concerning climate-related responses make species distribution modelling a key tool in marine research and future forecasting. This potential is reflected in an increase in studies developing and applying species distribution models in the marine environment over the last year (Albouy *et al.* 2012; Arcos *et al.* 2012; Ballard *et al.* 2012; Gorman *et al.* 2012; Russell *et al.* 2012) and also in the wider use of the work presented in this thesis. For example, results and data presented here have been used to inform a government report on the 'Economics of Climate Resilience' (DEFRA 2012) and have been incorporated into the Marine Climate Change Impacts Partnership (MCCIP) Annual Report Cards 2012 (MCCIP, 2012) and 2013 (MCCIP, in press). The application of predictive models and assessments seems particularly important for shelf seas and coastal marine ecosystems. Not only are these ecosystems highly dynamic and impacted by atmospheric, oceanic and terrestrial influences (Holt *et al.* 2010), they are also regions of great socio-economic importance, with the majority of the world fish catch being made in coastal seas (Watson and Pauly, 2001). Furthermore, shelf seas are warming substantially quicker than the open ocean. For example, sea surface temperatures in the North Atlantic and UK coastal waters are warming faster than the global average (Mackenzie and Schiedek, 2007) with the fastest warming occurring in the English Channel, North and Baltic seas (IPCC, 2006; Marsh and Kent, 2006).

Studies undertaken in this thesis attempted to further the application of predictive species distribution models, comparing and validating approaches that best suit the study of marine species and investigating the impact of climate change on species' distributions. The linking of species distribution model results with a cost-benefit analysis sought to exploit a variety of methodologies and spatially explicit data. To my knowledge this is the first study to link ecological and economic modelling techniques to investigate the quantitative effects of climate change on the fishing industry in the United Kingdom, through the availability of fishery resources. Furthermore, this thesis has sought to present findings in such a way as to make them useable and applicable to the non-modelling community, to inform policy or management decisions. Although there are assumptions integral to this work and limitations that must be considered, it is hoped that the ideas and modelling approaches discussed in this thesis may be updated and refined as modelling techniques are developed and more, or better, data become available. The following sections summarize the key findings of this work before outlining its limitations and the opportunities for improvement and development. Finally we will discuss the implication of findings in the wider policy context of fisheries management and adaptation to climate change.

1. Key Findings

i) A range of equally valid predictions of species' current distributions may be obtained through applying a multi-model approach.

The model comparison study that begins this thesis (Chapter 2) informed subsequent model applications and interpretation of results. This study found that a suite of varying predictions of species' current distributions could be made that were equally plausible given the available input data and model testing methodologies. Results highlighted the considerable uncertainty in species specific predictions introduced through the species distribution modelling procedure, the data input and the algorithms applied. However, as discussed, difficulties in model testing and its likely bias depending on model characteristics complicate selection of the most accurate or reliable model. Thus although an effort was made to rigorously clean and check environmental tolerance limits and species occurrence data to minimize error in constructing environmental envelopes, the variations between these data sources, as well as the parameterization and weighting of environmental variables masked real uncertainties in the true species' distributions and their responses to climate change. Testing these predictions and species' responses to climate change over time might enable future model testing on a temporal scale. However, while uncertainties exist in the true response of species to climate change, a multi-model approach is vital to avoid substantial inaccuracy if assumptions, selection of input data or model design are mis-informed. This is especially important for the marine environment, where validating model predictions using empirical data may be difficult due to the expense and logistical difficulties of obtaining reliable data, and where species' occurrence data may thus be hampered by issues of data quality. Applying a suite of models to draw conclusions from the range of results reflects ideas proposed to achieve a more robust approach in the terrestrial sphere (Araújo and New 2007) as well as in climate modelling

(Stainforth *et al.* 2005). Although variation resulted from the choice of climatic datasets and downscaling techniques used to make predictions, the species distribution models provided the greatest source of variation, with differences reflecting model characteristics and techniques.

ii) When projecting species' distributions into the future, including variability from alternative climate models and distribution modelling procedures allows inherent uncertainties to be captured and a precautionary approach to assessing the impact of climate change on species' distributions applied.

The second key finding relates to the projection of species distribution models under climate change. Problems of testing species distribution model outputs are enhanced when projecting models under future climatic scenarios, for which no current analogue exists, or similarly for invasive species, whose current observed niche may result from time-limited dispersal. This study thus advocated that, as when modelling current distributions, aspects of the modelling procedures and key uncertainties should be taken into account when drawing conclusions concerning climate change impacts. For example, when modelling commercial and threatened marine species in Chapters 3 and 4, this involved assessing a range of predictions and treating variations in species specific indicators of change as best and worst case scenarios. If predictions are used to inform management decisions, a multi-model procedure allows a precautionary approach to be taken. For invasive species, which may not have had sufficient time to disperse and fully exploit their full potential niche, relative environmental suitability maps provide information on sites of likely invasion both currently and under future climate change.

Chapters 3, 4 and 5 further explored the sensitivity of results to variations in the application of thresholds and alternative downscaling methodologies. Considering the effects of input data and post-model processing on conclusions made is vital to prevent certain assumptions or choice of data leading to incorrect conclusions and misinformed management decisions or recommendations.

iii) Species' potential distributions are predicted to move poleward in response to climate change between 1985 and 2050.

Despite large uncertainties, projections of species' distributions made throughout the thesis support hypotheses for a poleward movement of species' potential ranges under climate change. These shifts occurred at rates comparable to those observed for marine species (Perry *et al.* 2005; Dulvy *et al.* 2008; Simpson *et al.* 2011). Pelagic species are predicted to show a greater distributional shift in to climate change, due to higher rates of dispersal.

iv) Protected Areas are predicted to change in relative environmental suitability under climate change. The direction and extent of change will depend on the species and model combinations used in predictions.

Change in the relative environmental suitability of protected areas for key threatened species was predicted to be less detrimental than might be expected given similar studies for terrestrial species. Although environmental suitability was predicted to change, there was little consensus in the magnitude and direction of change for particular protected areas across model combinations. Undertaking a similar analysis of protected areas designed for particular commercially targeted species highlighted the importance of considering the changing suitability of protected areas in terms of specific species, as well as the position of the protected area within that species' range. Maintaining a range of predictions from equally plausible models is particularly important in presenting a best and worst case scenario of change for species under threat or those of commercial importance. Techniques such as those applied here may thus inform management strategies that enhance the protection afforded currently and in the future, and the resilience of species to both climate change and fishing pressure.

v) The profitability of UK fisheries by 2050 will decrease in responses to declining maximum catch potential for key species in UK waters.

The final key finding of this thesis relates to how predicted changes at a biological or ecological scale might impact the fishing industry. Results presented here show that although relative environmental suitability may be projected to increase for some species using particular model combinations, total maximum catch potential is predicted to decrease. This decrease is primarily driven by a fall in primary productivity in UK waters by 2050. The decline in catch potential subsequently leads to a substantial decrease in the profitability of UK fisheries between 2005 and 2050, with the extent of this decrease depending on changes in particular costs and the ability to re-build fish stocks to more sustainable levels. Exploring key influences on the profitability of UK fisheries reflects the importance of considering a range of possible predictions in predictive modelling expressed previously, not only encompassing uncertainties in modelling procedures but also possible future socio-economic scenarios. As mitigation and adaptation at all levels investigated in this thesis may incur substantial social and economic costs, explicit consideration of uncertainty may in future be used to compare such costs with the likelihood of projections and the degree of risk they pose. The implications and applications of this work to climate change adaptation are discussed below.

