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A multivariate spatial analysis of northeast Atlantic fish stocks over time

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Submission Date: February 12th 2013
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Thesis Abstract

Describing a population in space and time may provide essential information to govern regimes for the effective and sustainable management of that population. Some fish species exhibit naturally complex and changeable patterns of distribution relating to their life history characteristics, biological requirements (which may vary between ages and seasons), the environment, climate change and human factors. Where this is the case, investigating a populations distribution in varying spatial (and temporal) scales has the advantage of being able to extract a more ecosystem focused and detailed pattern of possible causes for and therefore implications of a particular distribution. The northeast Atlantic supports some of the world’s most highly productive fish stocks and as a result is impacted heavily by human activity. Northeast Atlantic waters are highly dynamic with complex oceanographic and hydrographic features which are responding significantly and variably to a changing climate.

In this thesis, results show that northeast Atlantic mackerel (NEAM) western spawning component (WSC) are moving north associated with a change in survey effort and warming waters, and that their distribution is related to local topographic features. Important fishing areas for Atlantic mackerel are the continental shelf edge, northern North Sea and southern Norwegian Sea. Shifts in NEAM catch have occurred 1977 – 2010 and show a northern and off-shelf preference in distribution. Cod in the North Sea and Celtic Sea and western Channel are examined to show a northwest shift in North Sea cod made up of spatially heterogenous local scale site specific changes. The Celtic sea and western Channel stock were not shown to display any density dependent habitat selection. An across species comparison of mackerel, blue whiting and horse mackerel suggested species specific responses to environmental variables as well as some biological species interactions. This thesis analyses important data sets whilst considering the limitations of the data throughout the methods and conclusions. The report is a significant contribution to understanding changes in spatio-temporal patterns of several commercially important northeast Atlantic fish species and fisheries. Based on the findings shown here future research would include in situ or modelled environmental data, especially temperature at depth, as well as a better understanding of fisheries effort data to ascertain a distinction between environment and anthropogenic drivers of changes in distribution of northeast Atlantic fish stocks.
## Acronym Table

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<tr>
<th>Acronym</th>
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<tr>
<td>AIC</td>
<td>Akaike Information Criterion</td>
</tr>
<tr>
<td>AMO</td>
<td>Atlantic Multidecadal Oscillation</td>
</tr>
<tr>
<td>CCMP</td>
<td>Cross Calibrated Multi Platform (model)</td>
</tr>
<tr>
<td>CDF</td>
<td>Cumulative Distribution Function</td>
</tr>
<tr>
<td>CEFAS</td>
<td>Centre for Environment Fisheries and Aquaculture Science</td>
</tr>
<tr>
<td>CFP</td>
<td>Common Fisheries Policy</td>
</tr>
<tr>
<td>CoG</td>
<td>Centre of Gravity</td>
</tr>
<tr>
<td>CPUE</td>
<td>Catch Per Unit Effort</td>
</tr>
<tr>
<td>CRAN</td>
<td>Comprehensive R Archive Network</td>
</tr>
<tr>
<td>CSE</td>
<td>Continental Shelf Edge</td>
</tr>
<tr>
<td>CSWC</td>
<td>Celtic Sea and Western Channel</td>
</tr>
<tr>
<td>EAFM</td>
<td>Ecosystems Approach to Fisheries Management</td>
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<tr>
<td>EEZ</td>
<td>Exclusive Economic Zone</td>
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<tr>
<td>EOF</td>
<td>Empirical Orthogonal Function</td>
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<td>EU</td>
<td>European Union</td>
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<tr>
<td>FAO</td>
<td>Food and Agriculture Organisation</td>
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<tr>
<td>GAM</td>
<td>Generalized Additive Model</td>
</tr>
<tr>
<td>GEBCO</td>
<td>General Bathymetric Chart of the Oceans</td>
</tr>
<tr>
<td>GOV</td>
<td>Grand Overture Verticale</td>
</tr>
<tr>
<td>Had</td>
<td>Hadley (sea surface temperature data set)</td>
</tr>
<tr>
<td>IBTS</td>
<td>International Bottom trawl Survey</td>
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<tr>
<td>IBWSS</td>
<td>International blue whiting Spawning Stock Survey</td>
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<tr>
<td>ICES</td>
<td>International Council for the Exploration of the Seas</td>
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<tr>
<td>IDW</td>
<td>Inverse Distance Weighting</td>
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<td>International Catch Data</td>
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<tr>
<td>IFD</td>
<td>Ideal Free Distribution</td>
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<td>IGFS</td>
<td>Irish Ground Fish Survey</td>
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<td>IPCC</td>
<td>Intergovernmental Panel for Climate Change</td>
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<td>IUCN</td>
<td>International Union for Conservation of Nature</td>
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<td>MCS</td>
<td>Marine Conservation Society</td>
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<tr>
<td>MTLI</td>
<td>Mean Trophic Level Index</td>
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<tr>
<td>MSY</td>
<td>Maximum Sustainable Yield</td>
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<tr>
<td>NAO</td>
<td>North Atlantic Oscillation</td>
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<td>National Centre for Atmospheric Research</td>
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<td>NEAM</td>
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<td>North East Atlantic - Western Spawning Component</td>
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<td>National Research Council</td>
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<td>NSC</td>
<td>Northern Spawning Component</td>
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<td>North Sea Ground Fish Survey</td>
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<td>OGCM</td>
<td>Ocean General Circulation Model</td>
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<td>Regional fisheries Management Organisation</td>
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<td>Sea Surface Temperature</td>
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<tr>
<td>SW</td>
<td>South West</td>
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<tr>
<td>TAC</td>
<td>Total Allowable Catch</td>
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<td>TSB</td>
<td>Total Spawning Biomass</td>
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<tr>
<td>UBRE</td>
<td>Unbiased Risk Estimator</td>
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<td>UNEP</td>
<td>United Nations Environment Programme</td>
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<td>UTM</td>
<td>Universal Transverse Mercator</td>
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<td>VIF</td>
<td>Variance Inflation Factor</td>
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<td>VMS</td>
<td>Vessel Monitoring System</td>
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<td>VPA</td>
<td>Virtual Population Analysis</td>
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<tr>
<td>WGCSE</td>
<td>Working Group for the Celtic Shelf Ecoregion</td>
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<td>WGMEMGS</td>
<td>Working Group of Mackerel Egg Survey</td>
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<td>WGNAPES</td>
<td>Working Group of the North East Atlantic Pelagic Ecosystem Survey</td>
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<td>WGNSSK</td>
<td>Working Group of the North Sea Skagerrak and Kattegat</td>
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<td>WGWIDE</td>
<td>Working Group for Widely Distributed Species</td>
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<td>WSC</td>
<td>Western Spawning Component</td>
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Chapter 1: Introduction
1.1 Thesis introduction

Throughout this thesis patterns of distributional change are examined through time for commercially important fish stocks in the northeast Atlantic. Possible drivers of change are identified and include: species specific habitat preferences, environmental (including climatic variables) and fishery related factors and intra-population dynamics. The study species presented in this thesis are Atlantic mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*), cod (*Gadus morhua*) and blue whiting (*Micromesistius poutassou*). The chosen species all support fisheries (some larger than others), and have ample data available to address issues from the perspective of a spatial analysis using scientific methodologies that render results supportive of an ecosystem approach to population ecology and fisheries management. The area of study includes waters around Ireland, and the wider northeast Atlantic, waters which are highly productive. Methodological approaches include novel applications of statistics on these data including univariate and multivariate approaches, spatial statistics and modelling.

This introduction will begin broadly with global fisheries, focusing on issues including climate change and over exploitation, before introducing the ecosystems approach to fisheries management and in particular the importance of spatial aspects within fisheries ecology. Finally the study species will be introduced, along with a summary of the data used, and a review of current research that used aforementioned study species within the northeast Atlantic.

1.2 The global importance of fisheries

In general, fisheries are receiving ever more attention in public as well as scientific literature (IUCN 1996; Hudson and Mace 1996; Roberts 1997; Scheiber 2001; Pauly and Zeller 2003; Allan et al. 2005). The oceans represent over 70% of the earth’s surface (Chu et al. 2003), with almost two-thirds of humanity occupying coastal areas most of which depend on marine habitats and environments for their livelihood (Ray 1988; UNEP 2006). Fisheries are socially and economically important as a food-supply with one-sixth of the world’s population relying on fish as a primary source of protein (Tidwell and Allan 2001). Income generation is provided by fisheries especially in the developing world, with some 45.5 million employees worldwide, and over 4 million fishing vessels (Sovacool 2009; Allan et al. 2005; Srinivasan et al. 2010). Annually, global trade includes almost half of the 90 million tons of fish caught, and $124 billion is spent on fishing, by fishers (FAO 1995).
Overfishing is ubiquitous throughout the globe with excess fishing capacity and increased demand for fishery products driving the exhaustion of the natural resource (Srinivasan et al. 2010). From 1950 to 2004 36-53% of commercial species within 55-66% of exclusive economic zones (EEZs) have been overfished (Srinivasan et al. 2010). In 2007 the FAO stated that 17% of the worlds fish stocks are overexploited, 7% are depleted and 1% are recovering from depletion (FAO 2007). Likewise it is thought global fishing fleets are now 250% greater than needed to catch sustainable yields (Eichenberg and Schapson 2004). Europe has incurred the greatest losses by fish mass, closely followed by North America and Asia (Srinivasan et al. 2010). Overfishing is thought to be the highest threat to the extinction risk of fish populations (Sadovy de Mitcheson et al. 2012), with the effects of fishing having been linked to changes in ecological communities (Jackson et al. 2001). Today numerous fish stocks have declined since their historical peaks and some have collapsed, leading to increased pressure on policy makers for more stringent and diverse measures in fisheries management (Sovacool 2009). Fisheries collapses have been considered to be the result of economic or administrative mismanagement (O’Leary et al. 2011) leading to a lack of control or enforcement to ensure the equilibrium theory of fishing effort is being maintained (i.e. fishing mortality at or below a threshold at which stock collapses should not occur). Since the 1950’s the rate of collapse has remained similar, indicative of little improvement in the effective management of fisheries (O’Leary et al. 2011).

Whilst overfishing might be one source of fish population depletion, other threats to the future success of fisheries include a multitude of sources. International distribution of fish populations often require transboundary management as well as agreements in fishing rights or quotas, both at international level. Climate change impacts are predicted to modify resources thereby driving some “winners” and “losers” at the micro and macro-spatial scale, particularly for poikilothermic marine species (FAO 2008). Habitat loss, conversion or degradation and over-exploitation of fish populations are also threatening some fisheries sustainability (Plater and Jake 2011). For example, trophic interactions means commercial fishing of a target species not only affects the fished population but also related communities of organisms (relative abundances of prey items), ecological processes (energy flow through the trophic web) and sometimes entire ecosystems (Plater and Jake 2011). For example, the removal of large fish in a coral reef system in the central Pacific Ocean accounted for altered behaviour of prey fish, changes in lower trophic feeding rates (grazing), direct positive and indirect negative impacts on coral recruitment and decreased abundances of marine benthic invertebrates (McCauley et al. 2010).
From an ecosystem perspective, dynamics of fish stocks affect and are affected by both anthropogenic and environmental impacts. The understanding of these interactions then feed into policy and management for sustainable exploitation which can in turn influence fish stocks productivity. Of particular focus in this thesis is the understanding of the physical environment, data limitations and anthropogenic influence as well as fish stock/population distribution. Response in population distribution to environmental impacts have been seen for a number of marine fish species (Brander et al. 2003; Rose 2005) and is a relatively recent focal point in the ecosystem approach to fisheries management.

