Understanding shifts in body size distributions – a comparative study of the impacts of fishing and climate on North Sea demersal fishes

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Abstract

The North Sea is a huge economic resource for millions of people and is undergoing dramatic changes due to overfishing and climate change. The extent to which fishing and climate are causing changes in the North Sea demersal fish community status and ecosystem health is difficult to quantify. This thesis implements newly combined empirical methods and adaptive modelling techniques in an attempt address this area of uncertainty. The first study develops a statistical framework for understanding variations in size-based indicators (SBIs), metrics for describing ecosystem health, across space and time simultaneously, as well as finding the most likely driver of observed changes. SBIs declined in the central North Sea due to fishing, but increased in the Norwegian trench region due to changing sea bottom temperature. This highlights the need to consider environmental and fishing impacts on the change in body size distribution of fish communities. The remainder of the thesis improves an existing multispecies, size-structured model by incorporating empirical relationships between growth and temperature and oxygen. Including temperature or temperature and oxygen leads to a smaller body size distribution under warmer, deoxygenated waters. When oxygen alone is included no significant effects on either the individual size or the community size structure are found. The temperature-oxygen size-structured model is subsequently used alongside extracted environmental data from global climate models (GCMs) to project a number of size-based indicators for 2100. The most striking result is the inconsistency of the GCM output, which results in huge differentials in size-based indicators depending on which GCM is used. Corrections to the GCMs must therefore be made before the use in ecological projections. The common result, however, is that temperature and oxygen will cause changes in the body size distribution. Although these effects are much smaller than fishing effects, they demonstrate that ignoring impacts of climate change could cause considerable overestimates in the biomass of North Sea demersal fish.

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> ...though he may stumble, he will not fall for the LORD upholds him with his hand
>
> Psalm 37:24

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Chapter 1

Introduction

The interactions and physiological parameters within an ecosystem are complex. Add to that a changing climate and other anthropogenic attributes forcing ecosystems to change, such as harvesting, understanding the already complex becomes significantly more difficult. The rate of climate change [Stocker *et al.*, 2013] and harvesting [Allendorf & Hard, 2009; FAO, 2014] are fast outpacing our knowledge of the baseline ‘pristine’ condition of many ecosystems [Pauly, 1995]. Therefore there is an urgent need to improve our understanding of ecosystems, especially due to the heavy reliance of humans on the services provided by these systems [Worm *et al.*, 2006; Daily & Matson, 2008; Mace *et al.*, 2012]. Obtaining the empirical data necessary to accurately represent ecosystems is a process requiring huge financial resources and time. Therefore one way to improve our current understanding of changes in ecological systems is through the use of mathematical, mechanistic models based upon existing data (*in situ* or experimental). In particular, by modelling fundamental processes emergent patterns occur, which can be tested against empirical observations [Follows *et al.*, 2007; Hartvig *et al.*, 2011; Bone & Altaweel, 2014; Stewart *et al.*, 2014]. This is not a substitute for continued data collection, but the use of current data and mathematical models can aid in making useful projections to help improve our knowledge of potential change and mitigate against ecosystem degradation under a changing environment [Delworth & Knutson, 2000]. This thesis uses both empirical data to understand large scale changes in the North Sea demersal marine ecosystem and biological theory to modify a mechanistic model in order to intertwine the environmental and harvesting impacts on a size-structured fisheries community. Throughout, body size is used as a unifying variable linking the physiological individual level to the higher ecosystem level. This introduction firstly discusses the importance and suitability of body size in ecosystem research. Secondly a variety of factors that are known to influence body size and the resulting community body size distribution are considered. Finally I conclude with the aims of this thesis that build upon body size distributions in the North Sea and modelling environmentally dependent physiological relationships.

1.1 Body size and the size spectrum

Midway through the 1980s Earl Werner and James Gilliam proclaimed in a review paper that "*Body size is manifestly one of the most important attributes of an organism from an ecological and evolutionary point of view*" [Werner & Gilliam, 1984]. This is supported by the century-long use of body size as a descriptor of organism traits where an easily measured single value holds a wealth of information regarding an ecosystem [Peters, 1983; Woodward *et al.*, 2005]. For example, body size is correlated with fecundity, birth weight, maturation time, metabolism, mortality, and life span at the individual level [Kleiber, 1932; Blueweiss *et al.*, 1978; Brown *et al.*, 2004; Savage *et al.*, 2004], growth rate [Blueweiss *et al.*, 1978; Savage *et al.*, 2004] and abundance [Sheldon *et al.*, 1972; White *et al.*, 2007; Xu, 2015] at the population level, and thus body size consequently manifests itself at the community level too [Peters, 1983; Brown *et al.*, 2004; Woodward *et al.*, 2005]. It is unsurprising, therefore, that body size is a key metric in describing the state and health of size-structured ecosystems [Shin *et al.*, 2005; European Parliament, 2008; Greenstreet *et al.*, 2011], as well as being a fundamental building block in a suite of models known as size-structured or size-based models [Andersen *et al.*, 2016; Blanchard *et al.*, 2017].

As mathematical models are often required to make simplifications (e.g. due to poor empirical data or to reduce computational time), the use of body size allows highly complex ecosystems to be described more easily through allometric scaling, that is scaling according to body size. The physiological individual or population metrics (E) listed above can often be described using mass (M) in the form:

$$E = aM^b$$

where a is a constant and b is the scaling exponent (if $b = 1$ this is known as isometric scaling). The value of the scaling exponent, b, depends on the trait being described and is derived from empirical data. Some have suggested universal rules exist across all species, such as the metabolic theory of ecology [Brown *et al.*, 2004], whereby the scaling exponent, b, is not species dependent. However, other scaling exponent values have been shown to be taxon–, if not species–, dependent (see Blueweiss *et al.* [1978] and Englund *et al.* [2011]). The use of species specific scaling factors, or factors that are averaged when assuming universal theories, are dependent upon the literature and data available. Ultimately, this allometric scaling allows complex ecological systems with different interactions and physiological attributes to be simplified under a size-structured modelling framework [Andersen & Beyer, 2006; Andersen *et al.*, 2016] (full details and derivations of a typical size-structured model are provided in Chapter 2).

The formation of a size-structured model uses body size relationships at the individual level. The models using these allometric equations have successfully predicted the emergence of the community level size spectrum [Hartvig *et al.*, 2011; Blanchard *et al.*, 2014; Andersen *et al.*, 2016]. The size spectrum describes the distribution of species (abundance or biomass) as a function of body size, such that few, large individuals co-exist with numerous, smaller individuals [Sheldon *et al.*, 1972]. Empirically the size spectrum slope is typically calculated by binning individuals into weight classes, regardless of species, and fitting a linear regression between size and abundance (on a log scale [Sprules & Barth, 2016], or a pareto fit [Vidondo *et al.*, 1997]). In an unexploited system the abundance–size slope is expected to be approximately -1, and the biomass–size slope approximately zero. In a remarkably consistent manner, these typical size spectrum slopes have been recorded for phytoplankton, fisheries, aquatic mammals, and even on land [Sheldon *et al.*, 1972; Rice & Gislason, 1996; White *et al.*, 2007; Pershing *et al.*, 2010; Barnes *et al.*, 2011; Roy *et al.*, 2013; Sprules & Barth, 2016].

Frequent observations in nature and theoretical expectations from models show that the size spectrum slope can be used as a descriptor of fishing impacts on ecosystem structure and function [Petchey & Belgrano, 2010]. The size spectrum slope is part of a descriptive class known as size-based indicators (SBIs) [Shin *et al.*, 2005; Greenstreet & Rogers, 2006]. Some SBIs, such as the Large Fish Indicator, have been accepted for use in policy-based decisions under the Marine Strategy Framework Directive [Greenstreet & Rogers, 2006; European Parliament, 2008], whereas other SBIs are used for research purposes. By calculating SBIs empirically, and parameterising size-structured models to specific ecosystems, models can be calibrated to replicate certain systems and calculate modelled SBIs [Blanchard *et al.*, 2014]. This allows predictions of future SBIs using mechanistic models to be based on empirical evidence. By using size-based relationships, there are two particular benefits in fisheries research. Firstly, allometric relationships can be used to simplify highly complex ecosystems for modelling purposes. Secondly, they can be used to calculate SBIs to aid our understanding of ecosystem resistance and adaptations under past and future environmental pressures. A wonderful overview of the history and theory of the size spectrum can be found by Sprules and Barth [2016] .

1.2 Changes in body size distribution

From the individual level perspective body size is controlled by the acquisition of energy from a food source. The way in which the energy is gained (e.g. the search for food, metabolism, digestion), and variability in the food source can both cause variations in how much energy, thus eventual mass, an individual gains (or, perhaps, loses). At the population and community level, the direct removal of size-specific fish through fishing or changes in habitat suitability affects body size distributions. While commercial fishing is a large factor in changes to ecosystems [Jackson *et al.*, 2001; Jennings & Blanchard, 2004; Genner *et al.*, 2010; Engelhard *et al.*, 2015], JH Steele claimed that the physical environment was not "*merely...a source of noise*" for changes in population and community dynamics [Steele, 1991]. With increasing knowledge on changes in the physical climate, particularly highlighted through the IPCC reports [Houghton *et al.*, 1991, 1995, 2001; Solomon *et al.*, 2007; Stocker *et al.*, 2013], the impacts of climate change on fisheries is an important research topic. There is great difficulty in separating the causes of change in community size structure, though attempts have been made at the population [Baudron *et al.*, 2014] and community [Rice & Gislason, 1996; Jennings & Blanchard, 2004; Marshall *et al.*, 2016] level in the North Sea. Contributing factors to changes in size through *in situ* and experimental works include temperature, oxygen, carbon dioxide, food, and fishing.

1.2.1 Temperature

The role of temperature in the distribution of species is founded in Bergmann's rule [Bergmann, 1947]: body size decreases with an increase in temperature. More specific rules derive from this such as warmer temperatures resulting in smaller hearts [Hesse *et al.*, 1937], larger relative appendages [Allen, 1877], and a smaller average body size within a given species (i.e. intraspecific version of Bergmann's rule) [James, 1970]. Many of these rules were originally applied to endotherms, and still the evidence is mixed for ectothermic marine species [Mousseau, 1997; Fisher *et al.*, 2010; Trip *et al.*, 2014]. The causes of these macroecological patterns are not well understood. It was originally postulated to be due to energy, such that larger species are found in colder environments due to a reduced heat loss from the smaller surface area:volume they have [Bergmann, 1947].

The body size distribution patterns seen across the world are underpinned by, as it stands, an unknown mechanism relating to temperature. Laboratory experiments on temperature effects on individual fish corroborate these macroecological patterns whereby increased temperatures cause a reduction in body size. Unusually, this coincides with a faster growth rate - something termed as the temperature size rule (TSR)[Atkinson, 1994, 1995]. Under temperature, this fast growth rate leading to a smaller adult size-at-age opposes other growth regimes [Angilletta *et al.*, 2004]. For example increased food availability increases the growth rate with the individual being larger than average. These opposing results have been regarded as a conundrum in the experimental world [Angilletta *et al.*, 2004]. A variety of theories have been put forward in an effort to explain the TSR: the occurrence of smaller cells (same quantity) due to higher activation energy of cell division relative to cell growth reducing overall body size [van der Have & de Jong, 1996; Atkinson *et al.*, 2006]; enhancement of catabolism over anabolism [von Bertalanffy, 1960; Berrigan & Charnov, 1994; Perrin, 1995]; reduced oxygen supply through a temperature increase thus limiting growth [Pörtner & Farrell, 2008; Pauly, 2010; Forster *et al.*, 2012]; maturation rate increasing at a faster rate than body size thus maturation occurs at a smaller size [Angilletta *et al.*, 2004]; optimal resource allocation [Kozlowski *et al.*, 2004]; ontogenetic timing [Forster *et al.*, 2011], and seasonality [Atkinson, 1995]. Ultimately, it is known unequivocally that temperature impacts fish through variation in bioenergetics – it is just not entirely known as to *how*.

There is a better understanding, however, of other aspects of temperature-physiology dynamics in fish. Increased temperatures cause a higher metabolic rate within an individual (here defined as the rate of change in energy and material used by an individual) [Brown *et al.*, 2004]:

$$I = i_0 M^b e^{\frac{-E}{kT}}$$

where I is the individual metabolic rate, i_0 is a normalization constant, M is body mass, b is the allometric scaling exponent (usually 0.67–0.75), T is the temperature (Kelvin), k is Boltzmann's constant (8.617×10^{-5} eVK^{-1}) and E is a given activation energy (eV). As k is constant and E is constant for each species, when temperature increases, so does the metabolic rate. When the scaling exponent, b, is set to 0.75, this broadly covers all species, and thus the metabolism formulation is known as the metabolic theory of ecology, and cited as "*the most fundamental biological rate*" [Brown *et al.*, 2004]. Specific to mass, larger species have a lower metabolic rate. Other rates have been shown to be influenced by temperature in a similar mathematical formulation such as feeding rates through searching, attack, and handling rates [Englund *et al.*, 2011; Vucic-Pestic *et al.*, 2011; Rall *et al.*, 2012], as well as general movement and digestion rates [Brose *et al.*, 2012].

Beyond influencing individual organisms, temperature can impact the population and community level. For example shifts in the distribution of a population to deeper, cooler waters has been seen in both empirical and modelling studies [Perry *et al.*, 2005; Dulvy *et al.*, 2008; Cheung *et al.*, 2013b; Pinsky *et al.*, 2013]. Causes of this are uncertain, but changes in migration patterns [Nye *et al.*, 2009] and reduced recruitment success in warmer than average waters [Clark *et al.*, 2003; Rindorf & Lewy, 2006; Rijnsdorp *et al.*, 2009] have been attributed to such population changes, as well as individuals growing to smaller final sizes providing a reduction in average population body size [Cheung *et al.*, 2013b]. Changes in fish communities, such as a reordering of food webs and abundance variations are predicted with warming [Simpson *et al.*, 2011; Shurin *et al.*, 2012]. This assumes fish are able to find a suitable habitat [Simpson *et al.*, 2011] and will not be constrained, such as by depth [Rutterford *et al.*, 2015]. It could be that the structure of ecosystems may change in terms of species makeup, but the overall ecosystem size structure and function is unaffected, such as suggested in bottom-up controlled systems [Heath, 2005].

It is categorical that temperature impacts fish at different levels. It is equally clear that research into the impacts of reductions in body size is high on the ecological agenda, especially for systems on which the livelihoods of communities rely [Sheridan & Bickford, 2011]. The three major changes an organism is likely to have in response to a change in temperature are a change in distribution, a change in phenology, and a change in body size [Daufresne *et al.*, 2009; Sheridan & Bickford, 2011]. It is the latter, and how it impacts the population and community structure, which is the focus here.

1.2.2 Chemical variability

As briefly mentioned, temperature increases have been hypothesised as indirectly causing reductions in body size through a lowering of oxygen. This is typically thought because warmer waters have a lower oxygen saturation limit than colder waters therefore an assumption is often made that the oxygen concentration will also be lower. However, this is not always the case. For clarification, the distinction between oxygen saturation and concentration is highlighted. While temperature dictates how much oxygen can be absorbed, such that the warmer the water, the lower the *maximum* oxygen saturation, this does not mean warm waters will always contain less oxygen than cold waters. Variations in phytoplankton, spring blooms, currents, and mixing can all alter the oxygen concentration of the water [Stendardo & Gruber, 2012; Queste *et al.*, 2013; Marshall *et al.*, 2016]. Therefore the reports of cold waters with a lower oxygen concentration than warm waters in parts of the North Sea [Marshall *et al.*, 2016] is not unexpected due to the localised oceanographic dynamics. Much of the research on oxygen effects on fish is undertaken in laboratory conditions where the physical world cannot replicate oceanographic complexities. Therefore research often assumes warming leads to lower oxygen availability for fish, because when only temperature alters the oxygen availability (such as in experimental setups), this assumption is correct. While there are times where the opposite occurs [Marshall *et al.*, 2016], in general as temperature is a key factor in oxygen saturation, reduced temperatures will normally reduce the oxygen content.

In the most extreme case, oxygen depletion leads to dead zones. Over the last 50 years these dead zones have increased exponentially [Diaz & Rosenberg, 2008] and increases are likely to continue [Keeling *et al.*, 2010] resulting in major negative impacts on marine ecosystems [Joyce, 2000; Diaz & Rosenberg, 2008; Stramma *et al.*, 2010]. In particular, lethal levels can impact reproduction [Wu *et al.*, 2003; Thomas *et al.*, 2007] and metabolism, thus growth [Schurmann & Steffensen, 1997; Nilsson & Östlund-Nilsson, 2004]. However, small declines in oxygen, which are synonymous across the globe [Schmidtko *et al.*, 2017], are of particular interest as these non-lethal levels are unknown in how they might affect fish communities.

Research of non-lethal effects on fish is somewhat limited though arguably a necessity due to the expected reduction in oxygen with climate change [Keeling *et al.*, 2010]. Active metabolism, thus aerobic scope, reduces with oxygen [Claireaux & Lagardère, 1999; Claireaux & Lefrançois, 2007; Chabot & Claireaux, 2008] which consequently influences physical activities such as swimming and feeding. Additionally, growth reduces with a lowering oxygen: reduced food intake explained 97% of growth reduction in Atlantic cod [Chabot & Dutil, 1999], and a reduction in digestion and metabolism occurs [Chabot & Dutil, 1999; Thetmeyer *et al.*, 1999; Buentello *et al.*, 2000; Claireaux *et al.*, 2000; Pichavant *et al.*, 2001]. In extreme low oxygen circumstances, fish have been known to vomit, then re-ingest once oxygen rises to more suitable levels to allow for the energetic costs of digestion [Claireaux *et al.*, 2000]. Though non-lethal levels of oxygen do not appear directly detrimental to individual physiology, they do influence the consumption, thus energy availability for growth, as an avoidance tactic for energy expenditure. Reduction in oxygen through a temperature increase has been suggested as causing changes in North Sea fishes [Baudron *et al.*, 2014] and potential future changes of global fish populations [Cheung *et al.*, 2013b]. These theories are further corroborated by evidence that aquatic species have a stronger response to temperature changes than terrestrial species making oxygen a possible candidate in temperature-driven body size reductions [Forster *et al.*, 2012].

Another worry of the changing chemical composition of marine waters is an increase in carbonic acid (reduced pH). This is currently occurring due to anthropogenic-released atmospheric carbon dioxide (CO_2) diffusing into the surface waters, something known as ocean acidification [Caldeira & Wickett, 2003; Doney *et al.*, 2009]. Concerns over increasing ocean acidity relates to the effect on biogeochemical cycles [Doney *et al.*, 2009], calcifying phytoplankton [Orr *et al.*, 2005; Iglesias-Rodriguez *et al.*, 2008], corals [Hoegh-Guldberg *et al.*, 2007; Anthony *et al.*, 2008], and even fish, sea urchins and arthropods [Fabry *et al.*, 2008]. Changes in fish habitat due to increased CO_2 are also thought to have a negative effect on populations [Nagelkerken *et al.*, 2016; Rossi *et al.*, 2016].

Direct effects of reduced pH on fish has been linked to impaired neuro-functions such as sound and olfactory senses [Nilsson *et al.*, 2012; Bignami *et al.*, 2013] which could indirectly affect productivity (e.g. reduced olfactory senses could impair hunting skills). Whether CO_2 levels will have population level consequences is less well known due to the large number of processes involved in sustaining a population (e.g. recruitment, reproduction, growth) which have been relatively under-researched in CO_2 studies [Ishimatsu *et al.*, 2008]. What has been established more recently, however, is the likely impact of CO_2 on early laval stages which could have ramifications through to adulthood [Franke & Clemmesen, 2011; Baumann *et al.*, 2012; DePasquale *et al.*, 2015]. As research into the effects of CO_2 on growth is either in its infancy, not conclusive at adult stages, or the CO_2 experiments that have been conducted use values beyond any realistic projection, CO_2 is not considered further in this thesis.

1.2.3 Food

Food sources need to be both abundant and of good quality in order for an individual to survive and grow. If food simply does not exist, energy is unable to be converted to weight to support the growth of the fish, which thus will consequently die of starvation. Equally, if the food is of low quality, the amount of energy acquired for new tissue, bones, and reproductive materials will be minimal. This latter effect can perturb negatively through ecosystems [Wanless *et al.*, 2005], starting from the lowest trophic level (i.e. plankton spectrum) through to the size distributions of fish communities.

Changes in turbulence (i.e. wind and/or stratification changes) increase phytoplankton biomass and reduce zooplankton [Alcaraz *et al.*, 1988]. This can result in a steepening of the size spectrum for these plankton functional groups. Additional correlations have been shown between temperature and phytoplankton [Barnes *et al.*, 2011], oceanic properties (e.g. currents and temperature) and zooplankton [Planque & Fromentin, 1996; Planque & Taylor, 1998; Reid *et al.*, 1998], and large atmospheric oscillations and zooplankton [Fromentin & Planque, 1996; Planque & Taylor, 1998; Piontkovski *et al.*, 2006]. However, these relationships are not always consistent [Planque & Reid, 2002]. It has also been postulated that different fish populations will be more or less affected by phytoplankton depending upon the number of trophic levels and zooplankton availability [Runge, 1988]. Importantly, it is known that primary production is key for the basis of ecosystems and the productivity of fish [Pauly & Christensen, 1995; Chassot *et al.*, 2010; Watson *et al.*, 2014], thus is a vital component of any marine ecosystem model.

1.2.4 Fishing

Marine ecosystems are being heavily fished, with 10.5% underfished, 58.1% fished at full capacity, and 31.4% overfished across all globally assessed stocks [FAO, 2016]. An overfished ecosystem is where a population of fish is unable to produce a sustainable yield, economically or ecologically. Commercial fishing is very much orientated around the size of fish, where landings must abide by a minimum size, dependent upon the species (i.e. size-selective fishing [Myers & Hoenig, 1997]). However in Europe, under the Common Fisheries Policy (CFP), individuals must now be landed regardless of size in an attempt to reduce discard [Borges, 2015], despite criticisms [Symes, 2012]. Fishing regimes tend to be split into size-selective (knife-edge) and balanced harvesting (or balanced exploitation). Size-selective is where the aim is to capture individuals above a certain size, whereas balanced harvesting encourages fishing across the whole size spectrum based on productivity, with the former the more common strategy.

In order to catch different fish species across various sizes, a number of fishing methods are employed. For example, beam trawls predominately target bottom-dwelling flatfish (e.g. plaice, sole, dab), whereas otter trawls target demersal roundfish (e.g. cod, haddock, whiting) in areas where species have a known high seasonal biomass [Jennings *et al.*, 1999; Law, 2000; Mills *et al.*, 2007]. These trawls, along with other fishing methods such as gillnets [Hamley, 1975], and hook fishing [Ralston, 1990] are designed to catch certain sizes. Trawl nets have specific mesh sizes at the codend to allow small individuals to escape whilst retaining larger individuals [Jørgensen *et al.*, 2009]. Gillnets allow too small or too large a fish to escape, and catch success depends on net size, colour, and construction [Hamley, 1975]. Hook-and-line and longline fishing use hook size [Ralston, 1990] and bait size [Løkkeborg & Bjordal, 1995] respectively, to alter the body size of the catch. The resulting catch of specific fish sizes, however, is not guaranteed due to a number of factors altering selectivity (though not always consistently) [Dahm *et al.*, 2002]. These different methods of size-selective fishing, therefore, are not always predictable in the biomass they are expected to catch.

Size-selective fishing can be directly and indirectly damaging to the population body size distribution. By catching the largest, and most fecund, individuals (BOFFFF - big old fat fecund female fish) this directly causes a truncation in the size structure, and indirectly impacts the population as BOFFFFs are notably better for successful recruitment [Hixon *et al.*, 2014]. An alternative regime, balanced harvesting, claims to garner a higher sustainable yield [Zhou *et al.*, 2010; Jacobsen *et al.*, 2014] and may ease the damaging effects fishing has on ecosystems [Zhou *et al.*, 2010]. Despite the potential use of this strategy in fisheries, the evidence and basic concepts have been questioned [Froese *et al.*, 2016; Kolding *et al.*, 2016]. Ultimately, fishing strategies are by no means flawless and many are not sustainable. Research is ongoing to find the optimum fishing regime that achieves maximum yield, sustainability, and stability of a fisheries. Currently, whether fishing under a size-selective regime for large fish, or across the size spectrum, both are expected to lead to a decrease in population biomass directly or indirectly [Jennings & Blanchard, 2004; Jacobsen *et al.*, 2014].

Fishing, in general, directly removes the larger individuals of a given species. The theory to remove large fish, despite being highly fecund, is to allow the immature individuals to mature and reproduce. Larger fish also tend to be of higher financial value, thus benefiting fishermen. This ultimately results in the removal of large fish reducing the average body size of a population [Jennings & Blanchard, 2004] and has been seen in a variety of places across the North Sea [Genner *et al.*, 2010; Heath & Speirs, 2012; Marshall *et al.*, 2016]. Consequently this direct act of fishing can result in an ecosystem regime shift through trophic cascades [Daskalov *et al.*, 2007] resulting in an increase of smaller fish, again reducing the body size distribution of a population, though this time indirectly [Daan *et al.*, 2005].

Another indirect effect of fishing lies in genetic heritability at the individual level [Law & Grey, 1989]. It has been proposed, through theory and experiments, that size-selective fishing of larger individuals will cause the population body size distribution to tend towards genetically (naturally) smaller body sized individuals [Law & Grey, 1989; Law, 2000; de Roos *et al.*, 2006; Audzijonyte *et al.*, 2013] though this is not always found [Ernande *et al.*, 2004]. Consequently, this selective evolution remains a highly contentious and complex puzzle [Browman *et al.*, 2008; Enberg *et al.*, 2012]. The traits affected by fisheries induced evolution (FIE) appear to be numerous [Gjedrem, 1983], with size [Swain *et al.*, 2007; Enberg *et al.*, 2012; van Wijk *et al.*, 2013], natural mortality [Jørgensen & Fiksen, 2010; Swain, 2011], and growth [Favro *et al.*, 1979; Swain *et al.*, 2007; Enberg *et al.*, 2012] being at the centre of this evolutionary research. Due to FIE potentially perturbing through the system, damaging higher order characteristics such as yield [Law & Grey, 1989], there have been calls for evolution to be recognised under management [Audzijonyte *et al.*, 2016].

Evidence for human induced evolution is seldom conclusive due to the alternative possibilities to genetic heritability [Kuparinen & Merilä, 2007]. Some even suggest that proving genetic changes can only be achieved by looking at the DNA, determining genes for traits, and consequently determining evolution from there [Browman *et al.*, 2008]. However, this is expensive and highly technical, therefore the use of maturation reaction norms which can determine between plastic and genetic changes [Olsen *et al.*, 2004; Kraak, 2007] are often used in support of FIE. Additionally, research through experiments [Conover & Munch, 2002; Enberg *et al.*, 2012; van Wijk *et al.*, 2013], *in situ* observations [Rowell, 1993; Grift *et al.*, 2003; Enberg *et al.*, 2012], and modelling [de Roos *et al.*, 2006; Dunlop *et al.*, 2009] have all strongly indicated FIE and the subsequent detrimental effect on the sustainability of fisheries. Furthermore, it has been suggested that heavy fishing can cause collapsed stocks to struggle in recovery due to FIE [de Roos *et al.*, 2006; Walsh *et al.*, 2006; Enberg *et al.*, 2009]. This will inevitably have economic and social implications [Eikeset *et al.*, 2013].

A mix of direct and indirect effects of environmental change and anthropogenic pressures have huge impacts on fisheries. Fishing is among the most destructive and unsustainable anthropogenic practices when poorly managed [Hilborn *et al.*, 1995; FAO, 2014]. Fully understanding the genetic ramifications is not easy, though potentially very important in terms of stock recovery [Walsh *et al.*, 2006]. The climate conditions are projected to result in an increasingly inhospitable environment for many species, and climate change is already a major threat [Stocker *et al.*, 2013; Hobday & Pecl, 2014]. Therefore it is important to understand the impacts of fishing and the environment on body size distributions. Combining experimental work and mechanistic models can allow a logical understanding of the magnitude of environmental and fishing contributions towards changes in a fisheries community. The modelling output can be compared to empirical ecosystem metrics. This thesis studies a variety of environmental and ecological fishing effects, in an empirical and modelling setting, in the hopes of furthering our knowledge of individual and combined drivers of body size distribution change.

1.3 Research Objectives

The aim of this thesis is to contribute to the body of research on how fishing and climate serve to alter the body size distribution of marine ecosystems. It is a small addition to the many notable contributions which have already been made in this area, as described above. A mix of empirical and modelling techniques are employed using the North Sea as a case study in order to address the following questions:

1. What changes in demersal community size structure have occurred in different regions across the North Sea over the last 30 years?
2. How does environmental change impact the physiology of individuals, and in turn the size structure of populations and communities?
3. Can we accurately model how much environmental change will alter the North Sea demersal community?

The first question leads to an empirical analysis to introduce the current state of the North Sea and how it has changed over the last 30 years. Using a new combination of statistics from an array of scientific disciplines this question has a dual purpose: (a) to highlight how the demersal community has changed at the highest possible spatial resolution, and postulations as to why, and (b) to introduce methods rarely used, if ever, in fisheries but are seemingly well suited to this field and general ecology.

The remaining questions are researched using a size-structured model parameterised for the North Sea [Blanchard *et al.*, 2014] but which has been adapted in this thesis to incorporate environment-dependent physiological relationships which are based on empirical studies. The first modelling question (second in all) looks at how environmentally driven growth of individual species can propagate through an ecosystem, to see how changes in the population and community occur, and at what magnitude. The second modelling question (third in all) has two aims: (a) to highlight the differences between using environmental data extracted 2 global and one regional model, and (b) see how climate change will impact the North Sea demersal community by 2100.

The questions are approximately analogous to how the thesis is ordered. Chapter 2 is an analysis of the empirical demersal North Sea size structure. Chapter 3 is the size-structured model theory and derivations. This is not taken as a research question as this base model has been well established in food web theory [Andersen & Pedersen, 2010; Hartvig *et al.*, 2011] and parameterised for the North Sea [Blanchard *et al.*, 2014]. However, as this base ecological model is used for the foundations of the second and third research questions, it is taken into a separate chapter to avoid repetition. Chapter 3 does however incorporate the corrections to errors found in previous models. Chapter 4 describes the environmental modifications and testing of the size-structured model. Chapter 5 uses the modified environmental size-structured model to test how environmental conditions have caused variations in the body size distribution of the North Sea demersal community, and what the next 80 years could hold under different IPCC scenario projections to 2100. Additionally, extracted environmental data from 2 global models and regional model are used to see how they impact on the output of the fisheries model. The final chapter (Chapter 6) draws to a close the various research, methods, and possible implications of this research in the wider field of fisheries and ecology. It is at this point that we can reflect on progress made in the community ecology of fisheries, and postulate ideas on some vital modelling questions that still need to be addressed.

Chapter 2

Quantifying heterogeneous responses of fish community size structure using novel combined statistical techniques

The majority of this chapter is made up of the following published work: Marshall AM, Bigg GR, van Leeuwen SM, Pinnegar JK, Wei H-L, Webb TJ, Blanchard JL (2016). Quantifying heterogeneous responses of fish community size structure using novel combined statistical techniques. *Global Change Biology*, **22(5)**, 1755–1768.

Instead of supplementary materials or appendices as given with the journal article, these have instead been incorporated throughout this chapter.

All authors reviewed and commented on the GCB manuscript, along with two anonymous reviewers. Explicit contributions are:

- A.M.M. and J.L.B. designed the study
- A.M.M. wrote the manuscript, conducted data collection and preparation, calculated size-based indicators and empirical orthogonal functions
- S.M.v.L. provided environmental data from the GETM-ERSEM-BFM hindcast model
- H-L.W. conducted the NARMAX modelling
- J.L.B. provided recent Norway fishing effort through contact with Jennifer Devine and Henrik Kjems-Nielsen

Additional acknowledgments go to Simon Jennings for providing fishing effort data, and to Georg Engelhard, Paul Dolder, and Kjell Nedreaas for discussions and help on North Sea fishing effort.

Abstract

To understand changes in ecosystems, the appropriate scale at which to study them must be determined. Large marine ecosystems (LMEs) cover thousands of square kilometres and are a useful classification scheme for ecosystem monitoring and assessment. However, averaging across LMEs may obscure intricate dynamics within. The purpose of this study is to mathematically determine local and regional patterns of ecological change within an LME using empirical orthogonal functions (EOFs). After using EOFs to define regions with distinct patterns of change, a statistical model originating from control theory is applied (Nonlinear AutoRegressive Moving Average with eXogenous input – NARMAX) to assess potential drivers of change within these regions. Spatial datasets (0.5 ° latitude x 1 ° longitude) of fish abundance from North Sea fisheries research surveys (spanning 1980–2008) were selected alongside temperature, oxygen, depth integrated net primary production and a fishing pressure proxy, to which the EOF and NARMAX methods were applied. Two regions showed significant changes since 1980: the central North Sea displayed a decrease in community size structure which the NARMAX model suggested was linked to changes in fishing; and the Norwegian trench region displayed an increase in community size structure which, as indicated by NARMAX, was primarily linked to changes in sea bottom temperature. These regions were compared to an area of no change along the eastern Scottish coast where the model determined the community size structure to be most strongly associated to net primary production. This study highlights the multifaceted effects of environmental change and fishing pressures in different regions of the North Sea. Furthermore highlighting this spatial heterogeneity in community size structure change shows how important local spatial dynamics are often overlooked when the North Sea is considered as a broad-scale, homogeneous ecosystem, as normally is the case within the political Marine Strategy Framework Directive.

2.1 Introduction

Determining the appropriate spatial scale for monitoring communities has been cited as one of the most important challenges in applied ecology [Johnson, 2009]. This challenge arises from the non-uniform response of species to their biotic and abiotic surroundings, many of which exist on different scales [Levin & Paine, 1974; Levin, 1992]. One approach to determine spatio-temporal patterns is by identifying areas of predicted rapid change known as 'hot spots', and to project expected ecological changes in these areas based on known physiological and community dynamics [Hannah *et al.*, 2002; Belkin, 2009; Hobday & Pecl, 2014]. An alternative approach is to quantify past, local ecological changes and attribute potential global, regional or local drivers to the corresponding changes. However, there is uncertainty surrounding the spatial scale at which to do this. For marine systems the global Large Marine Ecosystem (LME) classification scheme [Sherman, 1991] may provide a suitable scale for such analyses, especially when one considers the climate patterns at even larger scales that influence LMEs [Gherardi *et al.*, 2010]. However, there can be considerable heterogeneity in both environmental and anthropogenic drivers within LMEs. For instance, the North Sea LME has a number of thermal oceanic fronts influencing density, currents and nutrients [Belkin *et al.*, 2009] which in turn influence the marine ecosystem [Olson *et al.*, 1994; van Leeuwen *et al.*, 2015]. Additionally, fishing effort, a huge driver of ecosystem change [Jennings & Kaiser, 1998; Jennings & Blanchard, 2004], is not homogenous across the North Sea [Jennings *et al.*, 1999]. Despite this, the North Sea LME is often characterised as a single cohesive ecosystem [European Parliament, 2008; Greenstreet & Rogers, 2006; Greenstreet *et al.*, 2011]. With abundant ecological data available, methods to appropriately quantify heterogeneous change and thus manage ecosystems must be reviewed as ecosystems adapt under a changing climate [Chave, 2013].

Many marine ecosystems are size-structured, where lots of small individuals and fewer large individuals coexist [Sheldon *et al.*, 1972], making body size of individuals a frequently employed proxy for ecosystem health and stability [Shin *et al.*, 2005; Woodward *et al.*, 2005; Greenstreet & Rogers, 2006; European Parliament, 2008]. Furthermore, trophic structure, a range of life history parameters, and biological rates correlate strongly with body size [Sheldon *et al.*, 1972; Blueweiss *et al.*, 1978; Calder, 1984; Gillooly *et al.*, 2001; Brown *et al.*, 2004; Savage *et al.*, 2004; Kingsolver & Huey, 2008; Rall *et al.*, 2012; Reuman *et al.*, 2014]. The multifaceted effects of climate and fishing are known to disrupt the size structure of marine communities [Rice & Gislason, 1996; Blanchard *et al.*, 2005]. Body size is thus an important indicator of size-structured, community-level properties and is consequently the basis of metrics used in policy [European Parliament, 2008] and an ecosystem approach to fisheries management [Jennings & Dulvy, 2005].

Explicit size-based indicators (SBIs) describe the distribution of body size and include the large fish indicator (LFI), mean maximum weight, length ($\overline{W_{max}}$, $\overline{L_{max}}$), size spectrum slope and mean maturation size [Nicholson & Jennings, 2004; Shin *et al.*, 2005]. European policy, in the form of the Marine Strategy Framework Directive, calls for the use of biomass and the proportion of large fish (by weight) as indicators for targets in defining good environmental status of food webs [Rogers *et al.*, 2010]. $\overline{W_{max}}$, LFI and the size spectrum slope have all been used in the evaluation of management and targets in the North Sea [Nicholson & Jennings, 2004; Blanchard *et al.*, 2014; Thorpe *et al.*, 2015]. Thus these three are used in this study.

In addition to using an indicator to describe the state of an ecosystem, such as body size distribution, drivers of ecological change also need to be examined. Environmental drivers [Daufresne *et al.*, 2009; Cheung *et al.*, 2013b; Gale *et al.*, 2013; Baudron *et al.*, 2014], fishing pressure [Rice & Gislason, 1996; Grift *et al.*, 2003; Jennings & Blanchard, 2004] and the interaction between them [Blanchard *et al.*, 2005; Genner *et al.*, 2010; Planque *et al.*, 2010; Engelhard *et al.*, 2014] have been found to cause changes in marine body size distributions.

Changes of the body size distribution in fish communities can be driven both directly and indirectly by increased seawater temperatures [Perry *et al.*, 2005; Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011]. Direct effects can cause a reduction in body size distributions by: (1) causing individuals to grow faster to a smaller size [Atkinson, 1994, 1995] although it is not fully understood why [Angilletta & Dunham, 2003; Atkinson *et al.*, 2006], and (2) causing a shift in the distribution of a given population to deeper, cooler waters [Perry *et al.*, 2005; Dulvy *et al.*, 2008; Cheung *et al.*, 2013b; Pinsky *et al.*, 2013] due to poorer recruitment success in warmer than average waters [Clark *et al.*, 2003; Rindorf & Lewy, 2006; Rijnsdorp *et al.*, 2009] and changing migration patterns [Nye *et al.*, 2009]. Indirect consequences of warmer waters on body size have been postulated to occur through lower oxygen saturation levels (causing a constraint on fish growth thus size [Pörtner & Knust, 2007; Pauly, 2010; Cheung *et al.*, 2013b; Baudron *et al.*, 2014]), and phytoplankton changes (causing a mismatch in timing for food sources and recruitment [Edwards & Richardson, 2004; Barnes *et al.*, 2011]). While temperature effects have been well explored, studies of oxygen effects are less numerous. They appear to influence physiology under lethal [Schurmann & Steffensen, 1997; Wu *et al.*, 2003; Nilsson & Östlund-Nilsson, 2004] and non-lethal conditions [Kinne & Kinne, 1962; Chabot & Dutil, 1999; Chabot & Claireaux, 2008]. A reduction of body size can also occur by the removal of large individuals through size-selective fishing which also causes an increase in small individuals due to reduced predation pressure [Daan *et al.*, 2005; Andersen & Pedersen, 2010]. Heavy fishing has also led to the idea of evolutionary adaptations in growth causing a reduced body size distribution [Rowell, 1993; Law, 2000; Grift *et al.*, 2003; Olsen *et al.*, 2004].

All of these drivers are rarely distributed homogeneously in space. The North Sea LME has undergone changes at different rates across the region [Beaugrand, 2004; Frost *et al.*, 2013] yet remains classified as a single ecosystem [European Parliament, 2008; Greenstreet *et al.*, 2011]. A marked recent warming in southern areas (∼1.15 °C over 20 years) is greater than that of northern areas (∼0.6 °C over 20 years) [Holt *et al.*, 2012a]. Primary production varies according to stratification, shelf exchange rates, riverine and atmospheric inputs, all of which are changing [Heath & Beare, 2008; Holt *et al.*, 2012b]. Oxygen levels have decreased with regions becoming hypoxic [Bendtsen & Hansen, 2013; Queste *et al.*, 2013]. Fishing, determined by effort and satellite-based vehicle monitoring, is distributed heterogeneously throughout the North Sea [Jennings *et al.*, 1999; Mills *et al.*, 2007; Stewart *et al.*, 2010]. It is therefore plausible, if not highly probable, to expect trends in the body size distribution of North Sea demersal fish to also be heterogeneous in space.