2. Limitations and Further Work

Dealing with uncertainty, in model inputs and projections, and how to present uncertainty has thus been a recurring theme throughout this thesis. Studying the impacts of climate change is necessarily restricted by limitations in data and knowledge and, as with any modelling procedure, involves the simplification of processes and reality using assumptions. This thesis attempted to take account of uncertainty in its assessments on the impact of climate change, for example through the ensemble approach applied in Chapter 5. However, although this approach allowed variation due to differences in component models to be captured, certain similarities in the models and input data excluded other sources of variation. There are thus additional uncertainties that challenge our ability to forecast the future and that might be reduced or incorporated as further models are developed and data becomes available.

Most notable are those uncertainties in the physical response of climate models, their resolution and process representation. Surface fluxes, for example, play a significant role in determining the fidelity of oceanic simulations and link the ocean and atmosphere in coupled Atmosphere-Ocean General Circulation Models (AOGCMs). However, as total heat and water fluxes are difficult to observe, they are generally estimated and parameterized using alternative variables such as SST and winds, thereby introducing large uncertainty into observational estimates (Randall *et al.* 2007). Furthermore, climate model error is not evenly distributed globally, with a large spread of model error occurring in the North Atlantic due to high SST gradients and poor simulations of the North Atlantic Current (Randall *et al.* 2007). Many models also have a warm bias at the eastern edges of tropical ocean basins, near the continental boundaries. This is associated with insufficient resolution, leading to problems in the simulation of local wind stress, oceanic upwelling and under-prediction of the low cloud amounts. As well as varying geographically, error also varies with depth (Randall *et al.* 2007). Further to the uncertainties surrounding the physical response of climate models (as discussed in Chapter 6) there are challenges in predicting the biological response of primary productivity to climate. Although this thesis placed a greater focus on variation in predictions resulting from alternative species distribution models (which was found to be greater), using more physical and biological datasets as model inputs might be useful in more accurately assessing the variability surrounding these data, particularly important for shelf seas.

Modelling continental shelf seas such as the North Sea presents particular difficulties in climate modelling as the present generation of climate models doesn't have sufficient resolution to resolve the shelf topography and many of the processes that influence primary production in the shelf sea ecosystem (such as run-off, seasonal stratification, tides, and nutrient recycling) (Ådlandsvik 2008; Holt *et al.* 2009). For example, with the increased resolution and process representation of a regional model, Holt *et al.* (2010) predicted that the effects of climate change effects on the Northwest continental shelf would be very different to those in the open ocean over the next 100 years (Holt *et al.* 2010, UKCP09). However, these predictions still contain unexplored uncertainty and differed from those made using a different regional model by Adlansvik *et al.* (2008). A broader ensemble of regionalized scenarios is needed to enable a more reliable assessment of the effects of future climate change in shelf seas, as well as the uncertainties involved (Ådlandsvik 2008).

The work commenced in this study could therefore be built on as more data become available. Furthermore, due to data availability for marine environmental variables, all projections made here used the medium emission scenarios (SRES A2) (Nakicenovic and Swart 2000). This scenario describes a global mean surface temperature rise of around 1.7–4.4°C during the 21st century, in response to atmospheric carbon dioxide concentrations of about 700 ppm, and depends on fast development and uptake of new, efficient technologies and a global population that reaches 9 billion mid-century before declining. If projections were to be extended beyond 2050, after which the range of greenhouse gas emissions between scenarios widens significantly as a result of different socio-economic scenarios (IPCC 2000), it would be beneficial to include a greater number of climate change scenarios in these studies.

Further to the particular climate signal, the likely impact of climate change resulting from a particular scenario is related both to the degree of mitigation and also to characteristics of the exposed system. Although this thesis discusses adaptive capacity in terms of resilience and possible responses to climate change, it would be beneficial to integrate environmental/bio-physical and socio-economic scenarios in a more systematic way that might be more broadly applied in further studies. For example, the development of Representative Concentration Pathways (RCPs) scenarios of potential greenhouse emissions (van Vuuren *et al.* 2011) has prompted calls for a 'parallel phase' of scenario development whereby integrated assessment modellers and those exploring vulnerability, impacts and adaptation jointly develop a new set of socio-economic futures (Moss *et al.* 2010). Methodologies have thus been proposed that incorporate the capacity of a system to adapt into a framework for climate change scenario analysis (van Vuuren *et al.* 2012). Vulnerability to climate change may be assessed as a function of the interaction between social and biophysical vulnerabilities, thereby enabling comparison across different communities, fishing fleets and countries. Further to key quantitative variables investigated here, such as fuel cost, factors that influence adaptive capacity and vulnerability but that are difficult to quantify may be integrated through the scenario framework. These factors might include social capital, governance, technological capabilities and levels of economic development. Although there are several challenges surrounding this aim, proposed frameworks provide a way to better co-ordinate and compare studies concerning climate change impacts and assessment across academic disciplines and research communities, thereby facilitating the assessment and application of adaptation or mitigation options (van Vuuren *et al.* 2012).

A further addition to this work might involve investigating the indirect impacts of climate change by incorporating known predator-prey interactions. Although an area might become suitable due to changes in climatic conditions, a species' ability to occupy this area will also depend on the provision of sufficient food and the occurrence of predators or competitors. The incorporation of trophic interactions into the speceis distribution modelling procedure therefore represents a valuable addition to forecasts of species' distribution shifts and is currently being developed (Fernandes *et al.* (2013), in press). As mentioned in above with reference to the Pacific oyster, the accuracy of distribution maps could also be enhanced by incorporating habitat types. Although habitat is included in the initial current distribution maps predicted by the DBEM, a greater number of categories are required to be applicable to many speceis in UK waters. This would be particularly beneficial for species which require specific habitats to breed, feed or attach to. However, as a speceis may have different habitat requirements at different points throughout its life, this may also involve modelling different life history stages separately.

Further to the trophic interactions between fish and invertebrate species, climate change is likely to have an impact on the distributions and breeding success of marine mammals, reptiles and sea birds. For example, although modelling studies of these impacts are at an early stage, there is evidence that climate-driven changes in both temperature and food supply are having severe negative impacts on seabirds, with declines in the numbers and diversity of seabirds breeding in the UK expected (Frederiksen 2006). Herring gulls and roseate terns, for example, have shown decreases of greater than 50% since the mid-1990s (Pinnegar *et al.* 2012). Although studying the impacts of climate change on seabirds would benefit from knowledge of the distribution of their prey species, species distribution maps and predictions would need to be carefully combined with abundance and fisheries data in order to model the combined effects of climate-related and fishery-related changes in food supply. For example, both fisheries and warming waters are thought to have caused the decline in sandeel and consequential decline in breeding success of black-legged kittiwakes and common guillemot (Pinnegar *et al.* 2012).