1.3 The ecosystem approach to fisheries management (EAFM)

The EAFM (although ambiguous in definition and continuously evolving) aims to relate to the impact of fisheries on the environment whilst at the same time taking into account the impact of the environment on fisheries (Garcia & Cochrane 2004). For accurate assessment of the health of a fish stock, the effects of environmental impacts beyond fishing must be understood including trophic interactions and multi-species assessments (Wilson 2009). First coined in 1972 in the Stockholm declaration, the EAFM was defined as the wish to work towards integrated, holistic, science based management employing decentralised transparent decision making involving local communities and users (The Stock Book 2006). The FAO code of conduct for responsible fisheries contains aspects for all approaches adopted by the EAFM (FAO 1995a). The challenge in implementing the EAFM is converting the multifarious consortium of international agreements and conceptual objectives and principles into operational measurable and definitive goals. In conjunction with policy applications, scientific knowledge and a full understanding of the compound and dynamic marine ecosystem is somewhat in its infancy. In Europe, fish stock/population data (fisheries independent and dependent) tends to be collected and collated for the purposes of single stock assessment, and as such is often overlooked as a useful source of time series data on most commercially exploited fish stocks, for aims other than stock assessment (Holm and Nielsen 2004). Although the data are used annually for working group reports through ICES, few other investigations use the data for ecological or climate based analysis, despite the wealth of data available. This may change with the more common application of the ecosystem approach to fisheries management (EAFM) which states that scientific based investigations should use existing data from fisheries dependent and independent sources (Wilson 2009). The need for the EAFM is driven by the complex set of related issues within the marine ecosystem, including impacts of fishing on the ecosystem in the immediate and broader context (Wilson 2009). Fishery focused aims of the EAFM includes limiting the impact of the fishery on the
ecosystem to the minimum, maintaining ecological relationships between species, consistent management measures across international territories, human and ecosystem well-being and the application of the precautionary approach (The Stock Book 2006).

Currently within Europe, the common fisheries policy (CFP) determines total allowable catch (TAC) allowances based on the population biomass, and the level at which is thought to be the biological reference point of a population (Blim). Blim relates to the lower level of a sustainable population (ICES 2012c). Environmental forcings such as the north Atlantic oscillation (NAO) or the Atlantic multidecadal oscillation (AMO), although well known, do not feature in management practices as they tend to be unpredictable with current knowledge, although including these would improve fisheries management practices (Cochrane and Starfield 1992; Buch et al. 2004). Similar variables such as climatic variables, fishing, salinity, temperature as well as life history characteristics and match mis-match situations (ICES 2006b) might have a small spatial scale/short term effect (e.g. fishing on life history traits (Rochet 1998)), or broader spatial temporal scale ecological effect such as regime shifts (Wilson 2009). Regime shifts have been shown to have occurred in the North Sea from 1983-1988 (Beaugrand 2004). On the Scotian Shelf there has been a regime shift over the last four decades which was reported as having occurred from the removal of a large number of fish (Choi et al. 2004). These factors might have an effect on the abundance, productivity, distribution, habitat, stock size and structure of fisheries, and according to the EAFM, should be taken into account in the management regime of fisheries and fish stocks.

There are a number of cases where environmental/biological relationships have been found such as Baltic herring year class strength and the severity of the winter (average winter temperatures), Bay of Biscay anchovy larvae survival and upwelling and stratification; however these relationships are not considered robust enough to reliably predict the population one year in advance (The Stock Book 2006, Stige et al. 2013). As well, problems with the data collection not being concomitant in time and space between the biological and environmental variables mean the data cannot be directly associated.

The distribution, biology and productivity of a population are often influenced to varying degrees by intra population dynamics, interactions with other populations, and the environment. In stock assessment there are few examples of quota limitations that are manipulated to accommodate the predation needs of another species, although one example is Arctic cod where mortality is adjusted for cannibalism in stock assessment models, and the predation pressure of cod is included in the mortality estimates of Capelin (The Stock Book 2006). For understanding inter/intra-population and trophic relationships, spatial distributions and associated favourable conditions should be ascertained.
so variability in accessible resources, and temporal match/mismatch situations can be determined.

1.4 Spatial scale fisheries analysis

Defining an appropriate spatial scale for the analysis of a population’s distribution should be from the perspective of the biology of the species, their environment and the data available (see figure 1.1). Identifying appropriate spatial scales is paramount for assessing health, designing data collection and guiding the management of river and marine ecosystems (Kneib 1992). Macro-scale ecological analysis (ocean basins, 1000 km) might include one or more populations of the same species, as well as different populations or different species, various broad spatiotemporal scale hydro-meteorological forcing as well as the effects of many small scale processes. As a result only large scale processes and relationships are identified and local heterogeneity and small scale relationships might be lost. In the same way, looking in the meso or micro-scale (regional areas such as a shelf area or the continental shelf area, 10-100 km), the effects of local impacts might be more pronounced but the broader scale forcing and responses thereof might be lost. As the spatial resolution increases, so does the complexity and heterogeneity of the study area, and the relationships within.

![Figure 1.1. Nested grid taken from Gerritsen et al. (2013) showing vessel monitoring system (VMS) point data, where cells with ≥20 VMS records are recursively divided. The figure illustrates the importance analysing VMS data within the correct spatial units.](image-url)
Local relationships can be of particular relevance for fish species and particularly helpful with their management. For example, nursery grounds where juvenile fish are present before recruiting to the population are often a focus for conservation and fisheries management, so as to maintain biomass of a fish population. Spawning might be favoured in a particular area or around a particular feature e.g. orange roughy, herring. Feeding distribution and success might be dependent on distribution and phenology of prey species. Distributional responses to the local environment have been seen in a number of marine fish species for example hydrographic features (Stepputtis et al. 2011; Hsieh et al. 2010; Simmons et al. 2010), hydrometeorological forcing (Hatun et al. 2009), substrate type (Snickars et al. 2010) and depth (Sandman et al. 2012) etc. In the same way the larger spatial scale environmental or hydrometeorological processes may have an impact on longer term processes such as the spawning distribution of blue whiting and the strength of the sub polar gyre (Hatun et al. 2009).

The ability to detect a scale for appropriate spatiotemporal analysis of a population can be guided by understanding a population’s distribution in space, relationships with particular biotic and abiotic features for all life history stages, the temporal regimes of climatic and oceanographic processes of the study area, and the interactive combinations of all these factors. Data collection and analysis should then reflect these qualities. Problems associated with describing a population in space and time include: annual migratory populations that may display non-stationary spatial and temporal distributions; heterogeneity in relative abundance such as site specific fidelity; intra-population distributional effects such as density dependent habitat selection, and inadequate spatio-temporal resolution. Habitat or environmental based requirements for an individual may change in space and time and life history stage, for example, during spawning some species leave the food chain, feeding success may depend on degree of spatial overlap and density of competitors, warmer waters may be needed for spawning whereas cooler waters are needed for feeding. Broad scale atmospheric/oceanic processes at the annual (seasonal), decadal (NAO) and multi-decadal (AMO) scales may interact with each other to impact the ecosystem in varying ways, necessitating the need for longer term (hundreds of years) of data to determine relative impacts.

Often metapopulations are made up of separate disaggregated stocks (Shepherd and Brown 1993), which complicate abundance distribution analysis if the appropriate scale is not taken into consideration. Successful management of a fish stock or population requires the ability to describe a population in space and time, so as to derive appropriate management operations (Keesing and Baker 1998). As part of the marine strategy framework directive there is a requirement for more spatially resolved data.
analysis in the marine environment (Cochrane et al. 2010), which has proved useful (Keesing and Baker 1998) and includes analysis on the local, regional and international scale, as well as the ability to scientifically define a spatial scale such as the ‘ecosystem’ (EC 2010). ICES have also adopted a spatial aspect into their research in terms of focusing research projects on an integrated, area based ecosystem approach that facilitates an increased exchange of spatial data throughout ICES expert groups and also the marine community in general (ICES 2011). As well, the United Nations Educational Scientific and Cultural Organization (UNESCO) have developed an initiative on marine spatial planning to operationalize ecosystem-based management by finding space for biodiversity conservation and sustainable economic development in marine environments. Despite more recent data becoming available in higher spatial resolution such as vessel monitoring system (VMS) data (Gerritsen and Lordon 2011), or genetic methods to explicitly differentiate spatial boundaries of populations, the majority of fisheries abundance distribution data are still at the resolution of the survey or catch/landings data (The Stock Book 2010).

1.5 Fisheries data in the northeast Atlantic

In the northeast Atlantic fisheries dependent and independent (survey) data are available for commercially important stocks, and both are used for stock assessment and scientific research. Both data sets are important, fisheries independent data are used to assess stocks, and fisheries dependent data are used to assess the fishing pressure on that stock. Each of the data sets includes different information and should be used according to the aims of the research question.

Biases exist in both data sets, although fisheries dependent data are generally less preferred than survey data for use in fisheries analysis for a number of reasons including: non random sampling is concentrated in locations where fish are (or are thought to be) most abundant; stock components rather than the whole stock might only be sampled (i.e. those closest to port); inaccuracies in reported abundance and location; management and market/fleet driven biases; inconsistent sampling; the data only include commercial species from those countries submitting catch data and bycatch and discards are not necessarily reported (Rotherham et al. 2007). The scale of misreporting in fisheries can be highlighted by recent reports of illegal landing of mackerel into Scottish ports which describes a 10 year scam that resulted in a total catch of £37 million worth of mackerel (and herring), surplus to quota limits (The Guardian 2010). The scam emphasises the increased fishing mortality of mackerel that would not be accounted for in official landings data. The danger of using fisheries dependent data has been demonstrated in some papers, where false conclusions have been made which were based on results from fisheries dependent data
where biases have either not been accounted for or acknowledged, such as that described in Mutsert et al. (2008) (see section 3.2 for more details).

Despite the known drawbacks to the data, there are also known benefits which have significantly advanced current understanding of fisheries and fish population ecology in the northeast Atlantic. Fisheries dependent data generally includes extensive time series, as well as high spatio-temporal resolution of catch and/or landings data on many important commercially exploited marine fish stocks. In the northeast Atlantic fisheries dependent data has been used to predict recruitment peaks of squid species (Denis et al. 2002), to identify changes in the timing of Atlantic mackerel pre-spawning migration (Reid et al. 2003), assessing spatio-temporal patterns in fishing effort over time (Jennings et al. 1999).

Likewise, there are biases with fisheries independent or survey data. Very often survey data has incomplete spatial and temporal coverage and inconsistencies in sampling gear or survey strategy in space and time (Blanchard et al. 2008). Resource constraints, particularly time and money, are very often the reason for limitations in data collection as well as the large amount of time required to process the data for collation, standardisation and dissemination. Fisheries independent data often gives a poor indication of the direct impact of fishing because assessment relies on the average area fished where as fishing is often concentrated on small localised areas (Jennings et al. 1999). In previous research, the use of fisheries independent or survey data has led to false conclusions when the ecology of the species is not well understood (Hixon and Carr 1997), leading to inadequate sampling techniques that are mis-aligned with the aims of the research.

However, fisheries independent data are essential in many stock assessments for multiple commercially important species, and the advantages of fisheries independent data have been well documented in the past (Hilborn and Walters 1992; Gunderson 1993). The use of fishery independent information can include important quantifications of relative abundance, rates of change in total population abundance, and biological data such as size and sex indices. As this data type is obtained from an experimental design and scientific sampling it is less prone to unknown factors that might otherwise confound analysis and interpretation of catch/landings data, and is regarded as a higher quality (Chang and Chou 2007).

Within the northeast Atlantic, fisheries dependent data are collected at the spatial scale of ICES statistical rectangles (Rijnsdorp and Pastoors 1995; Jennings et al. 1999), however fisheries independent (survey) data are collected at the resolution of both ICES statistical rectangles alongside ICES division and depth strata (i.e. the Irish Groundfish survey see Figure 1.2) (see Sections 2.3.1; 4.3.1.1 and 4.3.1.2 for more details on survey methodologies).
Catch data can be used in conjunction with survey data, which has been shown in the past to be a useful technique to validate spatial and/or abundance patterns (Rotherham et al. 2007; Booth 2000; Pecquerie et al. 2010). In the northeast Atlantic the combined (fisheries dependent and independent data) approach has been adopted to reveal a significant relationship between temperature and mackerel migration/distribution using mackerel catch data from commercial fisheries as well as scientific bottom trawl surveys (Jansen et al. 2012). Commercial landings and groundfish survey data (for example, see figure 1.2) have been used to detect changes in the abundance of the mean trophic level of fish assemblages in the Celtic Sea (Pinnegar et al. 2002). Virtual population analysis (VPA) used in stock assessment uses commercial landings data and pre-recruit surveys (Rjinsdorp et al. 1992).
The northeast Atlantic is a bathymetrically complex region (see figure 1.3) that supports a high level of productivity. In the northeast Atlantic there are a number of surveys which are coordinated by ICES including bottom trawl surveys, beam trawl surveys, pelagic surveys, ichthyoplankton surveys, continental shelf trawl surveys, acoustic surveys and red fish surveys (see http://www.ices.dk/products/surveyprotocols.asp for more details). Data available for this thesis comprises fisheries independent and dependent data. Fisheries independent data includes the ICES mackerel and horse mackerel egg survey (see Section 2.3.1 for more details); international bottom trawl survey (IBTS; see section 4.3.1 for more details) and the blue whiting acoustic survey (see section 5.3.2 for more details). Fisheries dependent data includes the mackerel international catch data (see section 3.3.1 for more details). Each of the data sets had to be analysed and results interpreted within the context of how the data were collected and collated (so that all biases and limitations were taken into account when interpreting the results). Whilst the aforementioned data sets were used, other data which were essentially derived from commercial and survey data were also analysed such as the VPA recruitment data used in Chapter 5, and in the ICES stock assessment. Similar to the survey data, the VPA data have drawbacks (for more details see Chapter 3), although as stated in Chapter 5, they are widely used in stock assessment,
including for the study species used in this thesis and they are considered the most accurate estimate (Myers and Pepin 1994; Lassen and Medley 2000).