Here a spatially explicit statistical framework is developed for highlighting local ecological change and investigating potential drivers of these changes using the North Sea demersal fish community as a case study. Firstly Empirical Orthogonal Functions (EOFs), commonly found in geophysics [Lorenz, 1956] though have recently been applied in a fisheries settings [Morfin *et al.*, 2012; Saraux *et al.*, 2014], are used as a tool for determining major areas of change in size-based indicators (SBIs). Secondly, SBIs are extracted from three regions showing different changes, along with the corresponding environmental and fishing conditions. Finally, using $\overline{W_{max}}$ as a case study, the use of Nonlinear AutoRegressive Moving Average with eXogenous input (NARMAX) modelling is employed as an illustrative example to investigate the potential drivers of size-based change. NARMAX has been used widely in the fields of engineering [Billings, 2013], neuroscience [Zhao *et al.*, 2013] and recently glacial climate dynamics [Bigg *et al.*, 2014; Zhao *et al.*, 2016]. However it has yet to be applied to fisheries. Using a highly spatial dataset covering 29 years, EOFs and NARMAX are applied in unison, for the first time, to highlight areas of major change and investigate potential reasons of these changes. The objective of this study therefore is twofold: (1) to mathematically quantify regional responses in size-based indicators and identify the main drivers, and (2) to introduce a new statistical tool in fisheries research to aid marine management. By highlighting areas of contrasting ecological change under different environmental and anthropogenic conditions, this combination of statistical methods provides increased awareness of multifaceted effects found across the North Sea fishery.

2.2 Materials and Methods

2.2.1 Study area

The study site is the North Sea (Figure 2.1): this northwestern North Atlantic shelf sea is of international economic importance and undergoing very marked changes (see Introduction). Trawl surveys for scientific research have been undertaken for over a century at various locations in the North Sea [Cefas, 2014].

However the bottom trawl survey data from 1980–2008 is used here to ensure the greatest spatial coverage to allow for methodological accuracy. While the spatial coverage improved dramatically in the 1970s, it was not until 1977 where ICES instructed the standardisation of trawls, where all surveys must be completed using the Grande Overture Verticale (GOV) trawl. Furthermore, it was 1980 where this standardisation was thought to be homogenous across surveying nations, hence this is the start of the time series used here. The end time period used, 2008, was chosen because the current best North Sea modelled environmental data has only been run to 2008. This environmental data were extracted across the North Sea from a validated GETM-ERSEM-BFM hindcast model of this area. A proxy for fishing pressure exists in the form of fishing mortality though 'patchy' fishing effort is discussed and reported. This study was carried out at the resolution of ICES statistical rectangles (0.5 ° latitude x 1 ° longitude) and for ICES divisions IVa, IVb, IVc.

2.2.2 Fish survey data

The North Sea International Bottom Trawl Survey (NS–IBTS) quarter 1 dataset is a collection of wintertime (January–March) fishery surveys taken annually from 1967 to present day in ICES statistical rectangles across the North Sea (downloaded from datras.ices.dk). The time period 1980–2008 was used here to ensure the greatest spatial coverage to allow for methodological consistency and confidence. Fish length was obtained for all demersal species caught during daytime GOV (Grande Ouverture Verticale) trawls. Individuals are identified to species level (if possible) and measured (cm). Data are converted to standardised units of catch per unit effort per length per haul (survey methodology and data processing are available at datras.ices.dk).

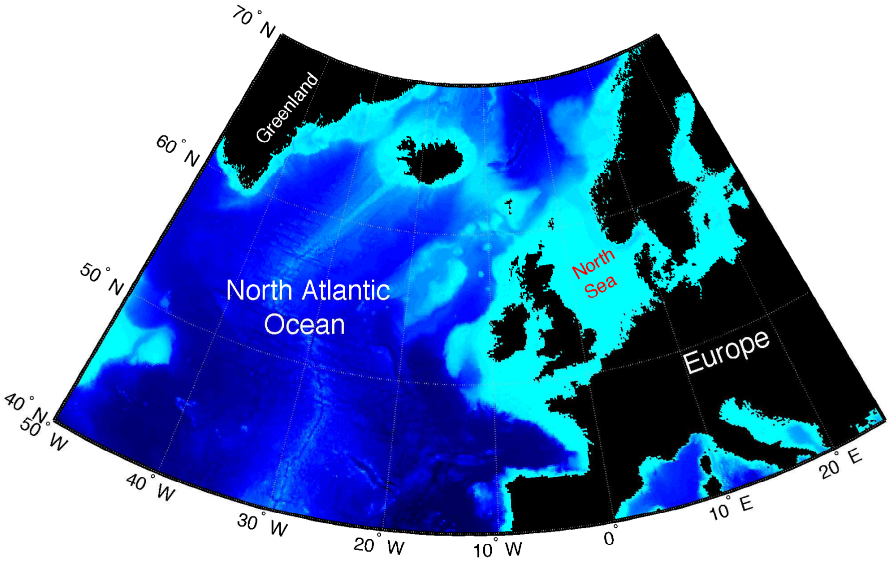

Figure 2.1: Map of the North Sea in the context of Europe and the North Atlantic Ocean (light blue <500 m).

Individual fish lengths (L) were converted to weight (W) using:

$$W = aL^b \tag{2.1}$$

where a and b are conversion factors provided by Fung *et al.* [2012]. If conversion values were not available, values from FishBase [Froese & Pauly, 2014] were used, or the same values from similar species were taken. If completely data deficient, the idealistic standard conversion factors $a = 0.01$ and $b = 3$ were used [Cheung *et al.*, 2013b]. Only two out of the total 159 taxa were converted using the latter process, *Micrenophrys lilljeborgii* (Norway bullhead) and any individuals labelled as 'Cottidae' (i.e. genus or species level unknown within this family).

All species recorded in the ICES North Sea International Bottom Trawl Survey were used and are found in Appendix A (Table A1). In the cases where species had alternative names, the same name as given in Fung *et al.* [2012] was chosen but alternative names have been declared. In accordance with quality control assessment guidelines [Daan, 2002] measurements that were less than 3 cm or greater than their species-specific Lmax were removed (taken from www.fishbase.org), the Lepadogaster record from 1991 and 1992, and the *Raja undulata* from 1990 were removed entirely and if *Leptoclinus maculatus* reached values greater than 20 cm, they were changed to *Lumpenus lumpretaeformis*. All pelagic species were removed.

2.2.3 Size-Based Indicators of demersal fish community structure

The IBTS dataset was used to calculate three size-based indicators (SBIs) at the resolution of ICES statistical rectangles over the period 1980–2008: the Large Fish Indicator (LFI), the mean maximum weight ($\overline{W_{max}}$) and the size spectrum slope due to their use in North Sea policy and research [Rice & Gislason, 1996; Nicholson & Jennings, 2004; Shin *et al.*, 2005; European Parliament, 2008, 2013; Blanchard *et al.*, 2014; Thorpe *et al.*, 2015]. Each SBI uses biomass (abundance multiplied by weight) as part of the main calculation – this biomass is the sum of each of the species' biomass per haul. If more that one haul existed in an ICES statistical rectangle in 1 year, the biomasses were averaged across hauls.

The LFI is the ratio between the total biomass of demersal fish greater than 40 cm in length (B_{40}) and the total biomass of all demersal fish (B_A):

$$LFI = \frac{B_{40}}{B_A} \tag{2.2}$$

The second SBI, the mean maximum weight ($\overline{W_{max}}$), calculates the maximum size relative to biomass across all species:

$$\overline{W_{max}} = \sum_i \frac{W_{max,i} B_i}{B_A} \tag{2.3}$$

where $W_{max,i}$ is the maximum observed weight of each species,i, found from the whole NS-IBTS quarter 1 dataset, B_i is biomass of species i, and B_A is the total biomass of all species. For the final SBI, the normalised biomass size spectrum slope, individuals were placed into size classes that conform to linear base two logarithms (e.g. 2-4 g wet weight, 4-8 g, 8-16 g ... 32678-65536 g) irrespective of species identity [Jennings & Dulvy, 2005]. The total biomass of all individuals falling within each size class was calculated and divided by the bin width of the corresponding size class to give the normalised biomass. The size spectrum slope was determined from a linear regression slope of $\log_2$(size class midpoint) against $\log_2$(normalised biomass) from the point of the highest normalised biomass across the remaining larger weight classes. This was performed for each year in each rectangle.

Not all rectangles had data every year owing to occasional gaps in the geographical coverage of the surveys or to the quality control procedures. In these cases the SBIs were interpolated using the mean value from all available adjacent rectangles (up to 8) for the specific year. Rectangles where fewer than 10 years of data existed were removed from the analyses after they had been used in the years they were present for, for greater interpolation accuracy. Consequently this meant the removal of 11.83% of data from the LFI and $\overline{W_{max}}$ leaving 164 rectangles. To have robust slope estimates ICES rectangles were excluded where fewer than 7 of the 14 observed size classes were recorded. Of the 5394 ICES rectangle-year combinations (186 ICES rectangles, 29 years), 810 (15.02%) were excluded for this reason; 91.60% of which (i.e. 742) were rectangles that contained no data. After this, ICES rectangles with fewer than 10 years worth of data of the 29 years were also removed leaving 161 rectangles (out of 186, so 13.44% removed altogether) in each year (4669 ICES rectangle-year combinations in total).

2.2.4 Environmental data – GETM-ERSEM-BFM Model

For a comprehensive coverage of environmental data, variables were extracted from a 51-year hindcast (1958–2008, although the first 20 years are considered spin up time for the benthic system) of the validated coupled hydrodynamic-biogeochemical model GETM-ERSEM-BFM [van Leeuwen *et al.*, 2013; van der Molen *et al.*, 2013; van Leeuwen *et al.*, 2015]. The General Estuarine Transport Model (GETM [Baretta *et al.*, 1995; Burchard & Bolding, 2002; Stips *et al.*, 2004; Burchard *et al.*, 2014]) is a fully 3D hydrodynamic, baroclinic, open source model which incorporates the 1D General Ocean Turbulence Model (GOTM) for vertical processes [Burchard & Bolding, 2002; Stips *et al.*, 2004; Burchard *et al.*, 2014] (www.getm.eu). GETM is coupled to ERSEM-BFM, developed jointly from the original ERSEM (European Regional Seas Ecosystem Model) and BFM (Biological Flux Model) codes by Cefas (UK) and NIOZ

(Netherlands) institutes.

ERSEM-BFM is a functional type model with integrated pelagic and benthic 'submodels' originally developed in the 1990s, specifically designed for temperate ecosystems. The biological dynamics are described separately under physiological processes (e.g. ingestion, respiration etc.) and population processes (e.g. growth, migration) along with trophic interactions within the food web [Baretta *et al.*, 1995]. The model provides both biological and chemical components such as phytoplankton, zooplankton and benthos biomass, organic and inorganic matter, bacterial biomass, primary production, oxygen levels, and dissolved nutrients such as phosphate, nitrate, ammonium and silicate. For more information on the ERSEM-BFM model, see van Leeuwen *et al.* [2013], van der Molen *et al.* [2013] and www.nioz.nl/ersem-getm.

The hindcast coverage, both spatially and temporally, was well suited to the rest of the data in this study. Spatially, the North Sea model setup of GETM-ERSEM-BFM covers the area $48.5 - 60.4\,°$N, 5.66W–16.20 °E with a resolution of $0.1\,°$ x $0.167\,°$. The northern and southern limits of the model are bounded by climatological averages which means the environmental variables in these areas do not change annually. Therefore, to avoid this static bias, the areas close to these boundaries were removed from the spatial grid.

The variables were extracted as monthly averages and were chosen to represent the demersal environment the species were most likely to experience. Therefore sea bottom temperature and sea bottom oxygen were used. Depth-integrated net primary production was taken as a proxy for food. For the purposes of this analysis, these extracted variables were averaged into ICES statistical rectangles to match the fish survey data.

2.2.5 Fishing pressure data – fishing effort and fishing mortalities

Data for fishing effort is restricted both spatially and temporally. The European Commission Scientific, Technical and Economic Committee for Fisheries (STECF), ICES and Jennings *et al.* [1999] (from now on referred to as J99) have collected a variety of data though they are not fully compatible to generate a full time series at the ICES rectangle level. An analysis of fishing effort and landings was carried out and is presented for ICES divisions IVa, IVb and IVc. However, due to the shortcomings of this combined dataset, the next best method was to construct a multi-species proxy based on annual fishing mortality rates weighted by biomass of the target species [Daan *et al.*, 2005]. This was applied to each ICES statistical rectangle in each year. Whilst both methods have caveats, the former is unusable for the spatial analyses.

Fishing effort and landings

Due to limited fishing effort data only certain countries could be used. The data used here were from England, Scotland, Wales, Germany, Norway, Denmark and Netherlands. This came from 3 sources: an international one-off collaboration in the late 1990s [Jennings *et al.*, 1999]; an ongoing, recently developed European Commission collection of EU countries fishing in the North Sea; and a collaboration with the Norwegian Institute of Marine Research (IMR) for independent Norway data since 2003. The expectation was that these data sources could be amalgamated in order to build a spatiotemporal time series, but this was unattainable due to the nature of the data. Hopefully, however, the collection and presentation of the current fishing effort here will highlight the need for standardising fishing effort across the North Sea. The assumptions made here were supported with the use of North Sea landings.

Landings data (in tonnes) are available from 1950–2010, however only data from 1977–2008 were used here. Data from the required divisions were kept: IVa, IVb and IVc. These three regions make up landings caught from the North Sea (subarea IV). All countries that had landings in these areas were kept for comparative purposes. If no ICES devision was specified they were removed. Only stock-assessed demersal fish were used: *Gadus morhua* (Atlantic Cod), *Melanogrammus aeglefinus* (Haddock), *Pollachius virens* (Saithe), *Pleuronectes platessa* (Plaice), *Merlangius merlangus* (Whiting), *Solea solea* (Sole) and *Trisopterus esmarkii* (Norway pout). Landing values which were recorded as '<0.5' were put at 0.25. While these are not the exact values; the values are so small relative to complete landings ($< 0.0001\%$) that the influence on the total landings is negligible, and 0.25 will be an overestimate for some, and an underestimate for others so will likely balance out. The landings from 1989 onwards include England, Wales and Northern Ireland as an aggregate thus were unable to be separated. Despite J99 not having Northern Ireland, the inclusion is unlikely to be a big influence. Landings from Northern Ireland in the North Sea only occurred in division IVa and the total landings from this region up until 1989 (i.e. before it became aggregated) was 106 tonnes, negligible compared to the total landings from the North Sea on an annual basis (<0.01%). Therefore it is unlikely that the inclusion of Northern Ireland as an aggregate will cause any bias in how the landings are interpreted.

The **first time window** for fishing effort was calculated over 1980–1999 using data provided by J99. The original dataset has two components: (a) 1977–1995 effort from England, Scotland, Wales, Norway and German otter and beam trawl fleets, and (b) 1990–1995 effort from these five countries with the addition of Denmark and Netherlands. The data were aggregated thus individual country effort is unknown and cannot be separated. The spatial patterns across 1990–1995 are all very similar (see Figure 5 in J99). Therefore the spatial pattern (i.e. *where* fishermen operated) was assumed to be the same from 1980–1999. Practically this means each individual ICES statistical rectangle over 1990–1995 were averaged and thus the resulting spatial pattern was the same each year across 1980–1999 to represent North Sea fishing effort. The use of all countries that fish in the North Sea as opposed to just seven was beyond any capabilities. The data simply do not exist. However, the 7 countries are a strong representation of North Sea fishing pressure as seen with landings (beam and otter landings data can be found in Appendix A - Tables A2 and A3, respectively. Beam trawl landings are taken as flatfish landings, and otter trawl landings as roundfish landings). From 1977–2008 in England, Scotland, Wales, Norway and Germany, landings of all flatfish species (vs stock-assessed flatfish: plaice and sole) accounted for 32.3% (vs 24.7%) of total annual beam trawl related landings relative to all countries that fish the North Sea (Figure 2.2). The inclusion of Denmark and Netherlands increased this to 91.0% (vs 91.2%). Therefore it was vital that Dutch and Danish fishing effort were included. The otter trawl related landings (vs stock-assessed roundfish: cod, haddock, saithe, whiting, Norway pout) from 1977–2008 in England, Scotland, Wales, Norway and Germany for all species account for 59.6% (59.6%) of total landings of otter trawl species likely to be caught relative to all countries that fish the North Sea. The inclusion of Denmark and Netherlands increased this to 89.3% (89.4%) again highlighting the importance of including these two countries (Figure 2.3). Therefore the spatial pattern of the 1990–1995 average (i.e. countries England, Scotland, Wales, Norway, Germany, Denmark, and Netherlands) is a good representation of fishing effort for the North Sea.

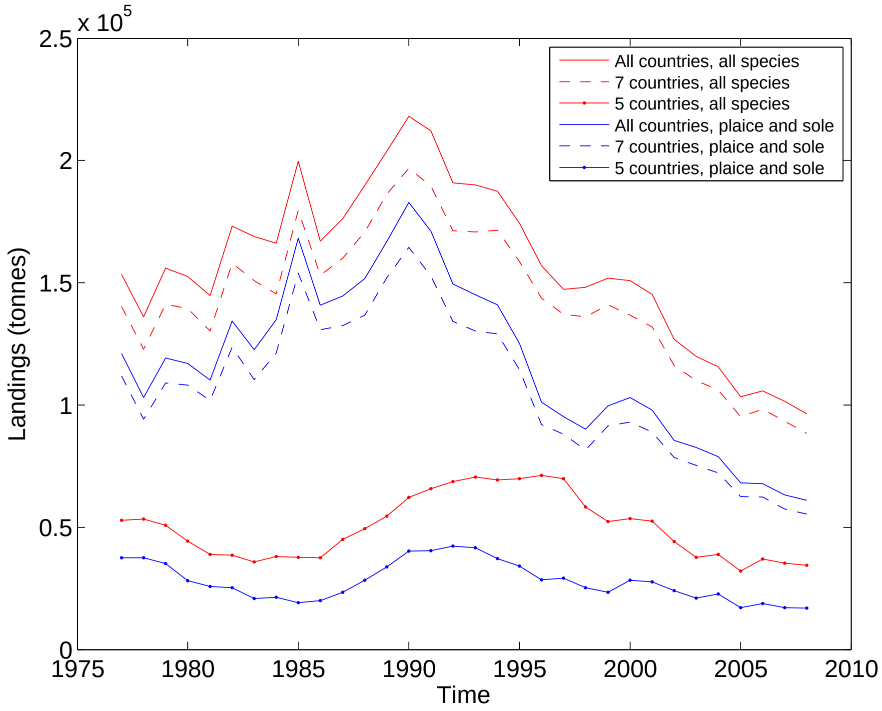

Figure 2.2: North Sea landings (tonnes) including all species most likely caught by beam trawls (i.e. flatfish) from: all countries (red solid); England, Scotland, Wales, Norway, Germany, Denmark and Netherlands (red dashed); England, Scotland, Wales, Norway and Germany (red dots); and just plaice and sole from: all countries (blue solid); England, Scotland, Wales, Norway, Germany, Denmark and Netherlands (blue dashed); England, Scotland, Wales, Norway and Germany (blue dots). Data from ICES catch statistics from 1977–2008.

The spatial pattern averages were separated for otter trawls and beam trawls. The hours were amalgamated into ICES divisions IVa, IVb and IVc - this is the best resolution that could be attained with the data to cover 1980–2008. To impose annual variability of fishing (i.e. *how much* the fishermen fished) the fishing effort was related to annual fishing mortality. Data from the seven stock-assessed demersal fish described above was used. Together this subsample of species made up an average of 68% of the total biomass of all demersal species in the IBTS trawl surveys. Furthermore plaice and sole have made up over 73% of flatfish landings since 1977. In the mid 1980s this was around 84%, but due to a severe decrease in plaice landings in the early 1990s they accounted for 61% of flatfish where it continued to fluctuate between 61% and 69% until the end of this time series, 2008 (Figure 2.2). For the otter trawl, the 5 specified species (cod, whiting, haddock, saithe, Norway pout - CWHSN) dominated with their combined landing weight often over 90% of all roundfish landings (Figure 2.3). Beam and otter trawls are thus shown to be dominated by these 7 species (Figures 2.2 and 2.3), making them a good representation of the demersal fish community that are targeted by fishing pressure.

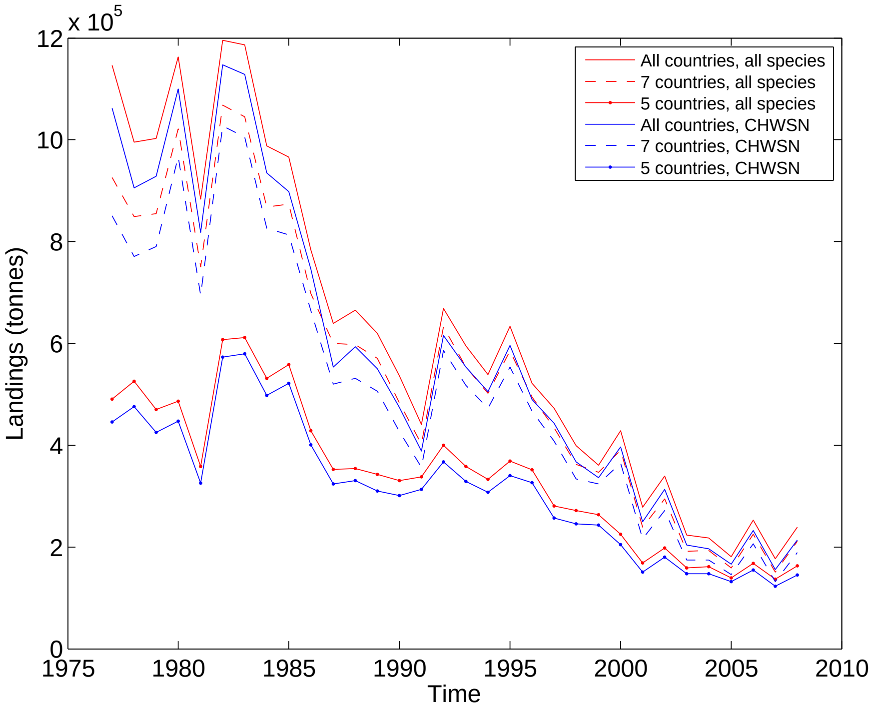

Figure 2.3: North Sea landings (tonnes) including all species most likely caught by otter trawls (i.e. roundfish) from: all countries (red solid); England, Scotland, Wales, Norway, Germany, Denmark and Netherlands (red dashed); England, Scotland, Wales, Norway and Germany (red dots); and just cod, whiting, haddock, Norway pout and saithe from: all countries (blue solid); England, Scotland, Wales, Norway, Germany, Denmark and Netherlands (blue dashed); England, Scotland, Wales, Norway and Germany (blue dots). Data from ICES catch statistics from 1977–2008.

Fishing mortalities for stock-assessed species are freely available from ICES (http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx) and can be found here in Appendix A (Table A4). Two species did not have fishing mortalities for the full time period of this study available from ICES. Whiting assessments began in 1990. However from 1990–2011 whiting mortality (F_w) was highly correlated with haddock mortality (F_H) with a simple linear regression explaining a large fraction of the variance (Figure 2.4, $r^2 = 0.87$). Therefore from 1980–1989, the whiting mortality was extrapolated:

$$F_w = 0.485F_H + 0.081 \tag{2.4}$$

The second species where the assessment did not extend to 1980 was Norway pout which began in 1983. Fishing mortality for Norway pout (F_{NP}) between 1980–1982 was calculated based on a strong linear relationship (Figure 2.4, $r^2 = 0.74$) found with fishing mortality of saithe (F_S):

$$F_{NP} = 1.8146F_S - 0.203 \tag{2.5}$$

The species used were split into two groups: those most likely to be caught by otter trawls (cod, haddock, saithe, whiting and Norway pout) and those by beam trawls (plaice and sole). To get an ‘average’ fishing mortality for beam and otter trawls the species values within the beam-based mortalities were averaged together, and the species values in the otter-based mortalities were averaged together to get two separate otter and beam trawl fishing mortalities over the last 29 years. The mortalities were standardised to the 1990–1995 mortality average. The 1980–1999 otter trawl spatial pattern (*where* fishermen fish) were weighted by the otter fishing mortality (*how much* fishermen fish) and the beam trawl spatial pattern by the beam fishing mortality. These two were added together to make an aggregate fishing effort distribution from 1980–1999. Distinguishing between the two trawls could be important, as they have not changed in unison over the last 30 years (i.e. compare Figures 2.2 and 2.3).

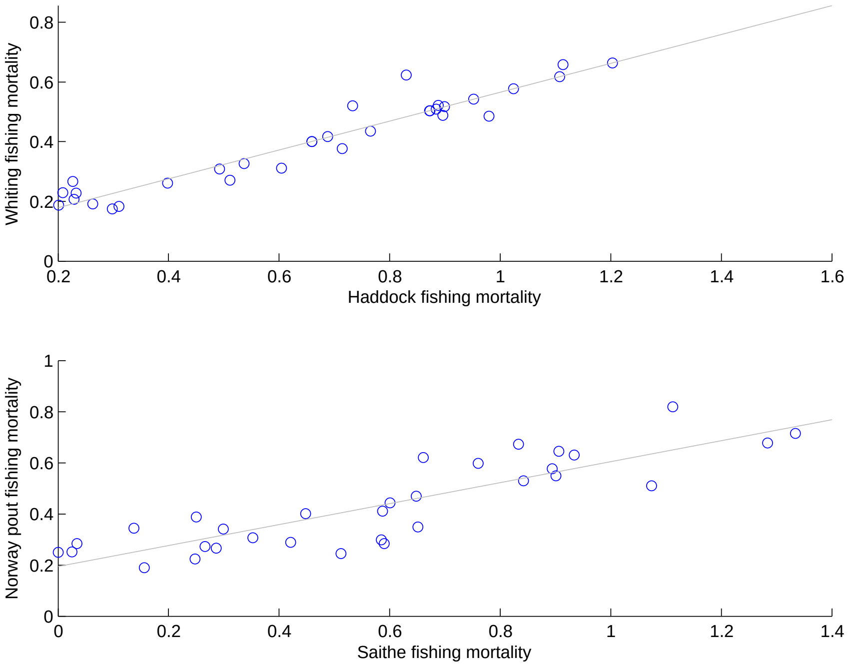

Figure 2.4: Relationship between (top) haddock fishing mortality and whiting fishing mortality in the North Sea ($r^2 = 0.87$) and (bottom) saithe fishing mortality and Norway pout fishing mortality in the North Sea ($r^2 = 0.74$). Data used from ICES catch statistics.

The **second time window** considered was 2000–2002. From 2000 a major EU decommissioning project was implemented to reduce fleet size and capacity with around 25% of vessels being taken out of service from 2000–2011 [European Parliament, 2013]. Therefore it was not appropriate to use data from J99 to extend into the new millennium. Instead, using the North Sea effort from 1999 and the North Sea effort from 2003, each ICES division (linearly for simplicity) was interpolated to calculate the intermediate 2000, 2001 and 2002 years.

The **third time window** was 2003–2008. England and Wales, Scotland, Germany, Denmark and Netherlands otter and beam (regulated and unregulated) fleets effort were obtained from the STECF and amalgamated for ICES statistical rectangles and divisions IVa, IVb and IVc. First England and Scotland fleets had to be readjusted. Data from England and Scotland is submitted to the STECF in days fished which is then multiplied by 24 to get hours fished. However, this is an unrealistic overestimation due to drive time and on-board processing [Engelhard *et al.*, 2015]. Therefore the use of recently calculated conversion factors were used (of days away from port and hours fished from

English and Scottish government fisheries management datasets) to calculate the adjusted hours fished [Engelhard *et al.*, 2015]:

$$H_{eb} = \frac{F_{eb}}{24}7 \tag{2.6}$$

$$H_{eo} = \frac{F_{eo}}{24}9.5 \tag{2.7}$$

$$H_{so} = \frac{F_{so}}{24}10.6 \tag{2.8}$$

where F_{eb}, F_{eo} and F_{so} is the fishing effort provided by STECF for English beam trawlers, English otter trawlers, and Scottish otter trawlers, respectively. The new adjusted values: H_{eb}, H_{eo} and H_{so} represent English beam trawlers, English otter trawlers, and Scottish otter trawlers, respectively.

As Norway is not part of the EU, it does not submit fishing effort data to STECF. However, as Norway is part of the compiled data in J99 it was crucial to have some representation of Norway in the later years. If not, a decline in fishing may well be an artefact due to the exclusion of Norway, especially considering their high landings contribution from division IVa relative to other countries (∼50% since the early 1970s). The only effort data available from Norway from 2002 onwards is for ICES subarea IV (i.e. the whole of the North Sea) for mixed fisheries. In order to disaggregate the data to improve the resolution an assumption that ∼95% of effort came from division IVa, ∼5% from IVb, and <0.5% from IVc (varied year by year) was taken. This was based on landings data where Norway landed this proportion of cod, haddock, whiting, saithe, plaice, sole and turbot species between 2002–2008 in division IVa, IVb, and IVc. These species were chosen as they are aggregated as such by the ICES Mixed Fisheries working group [WGMIXFISH, 2014], from which this effort data were originally collected for. The data were given in kW days and as the fleet size, engine size and power were not submitted, this series was unable to be converted appropriately in order to be amalgamated with the STECF data. As this Norway data are not directly compatible with the STECF data or effort data, it cannot be quantitatively included. Therefore the Norway fishing effort data will be discussed in light of the other countries that fish in the North Sea, though not in an explicitly, mathematical comparative way.

Fishing mortalities weighted by biomass

As has been shown in the previous section, attempting to collect and amalgamate fishing effort at the required spatial resolution is not possible. For an alternative fishing pressure metric the use of fishing mortality, as a proxy of fishing pressure, was weighted by biomass for greater spatial resolution (i.e. to ICES statistical rectangles) [Daan *et al.*, 2005]. The same sub-sample of species was used here as in the fishing effort: cod, haddock, plaice, whiting, saithe, Norway pout, and sole. Where biomass data did not exist, spatial interpolation was conducted as in the size-based indicator section. To get an individual fishing mortality F_m for each ICES rectangle each species' mortality was weighted by biomass:

$$F_m = \sum_i \frac{B_i}{B_{SA}} F_i \tag{2.9}$$

where B_i is the biomass of the specific species, i, B_{SA} is the biomass of all the demersal stock-assessed species, and F_i is the fishing mortality of the specific species, i. With biomass for individual species in each ICES rectangle, fishing mortality at this level of resolution was effectively calculated. It is this fishing proxy that had to be used in the NARMAX modelling analysis.

2.2.6 Data analysis

Spatial heterogeneity of change – Empirical Orthogonal Functions

The purpose of the Empirical Orthogonal Function (EOF) analysis was twofold: (1) to understand the spatial variation in temporal trends, and (2) to highlight particular areas of interest that explain the maximum amount of variance. Mathematically, an EOF analysis is identical to principal component analysis. However when used to define the spatio-temporal variation with spatially weighted data, the resulting functions are more commonly known as EOFs [Lorenz, 1956]. Using a gridded latitude-longitude dataset, the data were weighted by $\sqrt{cos(latitude)}$ [Baldwin, 2001; von Storch *et al.*, 2004] where *cos(latitude)* represents the length of the parallel at the specified latitude relative to the length of the parallel at the equator. A square root transformation was performed because the data were subsequently used to create a covariance matrix for EOF analysis (the data were thus weighted by *cos(latitude)* as variance involves a squaring term effectively nullifying the square-root). Importantly, any data being analysed by EOFs needs to be weighted if the geographic regions are not of equal area.

Once the data had been standardised (i.e. removal of the 29 year time-averaged mean for each ICES rectangle) and weighted spatially, a covariance matrix was calculated. The data input was therefore a year x location grid (e.g. for the LFI: year = 29, location = 164 rectangles so a 29 x 164 grid). The covariance matrix was used to retrieve orthogonal predictors. Using singular value decomposition, a matrix algebraic method, eigenvectors and eigenvalues were calculated which were taken as the EOF modes and EOF principal components, respectively. The first mode of the SBIs was the only one extracted as this captures the pattern of greatest explained variance (here, ~28%). Additional EOF modes capture much less variance (<9%) making the first EOF mode the key pattern. However, additional modes can be extracted based upon their statistical differences based on North's rule of thumb [North *et al.*, 1982] by calculating the approximate sampling error ($\delta\lambda$) of a certain eigenvalue (λ):

$$\delta\lambda \approx \lambda\sqrt{\frac{2}{N}} \tag{2.10}$$

where N is the number of independent samples (i.e. number of ICES rectangles being used). The lower error for each eigenvalue is compared to the neighbouring upper error. If a group of eigenvalues lie with 1-2 $\delta\lambda$, the eigenvectors are assumed to be a random mixture of true eigenvectors [North *et al.*, 1982]. However, the mode of greatest explained variance is of greatest use here. Extracting the first mode meets the first objective in the EOF analysis: quantifying the spatial variation in temporal trends.

To address the second objective, finding areas of interest, two extremes were chosen in terms of eigenvector values. An area of positive change (e.g. a location where body size distribution increased) was compared to an area of negative change (e.g. an area where body size distribution decreased). Additionally, an area no change was also extracted. Areas of interest were used to investigate potential relative effects of different drivers on size-based indicators.

The average annual rate of change in SBIs and drivers were calculated by fitting a linear regression model at both the resolution of ICES statistical rectangles and for the North Sea as a whole. For environmental variables, monthly data were used that covered the same time period as the SBIs (1980–2008). A seasonal 30-year average (1971–2000) was calculated and removed to normalise the data prior to computing the yearly averages that were subsequently used in the trend analysis. The estimated trends and associated spatial standard errors were used to test the significance of temporal change in SBIs and drivers across the North Sea. This was performed using the Mann-Kendall test where the null hypothesis was rejected at the 95% level.

Relative effects of drivers on size-based change – NARMAX modelling

The use of the statistical model NARMAX (Non-linear AutoRegressive Moving Average with eXogenous input) in the final stage of analysis simply provides a demonstration of one way in which to use the results obtained through the EOF analysis. The popularity of NARMAX stems in part from its ability to (1) identify linear and non-linear relationships in data, (2) highlight quantitatively key explanatory variables that most strongly influence the dependent variable, (3) find the most likely relationship over a range of time lags, and (4) highlight whether explanatory variables change in importance over time. Full methodological details are provided in NARMAX specific papers [Wei *et al.*, 2010; Billings, 2013]. Provided here is a brief overview of the NARMAX concept. Below is the commonly used power-form polynomial representation of NARMAX:

$$
\begin{aligned}
y(t) = \theta_0 &+ \sum_{i_i=1}^{n} \theta_{i_1} x_{i_1}(t) \\
&+ \sum_{i_1=1}^{n} \sum_{i_2=i_1}^{n} \theta_{i_1,i_2} x_{i_1}(t) x_{i_2}(t) + \dots \\
&+ \sum_{i_1=1}^{n} \sum_{i_2=i_1}^{n} \dots \sum_{i_L=i_{L-1}}^{n} \theta_{i_1,i_2,\dots,i_L} x_{i_1}(t) x_{i_2}(t) \dots x_{i_L} + e(t)
\end{aligned}
\tag{2.11}
$$

where y is the measured output (here, a size-based metric), θ values are autoregressive, moving average and exogenous model parameters. The variable x is defined as:

$$
x_m(t) = \begin{cases} y(t-m) & 1 \leq m \leq n_y \\ u(t-(m-n_y)) & n_y + 1 \leq m \leq n_y + n_u \\ e(t-(m-n_y-n_u)) & n_y + n_u + 1 \leq m \leq n_y + n_u + n_e \end{cases}
$$

where x is made up of 3 terms: the measured output, y, which was taken as the mean maximum weight, a noise term, e, to allow error modelling, measurement errors/noise and unmeasured disturbances to be accounted for, and the explanatory variables, u, which was taken as sea bottom temperature, sea bottom oxygen, depth-integrated net primary production and fishing mortality, as well as their associated lags and all possible interactions between each individual and combined explanatory variable. The output term, y, explanatory terms, u, and noise terms, e, all have associated maximum time lags (therefore the number of variables between no lag and the maximum lag equals n_y, n_u, n_e, respectively).

The number of model terms included in the initial NARMAX model, M, is based on the degree of non-linearity, L, and the combined number of variables for output, explanatory, and error terms, n:

$$
M = \frac{(n+L)!}{[n!\,L!\,]} \tag{2.12}
$$

where $n = n_y + n_u + n_e$. For the model used here, this results in 84 potential model terms as $n = 6$ and $L = 3$. Running a model with this many variables is unrealistic, especially when so often in models and regressions there are only a few significant model terms (regressors) which account for the greatest variance. NARMAX is powerful in determining which and how many model terms should exist in the final model using the forward regression orthogonal least squares algorithm (FROLS) [Chen *et al.*, 1989; Wei *et al.*, 2004, 2010]. FROLS is efficient in model term selection and structure detection under a non-linear premise. In the most simplistic sense, the algorithm varies and tests each model term, and by comparing the corresponding output, each term is rated under the error reduction ratio (i.e. % variance change in the system when the individual model term is included – it is this metric that is used in the results). Terms that cause a statistically significant change in the output, even if small in variance, are included. If any explanatory variables are identical or very closely correlated, NARMAX will only choose one of the variables to avoid co-linearity. The FROLS algorithm thus forms a final parsimonious model. Readers are directed to Wei & Billings [2008] and Wei *et al.* [2010] for a comprehensive detailing on the iterative algorithm that includes the code to instruct the FROLS algorithm. These papers, and references within, provide detailed formulation and derivation of NARMAX, NARX and algorithms.

The model validation is complex as many 'standard' methods used to validate models are based on linear systems and thus are not suitable in nonlinear models. Therefore extended statistical validations (e.g. statistical correlation tests) and model predictive performance validation methods (e.g. reproduction of the system characteristics) were used to test the model following the protocol described in Chapter 5 of Billings [2013].

$\overline{W_{max}}$ was used as the measured output. This output and the explanatory variables were extracted from each area of interest as identified by the EOF analysis. To reduce bias, the same number of ICES rectangles were chosen ($I_n = 8$) in each area. The model estimation was conducted over 26 years (1980–2005), and the model test over the last 3 years (2006–2008), following a 90%/10% split which is the conventional practice for small sample modelling problems.

The strength of correlation between the model and empirical data was calculated using an r-squared value. The r-squared value (r_e^2) measures the ability of the model to characterise the trend in the output metric ($\overline{W_{max}}$) by comparing the error amplitude to the observation observation:

$$r_e^2 = 1 - \frac{\|E\|^2}{\|Y\|^2} \tag{2.13}$$

where E is an error vector $E = [e(1), e(2), ..., e(N)]^T$ where $e(t) = y(t) - y(t|t-1)$ and $t = 1, 2, ..., N$ with $y(t|t-1)$ being an instantaneously predicted value from the model, Y is a measured system response vector $Y = [y(1), y(2), ..., y(N)]^T$ and the symbol $\|\|$ is the norm of the vector. This r-squared value is used because $\frac{\|E\|^2}{\|Y\|^2}$ is known as the error-to-signal ratio in dynamical data modelling [Wei & Billings, 2008; Wei *et al.*, 2010; Billings, 2013]. This r-squared value thus gives an index of the models ability to follow the target output trend. As the model test only ran for three years, calculation of r_e^2 was problematic, particularly when the amplitude of observations was close to zero. Therefore, the Pearson correlation coefficient (r_p^2) was provided for the final 3 years to indicate the linear relationship between the model and empirical data when r_e^2 was unable to provide a value for the model performance.

2.3 Results

2.3.1 Spatial variation in temporal trends of size-based indicators

A significant trend in the North Sea LFI was identified as -0.0087 ± 0.0007 y^{-1}, equivalent to a reduction of 0.25 ± 0.021 between 1980 and 2008. Significant linear trends occurred in 96% of ICES statistical rectangles. Approximately 88% of ICES statistical rectangles showed a decline, with the remaining increasing. From the EOF analysis, the first mode accounted for 27% of the variance seen in Figure 2.5(a). The central North Sea LFI showed the greatest decrease whereas the Norwegian trench region showed the greatest increase. Waters east of northern England and Scotland showed, on average, very little change. The Skagerrak and Kattegat exhibited a slight decrease in LFI, whereas the southern North Sea exhibited variable results.

$\overline{W_{max}}$ showed the most prominent decline in size with a North Sea average annual change of -204 ± 21.5 gy^{-1} which equates to a reduction of 5916 ± 622

g between 1980 and 2008. Significant trends occurred across 48% of ICES statistical rectangles in the North Sea. The North Sea exhibited predominately a decrease in $\overline{W_{max}}$ with 79% of ICES rectangles showing a decline over the 29 years. In terms of spatial changes through time, the first mode accounted for 28.3% of the variance and followed the pattern seen in Figure 2.5(b). Similar to the LFI, the central North Sea exhibited the most substantial decline, whereas the Norwegian trench region witnessed the biggest increase in $\overline{W_{max}}$ values, although changes were an order of magnitude lower compared to the central North Sea increase. Results for the southern North Sea, Skagerrak and Kattegat were consistent with LFI changes.