For marine mammals also, climate change may have direct effects, such as temperature induced changes in distribution or the impact of rising sea levels on sea haul out sites (Learmonth *et al.* 2006; Kaschner *et al.* 2011), or indirect, with changes in prey distribution and abundance at lower trophic levels altering species interactions and trophic pathways. It has been speculated that the marine mammal species that may be most affected by reduced availability of environmental space following climate-induced range shifts will be those with relatively narrow environmental requirements (Evans *et al.* 2010). In in North West Europe these include shelf sea species such as harbour porpoise, white-beaked dolphin and minke whale. Furthermore, declining abundance of sandeel may also be responsible for the recent shift in abundance of harbour porpoises from the northern to southern North Sea (MacLeod *et al.* 2007). Techniques applied here to assess the relative environmental suitability of protected areas and the spatial overlap of species' ranges may thus also be useful in assessing management opportunities to enhance the resilience of forage fish species and the sea birds and marine megafauna that depend on them for food.

As mentioned in the Introduction of this thesis, the marine environment and the species that inhabit it are currently under threat from multiple, anthropogenic sources acting at a variety of scales. Fisheries are removing predator and prey species while invasive species are being introduced to novel locations with the potential to unbalance food webs and disrupt species interactions, while habitats are being lost and polluted. Although studies undertaken here consider the possible consequences of climate change, and to a lesser extent fishing, the combined impact of these factors, and potential interactions between them have not been investigated. Pressure from multiple stressors such as climate change, acidification, and overfishing may combine synergistically, exacerbating the potential threat from each. Future studies would thus greatly benefit from integrating assessment of these different threats and, if synergistic interactions are poorly understood, management plans must err on the side of caution in assessing the adaptability and resilience to each specific threat.

It is evident throughout this thesis and further highlighted in the preceeding paragraphs that the DBEM model has the capacity to incorpate a greater number of biological processes and mechanisms than either AquaMaps or Maxent. Inclusion of factors such as species specific dispersal and trophic interactions represent important advances in the development of species distribution models and allow a more comprehensive investigation of direct and indirect impacts of climate change on species' distributions. Thus although studies undertaken here have found that all models perform well according to model testing statistics, the biological justification and ecological reasoning behind the DBEM give it a strength that the purely statistical models do not have. However, the species specific data required by the DBEM may not be available for all species. Methods such as Maxent and AquaMaps therefore continue to have a use and provide a valuable comparison or first step if little data or knowledge concerning a species' life-history parameters and habitat preferences is available. Therefore although I continue to support the application of a multi-model approach I suggest that a development to this work might involve factors such as dispersal, pH and oxygen, incorporated mechanistically into the DBEM, being applied to distribution maps formed from AquaMaps and Maxent and the outputs compared. Furthermore, experiments to relax the constraints imposed on the current distributions maps of both statistical models and the SAUP model could be undertaken. This would allow the potential of species adaptation or acclimatisation and their impact on future distributions to be investigated.

3. Policy relevance and Adaptation to Climate Change

Uncertainties surrounding the biological and social responses to climate change adds additional pressure to a policy framework already facing challenges such as overfishing, overcapacity and discarding. This thesis has attempted to present results in a policy relevant format, outlining the uncertainty involved in predictions and presenting best and worst-case scenarios of change in both the ecological and socio-economic spheres. This reflects the UK governments' approach to climate change adaptation, which works to support people and organisms in preparing for its effects by disseminating information to the public, stakeholders and policy makers. For example, information on climate change is amalgamated and disseminated by projects such as the Marine Climate Change Impacts Partnership (MCCIP, www.mccip.org.uk), UK Status of the Seas Report: Charting Progress 2 (chartingprogress.defra.gov.uk) OSPAR Commission's Quality Status Reports (qsr2010.ospar.org). The UK's Climate Change Act (2008) further aims to enhance adaptive capacity through regular publication (every five years) of risk assessments and adaptation plans (such as the 2012 Climate Change Risk Assessment, www.defra.gov.uk/environment/climate/government/risk-assessment) while also recognising the need for policies to stimulate and co-ordinate adaptation.

Chapter 6 of the thesis emphasises the importance of adaptation at all levels of the socio-ecological system, thereby coinciding with the approach to fisheries management taken in recent UK legislation. The UK Marine and Coastal Access Act (2009) recognises the complex interactions between marine conservation and resource exploitation and wealth creation, interactions that will likely become more volatile with climate change. For example, although the effect of climate change on the relative environmental suitability of protected areas for particular species was here found to be relatively low, all species were predicted to show northward shifts in distribution, according to environmental suitability. Depending on a species' ability to occupy predicted potential niches, community structure and food web dynamics may change, negatively impacting a species. Predictions do, however, highlight factors and changes that must be considered at the biological/ecological scale for successful adaptation and resilience for both fish and fisheries. The EU Marine Strategy Framework Directive (2008) as well as 'Fisheries 2027, a long-term vision for sustainable fisheries' (DEFRA 2007) explicitly integrate the goal of healthy fisheries into the wider ecosystem and socio-economic context, using both an adaptive and precautionary approach and the application of the ecosystem based approach to fisheries (EAF) management. The EAF requires fisheries managers to take a wide range of fisheries impacts into account before defining objectives. It intends to ensure that the planning, development and management of fisheries will meet social and economic needs without jeopardizing the options for future generations to benefit from the full range of goods and services provided by marine ecosystems (FAO 2003). To achieve this goal, the EAF seeks to develop pressure-state-response models that support the decision-making process through indicators. The value of indicators in relation to a reference or target value may thus guide decisions and management actions. Most specific issues in EAF relate to the impact of fisheries on the environment and the effect of the environment on fisheries (Garcia and Cochrane 2005) and understanding of the relationships and links between these two is therefore key.

Although the overarching principles of the EAF stipulate that aquatic ecosystems' ability to support essential services and livelihood must be maintained despite variability, uncertainty and natural changes in the ecosystem (FAO 2013), explicit consideration of adaptation to climate change and it's interaction with environmental resilience is not specifically addressed in this legislation. However, if the relationship between the environment and fisheries subject to climate change is not adequately understood, indicators such as those for individual species may either not be achieved or may provide a misleading assessment of a population's status. Alternatively, management actions such as spatially explicit policies and protected areas may not have the desired effect, or their impact might be masked by those of climate change and environmental variability. Studies undertaken here highlight ways in which climate change may impact marine biodiversity and thereby fisheries which depend on it. Taking into account these impacts is vital if EAF indicators are to be appropriate and effective and the goal to 'meet social and economic needs without jeopardizing the options for future generations' is to be upheld. Although all key international agreements adopted over the last two decades have stressed the need for the adoption of the EAF, its implementation has lagged behind uptake on its concepts and values (FAO 2013). In addition to required changes in governance systems and processes required for its implementation (Cury *et al.* 2005; Jennings 2005), bringing adaptive capacity more to the fore of the EAF and emphasising the interconnected responses of ecological and socio-economic systems to climate change may help overcome these barriers.