### 1.6 Study area: The northeast Atlantic

The geographical area of focus for this thesis is the northeast Atlantic. The northeast Atlantic contains some of the most productive waters globally (Profish 2006), sustaining a number of economically important fisheries for Europe, and includes one of the areas that is expected to undergo some of the greatest climatic changes globally (Hughes et al. 2009; Drinkwater 2005). The catchment area of the northeast Atlantic includes some 700,000 km$^2$ with a coastal length of 20,585 km, average surface temperature between 7-15 ºC with a salinity of 35 psu (OSPAR 2000).

In this region, primary productivity increases with latitude and is particularly high southwest of Iceland (Johnsen et al. 2002). In the northeast Atlantic some 1100 species of fish are known, 600 of which are pelagic and the rest are demersal, with a high level of species diversity in the shallow inshore areas particularly the Celtic Sea due to the large range of habitats (Johnsen et al. 2002). The shelf topography changes from the Celtic Sea and Irish Sea which is shallower than 100 m to the steep rocky slope along the Porcupine Bank and the Rockall Trough (The Stock Book 2006), to the North Sea which has a smoother topography of gentle slopes.

![North Atlantic water mass movement systems showing the sub polar gyre in white. Taken from Marine Scotland 2011](image)

A large subpolar gyre (see figure 1.4) plays a central role in the distribution and ecology of fish stocks in the northeast Atlantic (Dickson and Brander 1994) which was arguably discovered by the “Great Salinity Anomaly” (Dickson et al. 1988). The subpolar gyre is an anticlockwise circulation (Hatun et al. 2005) of water where currents are forced by buoyancy contrasts and overflows from adjacent seas, likely as much as by the wind (Treguier et al. 2005).
Hatun et al. (2009) suggested that the subpolar gyre might influence the spawning distribution of blue whiting, showing that when the gyre is strong (resulting in cold fresher water spreading east over the Rockall Plateau) the spawning distribution of blue whiting is constrained to around the European continental slope and south around the Porcupine Bank. Likewise when the gyre is weak allowing warmer more saline water around the western British Isles, blue whiting spawning distribution moves northwards along the slope and over the Rockall Plateau. In another paper, Hatun et al. (2009a) demonstrated the links between the gyre and changes in the bio-geographic distribution of four different trophic levels in the marine food chain, from plankton to zooplankton, blue whiting and pilot whales.

In Europe, most fisheries are managed by the common fisheries policy (CFP) which serves to protect Europe’s fisheries – necessitating the need for cooperation between countries through a range of measures designed to achieve a thriving and sustainable European fishing industry. The common fisheries policy (CFP) seeks to engage rules and controls of; fleet capacity and capability; abundance of landings and habitat protection, as well as encouraging initiatives to increase the sustainability of Europe’s fisheries, all based on scientific research and data for sound policy and decision making (EU Fisheries 2012 http://ec.europa.eu/fisheries/cfp/index_en.htm).

The northeast Atlantic has a number of organisations acting for fisheries management and data collection. The north east Atlantic fisheries commission (NEAFC) is the regional fisheries management organisation (RFMO) for the northeast Atlantic, outside the European Community (EC), which spans the area from southern Greenland, to the eastern Barents Sea and south to Portugal. The NEAFC main fisheries include redfish (Sebastes mentella), mackerel (Scomber scombrus), haddock (Melanogrammus aeglefinus), herring (Clupea harengus), blue whiting (Micromesistius poutassou) and deep water species. The international council for the exploration of the seas (ICES) is an independent scientific body which provides advice to the parties of the NEAFC, and mainly the European Commission, for conservation and/or management measures for the regulatory area.

According to the OSPAR convention (OSPAR 1992) the northeast Atlantic can be split into five areas: Arctic Waters; Greater North Sea; Celtic Seas; Bay of Biscay and Iberian Coast and the Wider Atlantic.

1.6.1 Iberian Peninsula

The Iberian Atlantic coast extends from the Gulf of Cadiz in the south to Galicia Bank in the north. The Iberian Peninsula is at the subtropical boundary of the North Atlantic, this determines the oceanographic and atmospheric characteristics for the region such as coastal upwelling during summer (Santos et al. 2001). The upwelling system apparent around the coast of Portugal is
part of a much larger system called the Canary Current Large Marine Ecosystem that extends south to 15°N (Wooster et al. 1976). Evidence suggest that systems such as these can have an impact on the biology of some fish species, such as the strength of the summer upwelling around the Portuguese coast and the poor recruitment success of horse mackerel (*Trachurus trachurus*) and sardine (*Sardina pilchardus*) (Santos et al. 2001). The region is also influenced by the Atlantic eastern boundary currents (Global Ocean Associates 2004). Upper ocean circulation is weak, with a mean southward flow of a few cm s⁻¹ (Mazé et al. 1997; Pailet and Mercier 1997), but the area is dominated by meso-scale activity (Memery et al. 2005). The continental slope has a poleward moving current known as the Iberian Poleward Current (IPC) (see Frouin et al. 1990; Peliz et al. 2005). Water inflow comes from the Atlantic where it mixes with northward flowing Mediterranean water, both the sub polar and subtropical gyres have an effect on the water masses in this region although in general the circulation follows the subtropical gyre (Mason et al. 2006). A westerly air circulation system brings a low pressure system which often covers the region and large storms occur particularly in the winter months (OSPAR 2013). Mediterranean water forms a prominent feature all along the European continental shelf edge, where the Mediterranean outflow meets the Atlantic water at the Gulf of Cadiz and travels north along the shelf edge (Prieto et al. 2013). The feature is characterised by a salinity maximum and forms a deep boundary current, and reaches as far as the Porcupine Bank west of Ireland at 52°N. A recent study characterised oceanic and climatic variables using a PCA of environmental variables to show three dominant modes of variation in this area which were sea surface temperature, oceanic transport indices (for example the Gulf Stream Index) and lastly meridional wind component and Ekman transport (Lavin et al. 2007).

There are a variety of interesting topographic features in this area including seamounts (450-600m depth) as well as deep submarine canyons which all contribute to the local circulation of water masses (ICES 2008b). A diverse coastline of estuaries, rias and wetlands are present which all support productive ecosystems (OSPAR 2013). The slope regions are generally steep with a rough bathymetry of muddy sediment, whereas the shelf regions are comprised of more sandy or rocky substrates (ICES 2008b). Anthropogenic influences include tourism, fishing and aquaculture, shipping, sand and gravel extraction and new developments of wave, tide and wind power (OSPAR 2013). These activities are not restricted to the Iberian shelf slope, but extend all the way up to northern European shelf break. In November 2002 a significant oil spill occurred affecting parts of northern Spain and in particular, Galacia (Martínez-Gómez et al. 2006). Whilst the spill has prompted monitoring of pollution levels in some fish species, results show there is a high level of background pollutants in the area anyway (Martínez-Gómez et al. 2006).
1.6.2 Bay of Biscay
The Bay of Biscay (43-49°N) is the area off the western French coast (Blanchard 2001), connected to the Atlantic Ocean to the west, and the Celtic Sea to the North. The area is divided in two parts which is separated by the continental shelf edge. The continental shelf area is very narrow in the south being only 12km wide in some areas (ICES 2008b) where it extends from the northern Spanish coast and French Basque country, and widens the further north, extending to about 200km at the entrance of the English Channel. A diverse coastline of estuaries, rias and wetlands are present which all support productive ecosystems (OSPAR 2013). The abyssal plain on the oceanic side of the shelf edge extends down as far as 4000m (Lazure et al. 2009). The shelf break occurs at 200m, except in the Gulf of Cadiz (ICES 2008b). The slope regions are generally steep with a rough bathymetry of muddy sediment, whereas the shelf regions are comprised of more sandy or rocky substrates (ICES 2008b).

![Figure 1.5](image.png)

Figure 1.5 The Bay of Biscay and Celtic Sea showing the bathymetric features of the area. Image taken from Gaba 2013

Throughout this area the circulation of water is relatively weak (Pingree and LeCann 1989), with the tidal wave entering the Bay from the wider Atlantic (Pairaud et al. 2008) from where is amplified as it travels across the shelf edge
When stratification is present, the tide drives large internal tidal waves (New 1988). At the location of the shelf break, vertical mixing is strong, the results of which can be seen at the surface (Lazure et al. 2009). From the shelf break, the tide plays a major role in mixing the water masses between the shelf waters and the deeper off shelf waters, the interface of which causes thermal fronts (Le Boyer et al. 2008). Throughout the Bay of Biscay, thermal stratification occurs between May and October over the shelf edge, with the thermocline depth varying between 20 to 50m. There are various localised fronts that are formed by local processes such as the Ushant front which is induced by tidal mixing in the north of the Bay, and in the south along the Spanish coast, upwellings induce thermal fronts (Froidefond et al. 1996).

In autumn there is a tongue of warm water centred over the 100m isobaths that extends northwards from the Basque country to south Brittany. In winter and early spring, there is a coastal strip of cold water, correlated with shallow depths and a particular salinity pattern. In general the Bay of Biscay has a large outflow of fresh water from the Loire and Gironde rivers which display strong seasonal variability (Puillat et al. 2004) depending on both runoff levels and winds.

1.6.3 Celtic Sea
ICES define the Ecoregion of the “Celtic Sea and West of Scotland” as the shelf areas west of Scotland, the Irish Sea, west of Ireland, the Celtic Sea proper, and the western Channel (ICES 2008a). The Celtic Seas extend from the coastal areas of the British Isles to the 200m depth contour, west of 6ºW (OSPAR 2013). The Celtic Sea is an extended shelf area with depths generally within 100m, limited to the west by the Porcupine Seabight and the Goban Spur (ICES 2008a). The Porcupine Bank is an extension of the shelf and to the west of this is the Rockall Trough (see Figure 1.5) (ICES 2008a).

The Rockall Trough has been extensively studied, although efforts have concentrated along the softer sediments of the continental slope as a result of ease of sampling in contrast to the rocky bottom (Howell et al. 2009). There is a variety of sediments present throughout the trough (Hitchen et al. 2002), and cold water corals (Lophelia pertusa and Madrepora oculata) have been found to depths of 1000m (Wilson 1979; Kenyon et al. 2003).

West of the Rockall Trough is the Rockall Bank which is 400km west of the Outer Hebrides and forms part of the wider region of the Rockall Plateau which comprises the Hatton Bank on the western side of the plateau and to the east is the George Bligh Bank (Howell et al. 2009). Rockall Bank itself is 450km long running northeast to southwest, and is a maximum of 200km wide (Howell et al. 2009). Depth ranges from 0 to 1000m, with the eastern and northeastern edge falling away very steeply although the western and southern slopes are less steep (Howell et al. 2009). The area is steeped in fishing history.
with records stretching back further than 2 centuries (Blacker 1982). Originally species such as cod, haddock and haibut were fished on the shallower parts of the bank but in the 1970’s trawlers have exploited blue ling, roundnose grenadier, black scabbardfish and deepwater sharks. In more recent years a small nephrops fishery has been developed as well as hake, blue whiting and monkfish and become targeted species (Howell et al. 2009).