The trend of the normalised biomass size spectrum slope was -0.021 ± 0.0015 y^{-1} and was significant when averaged over the entire region with 98% of ICES rectangles exhibiting significant temporal changes. Spatially, 86% of the ICES statistical rectangles showed a steepening of the size spectrum slope, with the remaining 14% showing an increase. The EOF first mode accounted for 26.6% of variance, the lowest of the three SBIs. This mode indicated decreased slope values (i.e. steepening of the slope) across large parts of the central North Sea, with increased slope values (i.e. slope becoming shallower) across north-eastern parts of the North Sea (Figure 2.5(c)). The southern North Sea showed patches of both increasing and decreasing slope values, but relatively low change levels compared to the central North Sea.

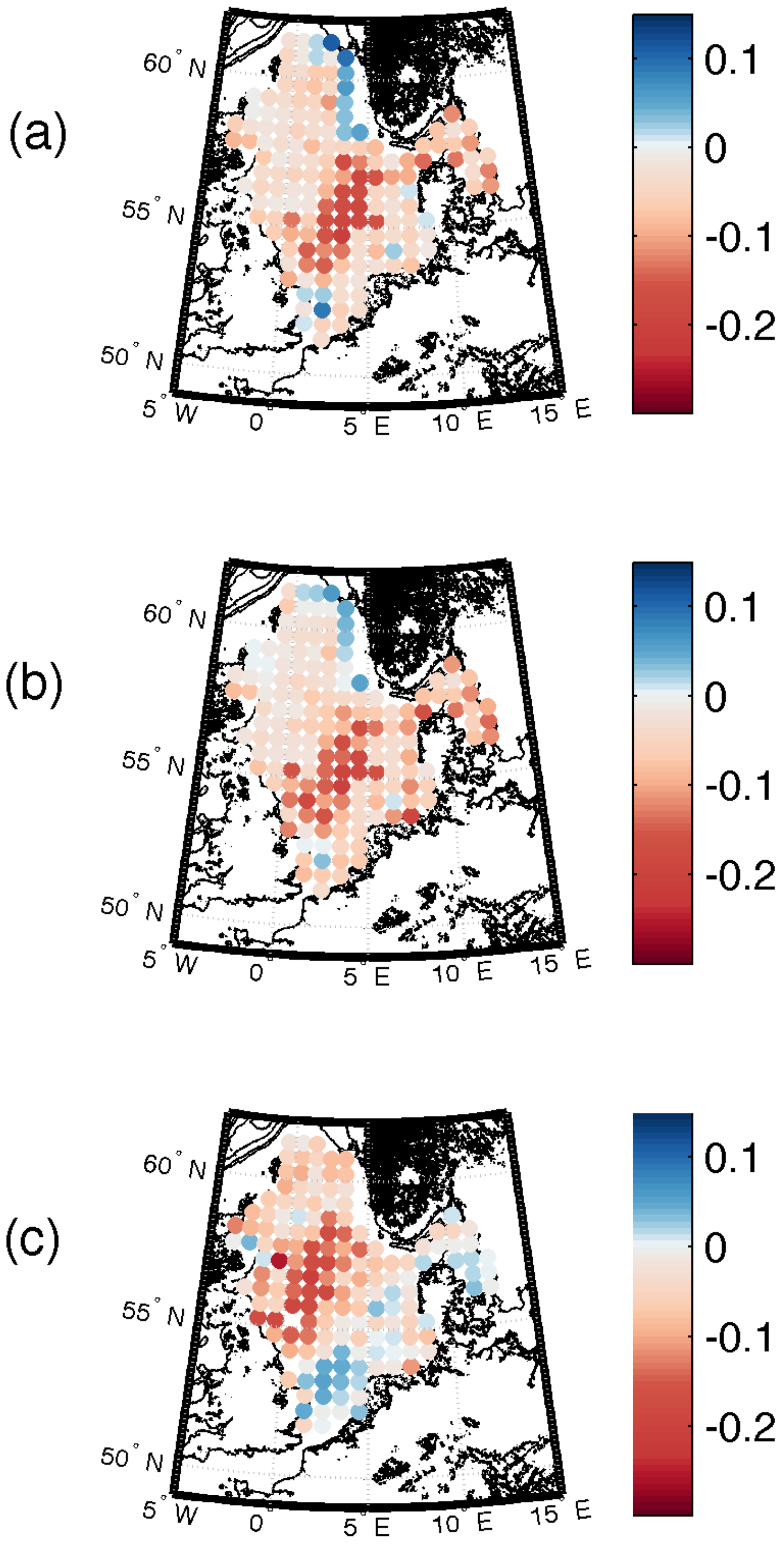

Figure 2.5: First mode from the Empirical Orthogonal Function analysis of three size-based indicators. This mode captures the main pattern of spatio-temporal variability. Modes are for (a) large fish indicator, (b) mean maximum weight, (c) normalised biomass size spectrum slope. All analysed over 1980–2008 using quarter 1 IBTS dataset.

To investigate the extreme values in SBIs, three contrasting areas ('areas of interest') were defined such that, after the EOFs were performed, eigenvectors (X) for the mean maximum weight acted as boundaries for the following areas:

$X < -0.157$ (and $< 6\,°$E) – central North Sea (negative change)
$X > 0.01$ – Norwegian trench region (positive change)
$\overline{X} \approx 0$ (58.5 – 59 °N, 2 °W–0.5 °E) – eastern Scottish coast (no change)

The area of no change was taken as the eastern Scottish coast as the EOF analysis indicated this to be an area of no change (i.e. mean of X, $\overline{X}$, ~0). This particular area is of interest, as opposed to other areas of no change, because previous research indicates communities are predicted to shift polewards due to climate change [Perry *et al.*, 2005; Pinsky *et al.*, 2013]. The selected no change region, however, has not shown this pattern. The boundaries of X were chosen to sample the same number of ICES rectangles ($I_n = 8$) from each region of change. Data from $\overline{W_{max}}$ were extracted for NARMAX, and the LFI and normalised biomass size spectrum slope in the same region were extracted for a comparison (Figure 2.6). The size spectrum slope was only averaged over seven ICES rectangles in the Norwegian trench region as rectangle 51F2 had been excluded for reasons explained in the Methods section. Similarities between the LFI and $\overline{W_{max}}$ compared to the size spectrum slope (Figure 2.6) are most easily seen in the central North Sea (-0.0029 ± 0.0008 y^{-1}, -857 ± 29.41 gy^{-1}, -0.053 ± 0.0033 y^{-1}, respectively). The size spectrum slope, LFI and $\overline{W_{max}}$ all indicate that the proportion of large fish declined from 1980 to 2008. Particularly from the late 1990s until 2005, the rate of decline of large fish proportionally was at its highest, picked up by all three indicators. In the Norwegian trench region, the size spectrum slope became slightly shallower throughout the time series (0.004 ± 0.0018 y^{-1}) despite more apparent increases in the LFI and $\overline{W_{max}}$ (0.009 ± 0.0023 y^{-1} and 218.69 ± 47.75 gy^{-1}, respectively). In fact, compared to the eastern Scottish coast (slope trend of -0.015 ± 0.0061 y^{-1}), the size spectrum in the Norwegian trench region was more steady. The LFI and $\overline{W_{max}}$ showed an increase off the east Scottish coast (17.51 ± 24.12 gy^{-1} and 0.0048 ± 0.0011 y^{-1}) although the trends were an order of magnitude lower compared to the other 'areas of interest'. The smaller changes along the eastern Scottish coast compared to the Norwegian trench region and central North Sea were expected as this area was highlighted by the EOF analysis of $\overline{W_{max}}$ to have seen little change over the 29-year period.

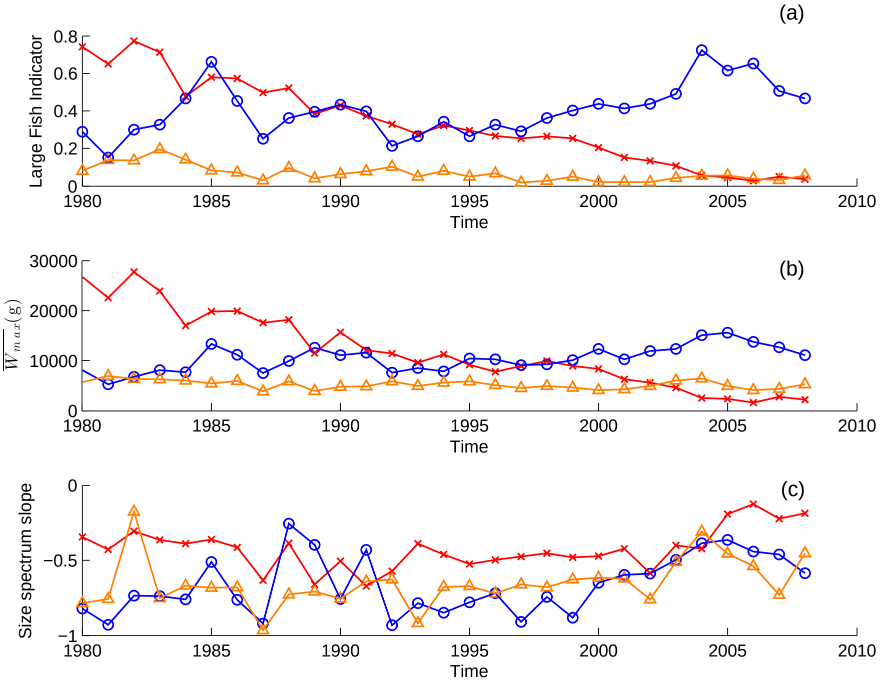

Figure 2.6: Time series of three size-based indicators in the three 'areas of interest' defined by EOF mode 1. Time series in 'area of interest' 1 (cross, red, central North Sea), 2 (triangle, orange, eastern Scottish coast), and 3 (circle, blue, Norwegian trench region) as defined by the Empirical Orthogonal Function analysis for (a) large fish indicator, (b) mean maximum weight (g), (c) normalised biomass size spectrum slope. Calculated over 1980–2008 using quarter 1 IBTS dataset.

2.3.2 Environmental conditions and fishing in the three 'areas of interest'

Sea bottom temperature, sea bottom oxygen, depth-integrated net primary production and relative fishing mortality were extracted in the three 'areas of interest' (Figure 2.7) for both comparative purposes and NARMAX analysis. However, due to the boundary of the GETM-ERSEM-BFM model being 60 °N, if a rectangle from $\overline{W_{max}}$ was at 60.5 °N, the closest rectangle was taken instead for environmental data.

Significant increases in sea bottom temperature change have occurred in

98.9% of the North Sea ICES rectangles with an average rise of $0.036 \pm 0.001\,^{\circ}$C y^{-1} equating to approximately $1.04 \pm 0.03\,^{\circ}$C increase over 29 years, in line with previous estimates [Holt *et al.*, 2012a]. In the central North Sea, eastern Scottish coast and Norwegian trench region, absolute temperatures were an average of $9.14 \pm 0.08\,^{\circ}$C, $8.09 \pm 0.06\,^{\circ}$C and $7.45 \pm 0.03\,^{\circ}$C and over the 29-year period trends were calculated as $0.05 \pm 0.002\,^{\circ}$C y^{-1}, $0.015 \pm 0.003\,^{\circ}$C y^{-1} and $0.008 \pm 0.004\,^{\circ}$C y^{-1}, respectively (Figure 2.7(a)).

A reduction in sea bottom oxygen was found across 87.6% of the North Sea. The average North Sea decrease in sea bottom oxygen was -0.26 ± 0.03 mmolm^{-3}y^{-1} over 1980–2008 which is an overall decline of 7.62 ± 0.73 mmolm^{-3}. The Norwegian trench region had much less oxygen available, an average of 223.7 ± 1.09 mmolm^{-3}, compared to the central North Sea with 249.5 ± 0.54 mmolm^{-3}, which itself was less than the eastern Scottish coast (256.8 ± 0.46 mmolm^{-3}) on average between 1980 and 2008. However, the central North Sea showed a greater decrease of oxygen of -0.50 ± 0.05 mmolm^{-3}y^{-1} compared to the Norwegian trench region of -0.36 ± 0.13 mmolm^{-3}y^{-1} and eastern Scottish coast of -0.18 ± 0.03 mmolm^{-3}y^{-1} (Figure 2.7(b)).

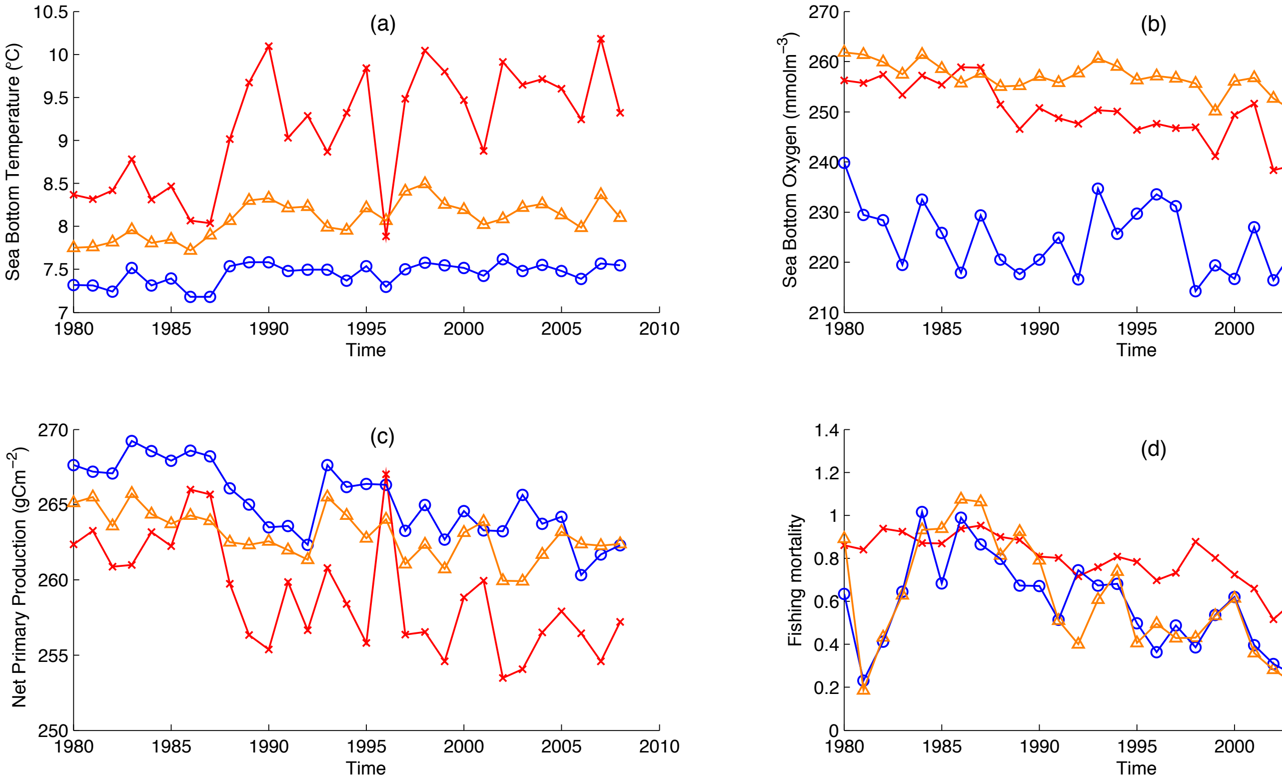

Figure 2.7: Time series of environmental and fishing data in the three 'areas of interest' defined by EOF mode 1. Time series over 1980–2008 in 'area of interest' 1 (cross, red, central North Sea), 2 (triangle, orange, eastern Scottish coast), and 3 (circles, blue, Norwegian trench region) as defined by the Empirical Orthogonal Function analysis for (a) sea bottom temperature, (b) sea bottom oxygen, (c) depth-integrated net primary production, (d) fishing mortality. (a)–(c) calculated from the GETM-ERSEM-BFM output; (d) calculated from the IBTS quarter 1 dataset and fishing mortalities from ICES.

Net primary production in the North Sea decreased in all areas, significantly so in over 94% of these areas. On average, primary production has decreased by -0.30 ± 0.02 gCm^{-2}y^{-1} equating to a 30-year decrease of 8.66 ± 0.47 gCm^{-2}. Regionally, the central North Sea averaged primary production was 259.0 ± 0.27 gCm^{-2} from 1980 to 2008, compared to a higher availability in the Norwegian trench region of 265.2 ± 0.35 gCm^{-2} and the eastern Scottish coast 263.0 ± 0.15 gCm^{-2}. Furthermore, the central North Sea primary production decreased by -0.27 ± 0.01 gCm^{-2}y^{-1} compared to the Norwegian trench region of -0.22 ± 0.06 gCm^{-2}y^{-1} and eastern Scottish coast of -0.11 ± 0.02 gCm^{-2}y^{-1}

(Figure 2.7(c)).

Over the course of 1980–2008, declines in the fishing mortality occurred in 96% of ICES rectangles. Across the North Sea, 93% of rectangles showed significant trends. At the North Sea scale, a trend of -0.018 ± 0.0005 y^{-1} was significant. Fishing mortality was highest, on average, in the central North Sea being 0.73 ± 0.07. The eastern Scottish coast and Norwegian trench region were broadly similar with averages of 0.51 ± 0.1 and 0.54 ± 0.08, respectively. Fishing mortality in the central region, eastern Scottish region and the Norwegian trench region decreased at similar rates of -0.020 ± 0.002 y^{-1}, -0.021 ± 0.001 y^{-1} and -0.016 ± 0.002 y^{-1}, respectively (Figure 2.7(d)).

The fishing effort shows differences between ICES divisions IVa, IVb and IVc (Figure 2.8). Division IVa, despite a sharp increase in the early 1980s, steadily declined until 1998 where a small rise has since occurred. Hours fished from 2003 showed a sharp decrease, which may coincide with EU fleet decommissioning, though it is somewhat sharper than has been recorded [European Parliament, 2013]. Effort in division IVb was an order of magnitude higher than in divisions IVa and IVc. Effort was steady from the early 1990s until a rise in 2000 but this is likely a mismatch in data. Data from Norway, however, show a substantial increase where effort tripled over a 6-year period. This increase is seen across the North Sea and while it has been weighted by landings, the relative change in all regions is the same. The missing Norway data (in hours fished) may account for some of the mismatches and for the sharp decline seen in hours fished in all the regions.

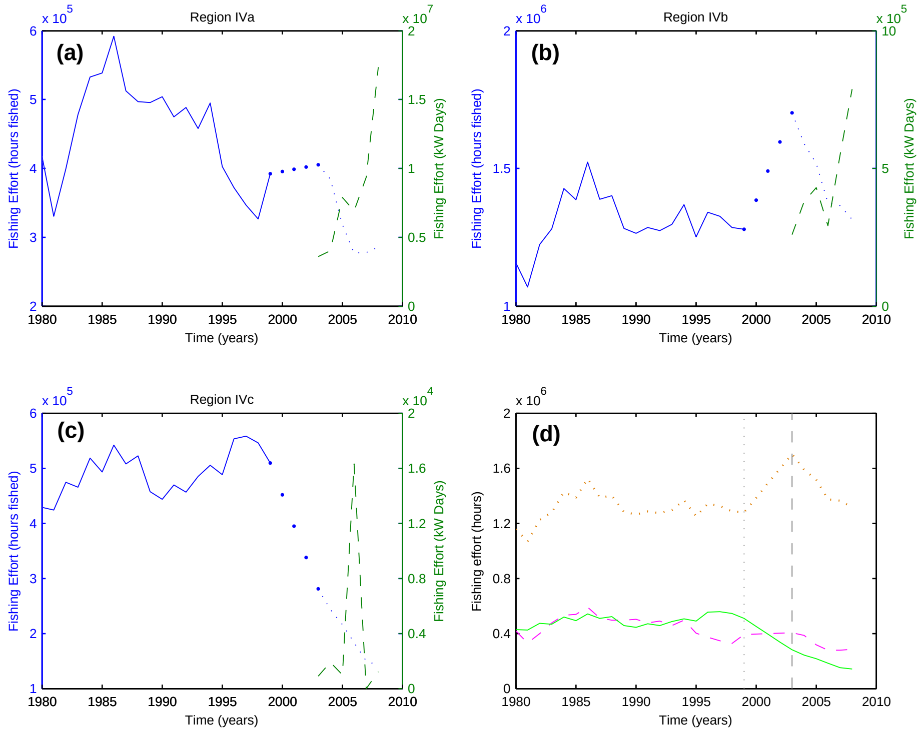

Figure 2.8: Time series of fishing effort for ICES division (a) IVa, (b) IVb, (c) IVc and (d) subarea IV. Time series where the line is straight is from Jennings *et al.* [1999] in hours fished, the single dots are interpolated points, the dotted line is data from the STECF in hours fished, and the dashed line is the Norwegian fishing effort in kW days in ICES division (a) IVa, (b) IVb and (c) IVc. All three divisions are shown in (d) with division IVa dashed, IVb dotted and IVc a straight line; the dotted vertical line is where the Jennings *et al.* [1999] data stops, and the dashed vertical line is where the STECF data starts. Effort data comes from England and Wales, Scotland, Germany, Norway, Denmark and Netherlands.

2.3.3 Relative effects of size-based change: implementing the NARMAX model

The NARMAX analysis showed that each 'area of interest' was influenced by different environmental and fishing conditions used in the model. Changes in the central North Sea were highly associated with fishing of the current year and the previous year (96%), along with temperature change and the interactions between these two (Table 2.1). Oxygen and net primary production showed little association with the decrease in $\overline{W_{max}}$ ($< 0.3\%$). The correlation between the model estimation and the raw data was very high ($r_e^2 = 0.993$ over 1980–2005). However, the amplitude of error in the original data compared to the model prediction was approximately the same (red line in Figure 2.9(a)) making the r_e^2 value for 2006–2008 unfeasible (therefore $r_p^2 =$

0.54). The trends between 2006 and 2008 in empirical and model prediction are very similar which is encouraging. However, the absolute values for the model prediction underestimated the $\overline{W_{max}}$ empirical data.

The NARMAX model suggested that the area of no change, the eastern Scottish coast, was most associated with net primary production (97%), with interactions of temperature, fishing and oxygen making up the final 3% (Table 2.1). The model estimation between 1980 and 2005 (Figure 2.9(b)) was able to track the data with confidence ($r_e^2 = 0.993$). Despite a changing environment with no obvious changes in the community size structure, the model still had good predictive accuracy for the final 3 years ($r_e^2 = 0.971$), especially for 2007 and 2008.

In the Norwegian trench region, where $\overline{W_{max}}$ increased, sea bottom temperature of 2 years prior was the main association (96%, Table 2.1). The remaining 4% was made up of the interactions of oxygen, fishing and temperature at different time lags. The correlation between the model prediction estimation and the raw data was very high ($r_e^2 = 0.991$ over 1980–2005). However, during the model prediction from 2006 to 2008, the model struggled to replicate the empirical data of $\overline{W_{max}}$ (Figure 2.9(c)) in 2008 with a resulting lower error-to-signal ratio ($r_e^2 = 0.951$ over 2006–2008).

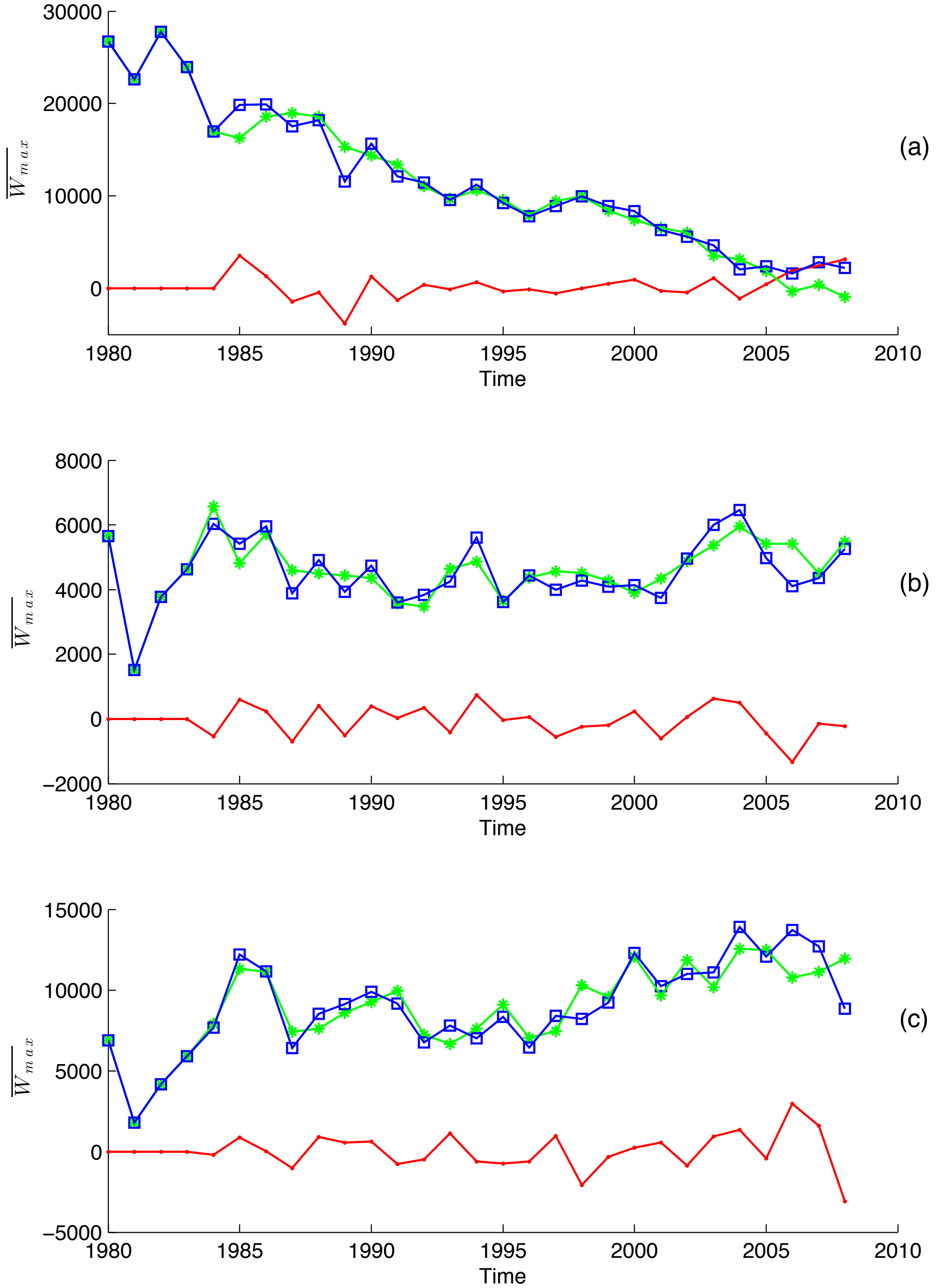

Figure 2.9: Results from NARMAX modelling of the mean maximum weight. Mean maximum weight in (a) 'area of interest' 1 - central North Sea, (b) 'area of interest' 2 - eastern Scottish coast, and (c) 'area of interest' 3 - Norwegian trench region. Blue squares are the observed data from the IBTS, green stars are the modelled data using NARMAX, red points are the difference between observation and prediction. The first 26 years (1980–2005) were used for model estimation; the final 3 years (2006–2008) were used for testing the model.

Table 2.1: NARMAX model results for 'area of interest' 1 (central North Sea), 2 (eastern Scottish coast) and 3 (Norwegian trench region). Index terms (Column 2) highlight order of importance of driving variable (i.e. environment/fishing) to the output (i.e. mean maximum weight). Model term (Column 3) describes each variable where Temp = sea bottom temperature, FM = fishing mortality, Netpp = depth-integrated net primary production, Oxy = sea bottom oxygen. All are a function of t = time (years). Contribution (Column 4) describes how much the model term contributes (%) to the change in mean maximum weight.

Area of Interest	**Index**	**Model term**	**Contribution (%)**
1 (CNS)	1	FM(t) * FM(t-1)	95.68
	2	Temp(t-1) * FM(t-1)	1.49
	3	FM(t-2) * FM(t-4)	0.91
	4	Temp(t) * Temp(t-1)	0.23
	5	Oxy(t-4) * FM(t-1)	0.17
	6	Netpp(t-1) * FM(t-1)	0.27
2 (ESC)	1	Netpp(t-3) * Netpp(t-3)	96.77
	2	Temp(t) * Oxy(t-1)	0.69
	3	Temp(t-2) * FM(t-2)	0.72
	4	Temp(t-2) * Oxy(t-3)	0.58
	5	Temp(t-2) * NetPP(t-4)	0.32
	6	FM(t-4) * Netpp(t-4)	0.06
3 (NTR)	1	Temp(t-2) * Temp(t-2)	95.78
	2	Temp(t-2) * Oxy(t)	1.51
	3	Temp(t-4) * FM(t-4)	0.72
	4	Netpp(t) * FM(t-4)	0.65
	5	Temp(t-2) * FM(t)	0.19
	6	Netpp(t) * FM(t)	0.35

2.4 Discussion

This study revealed substantial spatial heterogeneity around a 30-year decline in community size structure for the North Sea Large Marine Ecosystem. All three size-based indicators (SBIs), which are widely used in research and policy, showed regions of distinct and opposing patterns at smaller spatial scales. The spatio-temporal heterogeneity was similar for the LFI and $\overline{W_{max}}$ but differed slightly for the size spectrum slope. The combination of EOF analysis with NARMAX showed how identification of this mathematically defined spatial scale could help guide subsequent investigation of key drivers of change. To illustrate this, the focus was on $\overline{W_{max}}$ as an indicator of community size structure and detected different patterns of change along with potential drivers in the contrasting 'areas of interest'. In the Norwegian trench, increasing community size structure corresponded with increasing temperature, whereas decreasing size structure in the central North Sea was more strongly associated with changes in fishing mortality rates.

Ecosystems such as the North Sea are often studied as uniform systems for the purposes of regional assessment [Greenstreet & Rogers, 2006; Blanchard *et al.*, 2012; Brotz *et al.*, 2012; Fung *et al.*, 2012]. Other approaches use the biological and physical properties of the system itself to define appropriate sub-regions *a priori* [Zwanenburg *et al.*, 2002; van der Lingen *et al.*, 2006; Wang *et al.*, 2010; van Leeuwen *et al.*, 2015]. This approach instead directly quantifies the spatial structure in the temporal trends, allowing for interactions between drivers such as fishing and the environment to influence the system without any one driver defining its state that might consequently be used in defining a certain spatial area. The resulting high-resolution outputs are especially appropriate for management and policy. For instance, using this EOF-NARMAX framework, the spatial breakdown of regions could be used to inform where regulations are most likely to be effective for safeguarding important ecological measures such as community size structure. Although larger scale assessments for size-based indicators, species biodiversity, abundance and trophic level are appropriate for reporting ecosystem states, the use of ecological indicators to support spatial management has thus far been limited. The finding that trends and potential drivers of community size-based indicators vary across the North Sea strongly advises against a 'one size fits all' approach to management, an approach which could simultaneously lead to both under- and over-regulation in different areas, potentially impacting the well-being of fishery and fishers.

The varying environmental conditions and fishing pressure in the different regions alone are noteworthy. For example, compared to the Norwegian trench, the central North Sea is warmer (with a greater trend of warming), shows oxygen decreasing at a faster rate, has lower primary production (with a greater decreasing trend), and has consistently higher fishing mortality rates. The eastern Scottish region is almost an environmental intermediate between these two areas, with only the sea bottom oxygen levels being the most favourable compared to each region. The fishing effort (hours fished) for both ICES divisions IVa (i.e. eastern Scottish coast and Norwegian trench region) and IVb (i.e. central North Sea) have decreased since 2000 although fishing in division IVb in absolute terms is far greater. These conditions point towards a more hostile environment for many demersal species across the North Sea, particularly the central North Sea. Whether the positive (negative) change in the community size structure in the Norwegian trench region (central North Sea) associated with temperature (fishing) is an indirect (direct) effect reflecting worsening habitat conditions in the central North Sea cannot be determined from this analysis. Changes in the community size structure can be altered from changes at the individual level (such as temperature driving growth variability, or human induced evolution) and/or the population level (through shifts and removal). The framework here is not able to definitively attribute mechanisms of any localised change but instead shows where the changes are and the relevant strongest environmental/fishing association. Unfortunately, environmental changes in the Norwegian trench region are tending towards less suitable conditions, though at a much slower rate. Despite the cold temperatures in this region, the oxygen concentration level is lower than the warmer central North Sea (Figure 2.7a,b) due to warm, salty, oxygen-deplete waters from the North Atlantic being forced into the deep trench. At this depth, waters cool but are unable to become oxygenated at the surface because of the year-round saline stratification resulting from the much fresher Baltic outflow (which is less dense than the saltier North Sea and Atlantic waters). Therefore, if demersal species deepen, as into the Norwegian trench region [Dulvy *et al.*, 2008], the species would be driven out of the warmer areas into cool areas but at a cost of reduced oxygen availability. However, a fish's metabolism reduces in cooler waters [Brown *et al.*, 2004] so an analysis of scope for growth for each species could help determine the true bioenergetic cost of this deepening [Claireaux & Lefrançois, 2007]. This also highlights that cold waters do not always have more oxygen than warm waters, thus species are not always likely to be better off in cold waters on the assumption that these contain more oxygen. Concentration is affected by spring blooms, currents, mixing, ventilation and water masses [Stendardo & Gruber, 2012; Queste *et al.*, 2013], whereas oxygen solubility and saturation (i.e. the amount of oxygen the water is capable of containing) are bounded by temperature.

The spatial heterogeneity in drivers of the observed indicators of demersal fish community structure revealed by the NARMAX analysis is in general agreement with previous findings. For instance, in the central North Sea fishing pressure is known to be heavy [Jennings *et al.*, 1999; Mills *et al.*, 2007], highlighted both by fishing effort and landings data. The direct removal of individuals, and the resulting released predation pressure [Daan *et al.*, 2005], has been reported as a primary driver of decreases in the abundance of large fish and community size structure [Jennings & Blanchard, 2004; Blanchard *et al.*, 2005] with potential induced evolution occurring [Rowell, 1993; Law, 2000; Grift *et al.*, 2003].

Differences in the temporal variability and changes in the size spectrum slope compared to LFI and $\overline{W_{max}}$ may reflect differences in their intrinsic variability and sensitivity to drivers. Across the North Sea, the EOF first modes are comparable. However, when specific regions are extracted, the size spectrum slope appears to track changes consistently with the LFI and $\overline{W_{max}}$ under fishing (i.e. central North Sea) compared to temperature changes (i.e. Norwegian trench region). The stronger response of the size spectrum to fishing compared with temperature has been suggested previously [Blanchard *et al.*, 2005], and will likely relate to the different time scales and mechanisms that temperature and fishing are associated with. This highlights the need to use a variety of size-based indicators to understand changes to the community size structure that are likely to be influenced by both fishing and environmental effects. While modelling work has shown effects of fishing on the community size structure, environmental variability is often assumed to be part of the modelling error [Blanchard *et al.*, 2014; Thorpe *et al.*, 2015]. Therefore, further work is required to understand how different mechanisms that influence the structure of body size distributions in communities respond to explicitly defined multiple stressors (e.g. environmental, fishing, chemical, pollution).

Fishing is known to have wide-ranging effects on North Sea fish abundance [Jennings & Blanchard, 2004]. However, the use of a proxy for fishing pressure had to be employed because long-term, continuous data of spatially-resolved fishing effort across all North Sea fishing nations does not exist. Recent advances in the use of vehicle monitoring systems [Mills *et al.*, 2007] and collections through the Scientific, Technical and Economic Committee for Fisheries (STECF) has brought together high-resolution fishing effort across the North Sea. Due to different measurements of fishing effort (e.g. days fished, kilowatts days, fleet capacity) and countries recording data at different spatial resolutions, it is still currently impossible to compile a complete fishing effort time series. Jennings *et al.* [1999] showed how international collaboration can provide high-resolution fishing effort whilst respecting fisherman confidentiality, and making such protocols routine practice would certainly improve the understanding of the true extent of fishing in the North Sea. Nevertheless, even with existing data, hopefully the EOF-NARMAX framework has proved effective in a fisheries context.

The implementation of an EOF analysis will often result in several modes, each one describing how much variance a spatial pattern can explain. In this study, all EOF modes, other than the first, for each SBI explained $< 9\%$ of the pattern variance thus only the first EOF mode was considered. However, it is always important when using EOF analysis to check modes beyond the first to determine whether the other modes need to be considered (i.e. ones of similar/large variance to the first mode). The use of North's rule of thumb can determine whether the modes are statistically different [North *et al.*, 1982]. Additionally, it is not unusual to look at several modes [Lorenz, 1956; Yeh & Kirtman, 2005; Messié & Chavez, 2011]. The number of extracted modes can be determined by having a mode threshold e.g. over 10% [Yeh & Kirtman, 2005] or extracting all modes which are significantly different from one another [North *et al.*, 1982]. While individual modes can be interpreted as being driven by individual dynamics, this is only the case when the dynamics are stable and linear [Monahan *et al.*, 2009] something often seen with geophysical parameters. Often using other methods such as VARIMAX to cross compare with standard EOF modes can strengthen the understanding of the dynamics underlying a mode, if it exists [Dommenget & Latif, 2002]. Here EOFs are simply used to determine the different spatial heterogeneity in the ecosystem response. The use of EOFs to breakdown (particularly) geophysical drivers can give greater insight though it is important to remember the stability of the driver and thus the interpretation of the EOF mode [Monahan *et al.*, 2009].

Due to the complexity of biological systems, EOFs for ecosystem response should be used primarily to determine heterogeneity and appropriate scale for investigation, not for predicting an individual driver for each mode.

A caveat to the NARMAX modelling in this specific study is that the measure of fishing mortality only represents 68% of the demersal fish community biomass. However, the remaining 32% are not target species and therefore the fishing mortality for those species is expected to be low. Additionally, both fishing mortality and the mean maximum weight use biomass in their calculation, potentially introducing a bias. In response to this, however, there are 4 opposing arguments: (1) these two calculations are different and relative, not absolute under biomass, (2) NARMAX performs autocorrelation checks to ensure there is no bias, (3) if there was a bias, all areas of interest would be dominated by fishing, which was not the case, and (4) as outlined above, the fishing effort data used, while imperfect, are currently the best available.

Fisheries provide an obvious application for the EOF-NARMAX framework due to the existence of spatially extensive long-term survey data as well as a good understanding of potential drivers of community change. However, these statistical techniques can be of use in other ecological contexts where both suitable biological data [Loh *et al.*, 2005; Cefas, 2014; McClatchie *et al.*, 2014] and long environmental time series [Robock *et al.*, 2000; Reynolds *et al.*, 2002; Rayner *et al.*, 2003; Gregg *et al.*, 2005; Garcia *et al.*, 2013b,a] are available. The use of kriging [Morfin *et al.*, 2012] or specially formulated EOF algorithms [Taylor *et al.*, 2013] allows the use of EOFs in the presence of data gaps. NARMAX is powerful over long time periods [Bigg *et al.*, 2014] as it has the ability to quantitatively determine the extent to which individual drivers are associated with changes, and when in time they dominate. It is recommended that the time series is not much shorter than 30 years to ensure the greatest accuracy from NARMAX. The EOF-NARMAX framework has great potential to spatially resolve past ecological changes and associations with potential drivers and to thus help predict how communities might respond to future global change scenarios.

As a specific case study of the utility of the EOF-NARMAX framework, in this analysis heterogeneity in patterns of three key size-based indicators of

North Sea demersal fish community structure have been revealed and subsequently an example was provided of how one indicator was associated under multiple conditions. This enabled the distinctive regions where community changes were strongly associated with temperature and fishing to be determined. These drivers are expected to change in the future [Stocker *et al.*, 2013; FAO, 2014], with possible negative consequences for dependent economic activities. Therefore, the management of North Sea fisheries should take into account the multifaceted effects seen across different regions.

Chapter 3

A size-structured model

In the 1970s the collection of empirical data on body size and other traits had become sufficient to allow the start of size-structured ecosystem modelling using basic trophic processes [Kerr, 1974; Sprules & Barth, 2016]. 40 years on, complex food-web models have been pioneered such that they are used for global research and fisheries management [Andersen *et al.*, 2016]. The use of size-structured models has two distinct advantages in the role of ecosystem modelling. Firstly, highly complex ecosystems can be simplified by the use of a single value, body size, due to the correlations between size and many life-history traits as described in the Introduction. Secondly, size-structured ecosystems are found across the globe from bacteria through to whales [Sheldon *et al.*, 1972; Blanchard *et al.*, 2017] making size-based modelling adaptable across marine ecosystems. Model development is an ongoing area of research with each mechanism within models being improved through statistical methods [Spence *et al.*, 2016], empirical investigation, and model testing [Andersen & Beyer, 2006; Andersen & Pedersen, 2010; Hartvig *et al.*, 2011; Blanchard *et al.*, 2014]. It is the latter of these which makes up the remainder of this thesis. By testing and evolving the growth section of an established, multi-species size-structured model with the inclusion of environmental and time-dependent factors, the aim is to improve our understanding of fisheries under a changing climate.