4. Adaptive Capacity

The adaptive capacity of the UK fishing industry has been broadly assessed to be high (DEFRA, 2012), and the cost of adaptation impacts of climate change, such as those investigated in Chapter 6, relatively low. For example, the annual cost of adaptation in Europe has been estimated at between 0.03 and 0.15 $ billion, compared to 1.05 to 1.70$ billion for East Asia and the Pacific (Sumaila and Cheung 2009). The fishing industry has developed and evolved to operate within a tight policy framework while maximising profits and realising the value available from temporary and changing fish stocks in unpredictable weather and economic conditions. Fishers respond to changes in abundance or distribution of fish stocks by altering their fishing locations, the duration of trips or by targeting alternative or a range of species. However, there will be large differences in the scope of vessels and crews across sectors and regions to adapt to or even benefit from the effects of climate change (Daw *et al.* 2009). If low adaptive capacity coincides with regions for which the fishing sector forms a significant part of local economies, the impact of climate change at the local level may be far greater than that projected for the UK as a whole. Low adaptive capacity may result from low initial profitability and capital as well as poor resilience to adverse weather conditions. Furthermore, an adaptive response may be prevented by barriers at a policy and institutional level, with quotas, licenses and effort restrictions limiting the short-term flexibility of fishers (DEFRA, 2012). The potential adaptive responses of fishers to climate change, and the surrounding policy context, are discussed in the following paragraphs.

If a key commercial species declines in abundance in an area due to decreasing environmental suitability, fishers may seek to switch target species. However, quota restrictions may prevent particular species being targeted or restrict effort to below economically viable levels. Although quotas within the UK are transferable, trading is not transparent, is limited for owners of small vessels and may incur substantial transaction costs (Inglis and MacLennan 2010). This barrier might have a positive effect in encouraging diversification and flexibility by targeting a range of species, including those that have moved northwards into UK waters and aren't subject to quota. However, challenges may still be faced though limitations on gear or time spent at sea. The proposed introduction of discard restrictions in the Common Fisheries Policy reform may also restrict mixed vessels, which must avoid the accidental 'bycatch' of quota species (DEFRA, 2012). Although quotas are important in ensuring long term sustainability and promoting resilience of the fish stocks to environmental change, the lengthy, backward-looking process of quota allocation may not reflect the exploitable surplus stock following climate induced distribution shifts (DEFRA, 2012). In the case of mismatch between fish abundance and quota, fishers may instead opt to 'follow the fish', tracking species' distributional shifts and altering the spatial allocation of fishing effort (Inglis and MacLennan 2010). However, altering fishing location may also be restricted by jurisdictional boundaries or forms of Marine Protected Areas.

The flexibility of fishers to switch target species may also be limited by lack of consumer demand and market failures for particular species. UK consumer demand for fish is dominated by cod, haddock, salmon, prawns and tuna and primarily met by imports, with the UK exporting 85% of fish landed by UK vessels (MMO 2010). This mismatch in production and demand in the UK restricts the adaptive response of changing target species and the ability of UK local economies to benefit from a value chain based within the UK. For example, poor communication between the supply of new, emerging species and demand may make marketing new species difficult. In particular, the ability of smaller vessels at remote ports to access larger, international markets may be challenging. Although there is evidence that preferences are diversifying to include a wider range of species, this is mostly restricted to niche markets and needs to be further developed to maximise profits obtainable from new species (DEFRA, 2012).

It is important to note that short term adaptability does not always imply increased adaptive capacity to climate change (DEFRA, 2012). Short term decisions to adapt, coupled with the reduced profits that forced the adaptation decision may reduce long term investments in vessels and gear. They may also result in neglect in adaptation at other points of the supply/demand chain that might promote profitability and persistence in the future. For example, the decision to follow the fish may increase a fisher's dependency on fuel, lowering profits if fuel prices increase, for example according to the extrapolated trends described here. Lowered profits may subsequently further reduce capacity to introduce more fuel efficient methods, enforcing maladaptation. This may be re-enforced by fossil fuel subsidies which disproportionally benefit more fuel-intensive, environmentally damaging fishing practices (Inglis and MacLennan 2010). It thus seems vital to consider adaptive capacity within the framework of the EAF to ensure that a push to maintain current profits and socio-economic resilience to environmental change does not come at the expense of ecological resilience and long term sustainability. This is made more challenging by the uncertainties surrounding future environmental and socio-economic change mentioned above, creating confusion over which adaptive strategy to take. Assessing the degree of certainty of change and the costs of adaptation to that change may thus be required for effective decision making. Within the EAF framework, adaptive management to climate change may be continually monitored using indicators at the pressure, state and response levels, thereby promoting fast decision responses to changing and uncertain conditions and allowing a suite of possible responses to be maintained. However, the inherent mistrust of uncertainty and scepticism towards uncertain forecasts also needs to be overcome to promote adaptive capacity. A range of options from different climatic and socio-economic scenarios must be viewed as a suite of possible scenarios, consideration of which will minimises the surprises and risks climate change may impose on the marine ecosystem and the people who depend on it.

References

Ådlandsvik, B. (2008) Marine downscaling of a future climate scenario for the North Sea. *Tellus* **60A**, 451–458.

Albouy, C., Guilhaumon, F., Araújo, M.B., Mouillot, D. and Leprieur, F. (2012) Combining projected changes in species richness and composition reveals climate change impacts on coastal Mediterranean fish assemblages. *Global Change Biology* **18**, 2995-3003.

Araújo, M.B. and New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution* **22**, 42–7.

Arcos, J.M., Bécares, J., Villero, D., Brotons, L., Rodríguez, B. and Ruiz, A. (2012) Assessing the location and stability of foraging hotspots for pelagic seabirds: An approach to identify marine Important Bird Areas (IBAs) in Spain. *Biological Conservation* **156**, 30-42.

Ballard, G., Jongsomjit, D., Veloz, S.D. and Ainley, D.G. (2012) Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. *Biological Conservation* **156**, 72-82.

Cury, P., Mullon, C., Garcia, S. and Shannon, L. (2005) Viability theory for an ecosystem approach to fisheries. *ICES Journal of Marine Science* **62**, 577–584.

DEFRA (2007) Fisheries 2027, a long-term vision for sustainable fisheries. Available at: http://archive.defra.gov.uk/foodfarm/fisheries/documents/fisheries2027vision.pdf [Accessed January 24, 2013].

Daw, T., Adger, W.N., Brown, K. and Bedjeck, M.-C. (2009) Climate change and capture fisheries : potential impacts, adaptation and mitigation. In: *Climate change implications for fisheries and aquaculture: overview of current scientific knowledge.* (eds D. Soto and T. Bahri). FAO Fisheries and Aquaculture Technical Paper. No. 530, FAO, Rome, pp 107–150.

DEFRA (2012) Economics of Climate Resilience: Natural Environment – Fisheries. September 2012. Frontier Economics Ltd for Department for Environment, Food & Rural Affairs (Defra), UK. 108pp.

Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmller, V., Dye, S.R. and Skjoldal, H.R. (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology* **45**, 1029–1039.

Evans, P.G.H., Boyd, I.L. and MacLeod, C.D. (2010) Impacts of climate change on marine mammals in: MCCIP Annual Report Card 2010-11, MCCIP Science Review, 14pp. Available at: www.mccip.org.uk/arc

FAO (2003) The ecosystem approach to fisheries. *FAO Technical Guidelines for Responsible Fisheries* **4**, 122 pp.

FAO (2013) The ecosystem approach to fisheries management. Available at: http://www.fao.org/fishery/topic/13261/en [Accessed January 5, 2013]

Fernandes, J.A., Cheung, W.W.L., Jennings, S., Butenschön, M., de Mora, L., Frölicher, T.L., Barange, M. and Grant, A. (2013) Modelling the effects of climate change on the distribution and production of marine fishes: accounting for trophic interactions in a dynamic Bioclimate envelope model. *Global Change Biology,* in press.