Further north towards Scotland and the Rockall Trough comes close to the coastline, and west of this is the Rockall Plateau which has depths less than 200m. In most cases the shelf areas have soft sediments in the west with rockier areas to the east (ICES 2008a). In general, water moves from south to north, with oceanic Atlantic water entering from the south and west and moving north to the Arctic regions (OSPAR 2013). Within the Irish Sea there are slightly more complex intermediate water movements (OSPAR 2013). The Irish Sea is shallow being generally less than 100m. Strong winds come from the south and west although the strongest winds are experienced in the north and west of the region. There are a large number of different habitats in the area which supports a variety of commercially important fish species (OSPAR 2013). There are significant knowledge gaps for the Celtic Seas, generally due to lack of data analysis for the region rather than the lack of data (ICES 2008a). One of the main problems is that the region is broken into component parts and collation and analyses of data for the whole region is lacking. ICES state that predator-prey and interdependent relationships between commercially important species should be examined (ICES 2008a).

### 1.6.4 The North Sea

The North Sea (see figure 1.6) lies on the continental shelf edge, and is made up of three areas, the Norwegian Trench, and the northern North Sea (above the Dogger Bank) and the southern North Sea (below the Dogger Bank) (Judd and Hovland 2007). In general the North Sea has a shallow (<50m) southeastern area, and a deeper (50-100m) central area running north along the British coast and slopes down to 200m before the shelf edge (ICES 2008). The North Sea is one of the most frequently negotiated Seas in the world (Weisse and Günther 2007), owing to highly industrialised and densely populated coastal cities in Europe, including two of the world’s largest ports (Rotterdam and Hamburg) (OPSAR 2013). Anthropogenic activities include fishing, the extraction of sand and gravel and gas exploitation. The sediment is mostly mud (deeper regions), sand (southern and coastal regions) and gravel (in the eastern and western sides) (ICES 2008) and there is a variety of different habitats including fjords, estuaries, sandbanks (some are protected by EU habitats directive (ICES 2008)) and intertidal mudflats (OSPAR 2013). The climate of the North Sea is heavily influenced by the inflow of Atlantic water from the Channel (Hughes and Lavin 2005), and also from the northern side shelf break
and also by the westerly winds (causing an anticlockwise gyre) that frequently bring a low pressure system.

Figure 1.6 North Sea showing the major sea currents and the bathymetry of the area. Taken from the European Environment Agency (EEA)

However, the circulation is changeable and has been recorded as clockwise, splitting into two gyres (north and south) and the total cessation of circulation during some periods (ICES 2008). Changes in the distribution of zooplankton and fish have been linked to the circulation in the North Sea (ICES 2008). There is a huge amount of biodiversity in the North Sea with some 230 species of fish and 10 million seabirds (OSPAR 2013). Gaps in knowledge of the North Sea include: what are the ecological effects of a shrinking size spectrum of predators such as herring; what are the effects of climate change on the reproduction, early life history survivorship and growth, as well as distributions of populations; what are the likely consequences of the loss of a meta-population structure and spawning groups in depleted populations and also finally, there is a need to improve estimates of reproductive biology of stocks (ICES 2008).

1.6.5 Norwegian Sea
The Norwegian Sea is located northwest of Norway, north of the North Sea, south of the Greenland Sea and joins the northeast Atlantic to the west with the
Barents Sea to the northeast. There are three ridges partitioning the Norwegian Sea from other water masses in the region. The Greenland-Scotland Ridge divides the Atlantic Ocean to the west and the Norwegian Sea to the east; the Jan Mayen Ridge separates the Norwegian Sea from the Greenland Sea and finally the Mohn Ridge separates the Icelandic Sea from the Norwegian Sea (Loeng and Drinkwater 2007).

Figure 1.7 Norwegian Sea bathymetric features which control many of the currents in the Norwegian Sea (Taken from Gernigan et al. 2009).

On average the depth of the Norwegian Sea is 2km as the continental shelf area is relatively narrow, between 40 and 200km wide with troughs extending across it (ICES 2008). The Norwegian Sea is made up of two deep regions, the Norwegian Basin and the Lofoten Basin (Loeng and Drinkwater 2007), where the depth is between 3000 – 4000m (ICES 2008), with an area of 1.1 million km$^2$, and a volume of 2 million km$^3$ (ICES 2008). The benthic substratum on the shelf area is mostly Moraine deposits whilst the deeper areas has more clay (ICES 2008). The Nordic Seas are made up of the Norwegian Sea together with the Greenland Sea and the Iceland Sea. The Norwegian Sea is a transition zone for warmer more saline waters coming from the Atlantic towards the cooler fresher Arctic waters, and vice versa (Loeng and Drinkwater 2007). The water flow in the Norwegian Sea is controlled mainly by the topography of the area and is made up of Atlantic water flowing northwards along the continental
shelf break, called the Norwegian Atlantic current (Loeng and Drinkwater 2007). On shelf areas the water is controlled more by seasonally varying temperature and has lower salinity, also transported North by the Norwegian Coastal Current, which is separated from the water mass of the general Norwegian Sea by a salinity front (Loeng and Drinkwater 2007). The upper water layers of the Norwegian Sea are made up of the warmer Atlantic water. There is a salinity minimum throughout the middle of the water column that comes from Arctic intermediate water slotting in between the Atlantic surface waters and the deeper colder Norwegian waters (Loeng and Drinkwater 2007).

1.6.6 Arctic waters
In Arctic waters, oceanic flow is dominated by the “Global Conveyer Belt” (Tomczak and Godfrey 2003) with warmer surface water arriving in the eastern area, and sinking at higher latitudes, with colder dense water flowing southward through the Denmark Strait into the west (OSPAR 2013). The harsh climate and extreme variation in light mean anthropogenic influence is limited, although major fisheries exist for Iceland, Faroe Islands, Norway and the north-western part of the Russian Federation with the main fisheries being cod, saithe, haddock, blue whiting, herring and capelin. The continental shelf regions of this area are important spawning grounds for many commercially important species (OSPAR 2013).

1.6.7 The wider Atlantic
In the wider Atlantic, the topography of the area includes continental slopes with a sharply fluctuating seabed which are as a result of seamounts, canyons along the shelf edge, the Mid-Atlantic Ridge to very large areas of featureless abyssal plains (OSPAR 2013). The north Atlantic in general is an important region for oceanic and climatic regimes. Upper layer water flow into the northeast Atlantic is chiefly from west to east from the northern and southern components of the North Atlantic Drift, whilst on the continental shelf currents are primarily tidal and wind generated with a general flow from south to north (Johnsen et al. 2002). In deeper layers, there exist inflows of bottom waters from the Mediterranean Sea (coming originally from the Southern Ocean), as well as cold water flowing out from the shallow banks of the Nordic Seas (OSPAR 2013). Outflows exist in the north-east Nordic Seas which are important for maintaining the mild climate in Europe (OSPAR 2013). Bottom sediments depend on the local topography and currents. Pelagic fauna are 100% more diverse south of 40ºN than north, although the biomass shows the reverse trend. Benthic communities are far richer in species diversity than the pelagic species. In the deeper areas of the northeast Atlantic the sediments are mostly clay or calcareous whereas over the continental shelf the sediments are sandy and/or muddy (Johnsen et al. 2002).
1.7 Climate impacts on fish stocks

In more recent years there have been a number of reported climate driven responses of fish stocks globally (Rose 2005; Drinkwater 2005; Simpson et al. 2011). These changes are not necessarily straightforward (Simpson et al. 2011) and rather involve a complex array of habitat suitability tradeoffs such as latitude (Perry et al. 2005) and depth (Dulvy et al. 2008; Simpson et al. 2011) and physiological or life history based modifications (Ficke et al. 2007). In the North Sea, 72% of commonly fished species (commercially) have been found to be responding to warming with a majority of species increasing in abundance (Simpson et al 2011). In the same study there was found to be a scaling issue whereby decadal stability in the organisation of the presence and absence of species was present despite evidence for profound changes in the local communities. There are also different scales between the responses to a warming climate from the genetic to the ecosystem level (Brierley and Kingsford 2009; Brander 2010; Hare et al. 2010).

Between species there is also a great variety in the potential for adaptation. There are some species that are able to respond with a strong and quick reaction to climate, such as small pelagics for example capelin (Mallotus villosus) and herring (Clupea harengus) where there is strong physiological limitations and the potential for fast population growth (Rose 2005). Some works have investigated warming and cooling periods and have shown a northward expansion of species ranges in warming periods and a latitudinal contraction to more southern localities during cooler periods (Rose 2005). Indeed some of the most commercially important north Atlantic species are known to oscillate north and south in response to climate (Eckman 1953). Time series data has shown distributional responses associated with annual and seasonal variations in sea temperature using both mean and maximum latitudinal data, including Atlantic mackerel (Scomber scombrus) and herring (Clupea harengus) (Murawski 1993). Whilst some species populations will be able to adapt to changes in climate, others will not. For example, cod (Gadus morhua) stocks in the Irish and Celtic Seas (the most southerly distributions of cod) are expected to have disappeared by 2100, whilst those in the southern North Sea and Georges Bank will decline, according to predicted ocean temperatures from Global Circulation Models (Drinkwater 2005).

The abiotic response of the Ocean to anthropogenic driven climate change on a global scale is highly heterogeneous and likely to be changeable in space and time. Over the past 100 years the oceans have risen in temperature by 0.7°C (Smith et al. 2008) and has been predicted to rise by a further 1.5C to 2.6C by 2100 (Meehl et al. 2007). Global circulation models predict significant warming throughout the global oceans as a result of increased greenhouse
gases in the atmosphere (IPCC 2001), with the Arctic and sub-arctic regions thought to be some of the strongest affected (Drinkwater 2005). Changes will act on all parts of the abiotic ecosystem functioning including storm tracks and paths, vertical water column stability, atmospheric precipitation, ocean circulation etc. (Drinkwater 2005). The current knowledge gap lies in understanding how these changes might affect populations and how human based management might best mitigate any potential changes to ensure sustainability within the marine ecosystem

1.8 Study species

The study species used in this thesis are Atlantic mackerel, horse mackerel, blue whiting and cod. The northeast Atlantic populations of these species are economically important to the Irish and European economy and have suitable survey data (and catch data for Atlantic mackerel), covering a large spatial and temporal frame which makes them suitable for spatial time series analysis. A number of large scale internationally coordinated surveys have been deployed for a few decades, including the mackerel and horse mackerel egg survey and the North Sea international bottom trawl survey, both of which started in 1977. However in Irish waters, the international bottom trawl survey only started from 2003, and therefore this time series is far shorter than in the North Sea, however the Celtic Seas have been less well studied than the North Sea cod stressing the importance of testing the Celtic Seas groundfish survey data, despite the shorter time series.

1.8.1 Atlantic mackerel (Scomber scombrus)

Atlantic mackerel are a migratory pelagic species that feed during the summer/Autumn months in the southern Norwegian Sea and northern North Sea (Iversen and Skagen 1989; Holst and Iversen 1992; Belikov et al. 1998), and spawn along the continental shelf edge from the Iberian Peninsula to west of Scotland and as far north as 60°N. Past studies have investigated the environmental associations between the timing (Reid et al. 2003) and distribution of mackerel spawning events and findings showed associations with temperature (Rose and Legget 1988; D’Amours and Castonguay 1992; Castonguay et al. 1992; Walsh et al. 1995; Reid et al. 1997; Bernier et al. 2000), the continental shelf edge and water currents (Walsh and Martin 1986; Castonguay and Glibert 1995; Overholtz et al. 1991). In more recent publications, a significant correlation between the timing of North Sea mackerel spawning events and sea temperature were reported (Jansen and Gislason 2010). Whilst variations in the timing of northeast Atlantic mackerel migration along the continental shelf edge have been shown to be significantly correlated with the temperature fluctuations with the shelf edge current (Jansen
et al. 2012). A recent investigation has shown how the distribution of Atlantic mackerel has expanded north and west during the feeding months in the Norwegian Sea from 2007-2011, and was hypothesised to be as a result of an increase in population size, new feeding opportunities and increased water temperatures (Nøttestad et al. 2012). In a study by Overholtz et al. (2010) the northwest Atlantic mackerel were shown to have moved north and east by approximately 250 km, with a shift from the deeper offshelf waters to the shallower on shelf waters, which were significantly correlated with interannual variability in temperature and gradual warming of the area.