The baseline model (i.e. no time dependence or environmental factors) described here is the multi-species, size-structured model of Blanchard *et al.* [2014] parameterised for the North Sea. The model mathematics come from the theoretical food web framework proposed by Hartvig *et al.* [2011], developed over a decade to incorporate the complexity seen today [Andersen & Beyer, 2006; Andersen & Pedersen, 2010]. This published model is used throughout this thesis with largely identical mathematical formulations. This chapter sets out the model in terms of ecosystem processes. Parameter estimation and some in depth mathematical derivations have been left out here, and instead the references (mainly [Hartvig *et al.*, 2011; Blanchard *et al.*, 2014]) are highlighted. Amendments to the published models are noted here. This provides the basis for the novel extensions developed in this thesis involving the incorporation of environmental modifications at the individual level (Chapter 4).

3.1 Individual level dynamics

3.1.1 Growth

The somatic growth ($\frac{dw}{dt}$) of an individual species (i), that is the change in mass over time, can be physiologically described by simple bioenergetics of an energy in and energy out process defined as:

$$\frac{dw}{dt} = (\alpha f_i h_i w^n - k_i w^p)(1 - \psi_i) \tag{3.1}$$

This equation will be broken down and derived in three separate components: (1) energy intake, (2) energy expenditure, and (3) reproduction.

Energy intake

The energy intake is represented by lefthand side of the first set of parentheses of equation 3.1 and is:

$$\alpha f_i h_i w^n \tag{3.2}$$

where α is the assimilation efficiency, f_i is the feeding level, and $h_i w^n$ is the maximum intake rate where h_i and n is the prefactor and exponent for the maximum intake, respectively. α is taken here as 0.6, estimated by energy expenditure of food processing and food lost through excretion [Hartvig *et al.*, 2011]. This value falls in line with other empirical assimilation efficiencies within aquatic species [Welch, 1968; Buckley *et al.*, 2000; Liu *et al.*, 2010]. The feeding level, f_i, is incorporated to allow for food-dependent growth, i.e. the food intake is not constant. Food intake varies according to prey size and preference of the predator, along with prey availability ($0 < f_i < 1$). This is calculated in part by using the interaction matrix described in the Community level dynamics section of this chapter.

The maximum intake rate prefactor (h_i) is notoriously difficult to define. Biologically, the maximum intake rate is the time a predator requires to consume its prey, whether limited by handling time or gut evacuation [Englund *et al.*, 2011]. Empirically, very little work has been done on this, and so often the calculation must be made by other mathematical means. Under different models, community, trait, and multispecies, the value of h_i is altered in order to parameterise the model [Scott *et al.*, 2014]. In Hartvig *et al.* [2011], the value of h_i is taken empirically, while Blanchard *et al.* [2014] calculate it theoretically but assume metabolism is zero (metabolism is used in the calculation of h_i). Here metabolism is assumed to be greater than 0. The inclusion of such is important as it is influenced by temperature, something incorporated later in this thesis. Using previous methods to calculate h_i [Blanchard *et al.*, 2014], the following is used:

$$h_i = \frac{3K_i \sqrt[3]{W_{\infty,i}}}{\alpha f_i - k_i} \tag{3.3}$$

where K_i is the von Bertalanffy growth factor, $W_{\infty,i}$ is the asymptotic weight, k_i is the metabolism, and the rest are as previously described. Blanchard *et al.* [2014] used the 97.5th percentile of the von Bertalanffy factors (K_i and $W_{\infty,i}$) for each species (i). Here, plaice, gurnard and haddock values are still taken from the 97.5th percentile, the remaining species use the mean von Bertalanffy factors. Ideally the mean would be used for all species (for reasons relating to changes in maximum size described in Chapter 4, and based on the work of Baudron *et al.* [2014] and van Rijn *et al.* [2017]). However the 97.5th percentile needed to be used for plaice, gurnard and haddock otherwise the growth of these would not conform to empirical data. Equation 3.3 is derived by equalling the growth seen in the first set of parentheses on the righthand side of equation 3.1 (growth = $\alpha f_i h_i w^n - k_i w^p$) to the von Bertalanffy growth of a juvenile fish [Andersen *et al.*, 2009]: growth = $3K\sqrt[3]{W_\infty} w^n$. This is then rearranged for h_i. In order for equation 3.3 to be solved for h_i, the exponents of metabolism (p) and the maximum intake rate (n) must be identical. This, along with the metabolism calculation, is described in the next section. In Blanchard *et al.* [2014] and Scott *et al.* [2014] there was an assumption that metabolism was negligible and was thus ignored for parameterising the model. It is reintroduced here due to the importance temperature has on metabolism.

The exponent of the maximum intake rate, n, is set to 0.7 [Jobling, 1994; Andersen & Pedersen, 2010; Hartvig *et al.*, 2011].

Energy expenditure

The energy expenditure (righthand side of the first set of parentheses in equation 3.1) is calculated as:

$$k_i w^p \tag{3.4}$$

where k_i and p is the prefactor and exponent for metabolism, respectively.

The exponent of metabolism has long been debated, initially with estimates between $\frac{2}{3}$ [Rubner, 1883; Winberg, 1956] and $\frac{3}{4}$ [Kleiber, 1932; Gillooly *et al.*, 2001; Brown *et al.*, 2004], though it is $\frac{3}{4}$ which is generally accepted and used under the universal metabolic theory of ecology (MTE) [Brown *et al.*, 2004]. Realistically, there is a wide range of p values both within and across taxa [Kooijman, 2000]. In teleost fish alone a wide range of exponent values has been found ($0.3 < p < 1.125$) though this research was conducted using species across polar to tropical climes [Clarke & Johnston, 1999]. Therefore due to the range of values found for individuals, a value for p is taken to be 0.7. This allows the model to be both biologically sound and allows for mathematical ease now that $n = p$.

The value of k_i is taken as $0.12h_i$. This has both an empirical and theoretical basis. Empirically it has been shown that the metabolic rate is approximately $10 - 20\%$ of the maximum intake rate [de Roos *et al.*, 2008; Hartvig *et al.*, 2011]. Theoretically, k_i can be calculated when $\frac{dw}{dt} = 0$. This can be determined by allowing the feeding level (f_i) to be at a critical level (f_c):

$$0 = (\alpha f_c h_i w^n - k_i w^p)(1 - \psi_i) \tag{3.5}$$

The biological meaning of f_c is such that the food eaten, once assimilated and digested, is just enough to cover metabolic costs. Therefore by dividing through by the second parenthesis and subtracting the metabolism from each side, and rearranging for the metabolic prefactor, the resulting equation is:

$$k_i = \alpha f_c \frac{h_i w^n}{w^p} \tag{3.6}$$

As $n = p$, and we know values for α (0.6) and assume a critical feeding level of 0.2 [Hartvig *et al.*, 2011], we are left with $k_i = 0.12h$.

As can be seen, if $n \neq p$ then the calculation of k_i would be (somewhat unnecessarily) more complicated. Additionally, k_i would not always be 12% of the maximum intake rate because the weight for the maximum intake and metabolism would have different scaling exponents. By allowing $n = p$ means additional numerical complications are avoided and computational time is saved by avoiding the recalculation of k_i at every time step and weight class for each species. Additionally, the calculation of the maximum intake rate prefactor is also simplified (as described in the Energy expenditure section above). This is satisfied by knowing, as shown with previous research, that $n = p$ is biologically plausible. Another process which benefits analytically from $n = p$ is the reproduction allocation ruling.

Reproduction

Before an individual is at a specified maturation size, no energy is used for any maturation or reproductive process. Therefore change in somatic weight for a juvenile is:

$$\frac{dw}{dt} = \alpha f_i h_i w^n - k_i w^p \tag{3.7}$$

When an individual reaches a preset maturation weight, $w_{m,i}$, energy is diverted into reproduction $(1-\psi_i)$ as described in equation 3.1. The maturation weight used for each species was taken from Blanchard *et al.* [2014] which used a variety of empirical data from the North Sea to determine the maturation size in the 95th percentile. When an individual reaches $w_{m,i}$, the amount of energy that is allocated for reproduction assumes the gonad size (i.e. allocation of energy to reproduction) is proportional to individual mass. This can be written as:

$$\psi(w, w_{m,i})\overline{E}(w) = cw \tag{3.8}$$

where $\psi(w, w_{m,i})$ is the allocation, $\overline{E}(w)$ represents the energy in and energy out under a fixed feeding level (f_f, i.e. $\alpha f_f h_i w^n - k_i w^p$), and c is a constant to be determined. This is rearranged to the form:

$$\psi(w, w_{m,i}) = \frac{cw}{\overline{E}(w)} \tag{3.9}$$

The constant c can be determined when an individual reaches their given maximum size, thus $\psi(W_{\infty,i}, w_{m,i}) = 1$. Using this in equation 3.9 results in $1 = \frac{cW_{\infty,i}}{\overline{E}(W_{\infty,i})}$ which can be rearranged to solve for c: $c = \frac{\overline{E}(W_{\infty,i})}{W_{\infty,i}}$. By putting the new c equation into the original allocation equation (equation 3.9):

$$\psi(w, w_{m,i}) = \frac{\overline{E}(W^n_{\infty,i})w}{\overline{E}(w)W_{\infty,i}} \tag{3.10}$$

In order to simplify this equation, it is assumed $n = p$ such that $\overline{E}(w) = \alpha f_f h w^n - k_s w^p$ becomes $\overline{E}(w) = (\alpha f_f h - k_s)w^n$. For ease, $S_i = (\alpha f_f h_i - k_i)$. This allows the righthand side of equation 3.10 to be written as:

$$\frac{S_i W^n_{\infty,i} w}{S_i w^n W_{\infty,i}} \tag{3.11}$$

Here the S_i values cancel out and thus with the use of exponent power laws we get:

$$\left(\frac{W_{\infty,i}}{w}\right)^n \left(\frac{w}{W_{\infty,i}}\right) \tag{3.12}$$

As $\left(\frac{W_{\infty,i}}{w}\right)^n$ can also be written as $\left(\frac{w}{W_{\infty,i}}\right)^{-n}$, this gives $\left(\frac{w}{W_{\infty,i}}\right)^{-n} \left(\frac{w}{W_{\infty,i}}\right)$ which can be simply written as $\left(\frac{w}{W_{\infty,i}}\right)^{1-n}$. Therefore the allocation final equation is:

$$\psi(w, w_{m,i}) = \left(\frac{w}{W_{\infty,i}}\right)^{1-n} \tag{3.13}$$

However in order for a smooth transition from just maturating (i.e. $w_{m,i}$) to fully grown (i.e. $W_{\infty,i}$) a step function needs to be incorporated into the equation [Hartvig *et al.*, 2011]. This allows the amount of energy being diverted to reproduction to go smoothly from 0 to 1 resulting in biphasic growth trajectories [Ursin, 1967; Lester *et al.*, 2004; Hartvig *et al.*, 2011], similar to that of the von Bertalanffy growth function (i.e. asymptotic but determined by different bioenergetic assumptions). Therefore the final allocation reproduction equation becomes:

$$\psi_i(w) = \left[1 + \left(\frac{w}{w_{m,i}}\right)^{-10}\right]^{-1} \left(\frac{w}{W_{\infty,i}}\right)^{1-n} \tag{3.14}$$

Both $W_{\infty,i}$ and $w_{m,i}$ are given values for each species, i.

3.1.2 Mortality

Each individual species at different weight classes is subjected to a certain mortality rate represented by 4 probabilities that are size-dependent: natural (μ_n), starvation (μ_s), predation (μ_p), and fishing (μ_f):

$$\mu_i(w) = \mu_{n,i} + \mu_{s,i} + \mu_{p,i} + \mu_{f,i} \tag{3.15}$$

Natural mortality is death through anything other than starvation, predation or fishing, such as senescence or disease. It is taken to be species dependent (determined through size) and uses the assumption that natural mortality in fish declines with size, in the postlarval stages at least [Peters, 1983]. Natural mortality is calculated here as $\mu_{n,i} = \mu_0 W_\infty^{n-1}$ [Peterson & Wroblewski, 1984; Andersen & Pedersen, 2010; Gislason *et al.*, 2010; Bevacqua *et al.*, 2011; Hartvig *et al.*, 2011] where μ_0 is the background mortality (0.6 – [Blanchard *et al.*, 2014]), and the resulting exponent here of -0.3 falls in line with empirical exponents of -0.24 – -0.43 [Peterson & Wroblewski, 1984; Lorenzen, 1996; Gislason *et al.*, 2010]. The use of *n-1* is used to reduce additional computational coding, thus merely a form of convenience.

The starvation mortality here is assumed to be negligible and so ignored.

Predation mortality is given for each species of each size that is ingested, calculated as:

$$\mu_{p,i} = \sum_{j} \int \phi \left(\frac{w_p}{w} \right) (1 - f_i(w)) \gamma_j w^q \theta_{j,i} N_j(w) dw \tag{3.16}$$

where ϕ is the predator preference (see the Community level dynamics section), w_p is the prey weight, f_i is the feeding level of predator j, γ_j is the search rate, θ is the predator-prey interaction matrix (see the Community level dynamics section), and N_j is the predator abundance.

Fishing mortality is calculated for each species and size class by multiplying the size-dependent selectivity, effort and catchability together. The selectivity can either be knife edge (where each population is caught above a certain weight), or trawling (selectivity is sigmoidal across weights), thus is determined by species, weight and gear type (i.e. the selectivity ranges between 0 and 1 to reflect the ability of gears to catch specific species of a given size). The effort is set by the gear, and here is set to one for the baseline model. Finally, the catchability is calculated using the mean fishing mortality for each species averaged from 1985–1995 from the North Sea ICES stock assessment database [Blanchard *et al.*, 2014].

3.2 Population level dynamics

In the Individual level dynamics section the equations described can be applied to any species as long as three values are provided for each species: asymptotic weight (W_∞), maturation weight (w_m), and the von Bertalanffy growth parameter (K). An assumption is made that each individual species is representative of their whole population (e.g. all cod individuals are identical), while being different from other species (so cod and haddock are different based on W_∞, w_m, and K). Therefore to scale from the individual to the population level the partial differential equation often used in age-structured modelling can be used here. It is synonymous with the conservation equation and known as the McKendrick-von Foerster equation:

$$\frac{\partial N_i(w)}{\partial t} = -\frac{\partial g_i(w) N_i(w)}{\partial w} - \mu_i(w) N_i(w) \tag{3.17}$$

where $N_i(w)$ is the number of individuals in weight class w, t is time (where ∂t is set to 0.25 to avoid mathematical oscillations [Spence *et al.*, 2016]), g_i is the growth of an individual (equation 3.1), and μ_i is the mortality (equation 3.15). The first term on the righthand side is shown as negative because this form represents a flux, effectively the movement of individuals across weight classes. This equation is bounded by recruitment.

3.2.1 Recruitment

Recruitment refers to the gain of individuals into a new stock group. In modelling terms, it is the number of individuals entering the smallest size group of a given species', i, size spectrum. Empirically, recruitment relationships are notoriously difficult to calculate and are a source of great uncertainty. Statistical methods have helped improve model parameters, particularly in the case of recruitment [Spence *et al.*, 2016]. Recruitment, R_i is density-dependent and calculated using egg production, resulting in the Beverton-Holt stock-recruitment relationship:

$$R_i = R_{max,i} \frac{R_{p,i}}{R_{p,i} + R_{max,i}} \tag{3.18}$$

where $R_{max,i}$ is the maximum recruitment flux of a given species taken from an updated and new analysis by Spence *et al.* [2016], as opposed to the values originally used in the North Sea study [Blanchard *et al.*, 2014]. The new analysis uses a Bayesian approach resulting in an improved assessment of parameter uncertainty. The egg production ($R_{p,i}$) is calculated by:

$$R_{p,i} = \frac{\epsilon}{2w_0} \int N_i(w) g_i \psi_i(w) dw \tag{3.19}$$

where ϵ is the efficiency of reproduction (proportion of energy used to reproduce, with the remaining energy lost), w_0 is the egg weight (0.5), g_i is the effective juvenile growth (equation 3.7), ψ_i is calculated from equation 3.14, N_i is the number of individuals in a given weight class, and $\frac{1}{2}$ is representative of half the population being female and able to produce eggs. Due to the sensitive nature of the parameter ϵ a given value of 1 (rather than an empirically founded 0.12) was determined to be mathematically the best value to use under calibration and validation [Blanchard *et al.*, 2014].

3.3 Community level dynamics

3.3.1 Predator-Prey interactions

The community level dynamics described here represent predator-prey interactions which allow species to interact with one another to influence both size- and species-based predation and feeding. These dynamics are made up of the implicit spatial distribution of predator relative to prey, the predator-prey preference, food availability, and search rate. These ultimately lead to an individual consuming a prey item, allowing it to grow and thus completing a full circle back to equation 3.1.

The predator-prey distribution is also known here as the species interaction matrix. This matrix (which is not size dependent) ranges from 0 to 1, where 0 means the species never interact with one another, whereas 1 means species always overlap. The interaction matrix used here was parameterised by Blanchard *et al.* [2014] and used in Spence *et al.* [2016]. The matrix was calculated using the North Sea IBTS dataset where catch densities were gridded at ICES statistical rectangle level and the proportions of each co-existing species were calculated relative to all rectangles [Blanchard *et al.*, 2014]. These were averaged across juvenile and adult individuals to create a final interaction matrix (Table 3.1). This matrix is used for calculating food availability thus represents what a predator potentially will eat should it overlap, but not definitively eat all that it overlaps with.

Table 3.1: Species interaction matrix (θ) whereby 0 means never any overlap, 1 means species overlap across all sizes. The diagonal (left-right, up-down) is not equal to one as the matrix is calculated across the species in different size categories (pre- and post-maturation).

Species	**Sprat**	**Sandeel**	**Norway pout**	**Herring**	**Dab**	**Whiting**	**Sole**	**Gurnard**	**Plaice**	**Haddock**	**Cod**	**Saithe**
Sprat	0.729	0.034	0.064	0.274	0.362	0.265	0.298	0.175	0.371	0.081	0.338	0.017
Sandeel	0.034	0.681	0.049	0.059	0.097	0.075	0.060	0.056	0.078	0.094	0.099	0.016
Norway pout	0.063	0.049	0.797	0.298	0.091	0.300	0.017	0.306	0.079	0.549	0.325	0.295
Herring	0.274	0.059	0.296	0.659	0.290	0.374	0.200	0.275	0.278	0.348	0.405	0.126
Dab	0.362	0.097	0.091	0.290	0.808	0.334	0.380	0.220	0.565	0.132	0.416	0.031
Whiting	0.265	0.075	0.300	0.374	0.334	0.709	0.192	0.371	0.295	0.392	0.441	0.102
Sole	0.298	0.060	0.017	0.200	0.380	0.192	0.716	0.107	0.391	0.034	0.258	0.012
Gurnard	0.175	0.060	0.306	0.275	0.220	0.371	0.107	0.880	0.165	0.357	0.352	0.124
Plaice	0.371	0.078	0.079	0.278	0.565	0.295	0.391	0.165	0.719	0.113	0.350	0.033
Haddock	0.081	0.094	0.549	0.348	0.132	0.392	0.034	0.357	0.1124	0.858	0.396	0.262
Cod	0.338	0.099	0.325	0.405	0.416	0.440	0.258	0.352	0.350	0.396	0.787	0.209
Saithe	0.017	0.016	0.295	0.126	0.031	0.102	0.012	0.124	0.033	0.262	0.209	0.664

The preference for prey can be described using a log-normal selection formulation [Ursin, 1973]:

$$\phi_i \frac{w_p}{w} = e^{\left[\frac{-\left(ln\left(\frac{w}{w_p \beta_i}\right)\right)^2}{2\sigma_i^2}\right]} \tag{3.20}$$

where w_p is the prey weight, w is the predator weight, β_i is the mean fixed (for each species) preferred predator-prey mass ratio, and σ_i is the width of the weight selection function (species-specific), also known as the standard deviation of the preferred predator-prey mass ratio. These latter two parameters were calculated by Blanchard *et al.* [2014] and full details can be found in their supplementary materials. Briefly, stomach content data was used to estimate β_i and σ_i for each species where possible (sole and Norway pout values were estimated using dab similarities, or other published research, respectively). Each species was subjected to a linear mixed effects model to determine β_i and σ_i as the mean and standard deviation of the log preferred predator-prey mass ratio, respectively. These values were subsequently log transformed to allow for a normal distribution. This was finally adjusted by finding available prey abundance and size selection under stable conditions. Equation 3.20 thus describes the size selection of food based on the ratio between predator and prey.

The interaction matrix and prey preference are used to calculate food availability for predator (E_a) for different predator species, i:

$$E_{a,i}(w) = \int (N_R(w) + \theta_{i,j} N_j(w)) \phi_i \left(\frac{w_p}{w}\right) w dw_p \tag{3.21}$$

where θ is the interaction matrix where species i has a preference on species j, N_j is the abundance of the prey, and ϕ_i is the size based prey preference (equation 3.20). N_R is the background resource density which represents size structured food of the smallest individuals like phytoplankton (sizes 6 x 10^{-10} g – 10 g):

$$\frac{\partial N_R(w,t)}{\partial t} = r_0 w^{p-1} \left[\kappa w^{-\lambda} - N_R(w,t)\right] - \mu_p(w) N_R(w,t) \tag{3.22}$$

where $r_0 w^{p-1}$ is the resource population regeneration rate, and $\kappa w^{-\lambda}$ is the carrying capacity [Hartvig *et al.*, 2011; Blanchard *et al.*, 2014; Spence *et al.*, 2016].

Whilst equation 3.21 calculates what food is available in the system, this is not necessarily what the predators will eat. The predators need to search for food, giving rise to actual food encountered E_e:

$$E_{e,i}(w) = \gamma_i w^q E_{a,i} \tag{3.23}$$

where γ_i is the species-specific search rate (volume per time), scaled using the exponent q (0.8) [Blanchard *et al.*, 2014]. γ is calculated using the initial feeding level ($f_0 = 0.6$): $\gamma(f_0) = \frac{f_0 h \beta_i^{2-\lambda}}{(1-f_0)\sqrt{2\pi}\kappa\sigma_i}$ where λ is the exponent of the resource spectrum, κ is the resource spectrum carrying capacity, and σ is the width of the size selection.

The resulting food ingested by an individual provides the feeding level (f_i):

$$f_i(w) = \frac{E_{e,i}}{E_{e,i} + h_i w^n} \tag{3.24}$$

where f_i leads back into equation 3.1, completing the model dynamics.

3.4 Conclusion

The size-based model described above will be known as the baseline model for the remainder of this thesis. Species-specific values for set parameters (i.e. parameters that are not calculated using equations such as γ and metabolism) are given in Table 3.2. An overview of the main equations can be found in Table 3.3. A shortcoming of the above model is the lack of physiological-environmentally mediated processes. In the following two chapters I develop and apply an extension of the model to incorporate different temperature and oxygen hypotheses. This allows the effects of environmental change to be studied and simulated.

Table 3.2: Species-specific parameters for asymptotic size (W_∞), von Bertalanffy growth parameter (K), predator-prey ratio (β), size-selection width (σ), and the maximum recruitment flux (R_{max}) from Blanchard *et al.* [2014] and Spence *et al.* [2016]

Species	W_∞	**K**	β	σ	R_{max}
Sprat	30.8	0.469	51076	0.8	26.76905
Sandeel	20.4	0.758	398849	1.9	26.03754
Norway pout	77.5	0.606	22	1.5	30.89954
Herring	254.7	0.505	280540	3.2	26.59404
Dab	190.2	0.375	191	1.9	23.15732
Whiting	472.7	0.457	22	1.5	26.16771
Sole	361.6	0.441	381	1.9	22.98764
Gurnard	668.1	0.266	283	1.8	25.48522
Plaice	833.1	0.255	113	1.6	30.80458
Haddock	3484.7	0.271	558	2.1	28.49626
Cod	30784.1	0.183	66	1.3	22.84691
Saithe	35918.0	0.075	40	1.1	27.05699

Table 3.3: A brief overview of the main equations of the size-structured model used in this thesis. The derivations, explanations and parameter values of the equations are found in the main body of the text.

Equation	**Description**
$\frac{dw}{dt} = (\alpha f_i h_i w^n - k_i w^p)(1 - \psi_i)$	Individual growth
$h_i = \frac{3K_i \sqrt[3]{W_{\infty,i}}}{\alpha f_i - k_i}$	Max intake rate
$\psi_i(w) = \left[1 + \left(\frac{w}{w_{m,i}}\right)^{-10}\right]^{-1} \left(\frac{w}{W_{\infty,i}}\right)^{1-n}$	Reproduction
$\mu_i(w) = \mu_{n,i} + \mu_{s,i} + \mu_{p,i} + \mu_{f,i}$	Mortality
$\mu_{p,i} = \sum_j \int \phi\left(\frac{w_p}{w}\right)(1 - f_i(w))\gamma_j w^q \theta_{j,i} N_j(w) dw$	Predation mortality
$\mu_{n,i} = \mu_0 W_\infty^{n-1}$	Natural mortality
$\frac{\partial N_i(w)}{\partial t} = -\frac{\partial g_i(w) N_i(w)}{\partial w} - \mu_i(w) N_i(w)$	Abundance
$R_i = R_{max,i} \frac{R_{p,i}}{R_{p,i} + R_{max,i}}$	Recruitment
$R_{p,i} = \frac{\epsilon}{2w_0} \int N_i(w) g_i \psi_i(w) dw$	Egg production
$\phi_i \frac{w_p}{w} = e^{\left[\frac{-\left(ln\left(\frac{w}{w_p \beta_i}\right)\right)^2}{2\sigma_i^2}\right]}$	Prey preference
$\frac{\partial N_R(w,t)}{\partial t} = r_0 w^{p-1}\left[\kappa w^{-\lambda} - N_R(w,t)\right] - \mu_p(w) N_R(w,t)$	Resource spectrum
$E_{a,i}(w) = \int (N_R(w) + \theta_{i,j} N_j(w)) \phi_i \left(\frac{w_p}{w}\right) w dw_p$	Food availability

Chapter 4

Effects of environmentally dependent individual growth on population and community size structure

Abstract

Size structure influences the resilience of populations and communities to top-down and bottom-up perturbations, such as fishing and climate variations. Size-structured models can therefore be used to predict population abundance and community size structure, and the individual growth process is a core part of these models. Different hypotheses exist for the environmental influences on growth. However, a comparison of how different environmentally driven growth processes impact size-structured populations and communities has not been conducted. Here empirically founded relationships between the environment and growth are integrated into a multi-species, size-structured model parameterised for the North Sea. By comparing temperature-, oxygen-, and combined temperature/ oxygen-dependent individual growth trajectories guided by historical values, variations are explored to see how they propagate through the system. Comparing the temperature scenarios it was found that individuals tend towards smaller sizes after an initial faster growth under warmer waters - an emergence of the temperature size rule. Oxygen in the scenarios tested here had minimal impacts on community level metrics. When oxygen and temperature effects were combined these changes were lower than temperature alone, but higher than oxygen alone. At the population level, some species' biomass and abundance were very sensitive to environmental change, whereas others were not, resulting in a shift in the food web structure under temperature-, oxygen-, and combined temperature/oxygen-dependent

hypotheses. As this study has shown individual variation in growth results in marked effects on fish population and community structure, alternative hypotheses should thus be considered in climate change forecasting of fisheries to capture the range of model uncertainty. Further empirical research on individual growth variability is required to ground truth models to improve estimates of fish community size structure in the future.

4.1 Introduction

Changes in the body size distribution of fish communities, shown by indicators such as the size spectrum and large fish indicator, have been seen in a variety of ecosystems across the global oceans [Rice & Gislason, 1996; Blanchard *et al.*, 2005; Wilson *et al.*, 2010; Greenstreet *et al.*, 2012; Marshall *et al.*, 2016]. These metrics are widely used for quantifying the health, stability, and resilience of an ecosystem [Graham *et al.*, 2005; Shin *et al.*, 2005; European Parliament, 2008]. The relationship between body size and numerous life-history traits makes these types of metrics beneficial descriptors of size-structured ecosystems [Sheldon *et al.*, 1972; Blueweiss *et al.*, 1978; Rall *et al.*, 2012; Reuman *et al.*, 2014]. While many causes, such as environmental change [Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Hobday & Pecl, 2014] and fishing [Rice & Gislason, 1996; Law, 2000; Jennings & Blanchard, 2004], appear to drive changes in ecosystem size structure, explicit mechanisms are hard to define despite strong associations between ecological change and the surrounding environment [Marshall *et al.*, 2016]. For example, changes in the size distribution may arise at the individual level, mediated through altered growth trajectories [de Roos & Persson, 2005; Cheung *et al.*, 2013b; Baudron *et al.*, 2014], or at the population level via biomass shifts due to preferential environmental conditions differentiated through ontogeny [Rindorf & Lewy, 2006; Engelhard *et al.*, 2014; Saraux *et al.*, 2014]. This chapter focuses on the former, the importance of individual growth processes, and asks whether growth variability influences population or community level characteristics in size-structured systems. The model used is parameterised for the North Sea [Blanchard *et al.*, 2014], a region where it has been predicted some species will be unable to move to more appropriate climes due to depth constraints [Rutterford *et al.*, 2015]. Therefore this environmentally modified model can be used to infer possible variations in the North Sea community size structure if species are forced to remain in their current location.

Size-based food web models capture the main processes of growth and death that depend on individual body size and drive size-structured population and community level dynamics [Andersen & Beyer, 2006; Andersen *et al.*, 2016]. This makes them ideal for understanding fishing impacts on populations and communities [Blanchard *et al.*, 2014]. These size-structured models describe, using fundamental ecological assumptions, systems found globally across the marine realm where abundant, small individuals coexist with fewer, large individuals [Sheldon *et al.*, 1972]. Some size-structured models hold growth curves constant through time to help simplify the complex processes that influence growth [Hall *et al.*, 2006; Pope *et al.*, 2006; Speirs *et al.*, 2010]. Others assume food-dependent growth, where energetic costs of growth and reproduction are balanced by mortality on prey items [Andersen & Beyer, 2006; Hartvig *et al.*, 2011; Blanchard *et al.*, 2014]. Extending beyond standard biological growth equations, the variability of ontogeny under changing environmental conditions has been shown empirically [Taylor, 1958; Jobling, 1981; Fonds *et al.*, 1992; Chabot & Dutil, 1999; Pichavant *et al.*, 2001; Thresher *et al.*, 2007]. Different modelling approaches have been used to incorporate environmental drivers to emphasise fisheries variability under climate change projections such as large-scale changes (e.g. population or community-dependent environmental change, see Blanchard *et al.* [2012] & Barange *et al.* [2014]), habitat suitability [Cheung *et al.*, 2013b; Jones *et al.*, 2013] or individual environmental effects at different ecological levels [Pope *et al.*, 2006; Maury *et al.*, 2007]. More detailed research is required on the importance of how different environmentally driven individual growth processes mechanistically affect population and community dynamics, and therefore model predictions.

Some of the initial foundations of growth date back to 1920 when Pütter described animal growth in different climates (see Weymouth *et al.* [1931] for a description of Pütter's original German papers [Pütter, 1920a,b]). High growth rates occur in early ontogeny before reducing asymptotically to a maximum theoretical weight over infinite time for species with indeterminate growth, such as fish. This form can be described by an exponential function [Pütter, 1920a; von Bertalanffy, 1938; Pauly, 1981; Lester *et al.*, 2004; Quince *et al.*, 2008a,b]. Von Bertalanffy in 1938 built upon Pütter's work more acutely by describing the build up of tissues as anabolic processes scaled to physiological surfaces, and the breakdown of tissues as catabolic processes scaled to the volume [von Bertalanffy, 1938], an allometric metabolic growth basis still used in modelling today [Andersen *et al.*, 2009; Pauly, 2010; Cheung *et al.*, 2013b]. The surface-volume ratio of an individual tends from a value greater than 1 to a value less than 1 over time forming an asymptotic growth curve. An alternative hypothesis to the metabolic growth curve, the reproduction allocation rule, assumes the increasing cost of reproduction controls the somatic growth and thus asymptotic size [Kooijman, 2000; Lester *et al.*, 2004; Hartvig *et al.*, 2011]. When the rate of somatic growth starts to decrease, it is presumed that at this point some energy has been diverted for reproductive materials [Day & Taylor, 1997; Charnov *et al.*, 2001; Lester *et al.*, 2004; Quince *et al.*, 2008a,b]. While debates continue over the growth curve formation (e.g. Cheung *et al.* [2013a] vs Brander *et al.* [2013] and Lefevre *et al.* [2017] vs Pauly & Cheung [2017]), the asymptotic shape is well documented and cemented in fisheries modelling.

Warming has been widely reported as causing a decrease in individual and mean population body sizes for fish and many other taxa [Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011; Forster *et al.*, 2012; Baudron *et al.*, 2014]. In order to calculate the effect temperature has on an individual's physiology, chemical reactions of body rate activation energies, such as metabolism, search rate, handling time, and attack rate can be used [Gillooly *et al.*, 2001; Brown *et al.*, 2004; Englund *et al.*, 2011]. It is generally assumed that all body rates across species have similar activation energies under the metabolic theory of ecology [Brown *et al.*, 2004]. Realistically, fish have lower activation energies for metabolism than other taxa [Gillooly *et al.*, 2001; Brown *et al.*, 2004], and the attack rate and handling rate used to calculate the functional response each scale differently to temperature [Englund *et al.*, 2011]. Thus various physiological rates appear to respond differently to temperature within an individual, as well as general rates differing across species and taxa. This impact of temperature on the physiology affecting growth has been classed as the third universal response of fisheries to warming resulting in a decrease of body size [Gardner *et al.*, 2011].

While the indirect effects of oxygen through temperature tolerance limitations have been postulated [Pörtner & Knust, 2007; Cheung *et al.*, 2013b; Baudron *et al.*, 2014], the direct effect of oxygen on the long-term condition of fish is still debated. It is accepted that under extreme hypoxic conditions metabolism and reproduction in fish deteriorates [Schurmann & Steffensen, 1997; Wu *et al.*, 2003; Nilsson & Östlund-Nilsson, 2004; Thomas *et al.*, 2007], however the effect of non-lethal levels being a controlling factor in growth is still being questioned [Brander *et al.*, 2013; Lefevre *et al.*, 2017]. Research into the effect of non-lethal hypoxic levels on growth is somewhat limited though arguably more of a necessity to research than lethal conditions due to the expected reduction in oxygen homogeneously across the globe with climate change [Keeling *et al.*, 2010; Schmidtko *et al.*, 2017]. Studies have shown that the aerobic metabolic scope, the difference between active and standard metabolic rate, reduces with a decrease in oxygen [Claireaux & Lagardère, 1999; Chabot & Claireaux, 2008] due to a reduced active metabolic rate. Additionally, growth has been shown to decline: decreased food intake with a continual lowering of oxygen explained 97% of growth reduction in Atlantic cod [Chabot & Dutil, 1999]. As oxygen is required to break food down for energy, it appears that individuals make a decision under lower oxygen conditions by simply not eating [Chabot & Dutil, 1999; Thetmeyer *et al.*, 1999; Buentello *et al.*, 2000; Claireaux *et al.*, 2000; Pichavant *et al.*, 2001]. In extreme low oxygen circumstances, fish have been known to vomit, then re-ingest once oxygen levels rise to more suitable levels for the energetic costs of digestion [Claireaux *et al.*, 2000]. Though the issue of the detrimental effect of non-lethal levels of oxygen on fish is still uncertain [Townhill *et al.*, 2017], reduced oxygen does influence the consumption, thus energy availability for growth, as an avoidance tactic for energy expenditure [Claireaux *et al.*, 2000].

Given the complex nature of growth processes, an important question arises: how do alternative assumptions about individual growth influence model predictions of fish population and community structure? This chapter explores the importance of growth trajectories in the context of a multi-species, size-structured fish community. By using the reproduction allocation rule to study the impact of an environment-dependent individual growth trajectory on the community, a suite of empirically founded relationships between growth and temperature and oxygen are incorporated into a size-structured, multi-species model. The influence of alternative growth formulations on population and community structure are tested by comparing modelled individual growth rates, population biomass and community level size-based indicators that are used in fisheries policy [European Parliament, 2010].

The multi-species model used for this chapter as the baseline model can be found described fully in Chapter 3. The dynamics are the same except for changes to the individual growth mechanisms. These changes are kept for the rest of the thesis. Two important environmental features are incorporated into this size-structured model: temperature and oxygen, as well as a mechanism to allow the expected maximum weight to change under temperature controls. The environmental additions are based on empirical work and are tested at different climate values guided by historical and model reanalysis values to determine how they influence population abundance, and community indicators in a typical, semi-enclosed temperate sea.

4.2 Methods: Incorporating environmental effects into a size-structured model

Three different, and independent, environmental-physiological theories concerning growth are tested for community perturbations, one of temperature change, one of oxygen change, and one where temperature effects are altered by oxygen saturation. The temperature changes modify the metabolism and maximum intake rate. Changes under oxygen fall under non-lethal and lethal oxygen conditions: the intake rate reduces at any decrease in oxygen, whereas the metabolism is only impacted under hypoxic conditions. For combined temperature and oxygen changes, the intake rate combines the two physiological relationships (simply through multiplication of the factors). However the changes to metabolism are derived from experiments which have altered temperature with oxygen simultaneously which resulted in a co-dependence of metabolism with temperature and oxygen. The modelled results are compared to empirical survey data that Blanchard *et al.* [2014] used in their original parameterisation for the North Sea. Blanchard *et al.* [2014] extracted individual weight and age data for species specific to this model from the ICES IBTS Sex-Maturation-Age-Length-Weight (SMALK) database in order to compare the modelled results.

4.2.1 Modifying the model

When an individual is recruited into the stock, it follows an environmentally dependent somatic growth function:

$$\frac{dw_i}{dt} = (\alpha f_i h_i w^n S_{O1} T_1 - k_{s,i} w^p S_{O2} T_2)(1 - \psi_i) \tag{4.1}$$

where, as before in Chapter 3, for each species i, α is the assimilation efficiency (0.6), f_i is the feeding level, h_i is the maximum food intake constant, w is weight, n is an exponent to scale maximum food intake (0.7), $k_{s,i}$ is metabolism $(0.12 * h)$, p is the exponent for scaling standard metabolism (0.7), and ψ_i is the proportion of energy for reproduction. The new additions are:

- T_1 & T_2: temperature Arrhenius scaling terms
- S_{O1}: a log-fashion oxygen saturation scaling factor,
- S_{O2}: a factor for when oxygen becomes lower than a given value forcing anaerobic respiration

Each of the newly listed environmental variables can be turned on/off. Therefore testing of temperature effects (i.e. S_{O1} and S_{O2} are set to 1) and oxygen effects (i.e. T_1 and T_2 are set to 1) independently can be achieved.

Equation 4.1 is used when temperature and oxygen are tested independently. When temperature and oxygen are tested in combination, the following growth trajectory is assumed:

$$\frac{dw_i}{dt} = (\alpha f_{T,i} h_i w^n S_{O1} T_1 - k_{s,i} w^p TO2)(1 - \psi_i) \tag{4.2}$$

where $TO2$ is an oxygen-dependent temperature effect on metabolism.

The two independent temperature scaling terms, T_1 and T_2 ensure a temperature-dependent response for maximum intake rate and metabolism, respectively. They are calculated using the Arrhenius equation:

$$T_x = e^{E_{a,x}(\frac{1}{RT_{ref}} - \frac{1}{RT_e})} \tag{4.3}$$

where R is the Boltzmann constant (8.617 x 10^{-5} eVK^{-1}), T_e is the environmental temperature (T °C + 273.15 °C for Kelvin conversion), $E_{a,x}$ is the activation energy for T_1: $E_{a,1} = 0.44$ eV (average metabolic rates in fish: 0.41 eV [Gillooly *et al.*, 2001] and 0.47 eV [Brown *et al.*, 2004]) and T_2: $E_{a,2} = 0.80$ eV (maximum intake rate in Englund *et al.* [2011]). T_{ref} is the reference temperature (9.6 °C + 273.15 °C = 282.75 K) where 9.6 °C is the average North Sea summer (June–Sept inclusive) sea bottom temperature from 1971–2000. The average was taken to be approximately within the ICES subarea IV: $51 - 62$ °N, 4W–8 °E. This average was calculated using monthly climatologies from Berx & Hughes [2009]. The use of the summer average temperature is threefold: (a) it is the more extreme end of a species' annual experience so acts as a useful upper boundary, (b) many of the individuals used in the model have the greatest growth during this season [Amara, 2003; Bolle *et al.*, 2004; Mello & Rose, 2005], and (c) the only available historical oxygen data (see below) is taken from June-September, and thus these months were used for the best consistency for the oceanographic inputs.