Fischbach, A.S., Monson, D.H. and Jay, C.V. (2009) Enumeration of Pacific walrus carcasses on beaches of the Chukchi Sea in Alaska following a mortality event, September 2009. Open File Rep. 2009-1291. 10 pp. Reston, VA.

Frederiksen, M. (2006) Impacts of Climate Change on Seabirds, in: Marine Climate Change Impacts Annual Report Card 2006 (Eds. Buckley, P.J., Dye, S.R. and Baxter, J.M.) Online Summary Reports. Lowestoft. Available at:

www.mccip.org.uk/media/2481/seabirds-report-from-ceh.pdf [Accessed January 5, 2013]

Garcia, S. and Cochrane, K. (2005) Ecosystem approach to fisheries: a review of implementation guidelines. *ICES Journal of Marine Science* **62**, 311–318.

Gorman, D., Bajjouk, T., Populus, J., Vasquez, M. and Ehrhold, A. (2012) Modeling kelp forest distribution and biomass along temperate rocky coastlines. *Marine Biology* **160**, 309-325.

Grebmeier, J.M., Moore, S.E., Overland, J.E., Frey, K.E. and Gradinger, R. (2010) Biological Response to Recent Pacific Arctic Sea Ice Retreats. *Eos, Transactions American Geophysical Union* **91**, 161–162.

Holt, J., Harle, J., Proctor, R., Michel, S., Ashworth, M., Batstone, C., Allen, I., *et al.* (2009) Modelling the global coastal ocean. *Philosophical transactions. Series A, Mathematical, physical, and engineering sciences* **367**, 939–51.

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

IPCC (2000) *Emission Scenarios, Summary for Policymakers*. Cambridge University Press, Cambridge.

IPCC (2006) *ICES Report on Ocean Climate 2005.* International Council for the Exploration of the Seas, Copenhagen, Denmark.

Inglis, K. and MacLennan, S. (2010) Fisheries governance in the UK: challenges and opportunities in a changing climate. In: *The Economics of Adapting Fisheries to Climate Change Economics*. OECD Publishing, 349–366.

Jennings, S. (2005) Indicators to support an ecosystem approach to fisheries. *Fish and Fisheries* **6**, 212–232.

Kaschner, K., Tittensor, D.P., Ready, J., Gerrodette, T. and Worm, B. (2011) Current and future patterns of global marine mammal biodiversity. *PLoS ONE* **6**, e19653.

Learmonth, J.A., Macleod, C.D., Santos, M.B., Pierce, G.J. and Robinson, R.A. (2006) Potential effects of climate change on marine mammals. *Oceanography and Marine Biology: An Annual Review* **44**, 431–464.

MacKenzie, B.R. and Schiedek, D. (2007) Daily ocean monitoring since the 1860s shows record warming of northern European seas. *Global Change Biology* **13**, 1335-1347.

MacLeod, C. D., Pierce, G.J. and Santos, M.B. (2007) Starvation and sandeel consumption in harbour porpoises in the Scottish North Sea. *Biology Letters* **3**, 535-537.

Marsh, R. & Kent, E. (2006) Impacts of climate change on sea temperature. Marine Climate Change Impacts Annual Report Card 2006: Online Summary Reports (eds P.J. Buckley, S.R. Dye & J.M. Baxter). Marine Climate Change Impacts Partnership, Lowestoft, UK. Available at: www.mccip.org.uk

MCCIP (2012) Marine Climate Change Impacts on Fish, Fisheries and Aquaculture. (eds. M. Frost, J.M. Baxter, P.J. Buckley, M. Cox, S.R. Dye and H.N. Withers) Summary Report, MCCIP, Lowestoft, 12pp. Available at: www.mccip.org.uk/media/8789/37453%20mccip%20final%20lorez.pdf

Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., van Vuuren, D.P., Carter, T.R. *et al.* (2010) The next generation of scenarios for climate change research and assessment. *Nature* **463**, 747–56.

Nakicenovic, N. and Swart, R. (2000) *Special Report on Emissions Scenarios. A Special Report of Working Group III of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK and New York, USA.

Perry, A.L., Low, P.J., Ellis, J.R. and Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–5.

Pinnegar, J., Watt, T. and Kennedy, K. (2012) Climate Change Risk Assessment for the Marine and Fisheries Sector. In: *UK Climate Change Risk Assessment*. Defra Project Code GA0204, p 222pp.

Randall, D.A., Wood, R.A., Bony, S., Colman, R., Fichefet, T., Fyfe, J., Kattsov, V., *et al*. (2007) Climate models and their evaluation. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* (eds D.Q.S. Solomon, M. Manning, Z.

Russell, B.D., Connell, S.D., Mellin, C., Brook, B.W., Burnell, O.W. and Fordham, D. a (2012) Predicting the Distribution of Commercially Important Invertebrate Stocks under Future Climate. *PLoS ONE* **7**, e46554.

Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller). Cambridge University Press, Cambridge, UK and New York, USA, pp 385–432.

Simpson, S.D., Jennings, S., Johnson, M.P., Blanchard, J.L., Schön, P.-J., Sims, D.W. and Genner, M.J. (2011) Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Current Biology* **21**, 1565–1570.

Stainforth, D.A, Aina, T., Christensen, C., Collins, M., Faull, N., Frame, D.J., Kettleborough, J.A. *et al*. (2005) Uncertainty in predictions of the climate response to rising levels of greenhouse gases. *Nature* **433**, 403–6.

Sumaila, R. and Cheung, W.W.L. (2009) The Costs to Developing Countries of Adapting to Climate Change; New Methods and Estimates. Global Report of the Economics of Adaptation to Climate Change Study (Consultation Draft). 102pp pp.

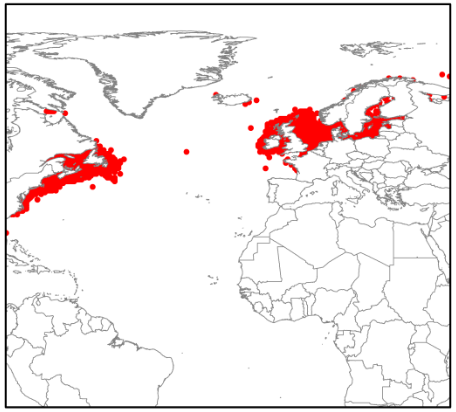
van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., *et al*. (2011) Representative concentration pathways: an overview. *Climate Change* **109**, 5–31.

van Vuuren, D.P., Riahi, K., Moss, R., Edmonds, J., Thomson, A., Nakicenovic, N., Kram, T., *et al*. (2012) A proposal for a new scenario framework to support research and assessment in different climate research communities. *Global Environmental Change* **22**, 21–35.

Watson, R. and Pauly, D. (2005) Systematic distortions in world fisheries catch trends. *Nature* **414**, 534-536.

Appendix

Occurrence records for each species investigated in this thesis, compiled from the three global online databases: the International Council for Exploration of the Sea (ICES) EcoSystemData database (http://ecosystemdata.ices.dk); the Ocean Biogeographic Information System (OBIS) (Vanden Berghe, 2007; http://www.iobis.org) and the Global Biodiversity Information Facility (GBIF) (http://data.gbif.org).