Other biological associations for Atlantic mackerel distribution have included predation on blue whiting young where mackerel spawning stock biomass (SSB) and blue whiting recruitment were hypothesised to be related (Payne et al. 2012). The distribution of mackerel (predator) was tested against the distribution of herring (Clupea harengus - prey) and were found to be related (i.e. that herring distribution influences mackerel distribution), alongside depth (Sveegaard et al. 2012).

The European agreement for mackerel quotas has broken down in the last few years as Iceland and the Faroe Islands have declared large unilateral TAC’s, (Marine Institute 2010) based on evidence that there are increased abundances of mackerel in their waters in more recent years (Astthorsson et al. 2012). Because there is no international agreement, the need to demarcate the distribution of mackerel is ever important. This is also true considering mackerel inhabit areas of the ocean that are warming (Reid et al. 2003), and mackerel have a high fidelity to particular sites such as the continental shelf edge (Walsh et al. 1995; Jansen et al. 2012) (see Figure 2). The associations between mackerel distribution and temperature, as well as the current gap in the scientific literature about changes in the spawning location of northeast Atlantic mackerel emphasise the need to establish whether changes in spawning distribution have occurred over time and also to what extent any changes are associated with the temperature of the area, or other habitat related variables. It would also be useful to use fishery dependent data to investigate spatio-temporal changes in fleet dynamics over time, such as to consider changes in locations of optimal fishing areas over time, possibly testing whether a shift in catch towards Icelandic waters is apparent, as well as changes in average distance travelled for catches (i.e. the profitability of the fishery).

The mackerel and horse mackerel egg surveys have varied throughout the 33 years of data collection in survey effort, area covered, days at sea and strategy. Initially, the survey was deployed in 1977 with the aim to cover the entire spawning area of Atlantic mackerel (and horse mackerel from 1992 (ICES 1992)) for the purposes of stock assessment. Mackerel are assumed to be a
determinate spawner which means spawning stock biomass can be deduced from an estimate of egg production, fecundity, atresia and a sex ratio. Whilst horse mackerel are an indeterminate spawner and so an index of egg production rather than SSB estimates are the focus. From the result of an adaptive design, aimed to survey wherever mackerel spawn, the sampling locations have changed over time, with an increase in the northern and western boundaries of the survey – and the earlier years of the survey not covering all of the spawning locations (seen from 1977 spot sampling further north than the surveys northern boundary). Furthermore, the survey effort has increased over time, initially two countries participated but now 13 countries are involved in the survey. There are some limitations of the data, such as the survey is only deployed every three years; samples are not consistent in their timing and location between years; not all the spawning area has been covered; there is an influence from survey effort etc. However, considering the long time series of the data, the large area covered the consistency in sampling strategy, the mackerel and horse mackerel egg survey data seems a likely candidate to test for changes in spawning distribution over time.

The mackerel international catch data set (1977-2010) also contains bias such as management implications, mis reporting, no record of bycatch and discards and an incomplete submission of data from all fishing countries (i.e. France does not submit catch data to ICES). However, due to its large and relatively highly resolved spatial and temporal time frame, accessibility and the good representation of landings data, if it is analysed and interpreted within the limitations of the data set, it is a good source for examining fleet dynamics such as changes in spatio-temporal distribution of catch over time, and identifying main fishing grounds to potentially isolate preferences in habitat type.

1.8.2 Cod (*Gadus morhua*)

The second study species is cod which, in the North Atlantic is a well studied species (Drinkwater 2005) found throughout the Atlantic shelf areas (Sundby 2000). Atlantic cod is one of the most important commercial species of fish and has a central role in many ecosystems (Ottersen et al. 2006). Depth preferences appear to be within 200m depth including shallow coastal waters with some catches being reported from the deepest parts of the Norwegian deeps at 500m (Bergstad 1991), making it a relatively straightforward species to gather information on from trawl surveys. As such, there is a wealth of data available from the international bottom trawl surveys. Shelf areas such as those occupied by cod have been recently documented as having warmed over the last years, with some areas warming at a faster rate than others (Simpson et al. 2011). Cod distribution and spawning sites as well as the existence and timing of migration have been linked to temperature (Drinkwater 2000). Temperature
has also been linked to growth rates and intrapopulation variability in cod size, as well as recruitment success (Brander 2000; O’Brien et al. 2000). Therefore in a region which has been reported as warming such as the Celtic and North Sea (Valentina et al. 2012), it is important to study spatio-temporal distributions and possible habitat associations with cod.

Spawning appears to occur throughout their distribution in the North Sea (ICES FishMap), although recent evidence reveals complex stock structuring in the North Sea that suggests four genetically distinct subpopulations are present (Hutchinson et al. 2001; See section 4.2.1 for more details). Whilst the biology and distribution of cod in the North Sea has been covered extensively in the scientific literature (Drinkwater 2005; Brander 1993), the Celtic Sea regions have been less well studied (ICES 2008a). The spatial structure of groundfish communities reflects essential habitat associations and ecological functions, for example spawning sites, feeding grounds and predator avoidance (Brander 1993; Hinz et al. 2006). Habitat specific preferences may change throughout an individual’s life-history stage (Shephard et al. 2011). Spatial heterogeneity of cod has been shown to vary in the North and Celtic Sea’s (Shephard et al. 2011), possibly suggesting highly spatially resolved analyses would be suitable for these areas; however regional analyses are useful with regards the spatial scales of the OSPAR regions, and management areas of ICES and should also be taken into consideration.

In general, cod are a prime study species due to their importance in the ecosystem. Cod are an essential top predator in the marine food web, whereupon removal can result in trophic cascades to lower levels (Frank et al. 2005) as well as the early life history stages acting as prey for herring and sprat (Köster and Schnack 1994). Cod are a long lived species (Ottersen et al. 2006) which means protecting their stocks is important due to their low resilience to fishing pressure. In the North Sea, cod are heavily fished and fishing mortality is above the maximum sustainable yield and North Sea cod have had poor recruitment since 2000 (ICES 2012). The Celtic Sea cod is assessed by ICES as the Celtic Sea and western Channel cod stock, and the stock is variable but currently SSB is higher than the maximum sustainable yield biomass trigger and fishing mortality is considered appropriate (ICES 2012a).

Given the recent understanding of the spatial complexities of the North Sea population; high fishing pressure; warming waters; the ecosystem approach to fisheries management adopted by the marine strategy framework directive and the biology of the species which makes it vulnerable to the effects of anthropogenic activities; it is important to understand habitat preferences and environmental variables associated with patterns and possible changes of the spatio-temporal distribution of North Sea cod. Given the large and accessible data from the international bottom trawl survey which has high spatial
resolution and has been conducted during the same period of every year since 1977, it is a suitable data set to use to investigate spatial relative abundance changes over time in North Sea cod. In contrast, the Celtic Sea is far less well studied and therefore warrants investigation into the spatial aspects of the cod population, particularly as the cod population here is at the southern range of their distribution, have had variable recruitment with extremely good years in 1987 and 2010. There is a knowledge gap for this cod population and due to the location between the shelf edge and the land mass of Ireland, are perhaps less well able to respond to the changes that warming waters might bring.

Data for the North Sea comes from the international bottom trawl survey which has been deployed annually, over (for the most part) the same locations during the same time of year from 1977-2010. For more information on the methodology of the survey refer to section 4.3.1.1. A similar survey is conducted for the Celtic and western Channel cod although a slightly different sampling design is used (See Figure 1) which is based on sampling over topographic features and substrate specific areas, rather than a gridded section such as ICES statistical squares. Data available for this stock starts only from 2003 (except slope strata see section 4.3.1.2) and therefore represents a much shorter time series, as well as not covering the entire stock area (See Section 4.2.2 and 4.3.1.2 for full details). In the North Sea the survey covers the majority of the cod population although may not fully capture the northern boundary.

1.8.3 Blue Whiting (*Micromesistius poutassou*)

Blue whiting have a large distribution from the Mediterranean to the Barents Sea, and populations exist on the continental shelves of both the eastern and western Atlantic (Payne *et al.* 2012), with high abundances along the continental shelf edge between 300 and 600m (ICES 2012).

The most recent ICES report taken from the working group on stock identification methods (WGSIM) uses genetic evidence which indicates that separate breeding units may exist between northern Scotland and the Bay of Biscay (ICES 2009a). In fact genetic samples between the Rockall areas and the Porcupine Bank appear strongly divergent, and even samples taken from the Celtic Sea in 2003 and 2004 appeared to show significant differentiation (ICES 2009a). There is combined larval and genetic evidence for the existence of a northern and southern population of blue whiting (Was *et al.* 2008; Skogen *et al.* 1999); however there is insufficient evidence overall to support multiple stocks with distinct spawning locations and times. The results suggest a single stock with a large biogeographical distribution which changes as a result of hydrography and stock size, called an abundance-occupancy
relationship. Currently blue whiting is managed as one single stock under a TAC regulation (ICES 2010).

Blue whiting is a pelagic gadoid and is of high commercial value (Ryan et al. 2005) with the fishery in general, in a state of decline and quota limits being cut by the EU (Villasante 2012). Recruitment of the blue whiting population is highly variable, although in recent years low fishing mortality and good recruitment have increased the SSB from a decline since 2004 (ICES 2012). Recruitment predictions have been poor in the last few years due to the lack of qualitative indices available for the assessment model (2012). Spawning takes place to the west of the British Isles around the continental shelf edge and the Rockall Bank (Villasante 2012); nursery grounds are thought to be in the Norwegian Sea (ICES 2011). Oceanographic variables have been suggested to exert influence over the survivorship of the survival of early life stage (ICES 2011) such as the subpolar gyre, which has been related to the spawning distribution (Hatun et al. 2009), and recruitment strength of blue whiting, although the latter is uncertain (ICES 2012).

Blue whiting are a keystone constituent of the pelagic marine food web (Langoy et al. 2012), feeding on zooplankton and small fish in the same area as Atlantic mackerel and herring (ICES 2012b). Adult mackerel are believed to prey heavily on blue whiting and possibly influence the recruitment of the blue whiting population, particularly considering their biogeographic overlap (Payne et al. 2012). The migration route of blue whiting is similar to that of Atlantic mackerel (ICES 2011).

The fact that the distribution of blue whiting and mackerel distribution overlaps significantly makes a comparative study between the two northeast Atlantic populations an interesting prospect, particularly considering the trophic links between the species and possible changes in mackerel distribution of spawning over time. Blue whiting are also important to study due to their economic importance to the Irish and European fishing industry – and in particular considering their variable recruitment and SSB, possible driving forces influencing recruitment would be a necessary starting point. Blue whiting are essential to the functioning of the ecosystem with their important position in the food web as predator and prey potentially especially for mackerel (Payne et al. 2012), and particularly as a migratory species whose distribution straddles several EEZ’s (requiring international agreement in their management) they are an important study species.

Data for blue whiting in Irish waters include fisheries dependent data as well as acoustic survey data during their spawning season over the Rockall Bank and continental shelf edge. The survey data are a relatively short time series from 2006 – 2010, although the spatial overlap with Atlantic mackerel and the
potential influence mackerel have on the recruitment success of the species warrants the use of this data set in a recruitment study, particularly with the availability of the mackerel spawning distribution data.