The first oxygen term, S_{O1}, is a log-based factor to scale feeding derived from Atlantic cod experiments under non-lethal oxygen conditions [Chabot & Dutil, 1999]:

$$S_{O1} = \frac{-74.22 + 54.51log(S_{ox})}{-74.22 + 54.51log(S_{ox_r})} \tag{4.4}$$

where S_{ox} is the predicted value of oxygen saturation and S_{ox_r} is the reference oxygen saturation, which is taken as the average saturation of the North Sea from 1970–2000 as 89.6% [Queste, 2013]. The data from Queste [2013] was compiled historical oxygen data for the central and northern North Sea between June–September in the bottom third of the sea. As this is the summer season, the waters are well stratified therefore we are able to assume this bottom third is representative of the near bottom conditions. While the southern North Sea has not been included in the historical data amalgamation, this could impact the overall reference value as often this region approaches 100% saturation. However, this area is not as large as the central and northern regions, therefore S_{ox_r} could never reach more than 95%. As historical data has been found to have errors of around 10% [Carritt & Carpenter, 1966], using

89.6% is well within the error range. The oxygen-dependent metabolic term (S_{O2}) is determined in a different way compared to S_{O1} and is incorporated for physiological accuracy to describe a switch from aerobic to anaerobic respiration. It only becomes effective under extreme oxygen saturation (<25% – see Schurmann & Steffensen [1997]; Cerezo & García [2004]; Nilsson & Östlund-Nilsson [2004]). When S_{O2} is implemented it is a fixed value of 20. While this increases the metabolism, and under anaerobiosis metabolism does not increase, this is purely a numerical exercise. Anaerobic respiration provides less energy for growth and reproduction due to ineffective metabolism (available energy for growth/reproduction is reduced by a factor of 20 under anaerobiosis compared to aerobic respiration [Lucas, 1996]). Therefore this balance can be achieved by increasing the metabolism (i.e. reducing effectiveness of converting food into available energy). The North Sea oxygen saturation will not be <25% for a prolonged time thus the S_{O2} modification is unused here.

The final environment model variable, *TO2*, represents the co-dependence of temperature and oxygen in influencing metabolism (whereas equation 4.1 showed temperature and oxygen as independent variables for the purpose of testing each environmental scenario separately). The empirical studies on temperature-oxygen interactions are specific to standard metabolism (resting, unfed fish), routine metabolism (unfed, natural swimming fish), active metabolism (highly active, unfed fish), and the metabolic scope (difference between active and standard metabolism) [Claireaux & Lagardère, 1999; Mallekh & Lagardère, 2002; Lefrançois & Claireaux, 2003]. The equation that determines the combined effects of temperature and oxygen relates to the metabolic scope. Here, this model has a metabolic term to indicate the loss of energy through the build up of tissue and body maintenance, in a food-dependent environment, so the different metabolic forms are not individually or explicitly defined. Therefore the metabolic scope (*MS*) equation is used as a reference. The experiments were conducted on sole [Lefrançois & Claireaux, 2003] and sea bass [Claireaux & Lagardère, 1999], so while the *TO2* parameter for all modelled species is here described by one equation, it at least derives from an empirical study of temperate, North Sea species [Claireaux & Lagardère, 1999; Lefrançois & Claireaux, 2003]:

$$MS = \left[\delta\left(\frac{T_m - T}{T_m - T_{opt}}\right)^{\omega} e^{\left[-\omega\left(\frac{T_m - T}{T_m - T_{opt}}\right)\right]}\right]\left[1 - e^{\alpha S_{ox}^{\beta}}\right] - ae^{bT} \tag{4.5}$$

where many of the values are statistical model parameters derived in the original paper: δ is 1038.41, ω is 1.870, α is -0.005, β is 1.320, a is 15.45, and b is 0.052 [Lefrançois & Claireaux, 2003]. As in previous equations, T is the temperature (°C), and S_{ox} is the oxygen saturation. The maximal temperature, T_m is 30.48 °C, and the optimal temperature, T_{opt}, is 19.74 °C. These values are kept the same, rather than changing them for specific species, as the statistical model used to calculate the metabolic scope is altered by these values. Changing T_m and/or T_{opt} would fundamentally alter the parameterisation of the whole statistical model for the metabolic scope. Reference temperature and oxygen values are used to calculate an initial metabolic scope value (MS_{ref}). When scenarios are tested (as explained in the next section), the metabolic scope ($MS_{scenario}$) is calculated for the temperature and oxygen, and the percent difference is used as *TO2*:

$$TO2 = \frac{MS_{scenario}}{MS_{ref}} \tag{4.6}$$

It is empirically known that with increased temperatures individuals tend to a smaller size [Atkinson, 1994, 1995]. However the mechanistic cause of this temperature-size rule (TSR) is unknown. Many theories are attributed under a large body of TSR research [Angilletta *et al.*, 2004]. The focus here is not to test these different theories. As long as individuals tend toward smaller sizes under warmer waters (preferably at a faster rate), then the TSR will be an integral part of the environmental growth trajectory. The rate at which the individuals grow is determined by the empirically founded equations incorporated above. However as the TSR final size is still a conundrum, the use of TSR emergent patterns can be used, namely from Baudron *et al.* [2014] and van Rijn *et al.* [2017]. Both of these studies have shown a change in the maximum size of fish, with both hypothesising that the cause is due to increasing temperatures. The differences between the two, however, are notable. Baudron *et al.* [2014] estimate an average 16% decrease in maximum size with a 2 °C rise in water temperature across all species studied. van Rijn *et al.* [2017] showed most of the fish that are able to attain that rate of change over 2 °C are substantially more active (thus more sensitive to change) compared to the North Sea species in the Baudron *et al.* [2014] study. Whether or not the fact fish from the North Sea are used [Baudron *et al.*, 2014] compared to Mediterranean Sea species [van Rijn *et al.*, 2017] can account for this difference remains to be seen (i.e. are tropical fish less susceptible to temperature effects on growth, or are there other underlying factors that differentiate North Sea from Mediterranean Sea fish?). In both cases, though different magnitudes of change, fish deemed typically less active (e.g. flatfish, gurnards) had a smaller rate of change than more active species (e.g. herring, gadoid group). Therefore the rates of change in maximum size in this model are split into two groups, less active fish (dab, sole, gurnard, plaice, and sandeel) and more active fish (cod, haddock, saithe, Norway pout, herring, sprat, and whiting) based upon their caudral aspect ratio values [Sherwood & Rose, 2003; Killen *et al.*, 2016]. The less active fish were given a rate of decrease of maximum size as 3% for every 1 °C, whereas the active species were given a value of 7%. Therefore over a 5 °C change, low and high active fish can change by 15% and 35%, respectively, an intermediate of the two empirical studies [Baudron *et al.*, 2014; van Rijn *et al.*, 2017]. Oxygen scenarios do not have this as the function describing change under oxygen is primarily a change in the amount of food being consumed (which causes a change in weight), whereas temperature relates to changes in the foundational bioenergetics.

4.2.2 Testing environmental resonance

Temperature and oxygen were incorporated into processes that influence individual level feeding and growth. Using this model framework, different scenarios were employed to determine how environmentally mediated processes at the individual level impacted the population and community levels. All model scenarios were relative to the original baseline model and changes in temperature and oxygen were based on a range of historical values over the past four decades – a period of major environmental change. Two runs for each environmental set up were chosen to be at the upper and lower boundaries of the empirical data. As the reference values described above were based on the mean North Sea, the baseline model is effectively the average North Sea.

For the sea bottom temperature, one run of cooler waters of 7.6 °C and one run of warmer waters of 11.6 °C were conducted, this is in line with there being a 4 °C difference between the 5th and 95th percentiles of June–September (1971–2000) North Sea sea bottom temperatures according to the GETM-ERSEM-BFM model [van der Molen *et al.*, 2013; van Leeuwen *et al.*, 2013, 2015].

The oxygen values were derived approximately from empirical data presented by Queste [2013]. Between 1970–2000, the lowest oxygen was 240 mmolm^{-3}, and the highest was 275 mmolm^{-3}, and these values were tested. However as changes of growth under oxygen in the fisheries model were determined by oxygen saturation (as the experimental work compares ingestion with oxygen saturation (%, [Chabot & Dutil, 1999])), an additional step had to be made within the model so that oxygen concentration, from ocean models, could be converted into oxygen saturation, for the fisheries model. First the oxygen solubility (O_{sol}, units μmolkg^{-1}) was calculated based on temperature and salinity using the following equation [García & Gordan, 1992]:

$$\begin{aligned} O_{sol} = exp[&5.80871 + 3.20291T_s + 4.17887T_s^2 + 5.10006T_s^2 \\ &+ 5.10006T_s^3 - 0.0986643T_s^4 + 3.80369T_s^5 + S(-0.00701577 \\ &- 0.00770038T_s - 0.0113864T_s^2 - 0.00951519T_s^3) - 0.000000275915S^2] \end{aligned} \tag{4.7}$$

where the most suitable constants came from previous research [Benson & Krause-Jr, 1980], S is the salinity, and T_s is the scaled temperature:

$$T_s = ln\left(\frac{298.15 - T}{273.15 + T}\right) \tag{4.8}$$

where T is the temperature in Kelvin. The temperature, T, used was taken from Queste [2013] as these correlated directly with the oxygen recordings. For the highest oxygen of 275 mmolm^{-3} a value of 7 °C was used, and for 240 mmolm^{-3} a value of 8.5 °C was used. The salinity, 34.9, was based on North Sea salinity climatologies from 1971–2000 for the months June–September [Berx & Hughes, 2009]. While salinity variability exists, the general trend, such as between the Great Salinity Anomaly where minimum salinities occurred in the 1970s [Dickson *et al.*, 1988], and 2009, is minimal with changes being been no more than 0.1 in the North Sea [Jenkins *et al.*, 2009]. Even a change of 1 psu at the temperatures of the North Sea mean changes in the saturation would be less than 1% [http://water.usgs.gov/software/DOTABLES/]. Therefore the use of one salinity value is sufficient for this purpose. These equations are based on fitting equations of seawater at 1 atm. However, as the oxygen solubility changes by <1% over even the deepest parts of the North Sea [Klotz, 1963; Uchida *et al.*, 2008] the equation is suitable for this model application. Equation 4.7 provides the oxygen solubility in μmolkg^{-1}. The oxygen concentration values from the ocean models were given in mmolm^{-3} which is equivalent to μmolL^{-1}. By calculating the density from the salinity, temperature and assumed averaged North Sea depth of 65 dbar [Davies, 1983], the oxygen solubility was readjusted to convert from μmolkg^{-1} to μmolL^{-1} using $density = \frac{mass}{volume}$ giving the same numeric value as mmolm^{-3}. The oxygen concentration from the ocean model is then divided by the calculated oxygen solubility (4.7) to give the oxygen saturation (%) for equation 4.4 and the subsequently equations 4.1 and 4.2. The equivalent calculated oxygen saturations therefore were calculated as: 240 mmolm^{-3} = 84.0% and 275 mmolm^{-3} = 92.2%. This fits well around the reference oxygen saturation of 88.75%.

Oxygen and temperature were tested independently (equation 4.1) as traditionally, due to data limitations, temperature is often the only variable modelled [Maury *et al.*, 2007; Blanchard *et al.*, 2012]. More recently, non-lethal levels of oxygen have been highlighted as potentially being important in growth [Chabot & Dutil, 1999; Cheung *et al.*, 2013b; Baudron *et al.*, 2014]. Therefore to see how these compare is of interest. However, it is known that temperature and oxygen have a co-dependence on one another to alter metabolism [Claireaux & Lagardère, 1999; Claireaux *et al.*, 2000; Pörtner & Knust, 2007]. Therefore an additional test (equation 4.2) was conducted. This was split into scenarios of high temperatures/low oxygen (11.6 °C, 240 mmolm^{-3}) and low temperatures/high oxygen (7.6 °C, 275 mmolm^{-3}). The reason the temperature values of 7.6 °C and 11.6 °C were used rather than 7 °C and 8.5 °C used in the oxygen conversion is because the former temperatures are more representative of the North Sea as a whole. The latter values are of a slightly reduced area, as explained above, and thus are used solely for the best conversions of oxygen.

The model was run under each fixed environment scenario to equilibrium. The sensitivity of the model was effectively tested by changing temperature and oxygen separately, and combined under the range of historical conditions relative to the baseline model. This ultimately allowed the model to output the population and community metrics assuming a world where the waters were consistently held in these conditions. The model outputs thus come from 6 runs: 2 temperature runs, 2 oxygen runs, and 2 combined temperature/oxygen, approximately distributed around the mean. The nature of the model, being parameterised for a number of North Sea species, allows a close examination across the individual, population, and community level. Therefore the different runs are examined at the individual level through changes in growth rate and maximum body size, the population level through biomass changes, and the community level through size-based indicators (SBIs), commonly used metrics to understand the health of an ecosystem [Greenstreet & Rogers, 2006; European Parliament, 2008].

4.3 Results

4.3.1 Individual level

The individual level growth trajectories under warmer temperatures and (independently and combined) lower oxygen concentrations showed individuals tending towards smaller sizes (Figures 4.1, 4.2, 4.3). The lower active individuals showed a change of 11 ± 3% across the 4 °C gradient, meaning these species converged to their upper limit (3% for 1 °C means a change of up to 12% in this study). The higher active individuals saw a change of 20 ± 8%, which is somewhat short of the upper boundary given (up to 28% across the 4 °C range). There are two particularly important results of the temperature tests. Firstly the growth curves for all but saithe fall within the empirical data, suggesting that the environmental conditions tested result in growth trajectories that are well within the confines of what is seen within nature. Saithe is slightly obscure, but when the calibrations were made [Blanchard *et al.*, 2014], metabolism was set to 0, which also has implications on the intake rate. Once these were reimplemented (Chapter 3), saithe struggled to conform to the data. Therefore the environmental changes made do not cause the problems with saithe, though they do exacerbate them. The second important result is that temperature-size rule is emergent across all species (Figure 4.1).

The oxygen conditions were fairly uniform, such that the high and low oxygen resulted in symmetrical increases and decreases, respectively in maximum size away from the baseline, though the minimal effects make this difficult to see (Figure 4.2). The maximum size variations were minimal (<2%) across oxygen gradients except for saithe, which had a greater change of 6%. While the foundations of the oxygen-physiology relationship established here was based on the inclusion of studies on food ingested, which as food is vital to growth is expected to be important, it is the small variation of oxygen that caused only a minor disruption to body size. This is due to two reasons. Firstly the physiological equation used showed that at high saturation levels the change of ingestion was not large, for example it took a drop from 100% to 60% oxygen saturation to cause a decrease of ingestion by a third [Chabot & Dutil, 1999], therefore the non-lethal levels of reduced oxygen still need to be substantially large to impact food uptake. Secondly, while the concentrations varied from 240–275mmolm^{-3}, which seems large, there was a small temperature variation alongside this (1.5 °C), resulting in the saturations being relatively small. This highlights that temperature does not dictate the concentration (things such as phytoplankton and water masses do [Stendardo & Gruber, 2012; Queste *et al.*, 2013]), but rather the maximum oxygen retention. Therefore by having a step change from concentration, typically extracted from global models, to saturation is hugely important.

The changes when temperature and oxygen were used together (which means the metabolism formulation was different) resulted in very similar pattern as the temperature scenarios, with the TSR pattern emerging and all growth trajectories falling into empirical ranges. This was expected as the boundaries for change were set the same for both scenarios. The minor difference in the growth trajectories was under the cooler and higher oxygen conditions where the growth rates were slightly higher than when low temperatures alone were tested.

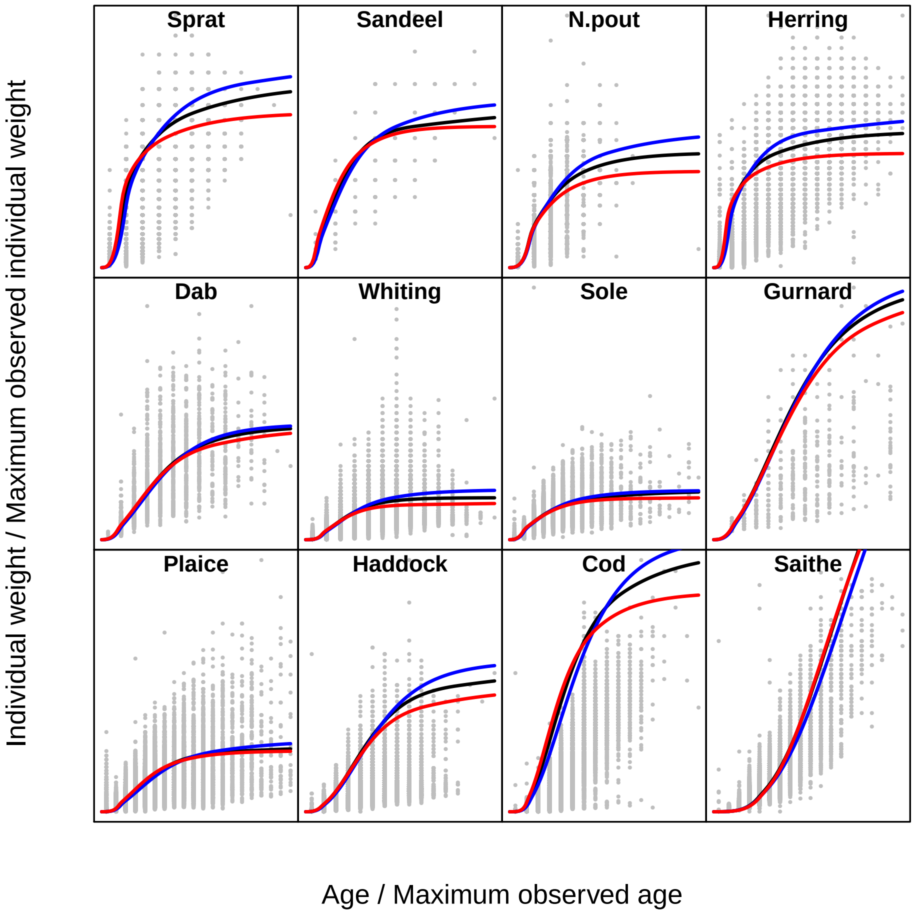

Figure 4.1: Growth trajectory for 12 different species of North Sea fish under 2 different temperature regimes. The blue trajectory represents waters of 7.6 °C and the red represents waters of 11.6 °C. The black line is the baseline model where no environmental conditions are implemented. The trajectories are superimposed over empirical North Sea length-age data from the International Bottom Trawl Survey dataset [Blanchard *et al.*, 2014].

4.3.2 Population level

At the population level the biomass of each species responded differently with changes from $1 - 23\%$ across the multiple environmental scenarios (Figure 4.4).

The expectation that small species will fair better under warming waters [Daufresne *et al.*, 2009] is supported in general here where species such as sprat, sandeel and herring had an increased biomass under the warmest waters, and large species such as saithe and haddock reduced. The largest species, cod, appeared to show great resilience to change either way with biomass changes being <4%. Despite all species having a smaller maximum size under warming waters, the abundance of small sizes increased, with medium–large species decreasing. There is a shift within the food web which accommodates these variations. Despite the very small changes in maximum size under oxygen variations, the biomass still altered by 3–4% for species such as sprat and cod. Perhaps most surprising is that the magnitude of change for cod under oxygen effects were the same as the temperature effects. The remaining species under oxygen varied by 1–2%, somewhat negligible compared to year on year natural fluctuations. Again, not all species responded in the same way to oxygen. Some species, such as sprat, sandeel, herring, Norway pout and cod increased in their biomass under the highest oxygen conditions. Other species, such as whiting, sole and gurnard increased under lower oxygen conditions, again a result of a changing food web structure. The combination of temperature and oxygen predominately followed the pattern of the temperature only scenarios, however, the effects were mitigated (Figure 4.4).

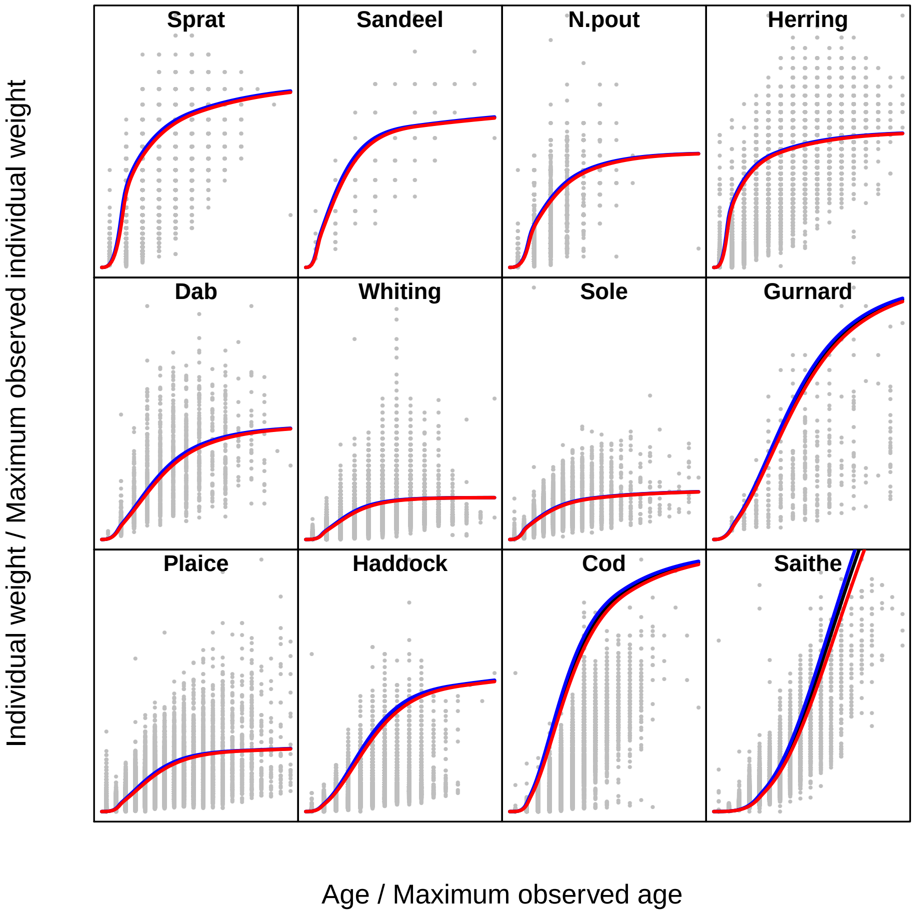

Figure 4.2: Growth trajectory for 12 different species of North Sea fish under 2 different oxygen regimes. The blue trajectory represents waters of 275 mmolm^{-3} and the red represents waters of 240 mmolm^{-3}. The black line is the baseline model where no environmental conditions are implemented. The trajectories are superimposed over empirical North Sea length-age data from the International Bottom Trawl Survey dataset [Blanchard *et al.*, 2014].

4.3.3 Community level

The directional effects on the community size structure changed in line with expectations. Warmer waters, lower oxygen, and their combination, all lead to reduced SBIs. The large fish indicator (LFI) and total biomass over the 4 °C range varied by approximately 12% and 13%, respectively. The mean maximum weight varied the most, by 49% under the warmest conditions compared to the coolest, meaning a loss of of nearly 3 kg. This coincides with the minor steepening of the size spectrum slope under warmer waters indicating relatively fewer large fish compared to small individuals, though this was a modest change comparatively (<4%). Under the range of oxygen values, a trend was found whereby higher oxygen levels led to larger size-based indicators (Table 4.1). However, these changes were negligible, varying by less than 1%. The changes under the inclusion of both temperature and oxygen scenarios showed a reduction in all SBIs with warmer, lower oxygenated waters. Across the temperature and oxygen gradients, the LFI varied by 6%, the total biomass by 8%, and mean maximum weight by 30% (change of 2.6 kg). Interestingly this shows the inclusion of an oxygen *and* temperature mediated metabolic response is less sensitive across environmental gradients compared to temperature alone.

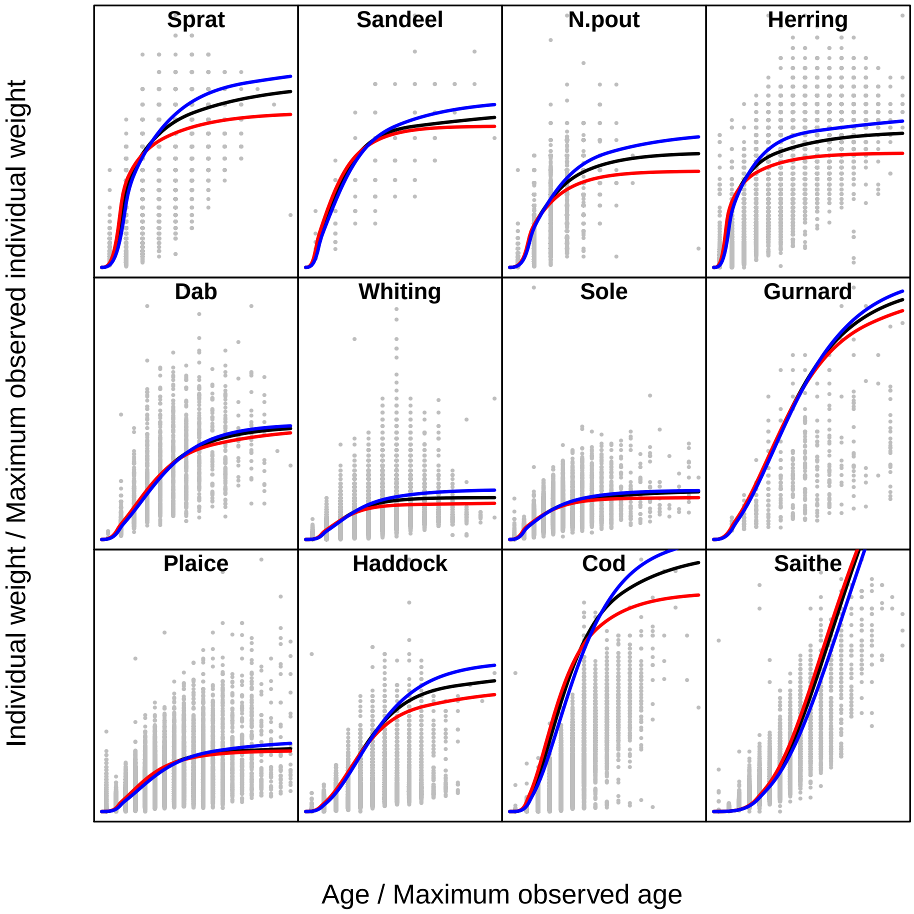

Figure 4.3: Growth trajectory for 12 different species of North Sea fish under 2 different temperature and oxygen regimes. The blue trajectory represents waters of 275 mmolm^{-3} and 7.6 °C and the red represents waters of 240 mmolm^{-3} and 11.6 °C. The black line is the baseline model where no environmental conditions are implemented. The trajectories are superimposed over empirical North Sea length-age data from the International Bottom Trawl Survey dataset [Blanchard *et al.*, 2014].

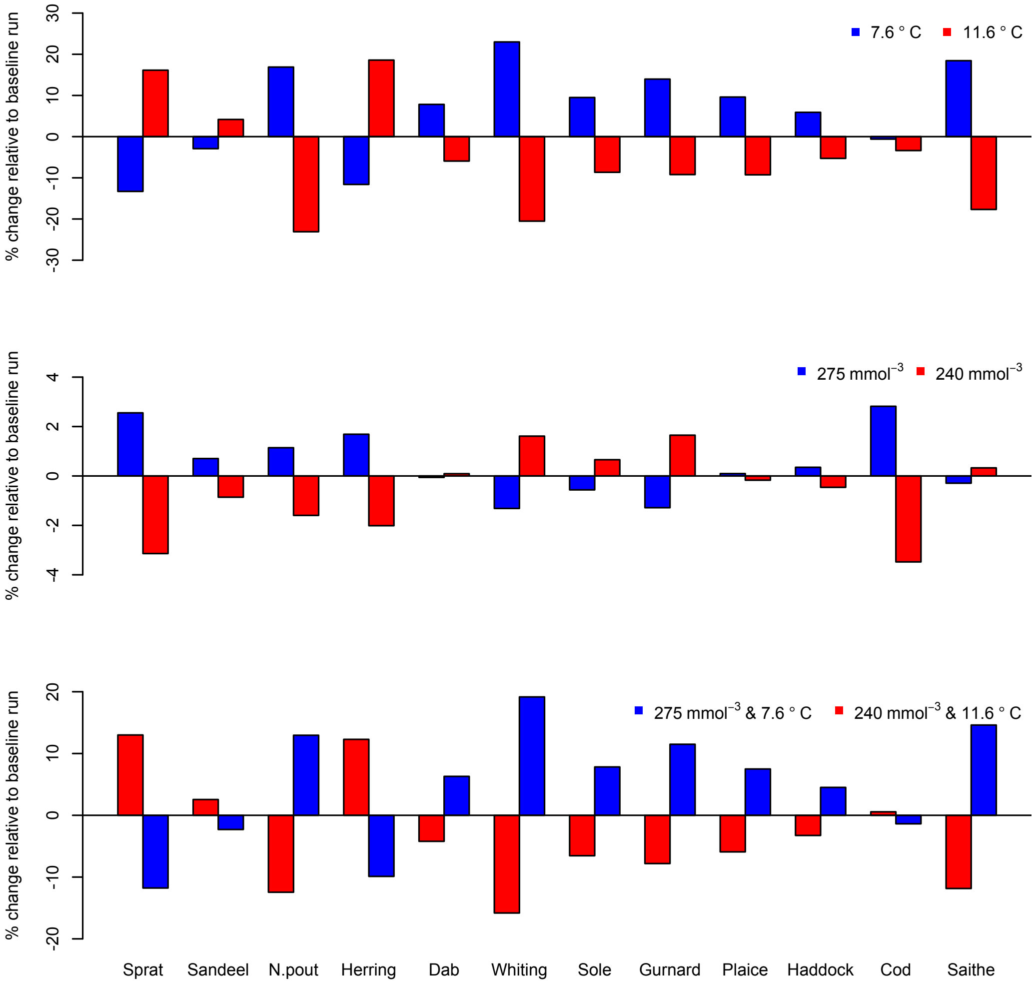

Figure 4.4: Population biomass changes (%) under different environmental scenarios relative to the baseline run. Top plot relates to changes under temperature regimes: 8.5 °C (blue), 10.4 °C (green), 12.2 °C (red). Middle plot relates to changes under oxygen regimes: 255.3 mmolm^{-3} (blue), 277.8 mmolm^{-3} (green), 209.6 mmolm^{-3} (red). Bottom figure combines temperature and oxygen regimes: 8.5 °C and 255.3 mmolm^{-3} (blue), 10.4 °C and 277.8 mmolm^{-3} (green), 12.2 °C and 209.6 mmolm^{-3} (red).

Table 4.1: 4 different size-based indicators (SBI) calculated under different environmental regimes, see Chapter 2 for SBI calculations. The two regimes for each environmental model represent upper and lower environmental conditions based on summer time empirical data. The size-based indicators use all 12 species from the North Sea parameterised size-structured environmental model.

Environmental model	**Input value**	**LFI**	**Size Spectrum Slope**	**Mean Maximum Weight (g)**	**Total Biomass (x 10^{12})**
None (baseline)	N/A	0.23	-2.35	7204	3.55
Temperature (∘C)	7.6	0.24	-2.36	8602	3.78
	11.6	0.21	-2.43	5763	3.34
Oxygen (mmolm^{-3})	240	0.22	-2.36	7203	3.53
	275	0.23	-2.33	7205	3.56
Temperature (∘C) & Oxygen (mmolm^{-3})	7.6 & 275	0.23	-2.36	8519	3.73
	11.6 & 240	0.22	-2.42	5949	3.42

4.4 Discussion

The incorporation of temperature and oxygen into food-dependent growth at the individual level within a size-structured model resulted in changes at the individual, population and community level. The growth trajectories predominately followed empirical expectations, with the temperature-size rule being an emergent pattern for each species, something not always achieved in fisheries modelling [Angilletta *et al.*, 2004]. The resulting differences in population and community level metrics across the alternative runs occurred due to a shift in the food web structure highlighting the advantage of a multi-species model where species interactions are incorporated. As many fishery policies are formed on community metrics [Greenstreet & Rogers, 2006; European Parliament, 2008, 2010], a multi-species modelling approach to future fisheries under climate change must start from the fundamental individual level, to allow changes to perturb through the system up to the community level.

The results in population changes have different implications depending upon the species. While it has been shown that the distributions of some species (exploited or otherwise such as cod, sole, mackerel, plaice) have extended northwards and/or deepened [Perry *et al.*, 2005; Dulvy *et al.*, 2008], other populations are postulated to now be constrained by depth in the North Sea, such as haddock and hake [Rutterford *et al.*, 2015]. The model here shows how species constrained by depth would have to adapt through changes in body size. With the North Sea predicted to warm further [Dye *et al.*, 2013] and reduce in oxygen concentration levels [Meire *et al.*, 2013], the study here implies that the future community structure will be reshaped and individuals will be substantially smaller. Individuals may grow to smaller sizes in response to environmental change, which has already been noted at the population level [Baudron *et al.*, 2014] and is a possible contributing factor for a decreasing community size structure [Marshall *et al.*, 2016]. Furthermore, regions such as the southern North Sea are likely to be under greater environmental stress: the increase of nutrient discharge from mainland european rivers has caused a large rise in eutrophication [Lacroix *et al.*, 2007]. This eutrophication leads to regions of progressively lower oxygen and consequently may result in major damage to marine life [Diaz & Rosenberg, 2008; Greenwood *et al.*, 2010; Queste *et al.*, 2013]. While here the perturbing oxygen changes were small, the population biomasses are nonetheless reduced. Therefore species such as cod and haddock, which are distributed almost homogeneously across the North Sea, might be less likely to be impacted to the same extent as southern dwelling species such as plaice and dab.

Across the North Sea, community size-based metrics have been in decline for some decades [Rice & Gislason, 1996; Shin *et al.*, 2005; Greenstreet *et al.*, 2011; Marshall *et al.*, 2016] though recent improvements have been seen [Engelhard *et al.*, 2015]. Changes have been linked to fishing and temperature [Baudron *et al.*, 2014; Engelhard *et al.*, 2015; Marshall *et al.*, 2016]. The improvement of the size structure, in particular, has been linked to the EU fleet decommissioning program which led to a decline in fishing effort [Engelhard *et al.*, 2015]. The role of temperature, and general environmental factors, are more difficult to explicitly prove [Marshall *et al.*, 2016]. For example, temperature has been suggested as an indirect cause of shrinking fish through reduced oxygen [Pörtner & Knust, 2007; Pauly, 2010; Cheung *et al.*, 2013b; Baudron *et al.*, 2014] though this has been contested [Brander *et al.*, 2013; Lefevre *et al.*, 2017]. It is shown here that size-based changes in characteristic North Sea species can be altered via temperature without the changes in oxygen. Furthermore, when studies are conducted that explicitly use temperature and oxygen [Claireaux & Lagardère, 1999; Lefrançois & Claireaux, 2003] it is found that temperature driven models indicate a higher reduction in the body size distribution. How this might impact future projections has yet to be determined.

Studies on the non-lethal impacts of oxygen on fish growth are limited with only a few species being studied [Chabot & Dutil, 1999; Thetmeyer *et al.*, 1999; Buentello *et al.*, 2000; Claireaux *et al.*, 2000; Pichavant *et al.*, 2001]. The debates surrounding oxygen use in models is therefore not surprising [Cheung *et al.*, 2013b,a; Brander *et al.*, 2013; Lefevre *et al.*, 2017; Pauly & Cheung, 2017]. Further experimentation of non-lethal hypoxia across species in a variety of marine environmental zones is key for confirming effects upon ecosystems. Whilst here the effects were minimal compared to temperature, the combined environmental scenarios with a temperature-oxygen dependent metabolism highlight that both play a role in reducing SBIs. The fact the use of an oxygen-temperature combined metabolic rate derived from a fisheries study, which is mathematically different to the widely used allometric exponential scaling, caused a substantial difference across environmental gradients, even compared to testing temperature and oxygen alone, suggests further expanded experiments should be completed. Additionally, studies of temperature on other fish stock variables, such as recruitment [Akimova *et al.*, 2016] and the plankton size spectrum [Barnes *et al.*, 2011] allude to indirect temperature effects on resulting SBIs. Effects of non-lethal levels of oxygen has not been researched at this larger scale, though it could prove important.

The activation exponent for different physiological rates under temperature is predicted to be 0.65 eV by the metabolic theory of ecology, regardless of the physiological rate considered [Brown *et al.*, 2004]. While here fish-specific rates were used in this model, such as the intake rate [Englund *et al.*, 2011] and metabolism [Gillooly *et al.*, 2001], a comparison of this to when a fixed value of 0.65 eV was used for all rates was conducted. For the temperature only runs the general changes under fixed activation exponent rates were the same (warmer waters resulting in smaller individuals, reduced mean maximum weight, a lower LFI, and a steepening of the community slope) though slightly less exaggerated. For example, the mean maximum weight was 45% larger under cold conditions than warm when the activation rates were equal. However, when activation rates were physiologically specified, the difference was 49%. The combined temperature and oxygen runs use a different formulation for calculating metabolism so only the rates affecting the energy intake would be impacted. The results were negligible in this instance (SBIs differed by $<1\%$ between fixed and physiologically-specified activation exponents), highlighting the sensitivity of metabolism in modelling the bioenergetics of growth. Ultimately, in a temperature only model, the assumption that the rates are equal could cause an underestimation in the expected decline in size-based metrics with a warming climate change. Further empirical work could help cement these important parameters for environmentally dependent models, helping reduce model uncertainty.

One of the greatest struggles in ecological modelling, particularly with fisheries, is understanding and constraining different forms of uncertainty [Chatfield, 1995; Hill *et al.*, 2007; Thorpe *et al.*, 2015; Spence *et al.*, 2016]. Despite these challenges, confidence in these models is still considered to be somewhat overestimated [Brander *et al.*, 2013]. Structural uncertainty, that of the model mechanistic equations, is most likely to be the greatest source of uncertainty [Chatfield, 1995] despite often being ignored [Hill *et al.*, 2007]. This study has implicitly shown how structural uncertainty manifests itself by allowing the growth equation to vary resulting in substantial changes to the population and community makeup. Using a fixed growth approach [Hall *et al.*, 2006; Pope *et al.*, 2006; Speirs *et al.*, 2010] may therefore cause an inaccurate picture of fisheries in the future under a changing climate of warming waters [Collins *et al.*, 2013; Dye *et al.*, 2013] and lower oxygen concentrations [Keeling *et al.*, 2010; Meire *et al.*, 2013]. Therefore the use of environmentally dependent growth trajectories should be encouraged. The different environmental growth trajectories were predominately within the bounds of the empirical data, in line with previous calibrations of this model [Blanchard *et al.*, 2014]. The use of statistical analysis can help identify sensitive parameters which may lead to focused empirical work [Spence *et al.*, 2016].

In addition to the environmental changes, the inclusion of known phenotypic and genetic variability under fishing [Rowell, 1993; Law, 2000; Grift *et al.*, 2003] would be an interesting next step. Shifts in individual growth and maturation dynamics from fishing impacts have been shown to alter population and community dynamics [de Roos & Persson, 2005]. In the North Sea, the changes in the community are likely attributed to a number of drivers, namely fishing and temperature change [Engelhard *et al.*, 2014, 2015; Marshall *et al.*, 2016]. The relative and combined effects of removal by fishing, fishing-induced evolution and environmentally mediated changes have not yet been considered together under a modelling framework. With the abundance of North Sea data, the model used here can be calibrated with greater certainty than many other ecosystems. However, more empirical validation is required to reduce overall model uncertainty such as by studying changes in individual growth in historical fish otoliths [Morrongiello *et al.*, 2012; Rountrey *et al.*, 2014], or further research in the topics mentioned above.

Ultimately, the progression of multi-species modelling for fisheries projections under climate change must incorporate environmental parameters. While the case for environmentally dependent growth has been made here, the incorporation of the environment at different ecological levels will no doubt further our understanding of the complex fisheries systems. This needs to be brought together with empirical relationships to allow for the greatest of confidence in projections of fisheries, one of the largest dependable trades in the world [FAO, 2014, 2016].

Chapter 5

Linking oceanic models to North Sea fish community dynamics: predicted changes and associated uncertainties

Abstract

One of the greatest threats to fisheries under a warming climate is the reduction in body size and body size distributions. Projections have indicated that the distribution of many species may move polewards, or deeper, in order to avoid increasingly inhospitable conditions. However for some species this may not be possible resulting in individuals having to adapt to warmer waters, and reduced oxygen availability. In this study a temperature-oxygen modified multi-species, size-structured model is used to project the North Sea demersal fish community size structure in 2100 under different IPCC scenarios. This is performed by extracting environmental data from two global (IPSL and GFDL) and one regional (GETM) models. Additionally, the results from the different climate models are compared to see if any divergence exists in the fish community projections. The most striking result is the large variations of projections across the climate models. For example the difference between the mean maximum weight using climate data derived from IPSL and compared to data from GFDL is larger than differences between the lowest and highest warming scenarios. Furthermore, the rate of change of the mean maximum weight is substantially higher using IPSL derived data compared to GFDL. However, the body size distribution in 2090–2100 is found to be lower than 2005–2015 average, regardless of which global model is used. The extent, however, cannot be quantified with confidence due to the large disparity between

models. Therefore it is imperative that an improvement in the environmental projections must be made at the regional scale as variations between these cause large differentials in the predications of fish communities under climate change.