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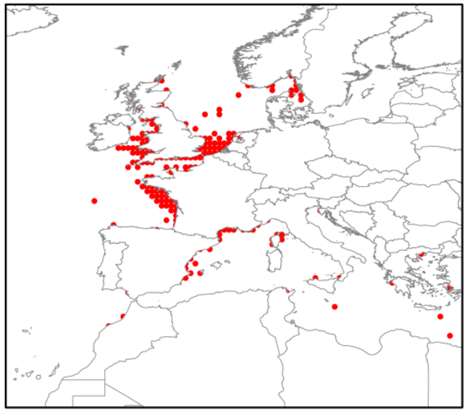

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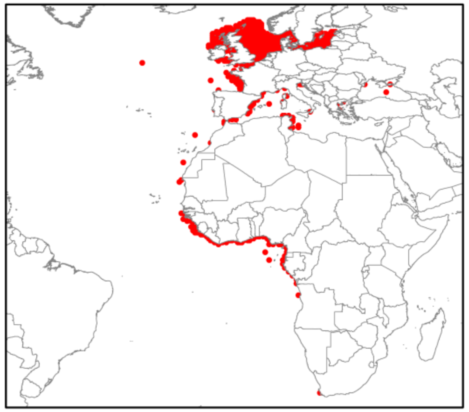

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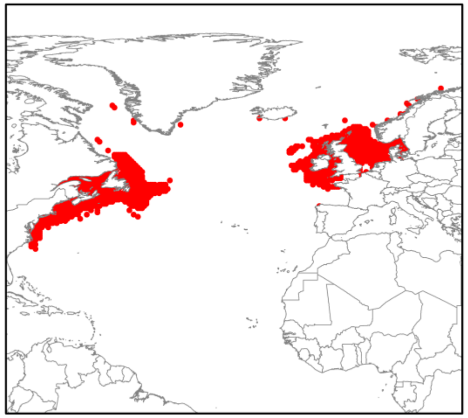

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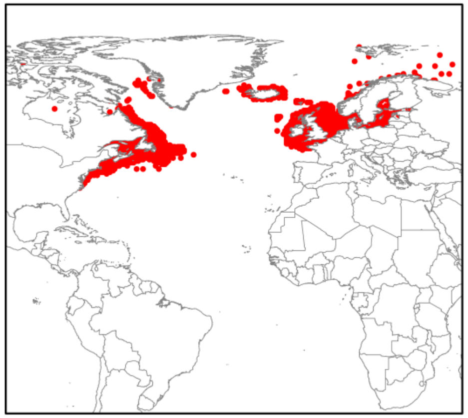

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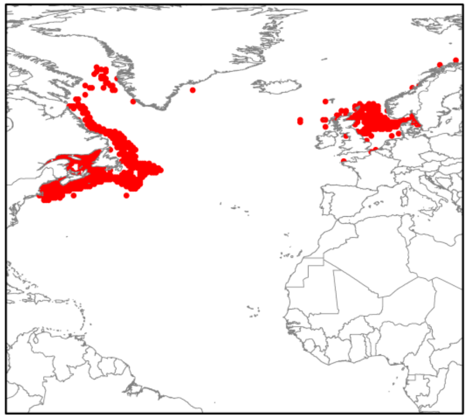

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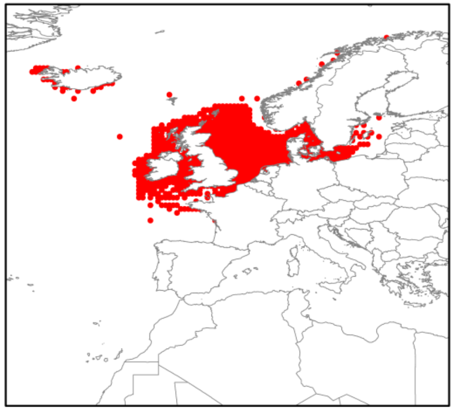

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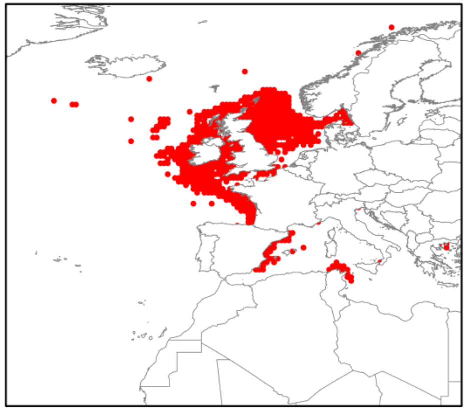

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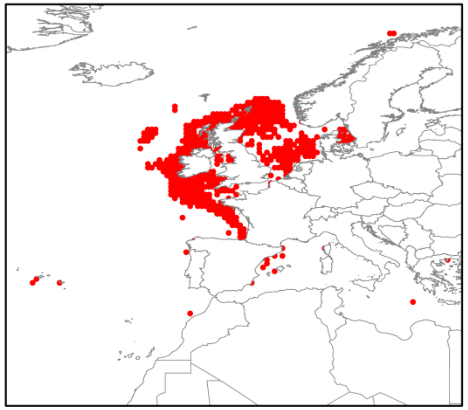

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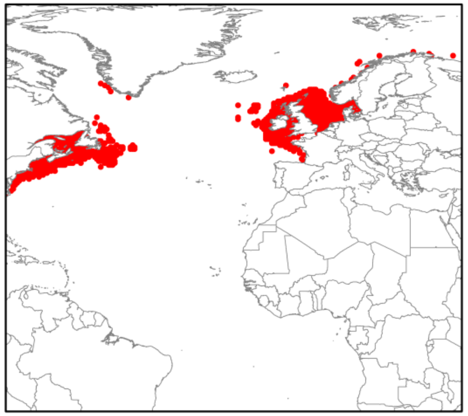

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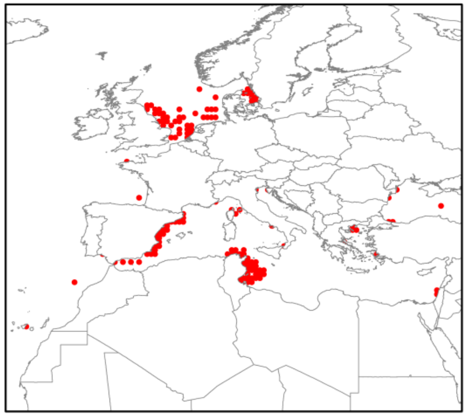

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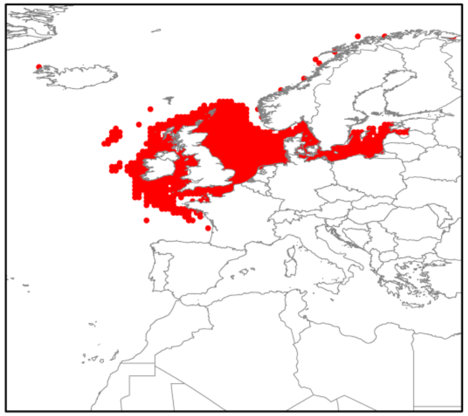