1.8.4 Horse mackerel (*Trachurus trachurus*)

Horse mackerel are an important study species for several reasons. The fishery for horse mackerel grew since 1982 when an anomalously high recruitment year caused a boom in the fishery. Due to the longevity of the species (30 years) the strong year class dominated the fishery and as such a substantial fishery remained for a decade and therefore the commercial importance of horse mackerel grew and they became one of the three most economically important European fisheries (Abaunza *et al.* 2003). The biology of horse mackerel is similar to that of Atlantic mackerel, with their migration route (Iversen *et al.* 2002), responses to particular temperature and to the continental shelf edge (Macer 1977; Eaton 1983) (for more information refer to section 5.3.1.2). Their close association with the shelf edge means that within the warming waters of the northeast Atlantic distributional changes may be occurring, and this has not been examined in the scientific literature. Typically their depth distribution is around 200m although specimens have been found as deep as 500m (Smith-Vaniz 1986). This also makes them an easy target for pelagic fisheries, which warrants a good understanding of their biology for the purposes of improved and sustainable management.
Horse mackerel undergo vertical migrations between the mid waters during the day, and disperse to just above the sea floor during the night (Macer 1977), although these migrations decrease during the winter when activity slows (Nazarov 1989). Horse mackerel occupy the North Sea although have been more associated with the south east area when large influxes of Atlantic water enter (Iversen et al. 2002), and in the winter the population largely disappears from the North Sea (Postuma et al. 1978). It has been noted that their habitat preferences are poorly understood but that a variety of hydrographic features may affect their distribution (Corten and Van de Kamp 1996). Horse mackerel are thought to be affected by density dependent controls, are slow growing although the rate varies, as does their age at maturity (ICES 1991). Egg development rates have been shown to be affected by temperature (Pipe and Walker 1987), which may be of concern as their distribution is within an area of warming due to climatic changes. Horse mackerel are important to the pelagic marine food web feeding on copepods and euphasiids (Macer 1977), with small fish becoming more important in the diet as they become older, particularly 0-group herring, cod and whiting (Dahl and Kirkegaard 1986;1987). For these reasons horse mackerel are an important study species and there is an ecological and commercial requirement to better understand their biology and environmental associations, as increased pressure comes from fishing mortality, a changing environment and their important trophic placement.

1.9 Thesis aims

Firstly distributional changes will be tested in the spawning locations of adult mackerel over time (1977-2010) using the mackerel and horse mackerel egg
survey data. Biases in this data such as the expanding survey effort should be taken into consideration, and if possible a biological shift should be separated from an anthropogenic shift. A number of specifics will be tested i) has there been a change in the centre of gravity of spawning location over time ii) can any change in spawning location be separated from the effect of an adaptive survey design iii) what are the smaller scale spatial changes involved such as a change in the amount or direction of spread of distribution and how might this be affected by local habitat.

Maintaining a spatial theme, the aim to test for similar patterns using the mackerel international catch data set. Firstly it was tested whether acknowledging the limitations of the data, useful information on changes in relative abundance can be obtained using a spatio-temporal analysis approach. Another aim was to verify known patterns (such as management changes i.e. quota restrictions in certain areas) in spatial catch abundance, to test for habitat associations and finally to detect changes in relative abundance throughout the year, not just the spawning season which is well covered by the egg data set.

Secondly the aim was to test North Sea and Celtic Sea cod for similar patterns in relative spatial abundance changes over time to better understand habitat associations, possible environmental influences and detect potential climatic changes. Higher spatial resolution patterns will be tested to examine to what extent the population centre of gravity can be explained by smaller scale changes in relative abundance. Another method will be used to test the same aim. Whether local areas respond similarly in terms of changes in relative cod abundance over time will also be tested; for example, are there simple increases in one area and decreases in another (local correlations in abundance fluxes), or are abundance fluctuations more spatially heterogeneous. Unfortunately the Celtic Sea and Western Channel data might not be appropriate for these analyses due to the small area covered and short time series. Density dependence will also be tested for distribution of cod in the Celtic Sea.

Finally, commonalities in the recruitment responses to environmental forcing in the distributionally overlapping populations of blue whiting, Atlantic mackerel and horse mackerel will be examined. First the aim is to detect significant changes in recruitment and environmental variations over time. Secondly the aim is to test whether multivariate combinations of both environmental and recruitment data better explain links between the environment and biological response. Considering mackerel and horse mackerel come from the same survey and therefore can be directly compared, and considering the literature supporting the importance of the survival of early life history stages on the recruitment of a population, a direct comparison between the survivorship of mackerel and horse mackerel egg stages will be
made. It will be tested whether egg stage transition mortality reveals a recruitment signal, and whether the spatial distributions of early life history stages respond to environmental forcing in the same, or a different way. Finally the aim is to test whether extremes of recruitment of all species have a common environmental signal.

1.10 Introduction References


Beaugrand, G. 2004. The North Sea regime shift: Evidence, causes, mechanisms and consequences. Progress in Oceanography. 60. 2-4: 245-262


FAO. 2008. Climate change for fisheries and aquaculture. Food and Agriculture Organisation of the United Nations, 7-9 April, Rome. HLC/08/BAK/6: 17pp


Gerritsen, H. and Lordan, C. 2010. Integrating vessel monitoring systems (VMS) data with daily catch data from logbooks to explore the spatial distribution of catch and effort at high resolution. ICES Journal of Marine Science. 68 1: 245-252


Hare, J.A., Alexander, M.A., Fogarty, M.J., Williams, E.H. and Scott, J.D. 2010. Forecasting the dynamics of a coastal fishery species using a
coupled climate-population model. Ecological Applications. 20: 452-464


Huthnance, J.M. 1995. Circulation, exchange and water masses at the ocean margin: the role of physical processes at the shelf edge. Progress in Oceanography. 35 4 353-431


Jansen, T. and Gislason, H. 2010. Temperature affects the timing of spawning and migration of North Sea mackerel. Continental Shelf Research. 31: 64-72


Langoy, H., Nottestad, L., Skaret, G., Broms, C. and Ferno, A. 2012. Overlap in distribution and diets of Atlantic mackerel (Scomber scombrus), Norwegian spring-spawning herring (Clupea harengus) and blue whiting (Micromesistius poutassou) in the Norwegian Sea during late summer. Marine Biology Research. 8 5-6: 442-460


Mutsert, K., Cowan, Jr., J.H., Essington, T.E. and Hilborn, R. 2008. Reanalyses of Gulf of Mexico fisheries data: Landings can be
misleading in assessments of fisheries and fisheries ecosystems. PNAS 105 7: 2740-2744


Overholtz, W.J., Hare, J.A. and Keith, C.M. 2010. Impacts of interannual environmental forcing and climate change on the distribution of


Reid, D.G., Eltink, A. and Kelly, C.J. 2003. Inferences on the changes in pattern in the prespawning migration of the western mackerel (Scomber scombrus) from commercial vessel data. ICES CM 2003/Q:19


Sadovy de Mitcheson. Y., Craig, M.T, Bertonicini, A.A., Carpenter, K.E., Cheung, W.W.L., Choat, J.H., Cornish, A.S., Fennessy, S.T., Ferreira,


Skogen, M.D., Monstad, T. and Svendsen, E. 1999. A possible separation between a northern and a southern stock of the northeast Atlantic blue whiting. Fisheries Research. 41: 119-131


Tidwell, J.H. and Allan, G.L. 2001. Fish as food: aquaculture’s contribution. Ecological and economic impacts and contributions of fish farming and capture fisheries. EMBO Reports. 2 11: 958-963


Chapter 2: Changes in the spatial distribution of spawning activity by northeast Atlantic mackerel in warming seas: 1977-2010

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2.1 Abstract

Migratory species with a broad geographic range, such as northeast Atlantic mackerel, may be amongst the fauna most able to respond to warming seas, typically with a poleward shift in range. Habitat heterogeneity could, however, produce more complex patterns than a simple polewards translation in distribution. We tested for changes in the central location and spatial spread of mackerel spawning over a 33-year period. Spatial statistics (centre of gravity of egg production, spatial variance and degree of anisotropy) were used to summarize interannual changes in the spawning locations of the western spawning stock of northeast Atlantic mackerel (NEA-WSC) using data from the ICES triennial egg survey. A northwards shift in centre of gravity of egg production estimates was observed, related to both an expansion in the distribution in survey effort and warming waters of the north east Atlantic. Sea surface temperature (SST) had a significant positive association with the observed northward movement of NEA-WSC mackerel, equivalent to a displacement of 37.7 km °C\(^{-1}\) (based on spring mean sea surface temperature for the region). The spatial distribution of spawning around the centre of gravity also changed significantly with sea surface temperature, with a less elongated spatial spread in warm years. An increase in the proportion of spawning over the Porcupine Bank demonstrated how habitat interacts with positional shifts to affect how northeast Atlantic mackerel are distributed around the centre of their spawning range.

Keywords: inertia, spatial statistics; spawning locations; distribution; Generalised Additive Models; survey effort.
2.2 Introduction

Many studies have reported changes in the distribution or phenology of species with increasing temperature (Bertin, 2008; Leech and Crick, 2007; Parmesan and Yohe, 2003). Spatial changes are often reflected through poleward shifts in range (Beaugrand et al. 2002; Brander et al. 2003, 2007; Sorte et al. 2010). However, poleward movements to maintain a thermal niche are not universal, reflecting other physical and biological constraints on species’ ranges. Species at high elevations such as mountains are limited in terms of latitudinal shifts and rely more on adapting their altitude to maintain microclimates (Sekercioglu et al. 2008; Galbreath et al. 2009). A similar pattern is apparent in marine systems, where changes in distribution with depth are associated with temperature changes (Perry et al. 2005; Dulvy et al. 2008). Some species may inhabit areas such as enclosed seas or fragmented habitats where range shifts to more favourable conditions are less likely due to constraints on dispersal (CIESM, 2008; Melles et al. 2011).

In contrast to species with restricted dispersal, migratory species might be less constrained in responding to climate change. Migratory species have been shown to have adjusted arrival or departure times from spawning areas and there have been shifts in the overall latitudinal position of populations (Sims et al. 2001; Dufour et al. 2010). However, a species tracking a thermal niche may face other challenges even if mean temperature conditions are maintained (Visser et al. 2005). The quality or availability of habitat used by a species may alter as environmental conditions change or as the population moves to different latitudes. For example, the spawning grounds of Japanese common squid, Todarodes pacificus, are defined by a depth range, a sea surface temperature (SST) range and the position of the Kuroshio current (Rosa et al. 2011). In some years the environmental conditions interact to result in a spawning area distribution associated with lower commercial T. pacificus catches. One potential approach to understanding how migratory species may respond under projected climate change is to define a thermal niche and then map the location and extent of suitable habitat, as has been attempted for Pacific saury (Cololabis saira) (Tseng et al. 2011).

North East Atlantic mackerel (NEAM, Scomber scombrus) is a pelagic species undergoing seasonal migrations (Molloy, 2004) and, as such, might be expected to have few constraints in adjusting latitude with warming seas. NEA Mackerel are distributed along the western European Continent from the west coast of Portugal and the Bay of Biscay to north of Norway, into the Arctic Circle (Bolster, 1974; Borchers et al. 1997; Uriarte and Lucio, 2001; Iversen, 2002; Borja et al. 2002); areas that are expected to undergo some of the most extreme climate changes globally (Drinkwater, 2005; Hughes et al. 2009). The strongest warming in the waters west of Ireland has occurred since 1994, with
2005, 2006 and 2007 being particularly warm years (Cannaby and Hüsrevoğlu, 2009). Seasonal migrations between wintering grounds and spawning areas occur throughout the range occupied by mackerel and the species supports one of the largest fisheries in European waters (in catch tonnes and biomass, Beare and Reid, 2002 or by landings tonnes and value, Tenningen et al. 2011). Since 1995 NEAM have been managed as one population (The Stock Book, 2009). However, the mackerel stock contains a number of subdivisions. The consensus view is that NEAM can be divided into three separate spawning components (North Sea, southern and western; Molloy, 2004; ICES 1999), although the structure of the stock is probably more complex than a simple division into these components (Uriate et al. 2001, Jansen and Gislason 2013).

Here we concentrate on the Western spawning component (NEA-WSC) as it has good coverage in triennial egg surveys and makes up the largest proportion of the commercial catch (ICES, 2011). Previous research on the NEA-WSC has identified spawning concentrated along the European shelf edge, with intense spawning around the Porcupine Bank, Goban Spur and Celtic Sea (Reid et al. 2001). The location of peak spawning (located off SW Ireland) may have shifted north between 1977-1998, associated with changes in sea surface temperature (Beare and Reid, 2002). Evidence suggests that the location of overwintering, and the timing direction and speed of migration are related to SST (Walsh et al. 1995; Reid et al. 2001). Analyses on the North Sea spawning component have demonstrated that SST is associated with the timing of pre- and post-spawning migration (Jansen and Gislason, 2011), and with the winter-spring migration path and distribution (Jansen et al. 2012). Northwest Atlantic mackerel distributions have also changed in association with warmer temperatures: mackerel are now more common on the North American continental shelf, with a distribution shift of approximately 250 km to the North and East (Overholtz et al. 2011).