5.1 Introduction

The rate of human induced climate change is unlike any environmental change seen before and, if continued in a similar trajectory, will cause detrimental, irreversible damage to ecosystems across the globe [Stocker *et al.*, 2013; Cheung *et al.*, 2016]. Of major concern in the marine realm is an increase in temperature [Stocker *et al.*, 2013], a reduction in pH [Sabine *et al.*, 2004], and a decrease in oxygen levels [Keeling *et al.*, 2010]. These changing conditions have already given rise to coral bleaching [Glynn, 1993; Brown, 1997], inhospitable dead zones [Joyce, 2000; Diaz & Rosenberg, 2008; Greenwood *et al.*, 2010], and potentially 'shrinking' fish [Sheridan & Bickford, 2011; Cheung *et al.*, 2013b; Baudron *et al.*, 2014]. Fishing additionally damages ecosystem health through habitat destruction [Rothschild *et al.*, 1994; Turner *et al.*, 1999], a decline in stocks [FAO, 2014, 2016], and reducing body size distributions [Law, 2000; Jennings & Blanchard, 2004; Marshall *et al.*, 2016]. Due to climate change and heavy fishing having occurred for over a century, where full-scale temporal and spatial environmental, ecological, and fish survey data is not always available, models are required to provide understanding of the past, and projections for the future.

Despite the patchy nature of ecological survey data over time, there are still strong conclusions that can be drawn about the North Sea through time. Data from both otter and trawl surveys (thus catching species in different numbers) have indicated a reduction in diversity, abundance, and size distribution of round- and flat-fish in snap shots of the early 20th century compared to 1990–1995 [Rijnsdorp *et al.*, 1996]. There has been some notable resilience to fishing impacts of non-target fish with some species increasing in abundance due to a changing food web structure [Heessen & Daan, 1996]. Additionally, different taxonomical groups have responded in a variety of ways, with huge changes in abundance in over half of the dominant benthic taxa [Callaway *et al.*, 2002], and shifts in the elasmobranch community from larger individuals to smaller over the last century [Sguotti *et al.*, 2016]. These general conclusions highlight the vast change within the North Sea, with both the environment and fishing being highlighted as drivers of change [Marshall *et al.*, 2016]. More specific studies, for example on individual species like plaice and sole [Engelhard *et al.*, 2011; Cefas, 2014], and cod [Engelhard *et al.*, 2014], or specific regions such as the English Channel [Genner *et al.*, 2010], also draw out conclusions of great change in response to fishing and climate.

While metrics such as diversity and abundance highlight changes, the use of size-based indicators (SBIs) are more commonly used in fisheries policy and management owing to their indicative nature of population and community level changes [Jennings & Dulvy, 2005; Shin *et al.*, 2005; Greenstreet & Rogers, 2006; European Parliament, 2008; Greenstreet *et al.*, 2011; Thorpe *et al.*, 2015]. Size-based indicators use body size to infer the health of an ecosystem. As body size is linked with a variety of life history traits, such as fecundity, maturation time, and physiological rates [Blueweiss *et al.*, 1978; Calder, 1984; Gillooly *et al.*, 2001; Brown *et al.*, 2004; Kingsolver & Huey, 2008; Rall *et al.*, 2012; Reuman *et al.*, 2014], as well as population parameters [Sheldon *et al.*, 1972; Blueweiss *et al.*, 1978; Savage *et al.*, 2004], this single numeric holds a wealth of information. Therefore understanding how changes in body size might alter the community body size distribution, such as via fishing and climate [Rice & Gislason, 1996; Blanchard *et al.*, 2005; Engelhard *et al.*, 2014; Marshall *et al.*, 2016], is of huge importance under a changing climate.

For the North Sea, in general the trends have decreased for different SBIs [Rice & Gislason, 1996; Jennings & Dulvy, 2005; Greenstreet *et al.*, 2011; Fung *et al.*, 2012], though dependent on the area [Marshall *et al.*, 2016]. The central North Sea has shown the greatest change in a reduced body size distribution in recent decades [Marshall *et al.*, 2016], though SBIs such as the large fish indicator have shown an improvement likely due to a reduced fishing fleet [Engelhard *et al.*, 2015]. Steepening of the size spectrum slope also appears to be indicative of heaving fishing in the 20^{th} century [Rice & Gislason, 1996; Jennings & Dulvy, 2005]. At the population level it has been shown that a decrease in maximum size of individuals has decreased, whether this is due to impacts on individual growth [Baudron *et al.*, 2014], or shifts in the centre of biomass for given populations [Dulvy *et al.*, 2008; Engelhard *et al.*, 2014] remains to be seen. Many of the studies mentioned either are only able to reveal trends across a 30–40 year period, or two distinct, averaged time periods.

Therefore dynamical mechanistic models that incorporate both environmental and fishing effects, such as developed in this thesis, affords an opportunity to reconstruct past changes in fish population and communities as well as future projections. Although time series of SBIs have been examined under past and future fishing scenarios for the North Sea [Blanchard *et al.*, 2014; Spence *et al.*, 2016] these multi-species models did not incorporate concurrent environmental drivers of change.

Dynamic models used for projecting fisheries in the future under climate change tend to fall into two categories, those that look at changes in species distributions [Hare *et al.*, 2010; Cheung *et al.*, 2013b; Jones *et al.*, 2013], and those that focus on fewer species or functional groups [Blanchard *et al.*, 2012; Barange *et al.*, 2014]. The species distribution models build upon what has been seen empirically at the population level [Engelhard *et al.*, 2014] and community level [Perry *et al.*, 2005; Dulvy *et al.*, 2008; Simpson *et al.*, 2011; Marshall *et al.*, 2016] where changes under temperature appear to cause populations to shift. However, it has been argued recently, using historical ICES North Sea data, that certain populations have reached the furthest they can go and will instead be constrained by depth and thus be forced to adapt, if possible [Rutterford *et al.*, 2015]. If this does happen, it is unclear how the North Sea community will look in the future as many models do not have depth as a constraining factor. The model described here, which does not include a spatial component (see Chapter 6 for more on this) thus implicitly constrains individuals. Therefore it is well suited for testing how species will change under the depth constrained hypothesis [Rutterford *et al.*, 2015].

In order to project future fish communities, global climate models (GCMs) are currently the only real prospect. Regional models, certainly for the North Sea, have yet to produce projections in line with IPCC scenarios [Stocker *et al.*, 2013], and instead have only been able to resolve small, characteristically different pinpoint sites across the North Sea [van Leeuwen *et al.*, 2016]. Unfortunately GCMs struggle to accurately resolve regional seas, so any results using GCM extracts must be viewed with an air of appreciable uncertainty [Cheung *et al.*, 2012], especially as error is often carried from GCMs to the biological model [Payne *et al.*, 2016].

In order to reconstruct the past community size structure and to discover the demsersal species “winners and losers” [Somero, 2010; Fulton, 2011] in the North Sea, an environmentally adapted size-structured model parameterised for the North Sea is used (Chapter 4). Although in Chapter 4 the equations were dynamic, the inputs were fixed over time as the objective was to test the impact of changing the individual growth through environmentally mediated change. In reality the environment and community dynamics change through time, particularly in this era of rapid warming and deoxygenation [Mann *et al.*, 2008; Keeling *et al.*, 2010]. Therefore using modelled annual sea bottom temperature and oxygen data from 1950 to 2100 this size-structured model is run to detect environmentally driven changes. Two different global climate models are used for extracting environmental data, along with a shorter dataset from a regional model. Therefore two objectives are formed: (a) to understand how much the environment plays a part in changes to the community body size distribution, and (b) to assess the variation in uncertainties with projected fish community metrics under the use of 3 different climate models.

5.2 Methods

The temperature-oxygen environmental multi-species size spectrum model (mizer - env) introduced in Chapter 4 (i.e. environmentally dependent individual growth) is used here in a time-dependent fashion. In Chapter 4, the aim was to understand the consequences of broad-scale time-averaged increases and decreases in temperature and oxygen on the population and community structure. Here the aim is to understand how climate change has influenced fish population and community dynamics over the past 70 years and how climate may impact the future of the North Sea demersal fish community. A brief overview of the environmentally modified model is given here, along with the environmental data used, and a variety of ecological indicators, ranging from individual to community, that are used in describing how the ecosystem responds to climate change.

5.2.1 Size-structured model: mizer-env

This full model has been described in Chapters 3 and 4, along with derivations and modifications. Equations overviewing the main compartments of the model can be found in Table 3.3, and particular ones are featured here in this brief overview.

An individual follows a temperature-oxygen growth dependent trajectory:

$$\frac{dw_i}{dt} = (\alpha f_{T,i} h_i w^n S_{O1} T_1 - k_{s,i} w^p TO2)(1 - \psi_i) \tag{5.1}$$

where for each species i, α is the assimilation efficiency (0.6), f_i is the feeding level, h_i is the maximum food intake constant, w is weight, n is an exponent to scale maximum food intake (0.7), S_{O1} is a log-fashion oxygen saturation scaling factor, T_1 is temperature Arrhenius scaling term for the maximum intake rate (activation rate of 0.80 eV), $k_{s,i}$ is metabolism ($0.12 * h$), p is the exponent for scaling standard metabolism (0.7), *TO2* is an oxygen-dependent temperature effect on metabolism, and ψ_i is the proportion of energy for reproduction. At a given weight, energy starts to be put into reproduction until it plateaus to its maximum size ($W_{\infty,i}$):

$$\psi_i(w) = \left[1 + \left(\frac{w}{w_{m,i}}\right)^{-10}\right]^{-1} \left(\frac{w}{W_{\infty,i}}\right)^{1-n} \tag{5.2}$$

where $w_{m,i}$ is the maturation size, and the above equation provides a step function to smooth the transition from juvenile to mature.

An individual needs to maintain its growth through feeding, which is determined by a background plankton resource spectrum(N_R), and the predation of other species on a given size-specific preference (ϕ), and if they overlap spatially (θ):

$$E_{a,i}(w) = \int (N_R(w) + \theta_{i,j} N_j(w)) \phi_i \left(\frac{w_p}{w}\right) w dw_p \tag{5.3}$$

This determines what species will eat what. A final rate on the ability of an individual to grow and prosper is the likelihood of death.

Each individual has mortality rate imposed on it made up for 4 components: natural (μ_n), starvation (μ_s), predation (μ_p), and fishing (μ_f):

$$\mu_i(w) = \mu_{n,i} + \mu_{s,i} + \mu_{p,i} + \mu_{f,i} \tag{5.4}$$

Only starvation is ignored here, with the remaining mortality functions being size-dependent. It should be noted that the calibrated baseline model includes time-averaged fishing mortality [Blanchard *et al.*, 2014].

This individual described above, growing, maturating, and dying is assumed to be characteristic of all the individuals in the same species population, and therefore can be scaled up using the McKendrick-von Foerster partial differential:

$$\frac{\partial N_i(w)}{\partial t} = -\frac{\partial g_i(w)N_i(w)}{\partial w} - \mu_i(w)N_i(w) \tag{5.5}$$

where the new abundance of a given species, N_i is dependent on the growth, g_i and mortality, μ_i. In order to differentiate the species, Winf, Wm and K are empirically founded [Blanchard et al., 2014] and used within the model.

5.2.2 Environmental input

To force the model with changing conditions in the North Sea through time outputs from two classes of oceanographic models are used, global and regional. Alongside these model outputs, empirical observations from two studies of the North Sea oceanographic climatologies are used here for further comparison [Janssen *et al.*, 1999; Berx & Hughes, 2009]. The fisheries model requires several environmental inputs: a reference temperature, a reference salinity, a reference oxygen, and a time series for each of these 3 oceanographic properties. The reference values are the same as in Chapter 4, empirically founded North Sea values: reference temperature = 9.6 °C (from Berx & Hughes [2009]), reference oxygen saturation = 88.75 % (from Queste *et al.* [2013]), and reference salinity = 34.9 (from Berx & Hughes [2009]). A time series for each of these environmental parameters is derived from each model class as described below.

Global Climate Models (GCMs)

Global Climate Models (GCMs), which can also be referred to as Global Circulation Models, are numerical formulations that describe the physical world. These are used primarily to make hindcasts and projections in an attempt to improve our knowledge of past and future climate change. GCMs are highly complex with interacting mechanisms describing atmospheric processes, energy fluxes, ocean circulation, the ice environment, and the terrestrial landscape. However many of the intricacies within these components are not able to be modelled acutely (i.e. there are large averaging assumptions made) – resolute details must be sacrificed so the desire to have global (as opposed to small-scale regional) projections can be achieved. Different GCMs created by different institutes make their own unique simplifications and assumptions, and thus no two GCMs are exactly alike. In order for a GCM to be considered in policy, certain standards must be met, continually compared with other GCMs, and to be constantly monitored and improved.

For individual GCMs be held accountable for reasonable projections, a large consortium of modellers, climate scientists, and mathematicians work together under the umbrella CMIP5 [Taylor *et al.*, 2012] – the 5th phase of the Climate Model Intercomparison Project (formally Coupled Model Intercomparison Project). The framework for CMIP5 allows different global climate models to be compared, the output studied, and the mechanisms driving changes to be determined. As many of the GCMs that are used under CMIP5 are dynamically different it is inevitable that the projections will vary. However the CMIP5 framework aims to disentangle what mechanisms drive the projections, why GCMs project scenarios differently, and to give an indication of what might happen in the future under human induced climate change. This is achieved by comparing modelled results (e.g. climate indices output, climate mechanics) from each GCM where each have all been implemented with the same initial conditions. Due to this vigorous process, the GCMs that have been studied and integrated as part of the CMIP5 framework are the best model projections of the environment that are available. Therefore the environmental data used here is taken from models that are part of the CMIP5 framework.

The data and comparisons under the CMIP5 umbrella can be freely downloaded. The CMIP5 project, however, also works in collaboration with other modelling projects where climate and environmental data are required. For example the Inter-Sectoral Impact Model Intercomparison Project (ISI-MIP) is a framework looking at how different sectors (such as agriculture, forests, fish, global water, biodiversity) are projected to change with the future climate. In this case ISI-MIP work with CMIP5 whereby CMIP5 provide the environmental climate data which is then used to drive the sectoral models. In the case of fisheries (FISH-MIP) climate projection data are used to force different ecosystem models, either global fisheries distributions or smaller, regional ecosystems. The fisheries model described here in Chapter 3 (based on Blanchard *et al.* [2014]) has been implemented as part of FISH-MIP for North Sea fisheries projections. Therefore it follows that using the updated, environmentally dependent model (i.e. Chapter 4) should use the same input for potential future use in FISH-MIP.

The extracted environmental data comes from two GCMs used under CMIP5: the Geophysical Fluid Dynamics Laboratory Earth System Model (GFDL–ESM2M) and Institut Pierre Simon Laplace (IPSL–CM5A–Low Resolution). These models have resolutions of 2° x 2.5°, which relates to approximately 60–70 miles when considering the North Sea. These GCMs have four major components, land, sea, air, and ice [Dunne *et al.*, 2012]. Within each of these components exist intricate modelled dynamics. For example the land model includes hydrology to allow for river runoff, vegetation dynamics and terrestrial ecology, and the sea ice model incorporates ice thickness and internal ice stress, and an additional iceberg component is also included. The atmospheric and oceanographic models are more complex with hundreds of separate equations required to describe their fluid natures, their ability to transfer and flux heat, momentum, and particulate, all of which dictate (directly or indirectly) the environmental characteristics of air and sea. These dynamics therefore allow hypothetical scenarios driven by changes to the atmospheric chemical composition (such as burning fossil fuels) to be tested for projections into human induced climate change.

The GCMs used here have the start of the modelled physical environment set to preindustrial years, circa 1800 (ignoring the spin up, which tends to be several hundreds of years prior to a given time point). However as empirical data for the 1800s is somewhat limited, and alternative must be sought. Models instead take the approach of initialising oceanographic systems (i.e. temperature and salinity) from empirical data in the 1980s, and force these conditions with atmospheric data to allow the model to run and stabilise. Solar and radiative forcing, which can be back calculated to the 1800s based on the known elliptical orbits the earth takes (Milankovic's cycles), are then imposed on this initial baseline [Dunne *et al.*, 2012]. This therefore gives a stable physical model prior to the industrial revolution. The pre-industrial values of greenhouse gases are taken as constant for the model spin up, taken from around the year 1750. At the point of calculating the historical environment (1950–2005), and projections beyond the present day (2006–2100), atmospheric greenhouse gases are taken from empirical records and from a variety of wide-ranging hypothetical scenarios, respectively.

The historical period under ISI-MIP runs from 1950–2005, and the future projections run from 2006–2100. Four different projections exist in line with the IPCC scenarios [Stocker *et al.*, 2013]: RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5, where each RCP (Representative Concentration Pathway) represents an increasing radiative forcing (Wmˆ-2) expected by 2100, respectively, noted by the numeric following 'RCP'. These radiative forcing values are dictated by the increasing greenhouse gases based on a variety of complex physical and socioeconomic scenarios [Moss *et al.*, 2010]. The data for the historical run and each RCP future run for the North Sea were extracted to be approximately in line with ICES subarea IV: $51 - 62\,^{\circ}$N, 4W–8 °E. The data required for inputting into the fisheries model were sea bottom temperature, sea bottom oxygen, and sea bottom salinity. The data extracted were then averaged across the whole of the North Sea for the summer months of June to September to remain consistent relative to the reference values. A spin up period for 300 years was done in the fisheries model prior to 1950 with the average historical temperature, oxygen, and salinity fixed during this period. One model run is therefore 450 years: 300 year spin up, 55 year historical run, 95 year projection. There are 4 runs for each global model making 8 model projections in all.

Regional model

As global models are often more easily accessible and available, it is rare for regional models to be used for fisheries projections. Additionally, projections are computationally costly and therefore are often done at a low resolution, something which would be ineffective for a regional model. However, in general, regional models are better validated. Therefore it can be asked whether there is any difference in the results (i.e. community size structure) when regional environmental data is used, rather than global data.

As it stands, North Sea environmental projections have not been completed [pers. comm Sonja van Leeuwen & Jorn Bruggeman]. However by using the regional model used in Chapter 2, the GETM-ERSEM-BFM coupled 3D hydrodynamic - biogeochemical model [van Leeuwen *et al.*, 2013; van der Molen *et al.*, 2013; van Leeuwen *et al.*, 2015], a 38 year comparison (1971–2008) between the regional and global models can still be made. The GETM-ERSEM-BFM model has been validated, and due to the high resolution (0.1° x 0.167°), it is able to resolve important small scale oceanographic processes through the inclusion of the 1D General Ocean Turbulence Model (GOTM) [Burchard & Bolding, 2002; Stips *et al.*, 2004; Burchard *et al.*, 2014]. The regional data were extracted in the same way as the global climate data, such that the sea bottom temperature, oxygen, and salinity were averaged across the same area ($\sim$ ICES subarea IV) over June through to September.

5.2.3 Ecological indicators

In order to assess how annual variations in the summer time environmental data influences the size-structured North Sea model, three aspects of the model output are assessed. Firstly the total biomass changes, along with species-specific biomasses, are calculated. A particular focus will be on the changes seen over the final decade modelled (2090–2100), which is commonly used in projection model comparisons. Secondly, the mean maximum weight will be calculated to assess how the community structure dynamics vary through time, and is calculated accordingly:

$$\overline{W_{max}} = \sum_i \frac{W_{max,i} B_i}{B_A} \tag{5.6}$$

where W_{max_i} is the maximum weight of each species i, B_i is biomass of species i, and B_A is the total biomass of all species. Finally, the large fish indicator (LFI) will be examined and is calculated as:

$$LFI = \frac{B_{40}}{B_A} \tag{5.7}$$

where B_{40} is the total biomass of individuals greater than 40 cm in length and B_A is the total biomass of all the fish.

5.3 Results

The primary purpose of this chapter was to investigate changes in the North Sea demersal fish community size structure through time, with an additional study into how global and regional model outputs effect the projections. The results are in two sections, the first describes size-based indicators for the North Sea over a 150 year period. The second section compares these results, derived using global model output, with results when data from a regional model is used instead.

5.3.1 North Sea size structure

For all species, a decline in maximum size was found between 10–28% across all projections. This resulted in substantial changes across the population and community level dynamics.

When the GCMs were used to force the fisheries model, the most striking result was the difference in initial overestimation of the mean maximum weight (Figure 5.1). The IPSL mean maximum weight at the steady state (i.e. before annual variations were forced) was 10495 g, over 3000 g greater than the baseline run (7204 g). However, while the GFDL did overestimate, it was only by ∼400 g, with a steady state value of 7735 g. Surprisingly, the regional model (GETM), struggled to replicate the baseline as closely as the GFDL, with a steady state mean maximum weight of 6113 g, over 1 kg less than the baseline (Figure 5.1). The projected expectation of change, taken here as the difference between the 2005–2015 average and 2090–2100 average, were highly variable in both GCMs, though clear differences were found (Table 5.1). For the GFDL runs, the RCP 2.6 and 4.5 scenarios showed no major changes through time (<3%), whereas RCP 6.0 and 8.5 saw a decrease in mean maximum weight by 793 g (10%) and 1167 g (15%), respectively. The IPSL showed greater expectations in change across all runs with the RCP 2.6, 4.5, 6.0, and 8.5 decreasing by 11%, 18%, 16%, and 24%, respectively.

The changes were calculated for the GCMs only as no projections exist for the regional model. However a historical comparison was still able to be made. GETM showed a step change with a sharp decrease of mean maximum weight from 6554 g to 5809 g in a three year period in the late 1980s, representative of a regime shift. To put this into context, over a 100 year period the GFDL predicted a reduction of size under the a more extreme scenario (RCP 6.0), very similar to the loss seen in the GETM 3 year step change (10% vs 11%). The GFDL also showed these step change characteristics throughout the time series, particularly seen in the early 1980s and 2000s with decreases in nearly 1 kg over a few years. Therefore in the case of GETM and GFDL, the sudden regime shifts associated climatic step changes (i.e. sudden rapid warming) have been picked up which could prove helpful for predicting times of sudden change.

The Large Fish Indicator (LFI) did not provide a coherent indication of change. Throughout all the scenarios, and across each model, the LFI never went beyond 0.20–0.25 (Figure 5.2), which is in line with the baseline run. The LFI showed huge fluctuations through time therefore only trends (as opposed to step changes) can realistically be determined. For the GFDL model there was a minor increase in the LFI under RCP 2.6 of 2%, whereas the remaining scenarios decrease by up to a maximum of 4% over the 100 year period (Table 5.1). The IPSL showed a range of increases between 1–3% across all scenarios.

The total biomass at the steady state for IPSL, GFDL, and GETM were 4.12 x 10^{12}, 3.61 x 10^{12}, and 3.43 x 10^{12}, respectively. Once again, it was the global model GFDL which gave results closest to the baseline run. GFDL estimated more moderate decreases in biomass by up to 4% in RCP 8.5, whereas

IPSL indicated a drop of 11% (Table 5.1). These are reflective of smaller fish in general increasing (e.g. sprat, sandeel, herring), and larger fish decreasing (e.g. whiting, sole, saithe). Some species showed no changes to the climate projections: dab and plaice. Unusually, cod and haddock appeared to increase in number under RCP 8.5, despite them being two of the largest fish in the model.

5.3.2 Comparison of global and regional climate model outputs

There was a stark contrast between the three model setups, both in terms of the environmental data (Figure 5.3), and the resulting fish community output (Figure 5.1). The historical average sea bottom temperatures were 4.7 °C, 8.7 °C, and 11.38 °C for the IPSL, GFDL, and GETM models, respectively. These are based on the summer months June–September. The GCMs underestimated, while the regional model overestimated. The IPSL model produced large underestimates with waters over 5 °C colder than the empirical North Sea climatology [Berx & Hughes, 2009]. In fact this average is lower than sea bottom winter temperatures seen in the early 1900s [Janssen *et al.*, 1999], a time before the first period of rapid warming [Delworth & Knutson, 2000]. On further investigation, it was found the English Channel had been closed (Figures 5.4 & 5.5), likely due to low resolution the model was set to, meaning the Atlantic waters were unable to mix into the southern North Sea. This closure is likely to have caused this cold, fresh depiction of the North Sea and is further discussed in the next section. The oxygen levels coincided with temperature boundary, such that the colder waters were able to retain more oxygen, and so did.

The waters in the GCMs were also substantially fresher than in the regional model and empirical data. A salinity value of 34.9 is the summer time average (June–September) in the North Sea [Janssen *et al.*, 1999; Berx & Hughes, 2009]. The GCMs were substantially lower in their historical averages, with the IPSL being 33.5, and the GFDL being 31.8. GETM was superior to these with a historical average of 34.5. While salinity does not impact the fish physiology directly, it is used in the conversion of saturation and concentration for oxygen. While the salinity does not have a huge impact on the oxygen conversion used here (i.e. it is not a sensitive parameter, certainly not at these minor levels of change), the major concern is what the salinity reflects in the hydrography of the models. The waters from the IPSL are characteristic of Arctic outflow waters [Dickson *et al.*, 2007; Bacon *et al.*, 2014], not a temperate semi-enclosed sea.

Table 5.1: Mean maximum weight, large fish indicator (LFI), and total biomass when using IPSL and GFDL derived environmental data. The values are calculated as the average of 2090–2100 ± the standard deviation, with the percent change in brackets relative to the 2005–2015 average.

GCM	**Scenario**	**Mean Max Weight (g)**	**LFI**	**Total Biomass ($x10^{12}$)**
IPSL	RCP 2.6	8801 ± 205 (-11%)	0.24 ± 0.004 (+ 2%)	3.75 ± 0.05 (-6%)
	RCP 4.5	8202 ± 70 (-17%)	0.23 ± 0.003 (+2%)	3.66 ± 0.03 (-9%)
	RCP 6.0	8293 ± 200 (-16%)	0.24 ± 0.006 (+2%)	3.67 ± 0.05 (-8%)
	RCP 8.5	7580 ± 303 (-24%)	0.23 ± 0.007 (+1%)	3.56 ± 0.06 (-11%)
GFDL	RCP 2.6	7570 ± 126 (-1%)	0.23 ± 0.005 (+0.2%)	3.58 ± 0.04 (-0.5%)
	RCP 4.5	7481 ± 95 (-3%)	0.23 ± 0.005 (-0.5%)	3.57 ± 0.02 (-0.7%)
	RCP 6.0	6812 ± 132 (-10%)	0.23 ± 0.004 (-2%)	3.48 ± 0.04 (-3%)
	RCP 8.5	6684 ± 313 (-15%)	0.22 ± 0.006 (-4%)	3.47 ± 0.05 (-4%)

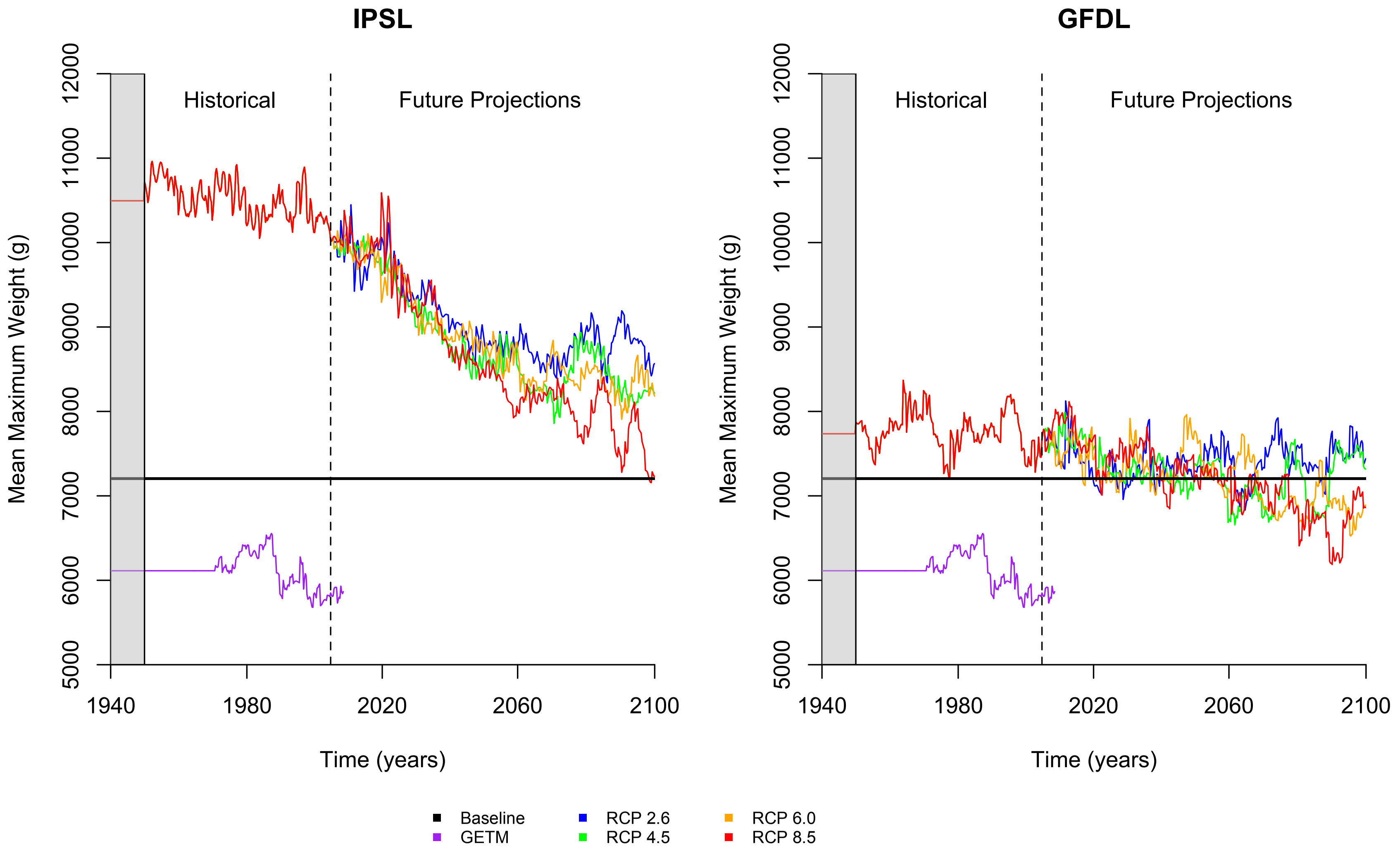

Figure 5.1: The lefthand figure is the mean maximum weight for a range of IPCC scenarios under IPSL forcing, and the righthand figure is under GFDL forcing. The different scenarios are plotted as RCP 2.6 (blue), RCP 4.5 (green), RCP 6.0 (orange), RCP 8.5 (red), GETM (purple), and the baseline run (black).

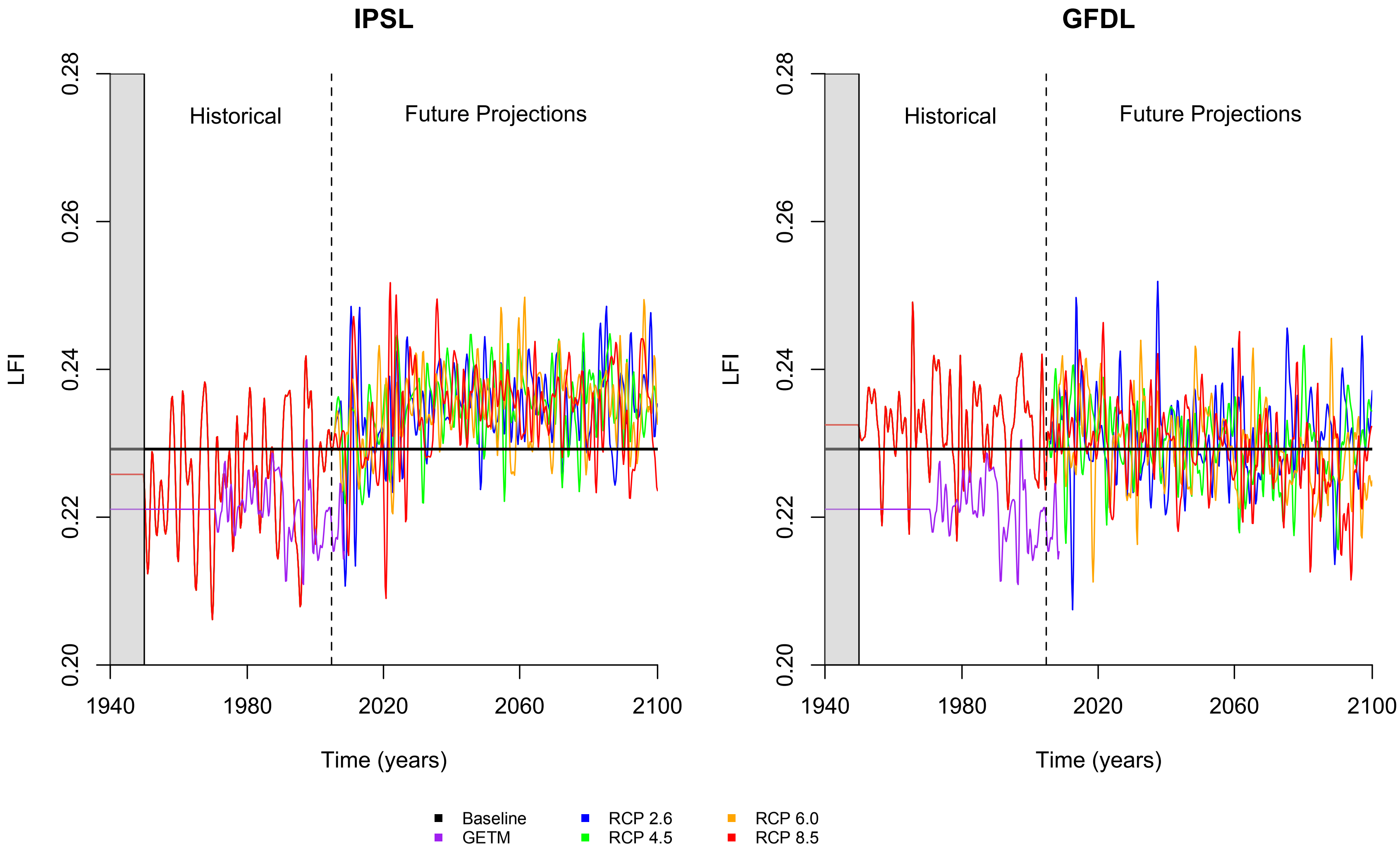

Figure 5.2: The lefthand figure is the Large Fish Indicator (LFI) for a range of IPCC scenarios under IPSL forcing, and the righthand figure is under GFDL forcing. The different scenarios are plotted as RCP 2.6 (blue), RCP 4.5 (green), RCP 6.0 (orange), RCP 8.5 (red), GETM (purple), and the baseline run (black).

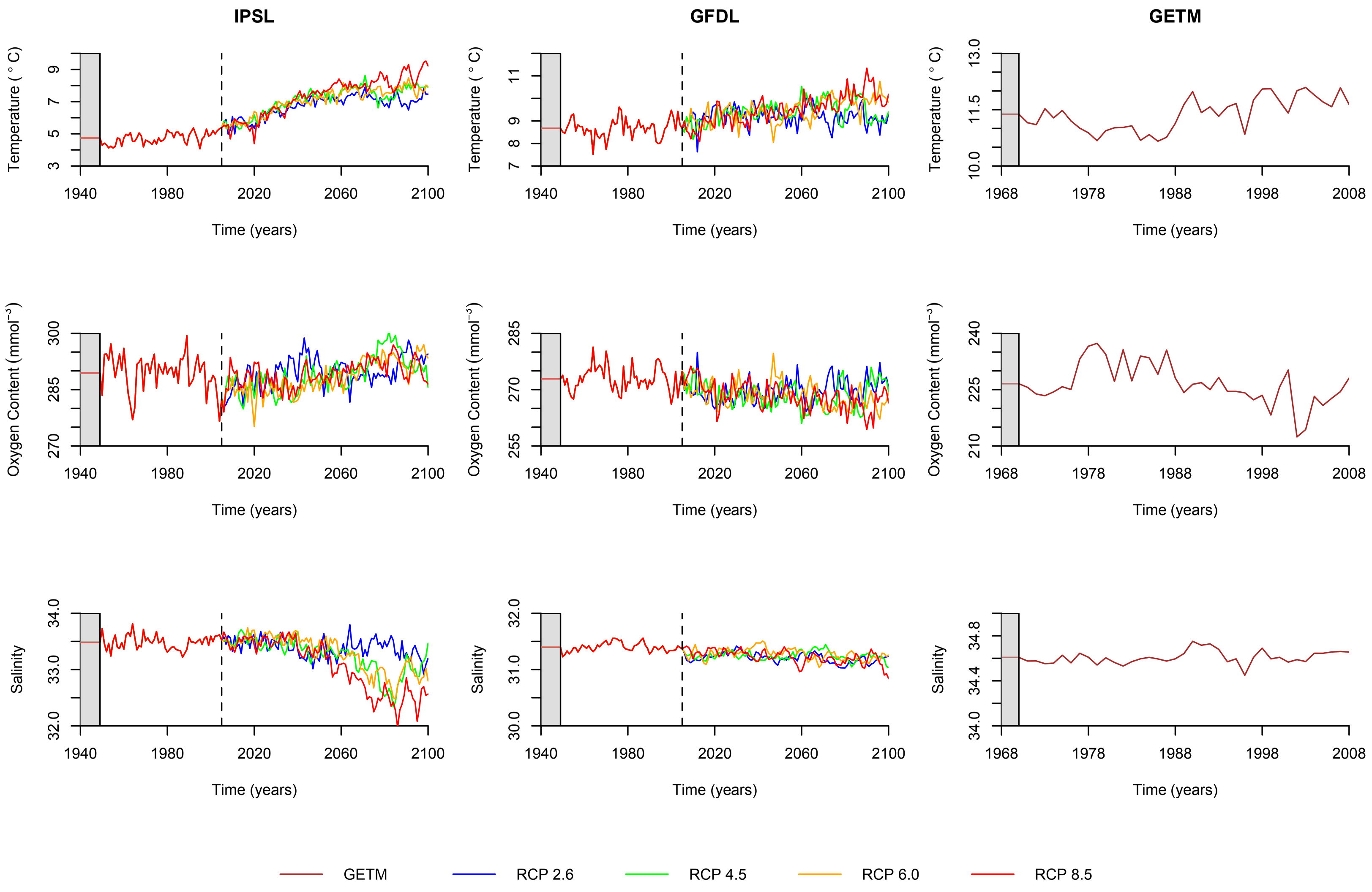

Figure 5.3: Figures in the lefthand column, centre column, and righthand column represent data from IPSL, GFDL, and GETM, respectively. The top row is the time series of temperature, the centre row the time series of oxygen, and the bottom row a time series of salinity. The different scenarios, where relevant, are plotted as RCP 2.6 (blue), RCP 4.5 (green), RCP 6.0 (orange), RCP 8.5 (red). The time limits are the same for the IPSL and GFDL x-axis. The y-axes for the same environmental parameter are often different due to the large differences in values would obscure the trends.