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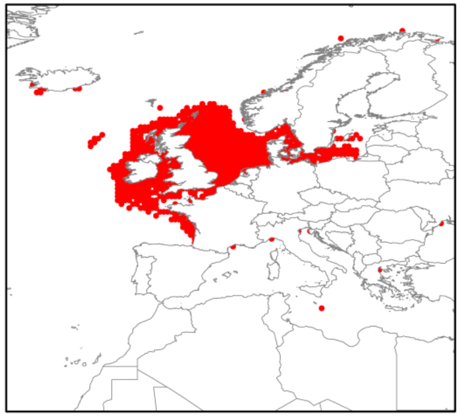

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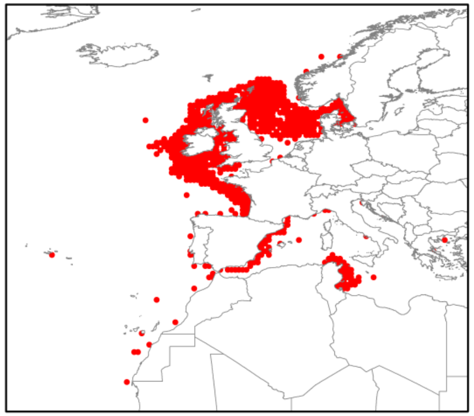

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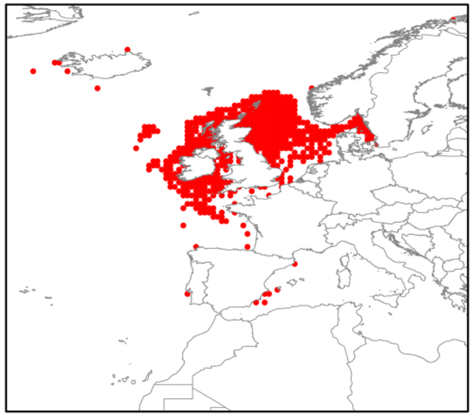

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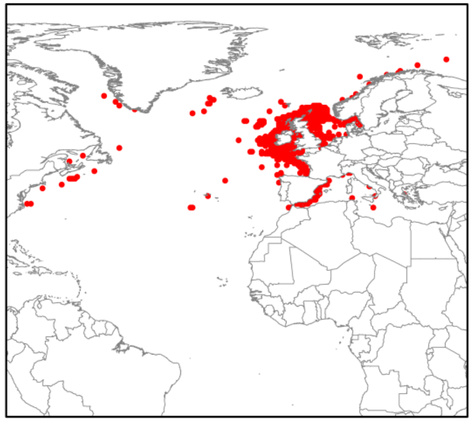

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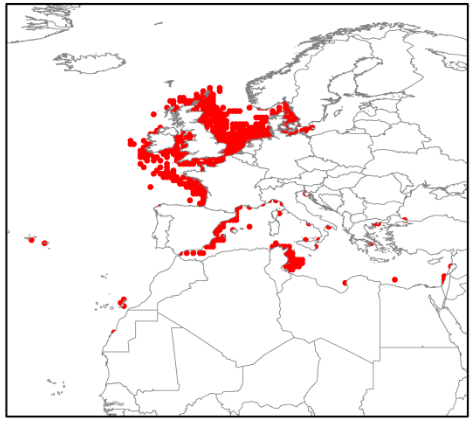

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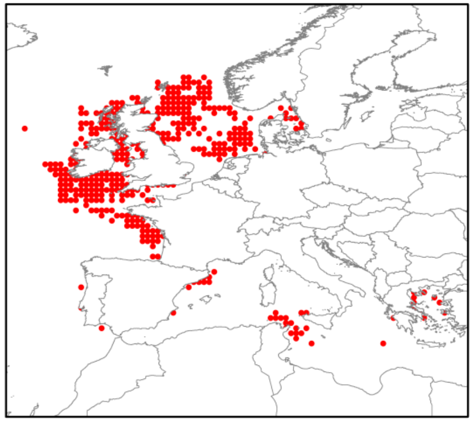

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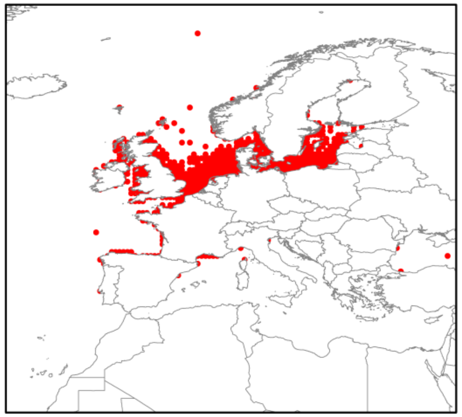

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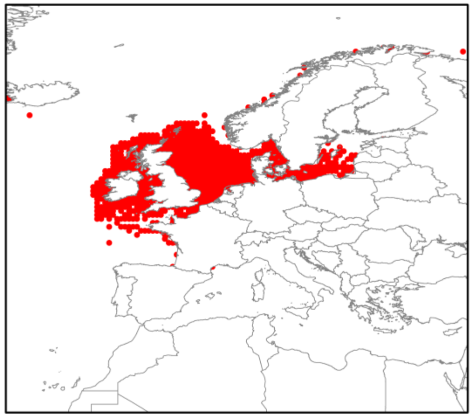

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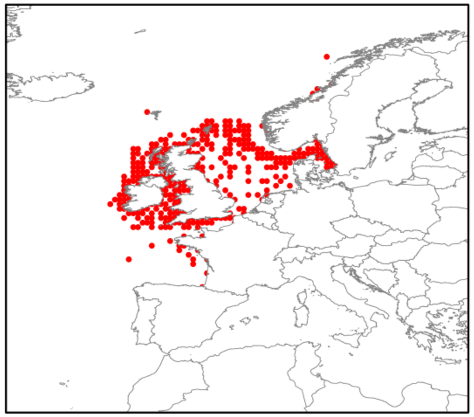

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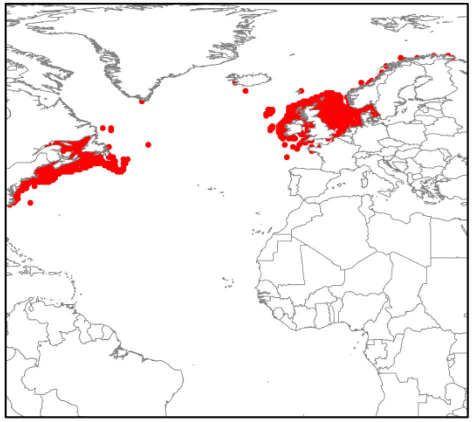

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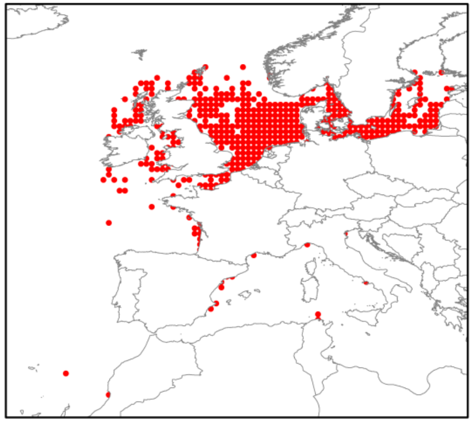