The aim of this paper is to examine the evidence for changes in the location and spread of mackerel spawning in the western stock using the ICES triennial egg survey, which provides a time series between 1977 and 2010. Changes in the spatial pattern of spawning may occur due to differential arrival of subpopulations in space and time and may be affected by other features of the habitat. While latitudinal shifts are not uncommon for fish, the complexity of the mackerel stock may obscure a simple northwards shift in activity. We use a measure of the location of activity (egg production centre of gravity) to test for polewards movement in the mackerel spawning area. In comparison to polewards movements, changes in spatial pattern are less well documented in the literature. The analyses in this study also test whether the spatial distribution of mackerel spawning retains the same orientation and spatial variance in response to any changes in the centre of the distribution.
The ICES mackerel egg surveys have used an adaptive approach, with changes in effort over time that includes a northward shift. The adaptive approach may produce a bias towards detecting latitudinal shifts, so an approach was developed to address the potential biases from changing survey effort. Due to inconsistencies in sampling effort in space and time within and between years, a generalized additive model (GAM) was also used to produce a smooth surface for summarizing broad scale changes in the spatial coverage of spawning grounds known to be highly productive for NEA-WSC spawning events.

2.3 Materials and Methods

2.3.1 Survey Background

The ICES triennial mackerel egg survey has been carried out since 1977, with the original aim (Lockwood et al., 1977a) of providing a fishery independent estimate for the spawning stock size of northeast Atlantic mackerel (NEAM). The survey involves plankton tows undertaken to a survey grid, generally centred on ICES statistical rectangles (ICES rectangle equals one decimal degree longitude x 0.5 decimal degree latitude). From 1977-2010, survey effort expanded in spatial coverage, accompanied by more survey days per year and a longer length of time between the start and end of the survey. In 1977 only 2 vessels from France and England were involved, sampling from March to July in the Bay of Biscay, Celtic Sea and to the west of Ireland. In the 2010 survey there were 13 vessels from 10 different countries with a greatly increased survey extent (Figure 1). The expansion of the survey reflects the aim of covering the main spawning area and an adaptive approach is followed where possible: sampling continues north and west until boundaries of egg distribution have been identified.

Eggs are collected using a Gulf VII sampler or similar, with onboard counting of samples to allow the edges of the egg distribution to be identified. Eggs are classified to a development stage. Subsampling is commonly used to save time when staging material from high density patches. This subsampling potentially leads to relatively greater variance around egg density estimates when egg density values are high in comparison to samples with a low egg density (where all the material is staged). Raw egg counts are converted to a density of eggs m\(^{-2}\) and subsequently to an estimate of egg production (m\(^{-2}\) day\(^{-1}\)) by adjusting for the temperature dependent stage duration of eggs (Lockwood et al., 1977b, 1981; ICES, 2010). A count of eggs in stage 1, the most recently spawned egg stage, in a subsample is converted to egg production (eggs m\(^{-2}\) d\(^{-1}\)) as follows:
Egg production = \left( \frac{n}{n_s} \right) \left( \frac{d}{v} \right) \left( \frac{24}{\exp(a(\ln(t_{20})+b))} \right)

(1)

Where \( n \) is the number of eggs in the sample, \( n_s \) represents the number of eggs staged in the subsample, \( d \) is the depth of water column sampled (m), \( v \) is the volume of water filtered by the sampler (m\(^3\)), \( t_{20} \) is the temperature at 20 m depth (\(^\circ\)C). Each variable is representative of a particular location at a particular day in a year, and therefore the egg production value is per survey tow. There are two species-specific constants \( a \) and \( b \), which for mackerel are -1.61 and 7.76 respectively (Lockwood et al., 1977b, 1981).

2.3.2 Summaries of spawning location

Egg production is based on stage 1 eggs and as mackerel eggs spend only 1-2 days in stage 1 (Lockwood et al., 1977b, 1981), it is a suitable proxy for the location of spawning adults. The locations of egg production in different years can be summarized using estimates of the annual centre of gravity (CoG), inertia and anisotropy (Bez and Rivoirard, 2001). To avoid distortion of units with latitude, the locations of egg survey samples were transformed to Universal Transverse Mercator (UTM) coordinates: eastings and northings (m). The CoG, is the location of the weighted average egg production in two dimensions \( x \) (eastings) and \( y \) (northings), with inertia \( (I_s) \) indicating the variance around the mean location:

\[
\text{CoG} = \left\{ \bar{x}_s = \frac{\sum_{i=1}^{N}(x_i s_i)}{\sum_{i=1}^{N} s_i} \right\}; \quad \bar{y}_s = \frac{\sum_{i=1}^{N}(y_i s_i)}{\sum_{i=1}^{N} s_i} 
\]

(2)

\[
I_s = \frac{\sum_{i=1}^{N} s_i ((x_i - \bar{x}_s)^2 + (y_i - \bar{y}_s)^2)}{\sum_{i=1}^{N} s_i}
\]

(3)

Where \( s \) is the egg production at location \((x, y)\) for tow \( i \), with \( N \) as the total number of locations within a survey year for which data are available. CoG values were therefore calculated for each separate survey year.

If egg production decreases evenly in all directions from the centre of gravity, then the distribution will be isotropic. More common is that the rate of change varies with orientation. We calculated the lowest rate of decrease and the rate of decrease orthogonal to this, with a principal components analysis of production estimates by location, with the ratio between the two axes indicating the degree of anisotropy (Wolliez et al. 2007).
The ICES mackerel egg survey includes the southern spawning stock of mackerel, which was removed using the boundary agreed on in stock assessments (ICES, 1999) so that analyses cover the consensus area accepted for the western spawning component.

2.3.3 Accounting for survey effort bias

The apparent northward shift of survey effort has the potential to confound estimates of change in the centre of gravity of egg production and related spatial statistics. All other things being equal, the estimated centre of gravity will move northward with sampling effort unless the expansion of sampling always reveals zero counts. The observation of non zero counts in the spot samples outside the main survey area (e.g., 1977) indicates that the northerly expansion of effort will have an apparent signal of change in location of centre of gravity, even in the absence of any underlying change in spawning distribution. To estimate the size of the potential sampling artefact, the egg production values were randomized in time and space giving a pattern lacking in spatial and temporal structure but containing variability from sampling. The randomization was based on the Mersenne Twister algorithm for generation of pseudo-random numbers (Matsumoto and Nishimura, 1998). The randomizing procedure was repeated 100 times with centres of gravity and inertia estimated for each year. The same numbers of observations as was actually sampled were assigned to each year so that annual randomized egg production distributions reflected appropriate sample sizes. The null hypothesis is that the observed changes in centre of gravity and inertia can be explained solely by changes in survey effort distribution, with the observed data having no additional signal associated with other variables.

A multiple regression was used to test which variables best explained changes in each of the observed egg production CoG, inertia and anisotropy. Variables examined as potential predictors for changes in observed CoG were randomized CoG, SST (March-June) and spawning stock biomass (SSB). Randomized CoG and inertia values provide a direct estimate of the change due to change in survey effort alone. The SST data were average values for the area surveyed for the months where peak spawning occurs (March – June). SST data were extracted from the Hadley (HadISST) data set (www.metoffice.gov/uk/hadobs/), which provides monthly SST data on a 1º x 1º latitude-longitude grid for all of the survey years (Raynor et al. 2006). The time series of NEA mackerel SSB was taken from ICES (2011) and can be seen in Figure 2. A Ljung-Box Q test was used to test for temporal autocorrelation, (Ljung and Box 1978) of variables as this may bias the estimates of the significance of different fits.
Candidate models for the changes in observed GoG, inertia and anisotropy were compared using an information theoretic approach (Burnham and Anderson 2002) to evaluate the support for different predictor variables. The advantage of an information theory approach based on Akaike’s information criterion (AIC) is in the ways that the evidence for different models can be compared. Hence, while the best model fit can be identified by the lowest AIC (or by AICc, the sample size corrected version of the AIC, used when the number of data points is small relative to the number of terms in the model, Burnham and Anderson 2002), the information in other candidate models can be evaluated using evidence ratios and by model averaging. Evidence ratios estimate the probability that one model is superior to another by comparing the ratio of respective Akaike weights ($w_i\text{AIC}$). Similarly, where fits are linear, the mean and standard error of a model term across different models can be summarised by weighting estimates so that the model with the largest $w_i\text{AIC}$ has the largest influence on the mean (‘model averaged’ term) and less likely models are reduced in influence. As the information theory approach involves judgements on the degree of support, it contrasts with a hypothesis testing approach, and providing significance tests relative to particular thresholds does not form part of candidate model evaluations (Burnham and Anderson 2002).

The randomization procedure on the entire data set was preferred to approaches seeking to use only locations that had been sampled in every survey year. A preliminary search indicated that only 10% of sample locations were surveyed in every survey year between 1977 and 2010. As more than one sample can be taken within a year in different months, the ‘sampled every year’ dataset still contains elements of changing sample effort and biases due to samples being taken in different months. Applying a stricter filter to address this reduces the data to fewer than 10 locations where egg production values are available within a specific month across all 12 survey years. Attempts to remove potential biases by pre-filtering the data were therefore not developed further.

2.3.4 Changes in temperature with a fixed spawning distribution

To examine what SST mackerel would have experienced for the years 1977-2010, had they remained in the 1977 distribution, a ‘pseudo’ CoG for SST was estimated using the HadISST data set. Associating a temperature with the 1977 survey locations requires an interpolation from the nearest HadISST data. Locations were associated with the temperature in the relevant month as this is the temporal resolution for the HadISST data. Spatial interpolation from HadISST to 1977 locations used Inverse Distance Weighting (IDW), where predicted temperature values are proportionally weighted by the inverse of the distance to the adjacent Hadley grid sample locations. The maximum distance
from a survey location to the nearest HadISST grid square mid point was 62 km. The pseudo centre of gravity for temperature was then calculated using the egg production values for 1977 using the temperatures from each subsequent survey year.

2.3.5 Modelling spawning distribution in different shelf edge areas

The spatial and temporal changes in sampling effort prevent a consistent comparison of the same sites across all sampled years. A smoothed surface (GAM modelled egg production) was therefore used to interpolate between measurements and summarize the broad scale changes in egg production over time. Generalized Additive Models (GAMs) were used to provide a non linear smoothing function (in this case using thin plate regression splines) that described the relationship between egg production and the variables of eastings, norings, survey years and fortnight (see equation 4).

\[
\ln \left( \frac{\mu}{1-\mu} \right) = \beta_0 + f(x_1, x_2, x_3, x_4) + \varepsilon
\]

(4)

Where \( \ln \left( \frac{\mu}{1-\mu} \right) \) represents the negative binomial logit function for the egg production, \( f(x_k) \) represents the smoothing functions of the four covariates used (\( x_1 = \) eastings, \( x_2 = \) norings, \( x_3 = \) survey year and \( x_4 = \) fortnight), and \( \varepsilon \) is the error term. The use of a GAM is similar to previous methods used with analyzing ICES egg survey data (Borchers et al. 1997; Augustin et al. 1998; Beare and Reid, 2002, Dates were aggregated into two week blocks (fortnights) as sampling periods were variable between years (Borchers et al. 1997; Augustin et al. 1998; Beare and Reid, 2002). Previous modelling work on NEAM egg production used distance along and from the 200m European continental shelf edge contour as a proxy for spawning position (Beare and Reid 2002). The northern expansion in survey effort means that features such as the Rockall Bank are included in the more recent years of the survey data, adding a second 200 m contour that makes definition of distance along the shelf edge problematic. Therefore eastings and norings were used for referencing locations. Predictor variables can be entered independently or as interacting terms. As the East-West spatial distribution of egg production is clearly not consistent from South to North (Beare and Reid 2002), eastings and norings were entered as interacting terms in the model.

The other covariates in the GAM describe the changes in egg production with time. The alternative models explored were that changes in egg production within and between years were independent, the within year pattern depended on the year (formally, a fortnight by survey year interaction) or that all covariates interacted. Clearly the case where all variables interact is the most complex model. The three candidate models are shown in Table 2.1.
GAM fitting was carried out in R (R development core team 2008) using the mgcv package (Wood, 2006). The optimum balance between overfitting and smoothing is found using penalised iteratively re-weighted least squares (P-IRLS). Model choice was based on information-theoretic approach and used comparisons of the unbiased risk estimator (Wood 2006), a rescaled Akaike information criterion (AIC).