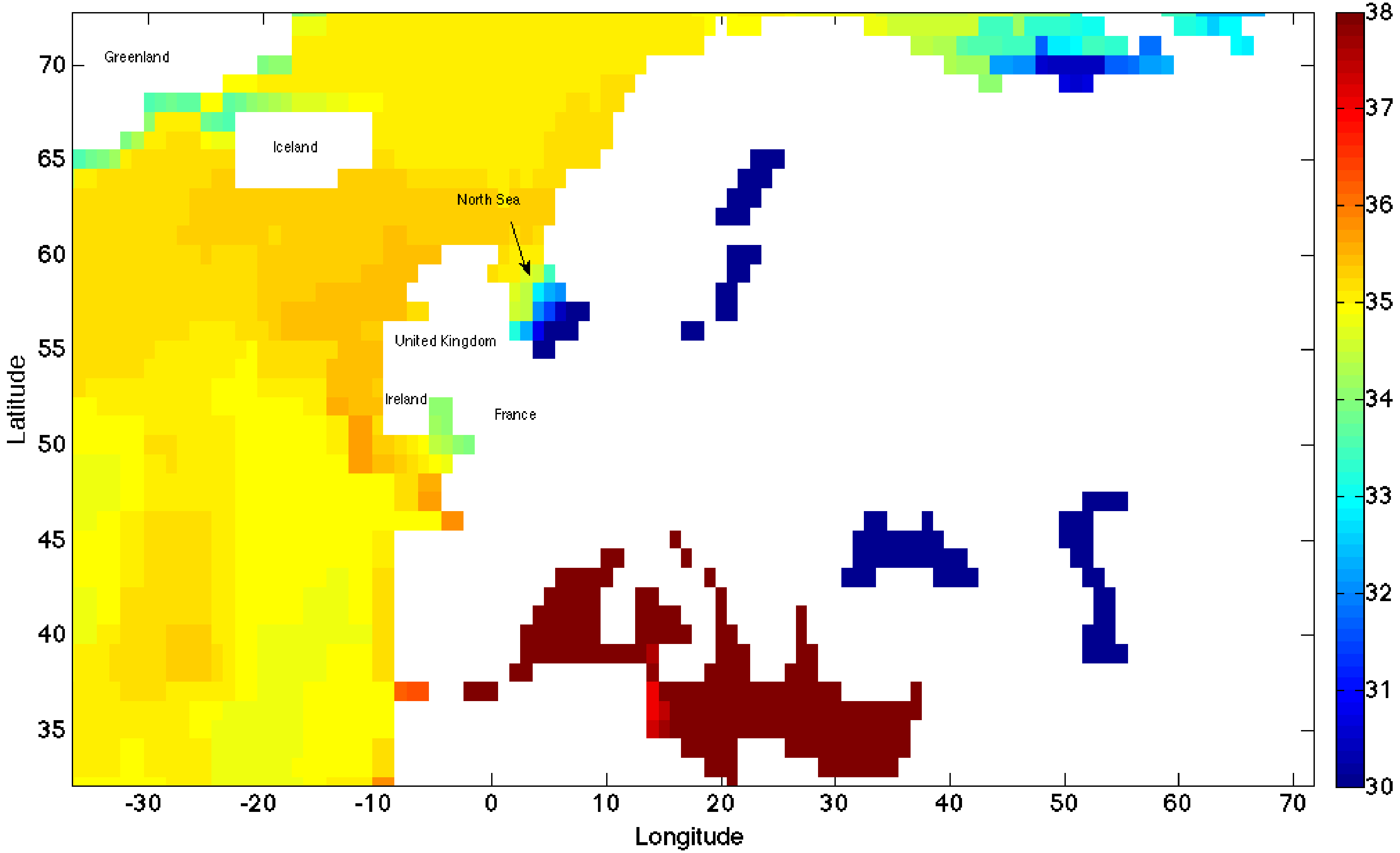

Figure 5.4: The salinity from the IPSL GCM is shown across the North Atlantic waters, with a particular note to the freshwater in the North Sea. The importance of this figure is the closure of two important hydrographic features: the English Channel and the Strait of Gibraltar. The impact of the closure of these is highlighted in the overly fresh, and overly salty nature of the resulting waters, respectively.

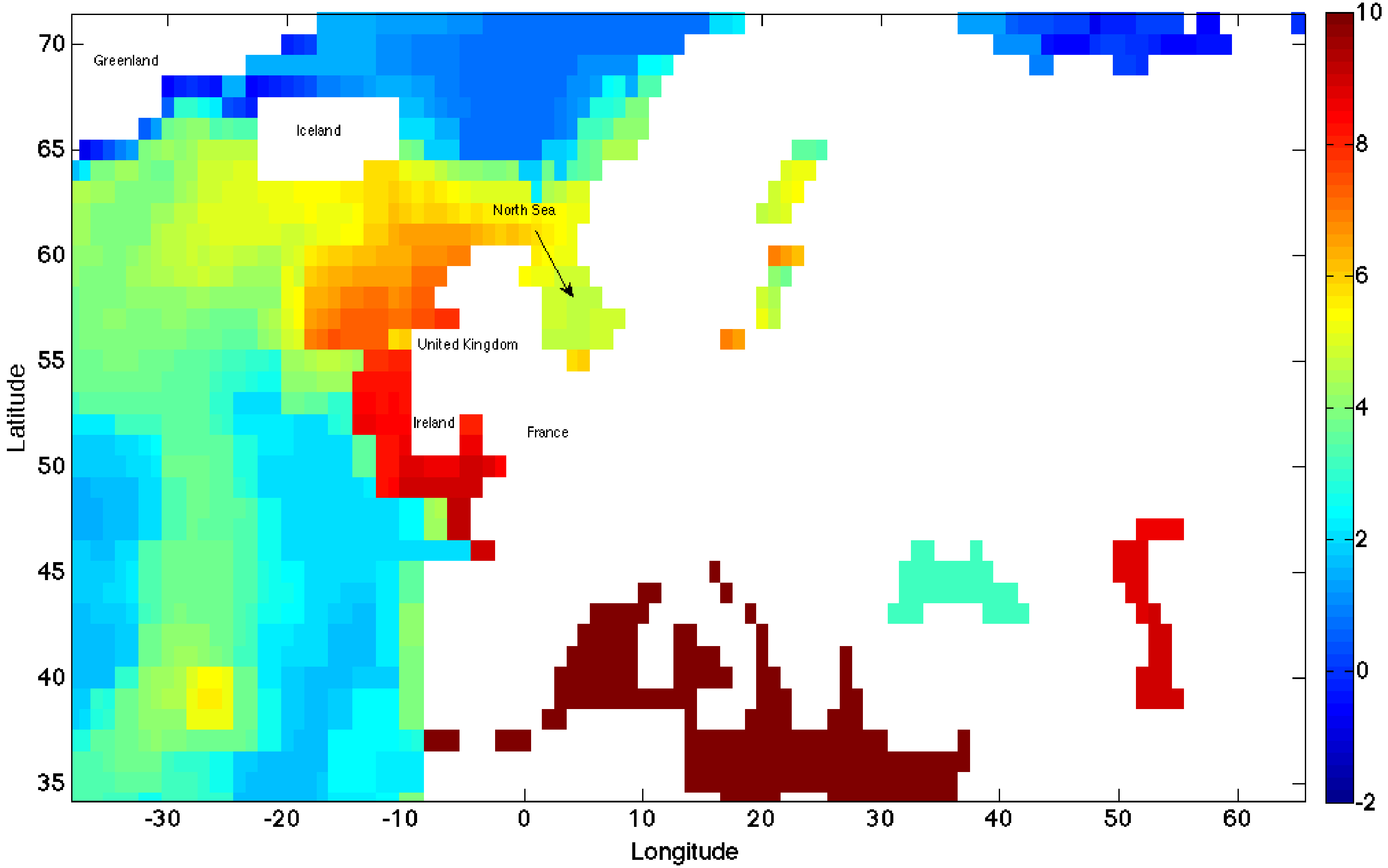

Figure 5.5: The temperature from the IPSL GCM (°C) is shown across the North Atlantic waters, with a particular note to the colder waters in the North Sea. The importance of this figure is the closure of two important hydrographic features: the English Channel and the Strait of Gibraltar. The impact of the closure of these is highlighted in the overly cold, and overly warm nature of the resulting waters, respectively.

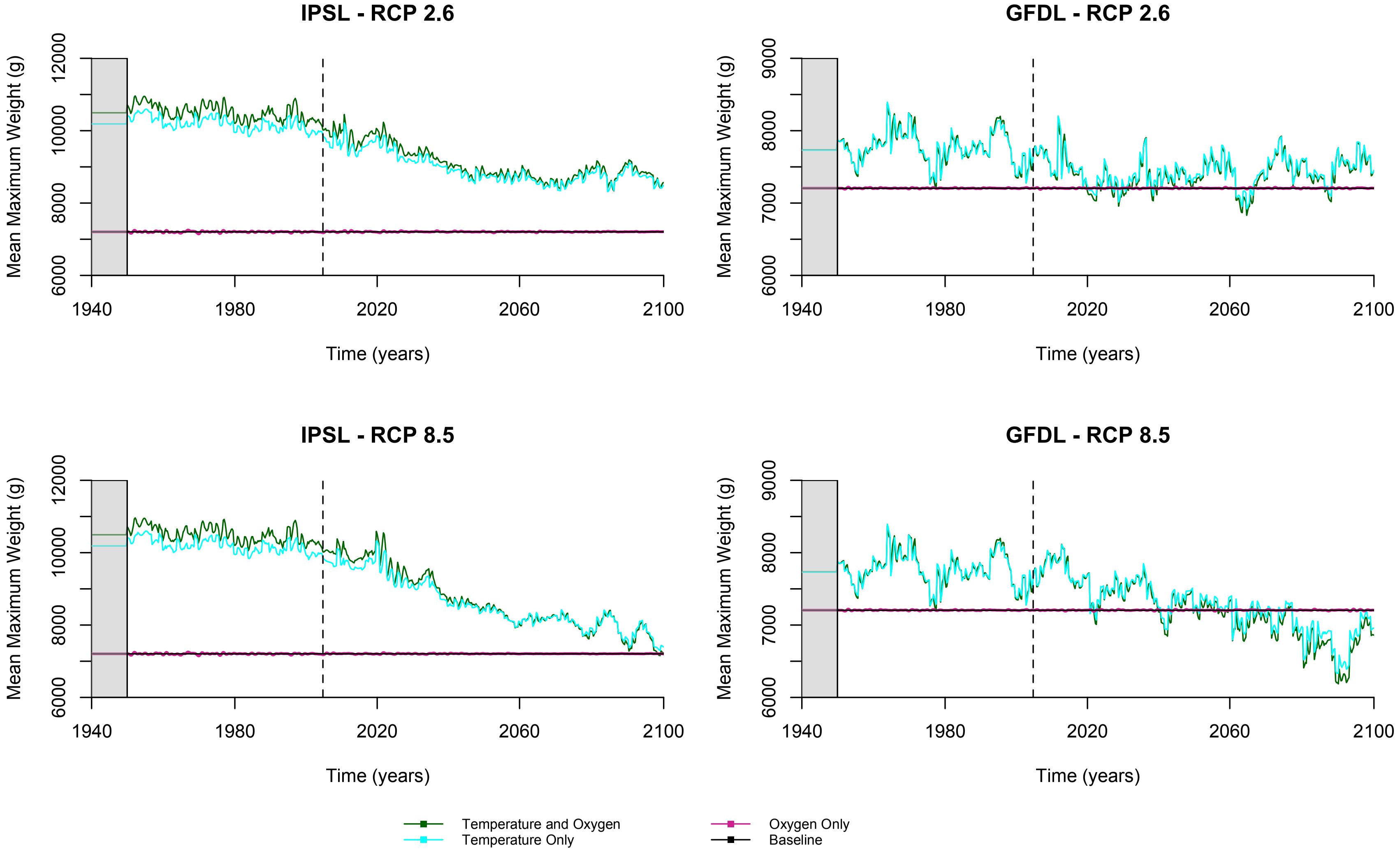

Figure 5.6: Each figure shows the mean maximum weight for three different environmental fisheries size structured model (derived in Chapter 3). The temperature only impacts maximum intake rate and metabolism (dark green), oxygen only impacts food intake (pink), temperature and oxygen combined impact maximum intake rate, food intake and metabolism. Black line is the baseline run. Rows represent the two lower and upper limits of climate scenarios, RCP 2.6 and RCP 8.5 (top and bottom, respectively). The columns indicate the global climate model used (left = IPSL, right = GFDL).

5.4 Discussion

The use of different global modelled environmental data has provided stark differences in the expectations of fisheries under a future changing climate. Due to the different oceanographic features and model resolution, the magnitude of ecological response that have been predicted are substantially different, such as varying from a 1% vs 11% change in mean maximum weight under RCP 2.6, and 15% vs 24% under RCP 8.5 for GFDL vs IPSL, respectively. However, it can be conclusively said that under either model all species decreased in size, but the response of abundance varied, with some species doing better, and others declining under warming. Therefore while an improvement on model estimation must be made, there are clear climate change impacts on the fish community size structure. Unlike fishing which can be managed locally, global climate change will continue (as it already has done) and thus policy makers, fishermen and scientists must develop adaptive ways to protect the sustainability of fish communities.

From all three model runs under each climate scenario, the LFI remained within 0.20–0.25 and was highly variable. Empirically derived LFI values have ranged from 0.07–0.47 across the average North Sea [Greenstreet *et al.*, 2011; Fung *et al.*, 2012], and 0.05–0.8 within spatially defined regions [Engelhard *et al.*, 2015; Marshall *et al.*, 2016] over the last 40 years. This study, therefore, seems to suggest that the LFI is not sensitive to changes in climate change, and certainly not to the same extent as it is to fishing [Houle *et al.*, 2012; Engelhard *et al.*, 2015]. However this model only includes environmental modifications at the individual level. Whether the LFI would respond more to environmental impacts on the population or community levels remains to be seen.

The mean maximum weight showed a greater sensitivity to climate change than the LFI. Across all scenarios using either GCM resulted in substantial losses by 2100. The most extreme scenario, RCP 8.5, showed the greatest change, as expected, and deviated from the other RCP runs around 2060. Comparing two time periods, 2005–2015 and 2090–2100 indicates that the mean maximum weight could reduce by up to 2.4 kg. The North Sea average change in mean maximum weight from 1980–2008 resulted in a nearly 6 kg loss [Marshall *et al.*, 2016]. Therefore climate driven changes are the same order of magnitude as what has already been seen. However, spatially, the central North Sea approached a 25 kg loss which was postulated to be due to fishing [Marshall *et al.*, 2016] indicating the greater damage caused by fishing over climate change. Empirically associating fishing and climate to changes in fish communities is difficult. The advantage of this model is the ability of it to predict that changes under climate alone could potentially cause a loss of 2.4 kg, especially if the fish are constrained to living in their current habitat [Rutterford *et al.*, 2015].

An interesting feature from the mean maximum weight is the sudden drop in the late 1980s as predicted when using the regional output. This coincides with a known regime shift in the North Sea during this time [Beaugrand, 2004; Alheit *et al.*, 2005]. As a regime shift is brought about through a change in climate, hypotheses such as temperature, wind, and phytoplankton have been put forward to explain the resulting higher trophic shift [Beaugrand, 2004; Alheit *et al.*, 2005]. What the size-structured model has shown here, when using regional environmental data, is that a drop in the mean maximum weight (i.e. a regime shift) has coincided to a dramatic warming of over 1 °C in a 2 year period. Furthermore, as this shift has been replicated in this particular environmentally adapted size-structured model, this would suggest the regime shift seen in the North Sea occurred due to temperatures driving a change in physiological growth rates. While neither GCM picked up this dramatic regime shift, the GFDL did show other step changes indicating it has the capacity for such changes, though relative to GETM, the temperatures are time-lagged. Using the GFDL data suggests that there have been two regime shifts in the last 70 years, and that we are currently in the middle of a shift. The IPSL does not appear to be able to detect such dramatic, short period changes.

The regional model used throughout this thesis has a resolution of 0.1 ° x 0.167 °, whereas the global models here are much lower, nearer to 2 °. This results in geographic disparities between global and regional models (and empirical data). For example, in the IPSL GCM used here the English Channel and Strait of Gibraltar, both of which are less than 2 ° at their narrowest points, are shut off from the main ocean circulation (Figures 5.4 & 5.5). By closing the Strait of Gibraltar the exchange of waters between the North Atlantic and Mediterranean Sea are effectively non-existent, a fundamental process that should not be ignored [Candela, 2001]. The North Sea has two inflows from the North Atlantic: the English Channel in the south, and the Fareo Island – Scotland Channel in the north, both bring in warm, salty, oxygen-deplete and nutrient-loaded Atlantic water [Winther & Johannessen, 2006; Holt *et al.*, 2012a; Marshall *et al.*, 2016]. By shutting the English Channel, the modelled North Sea is substantially colder and fresher than what it should be [Janssen *et al.*, 1999; Berx & Hughes, 2009], and slightly higher than expected in oxygen concentrations [Queste *et al.*, 2013]. Additionally, as the Atlantic waters are nutrient-rich, this could severely hamper the effectiveness of the GCMs to predict phytoplankton. The cooler waters in the GCMs are a result of the lack of warm Atlantic water inflow (Figure 5.5), and the riverine input from mainland Europe dominates the salinity profiles for much of the southern North Sea region (Figure 5.4). Ultimately this results in a North Sea which is as cold and as fresh as some Arctic outflow waters [Dickson *et al.*, 2007; Bacon *et al.*, 2014], and thus is completely uncharacteristic of the North Sea [Janssen *et al.*, 1999; Berx & Hughes, 2009]. However, it is not just the absolute values that are problematic, the rate of change also seems somewhat variable.

The noticeable difference between the IPSL and GFDL rate of change in environmental conditions is reflected in the projected fisheries metrics. In the most extreme case projection (RCP 8.5) IPSL predicts a change of 3.5 °C, whereas GFDL is only 1.2 °C. An increase of 3.5 °C is the maximum prediction in global sea surface temperature rises [Mora *et al.*, 2009]. The global near bottom water warming is about 0.5 °C [Mora *et al.*, 2009] - however this does include very deepest waters therefore is bias when attempting to understand the shallow North Sea. Therefore a 3.5 °C is likely to be closer to expectations than 0.5 °C, but is likely to be substantially overestimated in light of the strong seasonal stratification [van Leeuwen *et al.*, 2015]. The reason for these extreme projections under IPSL will require further investigation as to avoid any overestimated conclusions, especially when such data is used for other purposes like ecological modelling. Alternatively, a bias reduction scheme may need to be implemented [Maraun, 2016].

There are a number of examples across different sectors, such as agricultural [Hawkins *et al.*, 2013; Ramirez-Villegas *et al.*, 2013] and atmospheric [Kodra *et al.*, 2012; Yang & Chong-Ha, 2012], that have called for improvements of GCMs before they are used at the regional level. As it stands, GCMs are the only models for extracting climate projections. One possibility on improving the data at a regional level is the use of climatologies. These can be used to reduce bias in the absolute values of extracted regional data [Maraun, 2016] in parameters such as temperature and salinity (though *not* the trend). A bias correction has been undertaken by ISI-MIP (the umbrella project which FISH-MIP falls under), and while the GFDL appears to have been improved, the IPSL is still of concern. It is recommended, therefore, that any study requiring downscaled data from GCMs to a regional area should assess the error between the modelled and empirical data, and take appropriate steps for bias correction if required (such as those provided by the GCM downscaled data portal).

The idea of improving environmental modelled output by adjusting it through climatologies and empirical data may be sufficient in certain areas. However there are regions that are heavily influenced by oceanographic features, and if these features are not resolved within the model but are thought to vary under climate change, a simple bias correction may not be sufficient for accurate projections. For example, the Mediterranean Sea and the (southern) North Sea described here were closed off to the open ocean and thus the overturning circulation. Projections have indicated that the meridional overturning circulation is likely to weaken by ~20% by 2100 [Schmittner *et al.*, 2005; Stocker *et al.*, 2013]. This will influence the mixing and water characteristics (temperature, salinity, nutrients, oxygen) of many seas directly impacted by the overturning circulation, such as the North Sea and Mediterranean Sea. Therefore as the hydrodynamics are misrepresented in the GCMs, a bias correction alone may not be able to resolve the inaccuracy of the projections. The best solution here is for regional models to provide projections, which, as needed, are now being undertaken.

A final comment on the future improvements of projection modelling is based on the inclusion of different environmental parameters at the individual level. In the previous chapter, three environmentally modified models were compared: temperature only, oxygen only, and combined temperature/oxygen. In order to see how these different setups compared in their projections a brief test was conducted using the GCMs across the three environmental models. Oxygen had very little effect whatsoever on the food web structure or biomass (Figure 5.6). This is largely due to the high oxygen saturation within the North Sea. Until the oxygen saturation gets below 70%, there will be no major impacts on the ingestion of food, and therefore growth [Chabot & Dutil, 1999]. As the saturation in the North Sea has never been below 75% in the last century [Queste *et al.*, 2013], which has included two periods of extreme rapid warming [Delworth & Knutson, 2000], it is unlikely that oxygen alone will have an impact on North Sea fishes. Furthermore, despite the wide ranging oxygen concentrations across the models, (IPSL = 265–300 mmolm^{-3}, GFDL = 250–280 mmolm^{-3}, GETM = 210–240 mmolm^{-3}), a difference of just under 10% for the oxygen saturation was actually found (IPSL = 92%, GFDL = 94%, GETM = 84%), all of which are too high to impact food ingestion. The temperature alone setup was found to be incredibly similar to the temperature-oxygen combination setup and they were statistical indifferent under IPSL, and marginally different under the extreme scenario, RCP 8.5, for GFDL (Figure 5.6). This difference between the GFDL and IPSL at RCP 8.5 could be because the GFDL oxygen and temperature were working in unison (higher temperatures and lower oxygen) to cause a reduction in overall size, whereas in IPSL, unusually the oxygen was predicted to increase (Figure 5.3) which may have mitigated against increasing temperatures under the growth trajectory. While this additional comparison means the use of temperature alone may underestimate the true extent of the climate impacts, it is likely to be a sufficient model if no temperature-oxygen relationships are suitable. Additionally, this indicates under the model bioenergetic framework used throughout this thesis that oxygen is not necessarily a dominating, constraining factor with temperature as has been suggested previously [Pörtner & Knust, 2007; Pörtner & Farrell, 2008], though this is largely due to the assumptions made on how individual fish grow (i.e. oxygen limitations vs reproduction).

The use environmental modelled data from two global climate models to force an environmentally dependent, multi-species, size-structured model of the North Sea has shown a clear reduction in body size distribution. By 2100, every species studied is likely to reduce in size, and while some species will see an increase in their numbers, the majority will decrease under climate change. Errors within the GCM have lead to the recommendation that the output of a regional hydrographical model (currently running projections in line with IPCC scenarios) should be used in order to help reduce the uncertainty of these North Sea predictions. However, it is categorical that a reduction in body size distribution under climate change will occur in some capacity, just by how much needs to be further quantified under improved climate projections.

Chapter 6

Discussion

The North Sea Ecosystem is a vital resource for millions, yet has increasingly become strained over the last century due to fishing and climate change. The reduction in large fish and the increase of small fish, relative to one another, has predominately been attributed to fishing [Rice & Gislason, 1996; Bianchi *et al.*, 2000; Shin *et al.*, 2005]. Climate change, until recently, has been seen as a secondary impact compared to fishing [Steele, 1991]. The empirical research presented in this thesis supports the idea that fishing is of greater detriment to a fishery than climate change (Chapter 2). That being said, in Chapters 4 and 5 a size-structured model was adapted to include environmentally dependent growth which provided results suggesting the climate changes predicted by 2100 will still cause a considerable decline in community size-based indicators. In this final chapter I review the work of this thesis by highlighting the key findings. Two sections follow this, one focussing model development (environmental/fishing drivers and spatial resolution) and one focussing on how climate and fishing might need to be addressed in the future, with a particular focus on the North Sea.

6.1 Key findings

The first aim of this thesis was to understand the spatio-temporal changes in the North Sea demersal size structure. While many studies have focussed on North Sea changes, these tend to average across the North Sea spatially or through time [Daan *et al.*, 2005; Heath, 2005; Fung *et al.*, 2012; Greenstreet *et al.*, 2012] or look at certain species [Bolle *et al.*, 2004; Baudron *et al.*, 2014; Engelhard *et al.*, 2014]. Here, as part of this thesis, the change in the demersal fish community as a whole across space and through time was studied – three important factors never considered simultaneously. This approach was achieved by using Empirical Orthogonal Functions (EOFs) which define spatio-temporal patterns of change. EOFs have a major advantage in studying regions where the scale of the area in which to research has not been predetermined, something of an ecological conundrum [Johnson, 2009]. EOFs have no *a priori* assumptions surrounding a given system or area. Any distinguishable spatial patterns therefore are purely statistically derived from the dataset, and these patterns describe the strength of covariance between each region through time and not within imposed boundaries (i.e. such as political, oceanographic properties, historical significance).

By using EOFs on the North Sea demersal fish dataset it was found that the body size distribution declined in the central North Sea and increased in the north-eastern regions, though by an order of magnitude less. Furthermore, these changes were attributed using a nonlinear model to fishing and temperature, respectively, which highlights how much more of an effect fishing, compared to temperature, has on body size distributions. There is no doubt that climate change in some capacity is impacting North Sea fish [Dulvy *et al.*, 2008; Baudron *et al.*, 2014; Engelhard *et al.*, 2014; Rutterford *et al.*, 2015], but this research supports other studies that postulate fishing to be a bigger driver in changing body size distributions than temperature changes [Jennings & Blanchard, 2004; Blanchard *et al.*, 2012; Engelhard *et al.*, 2015]. The explicit mechanisms behind the EOF patterns are not known, though postulations can be made (i.e. see Chapter 2). Further research into how to approach disentangling effects from empirical ecosystem data is one of the hardest challenges faced in fisheries ecology. Despite this, it can be concluded that the North Sea should not be considered as one homogeneous system, as the Marine Strategy Framework Directive encourages, as this can easily cause an oversight in how fishing is managed, particularly under a changing climate.

These empirical findings paved the way for the remainder of the thesis, with evidence for both the environment and fishing able to cause changes in body size distributions. In order to further investigate changes of the North Sea demersal community, a mechanistic model previously parameterised for the

North Sea [Blanchard *et al.*, 2014] was adapted to incorporate temperature and oxygen dependent physiological equations at the individual level (Chapter 4). After the model was successfully verified different projection regimes from global climate models were implemented. There are three important conclusions that can be drawn from this: (1) the stark differences between the global climate model outputs, (2) the differences between the fisheries model used here compared with other published fisheries models, and (3) the ability of the GCM-forced fisheries model to project step changes (representative of regime shifts). The difference between the GCMs output, regional model output and empirical data were dealt with in some detail in Chapter 5 and thus here will simply be the recommendation that model output users should compare the data they extract before assuming its validity.

The fisheries projections found here are different to one particular suite of fisheries models, gill oxygen limiting theory (GOLT) based models. The GOLT based models discussed here [Cheung *et al.*, 2013b,a, 2016] have two components. The first is latitudinal shifts in fish distributions, something which the model in this thesis does not contain. The second component is to model the shifts in body size at the individual level, before scaling up to the population and community level, an approach used here in this thesis. The basis of the fish growth in the GOLT based models is fundamentally different to the growth defined in the model used throughout this thesis. Here the model assumes the asymptotic growth of a fish is due to the reproductive drain hypothesis. The GOLT models assume that the asymptotic growth of fish is due to oxygen limitations whereby the gills grow (mathematically) as a surface and therefore increasingly with size constrain the oxygen requirements of the whole fish (which grows as a volume).

The use of GOLT to drive fish growth is unusual and, as far as I am aware, is only done by, or those working with, the GOLT pioneer, Daniel Pauly. Yet the results of this tiny proportion of fisheries models has garnered worldwide publicity like no other. In reality, the evidence for the GOLT is not as strong as other theories, the basis is can be found to be theoretical and the support for the theory is often implicit purely by denouncing other hypotheses, mainly the reproductive drain hypothesis [Pauly, 2010]. Using reproduction as the basis of asymptotic growth has a wide empirical foundation [Lambert & Dutil, 2000; Lester *et al.*, 2004; Shuter *et al.*, 2005; Folkvord *et al.*, 2014], and recent research suggests that the gill physiology of GOLT is incorrect [Lefevre *et al.*, 2017]. In a response to this, Daniel Pauly and William Cheung described a number of outliers in an attempt to refute the reproduction theory rather than to explicitly support GOLT. However these outliers were not without their problems. For example sexual dimorphism is frequently used as evidence against the reproduction theory on the assumption female reproduction is more energetically demanding than male therefore females should be smaller, which they are often not. However Rijnsdorp & Ibelings [1989] found the reproductive energy requirements in male and female plaice were all but identical, despite them being sexually dimorphic. Furthermore, recent research has found that the gonad hormone rather than energetic costs are key in sexual dimorphism and teleost growth [Bhatta *et al.*, 2012] which questions the gonadectomy experiments that Pauly [2010] often refers to in support. Much of the GOLT proposals are somewhat theoretical [Pauly, 2010], or even misunderstood [Lefevre *et al.*, 2017], yet it is this fish growth formulation that is the basis of models whose output has captured the world press, twitter and Facebook - reaching across to billions of people. The news reports are somewhat bias, in that the underlying and unmentioned assumption of the story is that GOLT is correct, and that 13% of the changes in body size distribution are due to oxygen limitations [Cheung *et al.*, 2013b]. By using an alternative model, based on reproduction driving fish growth, this thesis has provided projections showing minimal, if any, impacts of oxygen on body size distributions. The oxygen physiology is based on experiments conducted on species found in the North Sea [Chabot & Dutil, 1999; Claireaux & Lagardère, 1999; Lefrançois & Claireaux, 2003], unlike other GOLT models which are less evidentiary [Cheung *et al.*, 2013b]. When one considers how much oxygen depletion is required for any substantial change to fish growth, shown experimentally [Chabot & Dutil, 1999],it is unsurprising that the expected changes are negligible. Therefore there are two clear lessons from this: (1) further research is required on the validity of GOLT and the reproduction drain hypothesis – both have merits and outliers, with the vast datasets a metadata analysis could be done to improve our knowledge surrounding fish growth, (2) fisheries scientists need to work together and not to mislead or scaremonger the public.

One way for comparing different model approaches is by creating ensembles, that is a collection of different models with identical initial conditions to compare their output. Despite some global climate models predicting rather unlikely scenarios, having CMIP5 as an umbrella framework to review all models within an ensemble helps determine the discrepancies and their importance [Taylor *et al.*, 2012]. Until recently, there was no equivalent for fisheries models. Over the last few years, FISH-MIP has evolved from the typical setup of CMIP (which, incidentally, has been running for over 20 years). FISH-MIP aims to compare mechanistically unique fisheries models across a range of ecosystems in order to see how they differ in their projections. There is no issue with taking the side of the reproductive drain hypothesis or GOLT, however there is a problem when one is taken to be far superior in its accuracy, especially when both theories are disputed. Therefore as a community of fisheries researchers, and scientists in general, we must endeavour to compare and improve models for needed climate predictions, not slander and hinder each others progress.

The final note to highlight from this thesis is the ability of the fisheries model to produce step changes, representative of regime shifts, when driven by one GCM (GFDL), and by the regional model (ERSEM-GETM-BFM). The regional model in particular picked up the regime change in terms of decreasing fish biomass during the 1980s, across the same time point when a large temperature increase occurred, found in the regional model and empirically [Beaugrand, 2004; Alheit *et al.*, 2005]. Capturing this step change is particularly encouraging because these types of changes are often unexpected and rapid. As such, from the 1980s regime shift the impacts were seen around the world across different biomes, from ocean biogeochemistry, to atmospheric composition, to fish catches [Reid *et al.*, 2016]. Having a fisheries model that is able to predict changes of this magnitude through time could help reduce the uncertainty associated with fisheries management. Arguably, being able to capture these rapid changes is more important than the 100 year projections. The dynamic and uncertain nature of fisheries means improving short term forecasts is more relevant and helpful to fisheries, fishermen, and fishery management than long term projections.

6.2 Future model developments

This thesis has added to previous North Sea work on changes to the demersal body size distribution, stressing the importance of models in a situation where historical data are in short supply or spatially inconsistent. Furthermore, projections of the future North Sea state are useful for policy and management. Unknown fish resilience and uncertainty (such as climate change) are often accounted for in future management scenarios, though it is useful to further improve our knowledge of such uncertainties in order to further clarify this ‘buffer’ within management regimes. However more consideration of model uncertainty is required. This section looks at two particular features of model uncertainty: parameter and structural. In addition, an approach to incorporate an explicit spatial dimension is proposed. As it stands this model assumes the North Sea is a single, cohesive ecosystem. However in Chapter 2 the use of empirical resources implied that a spatially explicit approach would be more reflective of the true North Sea [Marshall *et al.*, 2016]. This section discusses these uncertainty problems, along with ideas on approaching a spatial dimension within the model.

6.2.1 Parameter uncertainty

Uncertainty of parameters is common across all models. This uncertainty derives from not knowing the exact value that one should attribute to a given parameter, largely due to little empirical research support. Even if the biological equation is correct, if it cannot be bound by appropriate values, it can become meaningless. Therefore ensuring the best possible parameter values is vital. A major advantage of size-based modelling is the relatively few parameters that are required compared to other more complex, and highly parameterised fisheries models. However, discerning the correct value for the variety of parameters is not always easy, and improvements are still required. This can be split between drivers of change (e.g. environmental and fishing) and ecological parameters.

One approach to increasing reliability in ecological and physiological parameters could be a wide-scale experimental study looking at parameters across species and up through the taxonomic hierarchy. Studying species such as cod, haddock and whiting would reveal how species vary from one another within one family (i.e. Gadidae). This could be compared to another family group, such as the Pleuronectidae, where individuals within this group (e.g. plaice, dab, sole) could be cross compared. While expensive, this could at least indicate what taxonomic rank is sufficient for parameters: do individual species need to be examined, or can just one species be used to represent one family or genus, or even just one species from a 'functional' group (e.g. assume one flatfish species either from Scophthalmidae or Pleuronectidae can be representative of both groups). Accurately determining the basic physiological values is vital for incorporating drivers of change. While further experiments are paramount, using statistical methods on the models and data could extract the best information from the data that already exists.

Another route into improving parameter uncertainty can be the use of Bayesian statistics. When experiments are unable to be conducted, increasing the statistical power of the current data is a logical, inexpensive and useful way to reduce modelling error. For over 20 years the use of Bayesian statistics for this purpose has increased [Cerezo & García, 2004]. Recruitment values (R_{max}), for example, were improved in a size-structured model using Markov Chain Monte Carlo (MCMC) Bayesian statistics [Spence *et al.*, 2016]. However this is computationally expensive, taking several weeks as it attempts to use a distribution to fit a variety of statistical models to the data, finding the best fit, in an iterative-type process. There are also limits to what additional information statistics can provide. Ideally, more experiments would be used alongside high level statistical methods. This is where interdisciplinary science could be helpful, having a statistician help design experiments based on what they require for improved model accuracy can guide experimentalists to only carry out studies on the necessary animals with the hopes of reducing costs, time, and unnecessary animal testing (a reduction in which complies with the aim of reducing animal testing under the House of Lords scientific procedure [https://www.nc3rs.org.uk/the-3rs]).

6.2.2 Structural uncertainty

Reducing structural uncertainty is predominately about formulating the correct mechanisms to best describe a given process, ranging from processes such as individual reproduction, population growth, or species-interactions. Determining whether an equation is correct is based on the biological plausibility represented by the mathematics, and how well the resulting equation fits to empirical or experimental data. Chapter 4 described how the inclusion of temperature and oxygen varied growth (implicitly showing structural uncertainty), something which is known yet has never been modelled in tandem explicitly at the individual level in a size-structured model. Not only did the modified growth, for the most part, match empirical data well, it also highlighted cascades through the system to the population and community level. Therefore it is important to continue modifying the model in a way that includes important known effects, such as the environment and fishing, but at different ecosystem levels, namely the population level. The incorporation of environmental factors may further increase the integrity of its structural state.

As the model currently stands, there is no inclusion of fisheries induced evolution (FIE), and there is no known model that incorporates both FIE and environmental changes. FIE is complex and difficult to definitively prove as both plastic and genotypic changes can give rise to changes in growth and size. FIE is the process whereby size-selective fishing of large individuals causes a given phenotype, such as size-at-maturation, to change over generations as the remaining individuals (which grow to a smaller size) become the norm within the population, and it is this smaller size-at-age genotype that succeeds into the next generations [Law, 2000; Conover & Munch, 2002; Law, 2007]. This gradually causes a reduction in the average size-at-age across the population as seen in the North Sea [Grift *et al.*, 2003; Mollet *et al.*, 2007]. While not all are convinced that evolutionary changes are the cause of a reduction in size at age, it is becoming more accepted with the aid of probabilistic maturation reaction norms (PMRN) [Olsen *et al.*, 2004; Dieckmann & Heino, 2007]. Already FIE has been incorporated into fisheries models [de Roos *et al.*, 2006; Enberg *et al.*, 2009; Kang & Thibert-Plante, 2017]. In one study, a size-structured model with FIE resulted in a step change: if a moratorium is put in place early enough, the size-at-age will return to the original, natural average, if too late then the size-at-age will decrease until a steady state is found [de Roos *et al.*, 2006]. These results make incorporating FIE, fishing mortality and environmental change within a single model an important next step. This could be particularly guided by multidimensional PMRN which incorporate fishing and other factors governing growth, such as temperature [Rijnsdorp *et al.*, 2005; Kraak, 2007].

According to quantitative genetics, an FIE response is dependent upon the heritability of a given trait and magnitude of selection (in a fisheries context selection magnitude is represented by how much of a cohort has been removed through fishing) [Kuparinen & Merilä, 2007]. This response effectively describes the rate of evolutionary change between generations of a harvested population. The heritability of fish traits are often approximated to be between 0.2 and 0.4 [Law, 2007; Kuparinen & Merilä, 2007] making changes in size-at-age likely to be over the order of decades rather than cohorts/years [Law, 2007]. Using this basic relationship, the foundations of FIE within a size-structured model have been developed [de Roos *et al.*, 2006]. While the evolutionary mathematics in de Roos *et al.* [2006] can applied in the model used here, the addition of two distributions rather than fixed weight sub-cohorts (implicit in a normal distribution but modelled discretely by de Roos *et al.* [2006]) can allow an element of stochasticity to be incorporated. The current set up of the model dictates that all individuals of a given population have the same maximum weight. Instead, for FIE, a distribution of maximum weights could be implemented by assuming a normal distribution with the current maximum weight used here representing the mean of the distribution. This mathematical set up represents – genetically – a population of individuals having different genotypes that result in different growth rates and maximum sizes. An additional distribution could also be included, this time a harvesting distribution which can either be a skewed normal distribution, or a beta distribution. The mean of this distribution represents the average size of targeted fish. This could be based upon the optimum size vs selling price of a species, which is known to be nonlinear [Beverton & Holt, 1957]. At each time step a selection of fish will be 'caught', with these values taken from the skewed distribution, and then removed from the normally distributed population. As most caught will be around the target size, which will inevitably be to the right of the normal distribution, there will be a shift in the population weight distribution. By mathematically harvesting in this manner, predominately bigger individuals will be removed, but there is an acknowledgement that smaller fish can be caught, an important inclusion as discard has been banned [Sardà *et al.*, 2015]. This should result in an ever increasing right skewed normal distribution of fish population through time. The inclusion of FIE should hopefully allow further investigation into separating fishing and climate impacts. Furthermore, different fishing regimes, such as size-selective or balanced harvesting, could also be examined. However, there are numerous physical and chemical environmental factors that could also be considered. As some reviews have previously been published [Brander, 2010; Koenigstein *et al.*, 2016], I will here only highlight a few components that could be relevant to the North Sea calibrated model used here.

Temperature, oxygen and salinity are important in the impacts they have on fisheries. In Chapter 4 of this thesis it was shown that temperature and oxygen influence the growth rate and final size, consequently perturbing through the system. This particularly emphasises the benefit of having environmentally dependent growth, as opposed to a fixed growth model [Pope *et al.*, 2006]. However the environment can impact at different ecological levels [Koenigstein *et al.*, 2016]. A recent study compared temperature and salinity to a variety of fish stock variables for certain North Sea species [Akimova *et al.*, 2016]. With correlations between recruitment and the pre-larval survival for species like sprat, cod and plaice, new environmentally dependent recruitment could be tested, especially as recruitment is such a sensitive parameter [Spence *et al.*, 2016]. Other studies into pre-larval development and the dispersion of eggs have noted water density changes (through salinity and temperature), wind-driven currents, and direct effects of temperature all to be contributing factors to the success or failure to the new cohort [Holliday & Blaxter, 1960; Harms, 1986; Stenevik *et al.*, 2008; Bolle *et al.*, 2009; Pacariz *et al.*, 2014; Vuorinen *et al.*, 2015]. Therefore applying a factor between these and larval dynamics/reproductive success would be a fascinating modification. Finally, there is the likelihood that temperature in some capacity can influence plankton [Barnes *et al.*, 2011], and the nutrient filled oceanic inflow can influence zooplankton [Reid *et al.*, 2003]. As a semi-chemostat model for phytoplankton has been used throughout this thesis, the influence of temperature on phytoplankton would be an important extension. However, phytoplankton is not just dependent on temperature, the influence of a decreased pH is likely to cause variations.