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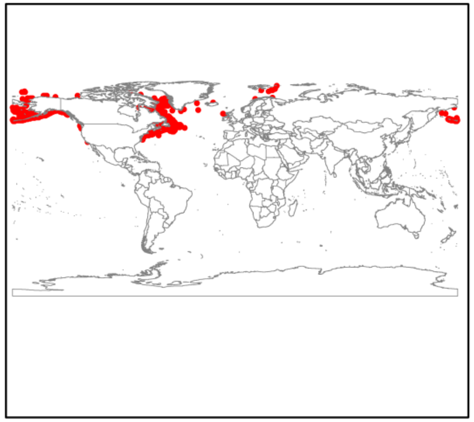

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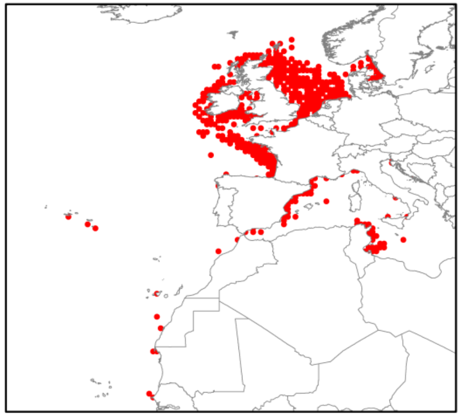

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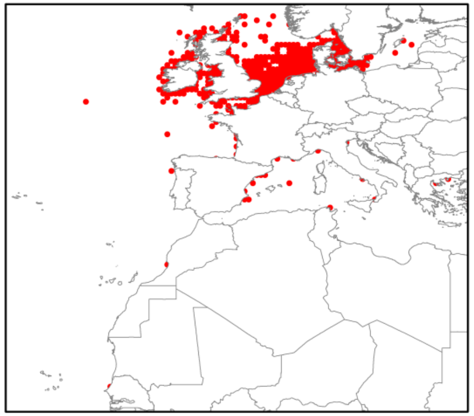

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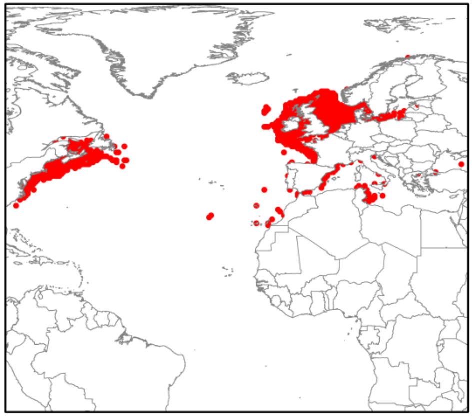

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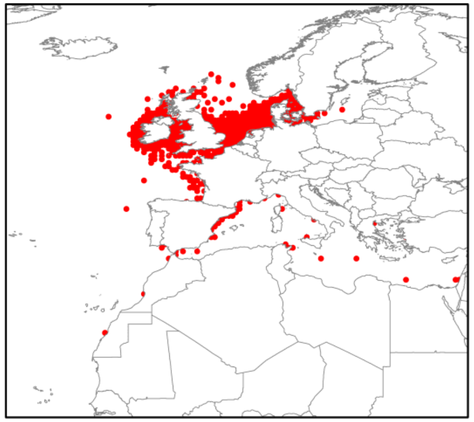

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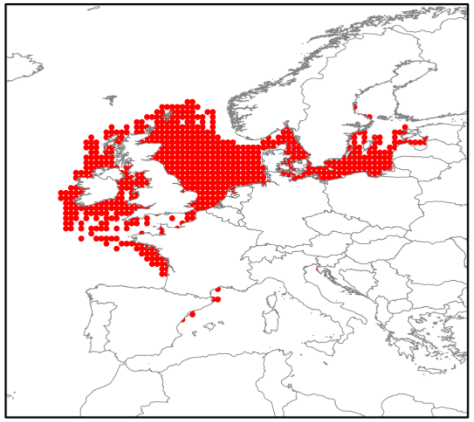

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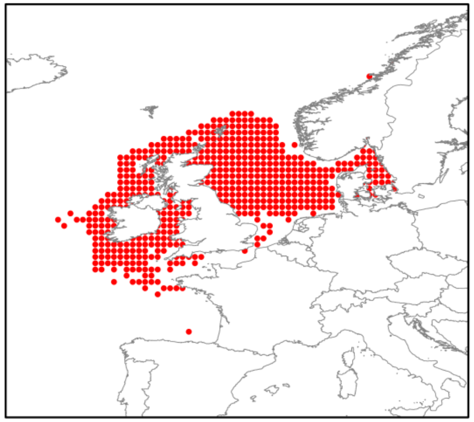

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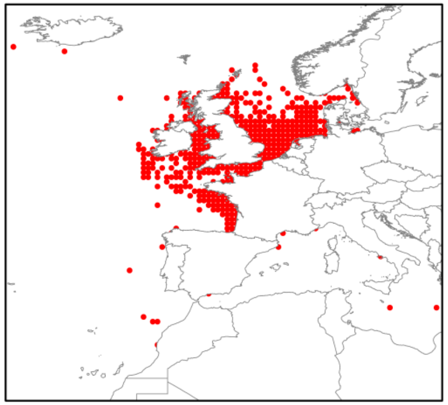

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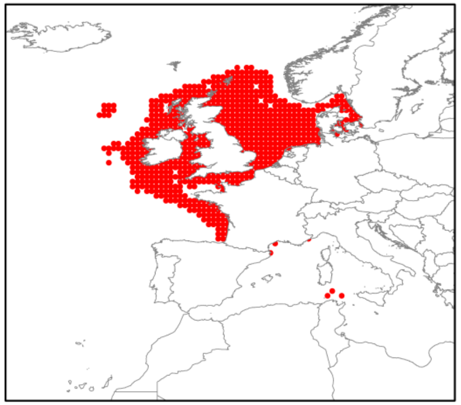

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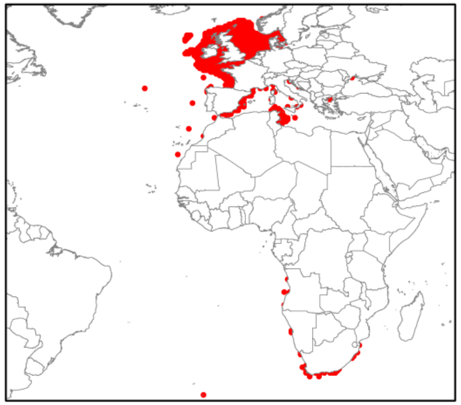

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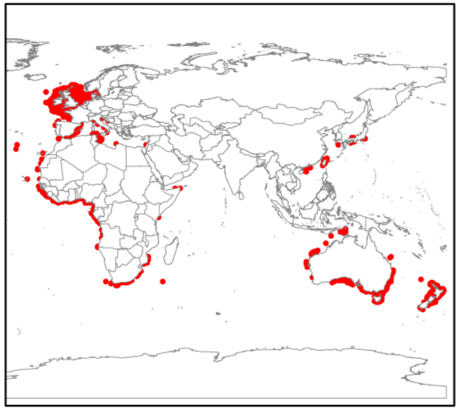

Zeus faber