The greatest threat to the chemical composition of the oceans is its increased acidity, and the North Sea is no exception to this threat. The indirect effect on fish growth stems from variations in the plankton. It was initially thought that carbon dioxide would damage calcifying phytoplankton [Riebesell *et al.*, 2000], however this is now being questioned for certain species due to the huge rise in coccolithophores in the North Atlantic, despite increasingly acidic waters [Rivero-Calle *et al.*, 2015]. Therefore the use of a carbon dioxide-dependent plankton spectrum is difficult to confidently calculate. Coupled biogeochemical-hydrographical models are starting to project the plankton spectrum [Cabré *et al.*, 2016], however as the mechanisms dictating the spectrum are not fully understood, as seen by unexpected results in nature [Rivero-Calle *et al.*, 2015], and the tenuous links to the environment (see the supplementary materials in Barnes *et al.,* [2011]), incorporating these direct projections could be misleading, especially as the size-structured model here is particularly sensitive to the plankton slope. Regional models with these projections offer the best solution as often they are verified to greater detail with better empirical data [van Leeuwen *et al.*, 2013]. The incorporation of direct effects of a decreased pH on fish are difficult to justify as experiments are largely based on unrealistic carbon levels [Ishimatsu *et al.*, 2008; Heuer & Grosell, 2014; Rossi *et al.*, 2016] relative to the IPCC pH predictions [Stocker *et al.*, 2013], and are often underestimated in the complexity on fish physiology [Heuer & Grosell, 2014]. Therefore any attempt to include carbon dioxide directly at the individual level (such as changes in reproduction [Miller *et al.*, 2013], or a reduced search rate to proxy impaired olfactory senses [Rossi *et al.*, 2016]) on fish must be done on a more theoretical level until more realistic empirical evidence is gathered. The other chemical change is the general reduction in oxygen, and certainly the reduction in oxygen capacity. Dead zones (hypoxic regions) are likely to be more frequent and sporadic in the southern North Sea due to excessive land use and temperature increases [Weston *et al.*, 2008] with damaging effects at such low levels [Greenwood *et al.*, 2010]. This hypoxic effect has been incorporated in the model through metabolism though did not come into effect. Model projections for climate change do not predict these extreme events as they are likely to happen over short time periods, something which models are unable to resolve. Non-lethal effects of oxygen are only partially understood at the individual level. Certain behavioural changes such as predator evasion tactics, predator performance, spawning regulation and habitat compression (lower oxygen forcing predator and prey to live in closer proximity) have been hypothesised to be due to oxygen variations [Townhill *et al.*, 2017]. As the mechanisms of these relationships are not fully understood, and there has been no evidence to suggest direct impacts at the population or community level, the inclusion of oxygen may, for now, be sufficient in this model.

As a primary purpose of including environmental relationships into the size-structured model is to decrease the structural uncertainty, the mechanisms included need to be founded on solid empirical research. However, at the population and community level this is incredibly hard to achieve in fisheries. Even at the individual level, while experiments are an excellent source of knowledge, they do not always reflect nature, such as highlighted by the case of the coccolithophores mentioned above. While structural uncertainty has been argued to be the greatest source of (ignored) uncertainty in models [Chatfield, 1995; Hill *et al.*, 2007], reducing parameter uncertainty is perhaps more achievable with improved statistics [Cerezo & García, 2004; Spence *et al.*, 2016]. Additionally, statistical inference of data can extract information that is not necessarily obvious, and can help direct what experiments can provide the best solutions, thus providing support in reducing structural uncertainty. Ultimately continued experimental research and interdisciplinary collaborations are imperative for the continual improvements of models.

6.2.3 Resolving the spatial dimension

The model developed in this thesis is not spatially resolved. The interaction matrix describes how species overlap providing an implicit spatial description of predator-prey interactions. However there are no explicit mechanisms describing spatial movements. The typical movements that could be mathematically modelled under environmental change can be derived from the movement of a population biomass due to climate vectors. Across different marine ecosystems it has been shown that the centre of biomass of populations are changing, likely due to warming waters [Dulvy *et al.*, 2008; Pinsky *et al.*, 2013; Engelhard *et al.*, 2014]. Therefore the inclusion of spatial movement to the size spectrum model could inform us of potential changes under climate change. Chapter 1 described how the North Sea Ecosystem should be seen heterogeneously, a model capable of replicating this would be a great help and improvement on the current set up.

While other ecosystem based models do include spatial dimensions, this often is accompanied by a variety of highly complex relationships. One of the major advantages of size-structured modelling is the ability to describe these complex ecological relationships in relatively simple mathematical terms, and without the need of high data input for model parameterisation [Blanchard *et al.*, 2014; Andersen *et al.*, 2016]. Therefore the progression of size-structured modelling should be kept in line with this ideology: simple mathematics describing complex ecology. For example, a spatial dimension has previously been included into a size-structured model by adapting the McKendrick von Foerster [Castle *et al.*, 2011] with the introduction of a population flux, ∇J:

$$\frac{\partial N_i(w)}{\partial t} = -\frac{\partial g_i(w)N_i(w)}{\partial w} - \mu_i(w)N_i(w) - \nabla J \tag{6.1}$$

The population flux, ∇J, is based on optimal foraging theory whereby individuals move to a place where growth is maximised (i.e. in the instance of Castle *et al.* [2011] species go where there is the most food), and where mortality is reduced [Castle *et al.*, 2011]. As previous studies have shown, the centre of biomass of certain populations have moved in response to temperature changes (though the exact mechanisms are not always clear) [Dulvy *et al.*, 2008; Pinsky *et al.*, 2013; Engelhard *et al.*, 2014]. Therefore it could be argued that the population flux should not just be driven by food but where the environment in general is better suited to growth. The population flux described by Castle *et al.* [2011] could be further adapted by incorporating temperature and oxygen as these impact the growth of an individual [Chabot & Dutil, 1999; Cheung *et al.*, 2013b; Baudron *et al.*, 2014]. By modifying this population flux to be temperature or oxygen dependent one would be able to hypothesise individual movement out of environmentally unfavourable conditions. However this model is more typical of an “open system”, where individuals are able to leave/return, but it is not known in a biological sense where they end up - do they end up impacting a different ecosystem? An alternative “closed” double model, i.e. conservation of mass, is proposed here.

A closed model could be formed by joining together two size-structured sub-models. The advantage is they can be parameterised to specific regions and species such as a northern North Sea and southern North Sea, or even the North Sea and the Norwegian Sea. The joining factor would be through a movement parameter which can alter depending on food, oxygen, or temperature, or any condition wishing to be tested (i.e. environmentally dependent ∇J). While this uses two models and doubles the size, the mathematics are still simple, just duplicated. Additionally, while this joining would double the parameters, this combination of submodels should only be done when data is available to parameterise both. This would be advantageous in somewhere like the North Sea that has stark contrasts between the north and south in terms of species and environment, and there is likely enough data to parameterise a both these regions individually. Currently there is some uncertainty as to whether North Sea species will be constrained by depth and so be unable to migrate [Rutterford *et al.*, 2015], or whether species will move to more ideal conditions which has already been seen [Dulvy *et al.*, 2008]. Using a closed, differentially parameterised size-structured model could test these hypotheses as data is readily available.

Environmental data is available at a relatively high resolution depending upon the source. Global data has the advantage of long term projections, but as seen here, the resolution can cause problems. Regional data is far better resolved, however as yet no projections are available. These are currently being undertaken [pers. comm Sonja van Leeuwen & Jorn Bruggeman]. Therefore retrieving environmental data ideal for a closed, coupled size-structured model is simple enough making parameterising the environmental conditions to a joint north/south North Sea model straightforward. Being a size-based model, species-specific parameters largely depend on weight or length, the most commonly measured metric in fish surveys. This, along with huge amounts of other fish stock variables, can be found on the ICES website. Environmental relationships between certain species and recruitment, as mentioned above, were studied at the level of ICES divisions (areas IVa, IVb, IVc: northern, central, southern North Sea, respectively) [Bolle *et al.*, 2009; Akimova *et al.*, 2016]. These could be used to strengthen the spatial contrasts. Therefore parameterising a joint model with specific species at the individual and population level could be feasible, especially in the instance of splitting the North Sea. The most difficult step would be the inclusion of fishing. Currently a fishing mortality is imposed across the species and sizes depending on gear type and catchability. One possibility is to use ICES catch data which describes what county has fished in what subregion (northern, central, southern North Sea). Under the EU directive, vehicle monitoring systems and fishing effort are now recorded at the ICES rectangle level by all vehicles longer than 15m and that are owned by countries within the EU. Having this type of data freely available [Mills *et al.*, 2007; Marshall *et al.*, 2016] makes it an attractive option to emphasise the spatial dimension of fishing in the model. With modelling there are no guarantees of success, however this could be a relatively straightforward way to incorporate the environment, fishing, and a spatially explicit North Sea and thus should be investigated further.

One of the most difficult parts of making a model work relies on correct parameterisation – this itself is based on getting the appropriate data and identifying the best way to mathematically describe the mechanisms. The size-structured model used here has been created and modified over the last decade [Andersen & Beyer, 2006; Blanchard *et al.*, 2014; Andersen *et al.*, 2016], and the research from this thesis is another layer. The mechanisms used to create this model are by and large accepted in biological theory and experiments. Furthermore through testing environmentally-dependent growth, chapter 4 highlighted the effective structural uncertainty at the individual level. However by allowing growth to vary, rather than keeping it constant [Pope *et al.*, 2006], environmental factors are considered resulting in them not being thought of as simply"noise" [Steele, 1991]. There are still difficulties in the parameterisation of the model. For example, in the trait based version of this model, originally metabolism was ignored to encourage better results [Scott *et al.*, 2014], but this vital component in environment-physiology relationships meant it was reincorporated. This unfortunately meant saithe became somewhat unrealistic. Therefore a new sensitivity analysis would help in securing better parameter values, and one such way is using bayesian statistics which have already been shown to reduce the inherent uncertainty in size structured models [Spence *et al.*, 2016]. With any model there has to be some give and take, and a thoroughly designed statistical sensitivity analysis could go a long way into pinpointing the parameters that dominate the model outcome and thus require further understanding (e.g. through more experiments) in order to improve the model. However this model has shown to be able to reflect the North Sea well under a variety of modelling dynamics [Blanchard *et al.,* 2014 & Chapter 5]. Therefore the remainder of this discussion looks at the potential changes the North Sea demersal community may undergo.

6.3 Fishing and climate: what next?

In order to fully appreciate the extent a changing environment will have on the North Sea demersal community, one must logically look to the past. We have been subjected to a rapidly changing climate for the best part of a century [Mann *et al.*, 2008], made up particularly of two periods of accelerated warming, one of which started in 1978 [Delworth & Knutson, 2000]. Chapter 2 of this thesis covered 30 years, all of which were in this period of extreme warming. Additionally, this period was a time where North Sea landings (for the majority of countries that fished there) decreased by nearly 3-fold [Kerby *et al.*, 2012]. Despite this reduction in fishing, and rapid increase of temperatures, fishing was still the dominant factor in changes to the body size distribution

[Mieszkowska *et al.*, 2009; Engelhard *et al.*, 2015; Marshall *et al.*, 2016]. From studies on the impact of fishing [Pitcher, 1998; Jennings & Blanchard, 2004], the results are perhaps somewhat unsurprising. However temperature here, and in other studies, has been highlighted as a cause for a reduction in body size. In particular, temperature was found to be important in the cooler and deeper regions, postulated to be due to the shifting of populations as already seen [Dulvy *et al.*, 2008; Simpson *et al.*, 2011] towards the Norwegian Trench region. While it cannot be definitively stated *where* Norwegians fish, there is strong likelihood that they fish in the northern waters of the North Sea [pers. comm. John Pinnegar]. With the increased fishing effort from Norway in the last decade (see Chapter 2), it is likely they are taking advantage of the increased body size distribution in this area. This brings two important points: (a) the future management of the North Sea should be heterogenous; having a homogenous 'one size fits all' rule would effectively say to reduce fishing in the Norwegian trench region by the same amount as the central North Sea, which is somewhat illogical, and (b) at different points in the climate cycle, fishing could be managed to take advantage of changes in body size distributions.

The idea of fishing and climate being harmonious in producing high volumes of stock may seem counter-intuitive. However a well managed fishery can take advantage of a changing environment. For example, the improved management of quotas, a reduction in illegal/unreported/unregulated fishing, the implementation of a discard ban, and warming waters leading to suitable grazing areas has resulted in a historical high spawning biomass of Barent Sea cod in recent years [Kjesbu *et al.*, 2014]. The key here is the management of fisheries but also taking advantage of the response of fisheries to oceanic change. As the environment is likely to keep changing for some decades [Stocker *et al.*, 2013], it is important under management to strategically propose where fishing should take place depending upon historical fishing and beneficial climate change. If species in the North Sea are to be constrained by depth [Rutterford *et al.*, 2015], many are likely to struggle to adapt with a reducing body size distribution likely – the focus on management must take this into account. While other regions may prosper in biomass, it is impossible to focus fishing solely on those areas for fear of overfishing. The complexities of fisheries management under a changing climate is vast. The message here is for heterogeneity across the North Sea to be taken into account along with environmental change. A changing climate might have some positives [Kjesbu *et al.*, 2014], though these will inevitably be short lived and ultimately the negatives will surpass the positives.

One of the important features for predicting North Sea fisheries is having a suitable, transparent, and improved model. The published size-structured model has provided a solid foundation for North Sea predictions of different quotas [Blanchard *et al.*, 2014]. Chapter 4 showed environmentally dependent growth to be an important mechanism within the model, and suggestions in the previous section here are aimed at reducing structural uncertainty. However even with improvements of the fisheries model, if the environmental data being used is overwhelmingly inaccurate compared to the natural system, the projections will inevitably be meaningless. The rates of changes can be used as a guide, but these are far from ideal. Therefore if projections are required, the first change *must* be getting the environmental projections to within reasonable limits. With regional models being tested for projections, these should be a requirement for regional fisheries projections. Global climate models are notorious for struggling to resolve at the regional scale [Cheung *et al.*, 2012], and using these for regional fish models carries a high uncertainty to the results [Payne *et al.*, 2016] which here has shown to be hugely substantial. Additionally if global data is expected to be used, such as under FISH-MIP, for a regional fishery, every effort to highlight the environmental discrepancies between the model and natural system should be made.

6.4 Final remarks

This thesis has attempted to improve the understanding of how much climate change has affected the North Sea demersal community. The importance of fully quantifying how the environment can alter fish population, biomass, and community size indicators cannot be underestimated. If the environment is put to one side and ignored, fishing quotas could be overestimated potentially resulting in an unanticipated stock crash. If the environment is considered too great a priority, this runs the risk that management puts fishermen out of work over-cautiously and unnecessarily, potentially leading to a major loss in this historical sector. By using a combination of models and data, this thesis has shown that both the environment and fishing are of huge importance. While fishing by far has the greater impact, temperature and oxygen also need to be considered. This has been supported by both empirical and modelling research. However this is not the end. Many questions need to be answered, and hurdles overcome. Models need to be improved to have a spatial dimension, an evolutionary layer, and further experiments are fundamental in cementing the validity of the models. One thing is for certain, climate change is happening, and ecosystem are responding to it. This can no longer be ignored under fisheries management.

Appendices

Appendix A

Data tables

Table A.1: Species used in the analysis of size based indicators found in chapter 2. These species come from the North Sea IBTS quarter 1 dataset, 1980-2008 with Latin name (column 1), common name (column 2), conversion factors a and b for length to weight conversion (columns 3 and 4 respectively). Species with more than one latin name found in literature are given in brackets

Latin Name	**Common Name**	**a**	**b**
Acentronura	Pygmy pipehorse	0.0002	3.2326
Agonus cataphractus	Pogge	0.0091	2.905
Amblyraja radiata	Starry ray, Thorny skate	0.0056	3.121
Anarhichadidae	Wolffishes, sea wolves	0.003	3.2491
Anarhichas lupus	Atlantic Wolffish, Catfish	0.003	3.2491
Anarhichas minor	Spotted wolffish	0.003	3.2491
Anguilla anguilla	European eel	0.0006	3.313
Anguillidae	Freshwater eels (spawn in seawater)	0.0006	3.313
Arnoglossus	Scaldfish	0.0047	3.218
Arnoglossus imperialis	Imperial scaldfish	0.0028	3.34
Arnoglossus laterna	Mediterranean scaldfish	0.0065	3.096
Artediellus atlanticus	Atlantic hookear sculpin	0.0065	3.096

Blenniidae	Combtooth blennies	0.0093	3
Bothidae	Lefteye flounders	0.0047	3.218
Brosme brosme	Tusk, cusk	0.0051	3.198
Buglossidium	Only one species exists in this genus: Yellow sole, solenette *Buglossidium luteum*	0.0078	3.128
Callionymidae	Dragonets	0.0135	2.6857
Callionymus	Dragonets	0.0135	2.6857
Callionymus lyra	Common dragonet	0.0086	2.927
Callionymus maculatus	Spotted dragonet	0.0162	2.5781
Callionymus reticulatus	Reticulated dragonet	0.0158	2.552
Caproidae	Boarfishes	0.2218	1.9707
Capros aper	Boar fish	0.2218	1.9707
Chelidonichthys cuculus	Red gurnard (*Aspitrigla cuculus*)	0.0045	3.2228
Chelidonichthys lucerna	Tub gurnard (*Trigla lucerna*)	0.008	3.061
Chelidonichthys lucernus	Tub gurnard misspelt	0.008	3.061
Chimaera monstrosa	Rabbit fish	0.0003	3.475
Ciliata mustela	Fivebeard rockling	0.0064	3
Ciliata septentrionalis	Northern rockling	0.0055	3.1785

Conger conger	Conger eel	0.0002	3.509
Cottidae	Sculpins	0.01	3
Crystallogobius linearis	Crystal goby	0.008	3.1614
Cyclopteridae	Lumpfishes, lumpsuckers	0.0587	2.939
Cyclopterus lumpus	Lumpsucker	0.0587	2.939
Diplecogaster bimaculata	Two-spotted clingfish	0.0141	2.737
Dipturus batis	Blue skate, Common skate, Grey skate, Flapper skate	0.0036	3.0787
Dipturus linteus	Sailray, pale rale, white skate	0.0036	3.0787
Echiichthys vipera	Lesser weever fish (*Trachinus vipera*)	0.0129	2.947
Echiodon drummondii	Pearlfish	0.059	3.1304
Enchelyopus cimbrius	Fourbeard rockling (*Rhinonemus cimbrius*)	0.0035	3.1062
Entelurus aequoreus	Snake pipefish (*Enterurus aequerius*)	0.0002	3
Etmopterus spinax	Velvet belly lanternshark	0.0019	3.212
Eutrigla gurnardus	Grey gurnard	0.0034	3.26
Gadus morhua	Atlantic cod	0.0039	3.2434
Gaidropsarus	Lotid fish	0.0072	2.865
Gaidropsarus macrophthalmus	Bigeye rockling	0.0063	2.95

Gaidropsarus mediterraneus	Shore rockling	0.0034	3.098
Gaidropsarus vulgaris	Three-bearded rockling	0.012	2.547
Galeorhinus galeus	School shark, tope shark	0.0098	3.0085
Glyptocephalus cynoglossus	Witch flounder	0.0013	3.435
Gobiidae	Goby	0.008	3.1614
Gobius	Goby	0.0119	3.0495
Gobius auratus	Golden goby	0.0119	3.0495
Gobius cobitis	Giant goby	0.0113	3.128
Gobius niger	Black goby	0.0124	2.971
Helicolenus dactylopterus	Blackbelly rosefish	0.151	3.0456
Hippoglossoides platessoides	Long rough dab	0.007	2.978
Hippoglossus hippoglossus	Atlantic halibut	0.235	1.797
Lampetra fluviatilis	European river lamprey	0.0011	3.141
Lepidorhombus whiffiagonis	Megrim	0.0134	2.746
Leptagonus decagonus	Atlantic poacher	0.0091	2.905
Leptoclinus maculatus	Daubed shanny	0.0244	2.0439
Lesueurigobius	Goby	0.0026	3.515

Lesueurigobius friesii	Frie’s goby	0.0026	3.515
Leucoraja circularis	Sandy ray	0.0024	3.233
Leucoraja fullonica	Shagreen ray (*Raja fullonica*)	0.0024	3.233
Leucoraja lentiginosa	Speckled/Freckled skate	0.0024	3.233
Leucoraja naevus	Cuckoo ray (*Raja naevus*)	0.0024	3.233
Limanda limanda	Dab	0.0071	3.119
Liparis	Snailfish	0.0207	2.9691
Liparis liparis	Seasnail	0.0122	2.9892
Liparis montagui	Montagu’s sea-snail	0.0292	2.949
Lophiidae	Goosefish	0.01	3.2
Lophius budegassa	Blackbellied angler	0.0044	3.345
Lophius piscatorius	Angler fish, monkfish	0.0166	2.9776
Lumpenus lampretaeformis	Snakeblenny (*Lumpenus lumpretaeformis*)	0.0244	2.0439
Lycenchelys sarsii	Sar’s wolfeel (*Lycenchelys sarsi*)	0.0417	2.2532
Lycodes vahlii	Vahl”s eelpout	0.0417	2.2532
Melanogrammus aeglefinus	Haddock	0.0052	3.156
Merlangius merlangus	Whiting/Merling	0.0042	3.1842

Merlucciidae	Merluccid hakes	0.0036	3.1469
Merluccius merluccius	European hake	0.0036	3.1469
Micrenophrys lilljeborgii	Norway bullhead	0.01	3
Microchirus	Soles	0.008	3.141
Microchirus variegatus	Thickback sole	0.008	3.141
Microstomus kitt	Lemon sole	0.0042	3.2695
Molva dypterygia	Blue ling	0.0019	3.149
Molva molva	Common/European ling	0.001	3.4362
Mugilidae	Mullet	0.0107	3.0328
Mullus barbatus	Red mullet	0.0139	2.9087
Mullus surmuletus	Striped red mullet, goatfish	0.0101	3.0201
Mustelus	Smooth-hounds	0.0041	2.9185
Mustelus asterias	Starry smooth-hound	0.002	3.079
Mustelus mustelus	Common smooth-hound	0.0062	2.758
Myoxocephalus scorpioides	Arctic sculpin	0.0178	3.0378
Myoxocephalus scorpius	Bull rout, Shorthorn sculpin	0.0126	3.1235
Myxine glutinosa	Atlantic Hagfish	0.0033	2.699

Nerophis ophidion	Straightnose pipefish	0.0004	3
Pagellus erythrinus	Common pandora	0.0171	2.906
Pegusa lascaris	Sand sole	0.007	3.13
Petromyzon marinus	Sea lamprey	0.0008	3.1956
Pholis gunnellus	Butterfish, Rock gunnel	0.0043	3.018
Phrynorhombus norvegicus	Norwegian topknot (*Zeugopterus norvegicus*)	0.0078	3.1457
Phycis blennoides	Greater forkbeard	0.0022	3.3892
Platichthys flesus	European flounder	0.0087	3.0978
Pleuronectes platessa	European plaice	0.0078	3.0541
Pollachius pollachius	Pollock	0.0061	3.115
Pollachius virens	Saithe	0.0042	3.1753
Pomatoschistus	Goby	0.0068	3.0965
Pomatoschistus lozanoi	Lozano’s goby	0.0068	3.0965
Pomatoschistus microps	Common goby	0.0068	3.0965
Pomatoschistus minutus	Sandy goby	0.0062	3.173
Pomatoschistus pictus	Painted goby	0.0073	3.02
Psetta maxima	Turbot (*Scophthalmus maximus*)	0.0046	3.3972

Raja	Rays	0.0035	3.1746
Raja brachyura	Blonde ray, Blonde skate	0.0028	3.233
Raja clavata	Thornback ray	0.0032	3.194
Raja microocellata	Small-eyed ray	0.0049	3.117
Raja montagui	Spotted ray	0.0023	3.2051
Raja undulata	Undulate ray	0.0042	3.124
Rajidae	Skates	0.0036	3.1632
Raniceps raninus	Tadpole fish	0.0062	3.2667
Scophthalmus rhombus	Brill	0.0055	3.3047
Scorpaena scrofa	Red scorpionfish	0.0121	3.124
Scyliorhinus	Catsharks	0.0031	3.029
Scyliorhinus canicula	Lesser spotted dogfish	0.0031	3.029
Scyliorhinus stellaris	Nursehound	0.0031	3.029
Sebastes	Rockfish	0.0093	3.1585
Sebastes marinus	Rose fish, ocean perch, redfish	0.0071	3.18
Sebastes viviparus	Norway redfish/haddock	0.0115	3.1369
Solea solea	Common sole (*Solea vulgaris*)	0.0038	3.2751

Soleidae	Soles	0.022	3.0848
Somniosus microcephalus	Greenland shark	0.0161	2.93
Sparidae	Porgies	0.1295	2.838
Spondyliosoma cantharus	Black seabream	0.0151	3.0233
Squalidae	Dogfish sharks	0.0034	3.0955
Squalus acanthias	Piked/spiny dogfish, spurdog	0.0034	3.0955
Stichaeidae	Pricklebacks	0.0244	2.0439
Syngnathidae	Pipefish and seahorses	0.0002	3.2326
Syngnathus	Pipefishes	0.0001	3.3877
Syngnathus acus	Greater pipefish	0.0001	3.527
Syngnathus rostellatus	Nilsson's pipefish, lesser pipefish	0.0001	3.414
Syngnathus typhle	Broadnosed pipefish	0.0001	3.222
Taurulus bubalis	Longspined bullhead	0.0154	3
Trachinus draco	Greater weever	0.0018	3.4099
Trachyrincus murrayi	Roughnose grenadier	0.0088	3
Triglidae	Searobins	0.0052	3.1457
Trigloporus lastoviza	Streaked gurnard	0.0049	3.039

Triglops murrayi	Moustache sculpin	0.0088	3
Triglops pingelii	Ribbed sculpin	0.0031	3.181
Triglopsis quadricornis	Fourhorn sculpin	0.0031	3.181
Trisopterus esmarkii	Norway pout	0.0046	3.1405
Trisopterus luscus	Bib, pouting	0.0038	3.3665
Trisopterus minutus	Poor cod	0.0092	3.0265
Zeugopterus	Turbots (genus)	0.0139	3.1457
Zeugopterus punctatus	Topknot	0.0139	3.1457
Zeugopterus regius	Eckström's topknot	0.0139	3.1457
Zoarces viviparus	Eelpout	0.0417	2.2532
Zoarcidae	Eelpouts	0.0417	2.2532

Table A.2: Expected beam landings data (dependent on species) for all countries that fished in the North Sea from 1977 - 2008

Country	**1977**	**1978**	**1979**	**1980**	**1981**	**1982**	**1983**	**1984**
Belgium	11030	10797.5	12075.5	10075.5	9916.25	11742	14811	17168
Denmark	23604	24435	31930	31917	28839	30911	28301	31501
Faeroe Islands	105	30	0	189	23	3	16	0
France	1944.5	2332.5	2701.25	2791.25	4543	3347.25	3199.25	3653
Germany	0	0	0	0	0	0	0	0
Germany Fed Rep	6537.5	5856.75	5185.25	5234.5	4215.5	4311	3502.5	3916
Greenland	0	0	0	0	0	0	0	0
Ireland	22	37.75	63	0	5.5	0	0	0
Netherlands	63825	45083.25	58487	63238	62657	88623.25	86769.75	75886
Norway	936.5	755	1195.75	1251.75	1060	897.75	971.75	999.5
Poland	1	0	0	0	0	0	0	0
Portugal	0	0	0	0	0	0	0	0
Spain	0	0	0	0	0	0	0	0
Sweden	0	0	14	12	4	14.25	30.25	23

UK - Eng + Wales + NI	0	0	0	0	0	0	0	0
UK - Eng + Wales	33598.75	34305.75	32195.5	24504.75	22048.25	21861.5	18358.5	18328.75
UK - NI	0	0	0	0	0	0	0	0
UK - Scotland	11783	12403.75	12152.5	13349.25	11495.25	11444.5	12957.25	14778.75
USSR	9	0	0	0	0	0	0	0

Country	**1985**	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**
Belgium	16655.25	11745.25	12707.75	15466	14632	18628	20231	17055
Denmark	35980	31510	27754.25	25985.25	29493	33550.25	31839.5	27782.5
Faeroe Islands	15	59	41	118	22	17	49	17
France	3369	2175	3431	3494	2961	2447	2064	2364
Germany	0	0	0	0	0	0	12480.75	10169
Germany Fed Rep	3053.25	2484.5	2718.75	3848	6913.5	12272.5	0	0
Greenland	0	0	0	0	0	0	0	0
Ireland	0	0	0	0	0	0	0	0
Netherlands	105933	84094	87247	95342.25	102226	100939	91938	74801
Norway	1085.75	671.5	896.5	717	1376	2903.75	2190.5	3297.75
Poland	0	0	0	0	0	0	0	0
Portugal	0	0	0	0	0	0	0	0
Spain	0	0	0	0	0	0	0	0
Sweden	26	24	16.25	9	29	250	219	119
UK - Eng + Wales + NI	0	0	0	0	25747.75	24993.75	24839.5	28047.5
UK - Eng + Wales	16786.25	17254.25	19899	22622	0	0	0	0

UK - NI	0	0	0	0.5	0	0	0	0
UK - Scotland	16733.75	17053.25	21471	22233.75	20478.75	22117.25	26221.5	27184.75
USSR	0	0	0	0	0	0	0	0

Country	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**
Belgium	17021	13870	12730	11142	8953	10418	10882.5	12039.25
Denmark	24583.5	24423.75	19850.75	18955	20104.25	15054	19127.75	19224.25
Faeroe Islands	13	124	732	0	16	13	8	0
France	2090	1928	2179	2229	1116	1551	0	1875
Germany	9649.75	9487.75	10628.25	7035.25	6922.25	5818	6290	7343
Germany Fed Rep	0	0	0	0	0	0	0	0
Greenland	0	0	0	0	0	0	0	0
Ireland	0	0	0	0	0	10	21	19
Netherlands	75756	77734	69010	53484	47113	62809	69577	64075
Norway	3977.5	3406.75	2253	3769.5	3636.25	3237.25	4602.5	3224.5
Poland	0	0	0	0	0	0	0	0
Portugal	0	0	0	0	0	0	0	0
Spain	0	0	0	0	0	0	0	0
Sweden	67	24.75	20	12.75	27.75	24.75	26	99.5
UK - Eng + Wales + NI	27947	25430.25	23354	20255.75	21651.75	17309.25	14798.75	17304.75
UK - Eng + Wales	0	0	0	0	0	0	0	0

UK - NI	0	0	0	0	0	0	0	0
UK - Scotland	28940.25	30994	33622	40191.5	37668.75	31842.5	26639	25656.25
USSR	0	0	0	0	0	0	0	0

Country	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**
Belgium	11236.5	8852	8220.5	8166	6846	6351	6891	6817.25
Denmark	19801.5	18325.5	20297.75	18442.75	17575	17374	12658.25	12934.5
Faeroe Islands	2	12	3	11	22	2	1	0
France	1221	1206	1280.5	1108.25	1858.5	1773.5	1570.5	1277
Germany	6070	6237.25	4345	4851	7208	5961	5877	5987
Germany Fed Rep	0	0	0	0	0	0	0	0
Greenland	0	0	0	8	0	0	0	0
Ireland	0	0	0	0	13	3	2	0.25
Netherlands	45551	43829	45373	40994	59752	53766	52090	48749
Norway	3253	2956.25	2553	2295	4028	3524.5	3498.5	3837.5
Poland	0	0	0	0	0	0	0	0
Portugal	0	3	0	0	0	0	0	0
Spain	0	0	0	0	0	0	0	0
Sweden	16	14.5	45	123	69	80.25	21	15
UK - Eng + Wales + NI	9122	9250.25	9290.5	8656.5	15102	11425	10066.75	10298
UK - Eng + Wales	0	0	0	0	0	0	0	0

UK - NI	0	0	0	0	0	0	0	0
UK - Scotland	13681	18626.25	19114.75	18640	26110	23195.25	18177.25	18813.75
USSR	0	0	0	0	0	0	0	0

Table A.3: Expected otter landings data (dependent on species) for all countries that fished in the North Sea from 1977 - 2008

Country	**1977**	**1978**	**1979**	**1980**	**1981**	**1982**	**1983**	**1984**
Belgium	18029	25026.50	19235.25	15871.50	13999.25	11273.25	12526	11052
Denmark	384794	255798	332549	471872	321051	408000	383794.50	300256.25
Faeroe Islands	50511	18889	23309	35646	17232	13407	32013	19067
France	78197.50	85447.75	94910	85681.50	100446.25	100302.50	93699	88399
Germany	0	0	0	0	0	0	0	0
Germany Fed Rep	55920.25	69730.50	44539.75	42109.25	42692	37642.25	39050.50	42643
Germany New	2465	2583	1659	1024	0	0	0	0
Greenland	0	0	0	0	0	0	0	0
Iceland	0	0.25	0	0	0	0	0	0
Ireland	1251	534	1	0	0	0	0	0
Lithuania	0	0	0	0	0	0	0	0
Netherlands	50832	68006.25	52369.50	63314.75	70842.25	52726.25	50378.25	35644
Norway	175873.25	183531.75	173702	198967.25	167635.75	276992.50	298220.50	296409.25
Poland	14039	5918	6392	2536	737	1219	642	441

Portugal	0	0	0	0	0	0	0	0
Russian Fed	0	0	0	0	0	0	0	0
Spain	0	0	0	0	0	0	0	0
Sweden	3820	0	1838.25	1880	1950.25	2696	2456	2851
UK - Eng + Wales + NI	0	0	0	0	0	0	0	0
UK - Eng + Wales	75702.25	99016.50	89898.75	83159	91924.50	86526.50	85238.75	65368.75
UK - NI	0	0	0	0	0	0	0	0
UK - Scotland	181110	170675	160889.75	163996	179518	206614	211159	197012.75
USSR	56810	10232	2082	0	0	0	0	0

Country	**1985**	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**
Belgium	8845.75	10192.25	9183	8775.50	5847	5636	4880	6328
Denmark	273889.50	228509.25	236789	231337	219597.50	140382	156288.25	215644.25
Faeroe Islands	10953	2735	5623	2032	1566	2665	2152	5232
France	69490	69114	65764	54230	43449	41082	25158	21266
Germany	0	0	0	0	0	0	29226	24226
Germany Fed Rep	33952.50	33054.50	32737.75	28265.75	27841.25	29387.25	0	0
Germany New	0	0	0	0	0	0	0	0
Greenland	0	0	0	0	0	0	0	0
Iceland	0	0	0	0	0	0	0	0
Ireland	0	0	0	0	0	0	0	0
Lithuania	0	0	0	0	0	0	91	0
Netherlands	42115	40776	31416	23718.75	17670	12357	11500	17308
Norway	245674.25	161089.75	165975.50	113173.75	169317.50	168387	172063	230268.25
Poland	0	506	868	1069	901	1350	1370	131
Portugal	0	0	0	0	0	0	0	0
Russian Fed	0	0	0	0	0	0	0	0

Spain	0	0	0	0	0	0	0	0
Sweden	4219	3936	3071.25	2153.50	2307	2617	4542	4143
UK - Eng + Wales + NI	0	0	0	0	31279.75	28243.25	26705	26537
UK - Eng + Wales	58037	45274.75	48731	40427	0	0	0	0
UK - NI	0	0	0	6.25	0	0	0	0
UK - Scotland	220475	223385	191812.50	176619.25	129294.50	108196	113708.25	119017.50
USSR	0	0	0	0	0	0	116	0

Country	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**
Belgium	6333	5597	7596	6164	7073	8139	6034.50	5433.50
Denmark	179780.25	158474.25	203723	130116.75	138576	75581	72889.25	154170
Faeroe Islands	5325	5541	13134	8502	7263	6197	3815	0
France	26643	23582	23844	21936	20393	18995	0	28791.25
Germany	23988	19738	24225	22869.75	20335	20515	15239	12290
Germany Fed Rep	0	0	0	0	0	0	0	0
Germany New	0	0	0	0	0	0	0	0
Greenland	0	0	0	0	0	0	0	601
Iceland	0	0	0	0	0	0	0	0
Ireland	0	0	0	0	0	7	41	33
Lithuania	0	0	0	0	0	0	0	0
Netherlands	15565	10699	15329	12940	15119	17010	11148	11245
Norway	168341.75	150747.75	185736.25	165899.50	102672.50	95209.25	122230.50	111944.75
Poland	1022	194	645	416	893	869	929	794
Portugal	0	0	0	0	0	0	0	0
Russian Fed	0	0	0	0	0	0	0	369

Spain	0	0	0	0	0	0	0	0
Sweden	3732	2472.25	3245	2495	2881	2706.25	3330	2877.50
UK - Eng + Wales + NI	27413.25	25705.50	26169.75	26208.50	23864.50	27704	19504	12656.75
UK - Eng + Wales	0	0	0	0	0	0	0	0
UK - NI	0	0	0	0	0	0	0	0
UK - Scotland	143372	146471.25	147888.50	139433.75	134103.25	129446.50	107333	89046.75
USSR	0	0	0	0	0	0	0	0

Country	2001	2002	2003	2004	2005	2006	2007	2008
Belgium 4467	4431.50	2752.50	2903.50	2708	2082	1771.25	1688.50	
Denmark 61651.50	89168.50	26285.25	26445.25	14051	51918.25	8902	43306.25	
Faeroe Island	353	4392	2892	1754	582	73.50	16.25	198
France	29629.25	33022.75	23677	17474.50	15333	21296	21588.75	21681.25
Germany	12794	14779	13370	13365	16187	17949	13872	14907
Germany Fed Rep	0	0	0	0	0	0	0	0
Germany New	0	0	0	0	0	0	0	0
Greenland	1526	0	0	0	1103	969	594	911
Iceland	0	0	0	0	0	0	0	0
Ireland	29	15	2	1	0	0	0	0
Lithuania	0	0	0	0	149	0	0	0
Netherlands 9546	10528	6463	5645	5421	5108	5161	5270	
Norway	76995.75	101101.25	87084.25	80614	80449	88322	66886.25	82942.75
Poland	781	843	812	0	1100	1092	1394	1425
Portugal	0	0	0	0	0	1053	0	0
Russian Fed	34	0	0	0	35	2	5	5

Spain	0	0	0	0	2	0	0	0
Sweden	3035.50	2681.25	2025.50	2141.25	2074	1455.50	1433	1791
UK - Eng + Wales + NI	10878	11549.50	6465.50	5273.75	6096	7496	9947.50	6753.25
UK - Eng + Wales	0	0	0	0	0	0	0	0
UK - NI	0	0	0	0	0	0	0	0
UK - Scotland 67823	76696.75	57032.50	61959.75	43067	58360.25	50735	58293.25	
USSR	0	0	0	0	0	0	0	0

Table A.4: Fishing mortalities for 7 North Sea stock-assessed demersal species from 1980 - 2011. All data is from ICES except in values in bold: Norway pout values calculated were calculated from saithe mortalities, whiting mortalities were calculated from from haddock mortalities

Year	**Cod**	**Haddock**	**Norway Pout**	**Plaice**	**Saithe**	**Sole**	**Whiting**
1980	0.860	0.899	**0.601**	0.555	0.443	0.452	**0.518**
1981	0.890	0.659	**0.352**	0.538	0.306	0.497	**0.401**
1982	0.983	0.659	**0.648**	0.602	0.469	0.543	**0.401**
1983	0.972	0.884	0.901	0.594	0.548	0.488	**0.510**
1984	0.916	0.873	1.284	0.585	0.677	0.618	**0.505**
1985	0.887	0.872	1.334	0.531	0.714	0.599	**0.504**
1986	0.936	1.203	1.112	0.662	0.819	0.580	**0.665**
1987	0.938	1.024	0.906	0.692	0.645	0.491	**0.578**
1988	0.948	1.108	0.661	0.666	0.621	0.566	**0.619**
1989	0.966	0.952	0.833	0.610	0.673	0.439	**0.543**
1990	0.906	1.114	0.760	0.567	0.598	0.440	0.659
1991	0.910	0.888	0.894	0.649	0.576	0.445	0.522
1992	0.877	0.980	0.934	0.631	0.630	0.421	0.485
1993	0.891	0.896	0.842	0.637	0.529	0.508	0.488
1994	0.906	0.830	1.074	0.619	0.509	0.567	0.624
1995	0.934	0.733	0.587	0.643	0.411	0.538	0.520
1996	0.955	0.688	0.448	0.673	0.401	0.706	0.417
1997	0.961	0.537	0.590	0.796	0.283	0.608	0.327
1998	0.980	0.604	0.299	0.735	0.340	0.646	0.312
1999	0.999	0.714	0.651	0.666	0.349	0.579	0.376
2000	0.995	0.765	0.585	0.475	0.299	0.608	0.436
2001	0.956	0.492	0.266	0.770	0.273	0.581	0.308
2002	0.926	0.229	0.512	0.580	0.244	0.578	0.206
2003	0.901	0.201	0.248	0.610	0.224	0.590	0.187
2004	0.857	0.263	0.156	0.481	0.189	0.514	0.192
2005	0.800	0.310	0.000	0.410	0.250	0.584	0.183
2006	0.723	0.511	0.286	0.375	0.266	0.455	0.271
2007	0.669	0.398	0.252	0.317	0.252	0.466	0.261

2008	0.630	0.227	0.137	0.237	0.344	0.369	0.266
2009	0.602	0.209	0.250	0.211	0.388	0.364	0.229
2010	0.583	0.233	0.421	0.206	0.289	0.355	0.228
2011	0.572	0.298	0.340	0.229	0.284	0.296	0.174

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