GAM predicted values of egg production were summarised using the partitioning of spawning into four distinct areas in each survey year. These four areas (Bay of Biscay, Celtic Sea, Porcupine Bank and Rockall Trough; Figure 3) represent shelf edge areas where spawning activity has been previously recorded. Partitions of the annual proportion of egg production into each area were correlated with annual mackerel SSB.

2.3.6 Choice of GAM structure: link function and offset

In the past, different approaches have been taken when modelling the distribution of ICES egg survey data (Augustin et al. 1998). Egg survey data have been modelled with egg counts or egg production as response variables. Subsampling during the survey may alter the precision of estimates, meaning that it is more appropriate to predict egg counts before estimating egg production. Predicting egg counts accounting for variability in precision can be done using an offset to describe the sample-specific conversion to egg production at each location (as the components of this conversion are known (equation 1) and do not have to be estimated). Despite the arguments in favour of using count data with an offset rather than modelling egg production directly, Augustin et al. (1998) found negative bias in GAM fit estimates based on egg counts and recommended use of egg production as the response variable. A second issue with fitting a GAM to an egg count or egg production surface is that the errors are not normally distributed. Egg counts are typically overdispersed, making the negative binomial an appropriate error distribution. The appropriate error family for egg production values is less clear a priori, although a negative binomial may again be suitable (Augustin et al. 1998).

We compared the alternative approaches of fitting a GAM using count data with offset with a GAM using egg production. Unfortunately, the data are available with count and associated subsample information for recent years only, so the comparison of models could only be made for survey years after 2001. Correlations of fitted egg production values from the different models were always significant. The centres of gravity in survey years were similar in the different models (mean north-south deviation between centres of gravity 90 km, SE 71.64 km). Therefore it seems unlikely that the details of the response variable would have a large influence on the egg production surface fitted in
separate years and GAMs fitted to egg production with a negative binomial error distribution were used for predictions.

2.4 Results

2.4.1 Changes in the spatial aspects of spawning

The centre of gravity for observed egg production rate moved north over successive survey years (Figure 2.1a) (correlation with year $r = 0.871$, $P < 0.001$). The displacement of the centre of gravity by 2010 was 272 km northward of the position in 1977. While there was a movement north, there were no equivalent relationships with the easting centre of gravity for egg production ($P > 0.05$) (Figure 2.1b). The inertia significantly increased over time (correlation with year $r = 0.925$, $P < 0.001$) (Figure 2.1c). The observed centres of gravity were generally associated with the shelf edge southwest of Ireland (Figure 2.2), reflecting peak egg production around the continental shelf edge, Porcupine Bank and Goban Spur.
Figure 2.1 Change in egg production centre of gravity and inertia in observed (dotted line) and randomized data (solid line; mean of 100 randomizations). (a) centre of gravity for northing (b) centre of gravity for eastings (c) spatial inertia (d) mean SST March-June for total survey area. To show inertia from randomization on the same scale as observed inertia, values for each line are standardised to 0 with a standard deviation of 1. Years are along the x axis.
Figure 2.2 Annual centre of gravity of egg production (survey data) with associated inertia (spatial variance of data) and anisotropy (main axis of variability and variability orthogonal to this). Contour lines (200m, 300m, 400m, 500m and 1000m) emphasize the shallower slope around the Porcupine Bank compared to more steeply sloping shelf edge along the Celtic Sea margin.
2.4.2 Survey effort, SST and SSB influences on spawning distribution

The apparent shift in the location and spread of adult mackerel spawning can be associated with a change in distribution of survey effort over the survey period (see Figure 2.3). The average centre of gravity generated by randomization, reflecting the change in effort alone without any interannual change in egg production distribution, also moved northwards (Figure 2.1a).

![Figure 2.3 Choropleth maps of annual mean raw egg production (eggs m$^{-2}$ day$^{-1}$) in ICES half statistical squares across all survey years (1977 – 2010). Latitude is along the y axis, and longitude is along the x axis.](image)

The patterns in the observed and randomized northing centres of gravity for egg production were similar. The observed values of easting centre of gravity were generally further west than in the randomised data (where CoG locations...
are generated solely by the pattern of sampling, see Figure 2.1b). The increased spread of sampling effort in more recent surveys affected the inertia around the egg production centre of gravity (Figure 2.1c). The SSB has no significant correlation with years (Figure 2.4)

![Figure 2.4](image)

*Figure 2.4* Spawning stock biomass of the western component of NEAM from 1977 – 2010 in millions of tonnes. Taken from ICES 2011.

A multimodel approach to predicting the observed northing centre of gravity for egg production, indicated that both the average temperature across the main spawning months of March to June (see Figure 2.1d) and the CoG for randomized survey effort were in the model with the best fit. The regression was not affected by temporal autocorrelation in any of the predictor variables (Ljung-Box Q tests for autocorrelation at lags up to 3 not significant). Similarly, variance inflation factors (VIF) =1 suggested that collinearity between predictors did not influence the regression. The evidence ratio calculated from Akaike weights suggested that the model with lowest AICc was 1.8 times more likely than the model with survey effort alone. The model-averaged estimate for the effect of temperature in the predicted model was 37.7 km °C\(^{-1}\) (SE 10.002). Hence, the distribution of mackerel spawning events is moving northwards at an estimated rate of 37.7 km for every degree of SST increase in the region, independently of the change in survey effort. The link between SST and position of the egg production CoG can be visualized if a regression is used to remove the influence of changing survey effort (Figure 2.5a). The partial regression for position of spawning CoG as a function of SST, while controlling for changes in effort, had an \(r^2\) of 39%.
Interannual changes in the eastings CoG mostly reflected the change in survey effort. The model with effort alone was 3.7 times more likely than the next most supported model (effort and SSB). Predictive relationships with observed CoG eastings were far weaker than with either inertia or CoG northings (on a comparison of $r^2$ values). Coefficients from model averaging for the effect of predictors on the observed centre of gravity were 14.6 km °C$^{-1}$ (SE 0.42) for SST and -0.04 km °C$^{-1}$ (SE 0.01) for SSB. Changes in inertia reflected survey effort, with effort alone being 2.8 times as likely as a model with effort and SST. The model average coefficient for SST was $1.62 \times 10^{10}$ egg production$^2$ °C$^{-1}$ (SE 0.267 $\times 10^{10}$).

The main axis of anisotropy (figure 2.2) generally lay parallel to the shelf edge. In more recent years, the ratio between the major axis of anisotropy and the axis orthogonal to this tended to decrease. Changes in the anisotropy ratio were related to SST, with little support for the distribution of sample stations (‘Effort’) or SSB having an effect (evidence ratio for SST model ≥ 8.6). The observed anisotropy ratio declined with increasing temperatures (Figure 2.3b, $r^2$ 48%). Egg production was therefore more evenly spread around the centre of gravity in warmer years (although the ratio between major and minor axes remains above two so the pattern has not become a circular, isotropic, spread of values).
2.4.3 CoG of observed and pseudo SST

An avoidance of warmer water associated with a northwards shift in egg production as a function of annual mean sea surface temperature (SST) for the spawning area. (a) Residuals from a regression of observed centre of gravity against mean centre of gravity from randomized data. Partial regression coefficient of determination ($r^2$) for CoG northing as a function of SST = 39%. (b) Anisotropy in the egg production distribution as a function of regional SST, $r^2 = 48\%$. The anisotropy ratio is derived from a principal components analysis of the egg production by location dataset and reflects the relative sizes of the main axis of variability compared to the orthogonal axis.

Figure 2.5 Changes in spatial location and spread of egg production as a function of annual mean sea surface temperature (SST) for the spawning area. (a) Residuals from a regression of observed centre of gravity against mean centre of gravity from randomized data. Partial regression coefficient of determination ($r^2$) for CoG northing as a function of SST = 39%. (b) Anisotropy in the egg production distribution as a function of regional SST, $r^2 = 48\%$. The anisotropy ratio is derived from a principal components analysis of the egg production by location dataset and reflects the relative sizes of the main axis of variability compared to the orthogonal axis.
production can be illustrated comparing the ‘pseudo’ and observed SST centres of gravity. The surface temperature associated with the average egg location would be on average 0.43ºC greater from 1977-2010 had the mackerel egg distribution remained in the 1977 pattern. The temperature difference between observed and pseudo centre of gravity increased over time (correlation with survey year, \( r = 0.66, \) \( p < 0.05 \)). The northward movement of mackerel distribution coincides with a regional increase in temperature (correlation between March-June SST and year (1977-2010), \( r = 0.811, \) \( p < 0.001 \)). A northwards shift in spawning distribution resulted in an absence of temporal trend for the observed mean SST of eggs produced (\( r = -0.152, \) \( p > 0.05 \)) and mackerel have therefore buffered the change in SST that would have occurred if the 1977 spawning distribution were maintained.

### 2.4.4 Changes in broad scale spawning areas

The GAM model with spatial and temporal variables interacting was a better fit than alternatives with non-interacting terms. The Akaike weights imply negligible support for the alternatives to a fully interacting model (Table 2.1). Visual examination of fitted values showed a good correspondence with observed patterns in egg production (\( r^2 \) analogue 0.178, deviance explained 34.5% \( n=11980 \)). The \( r^2 \) analogue used here is based on the likelihood ratio test comparing explained variation between the observed model and a model with no predictors (Mernard, 2009). Using an \( r^2 \) analogue provides a conservative estimation of the strength of the relationship between the predictors and the dependent variable, rather than summarizing the differences between fitted and observed values. The \( r^2 \) analogue is a more valid expression of model fit than conventional \( r^2 \) in cases such as that of mackerel egg production, where the errors are not normally distributed.
Table 2.1 Alternative GAM models for egg production in different locations and as a function of fortnight within year and year. The predictor variable for Y is northings with X as eastings on a UTM grid. UBRE is the unbiased risk estimator, a model selection tool suggested by Wood (2006). AIC is the Akaike Information Criterion, with Akaike weights showing the relative support for different models. Interacting terms are shown as A*B

<table>
<thead>
<tr>
<th>Model</th>
<th>$r^2_{adj}$</th>
<th>% deviance explained</th>
<th>UBRE</th>
<th>AIC</th>
<th>Δ AIC</th>
<th>$w_i$AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>(X<em>Y</em>Year*Weeks)</td>
<td>0.124</td>
<td>34.5</td>
<td>2.116</td>
<td>8893</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>(X*Y</td>
<td>Year*Weeks)</td>
<td>0.118</td>
<td>26.0</td>
<td>2.464</td>
<td>9326</td>
<td>432</td>
</tr>
<tr>
<td>(X*Y</td>
<td>Year</td>
<td>Weeks)</td>
<td>0.114</td>
<td>24.2</td>
<td>2.545</td>
<td>9423</td>
</tr>
</tbody>
</table>
Table 2.2 Relationships between observed spatial statistics and predictor variables based on SST for the survey area, distribution of sample effort (Effort) and stock biomass (SSB). The small sample corrected AIC (AICc) was used to compare models. \( \Delta \text{AICc} \) is the difference between the model with the lowest AICc and other models, \( w_i \text{AICc} \) are Akaike weights used to compare the support for different models and to calculate model average coefficients.

a) CoG northing

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>( r^2 )</th>
<th>AICc</th>
<th>( \Delta \text{AICc} )</th>
<th>( w_i \text{AICc} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effort, SST</td>
<td>0.922</td>
<td>292.19</td>
<td>0</td>
<td>0.6004</td>
</tr>
<tr>
<td>Effort</td>
<td>0.873</td>
<td>293.38</td>
<td>1.19</td>
<td>0.3313</td>
</tr>
<tr>
<td>Effort, SSB</td>
<td>0.876</td>
<td>297.79</td>
<td>5.60</td>
<td>0.0365</td>
</tr>
<tr>
<td>Effort, SSB, SST</td>
<td>0.925</td>
<td>298.06</td>
<td>5.88</td>
<td>0.0318</td>
</tr>
<tr>
<td>SSB</td>
<td>0.025</td>
<td>317.82</td>
<td>25.63</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>SST</td>
<td>0.001</td>
<td>318.12</td>
<td>25.93</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>SSB, SST</td>
<td>0.922</td>
<td>322.33</td>
<td>30.14</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

b) CoG eastings

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>( r^2 )</th>
<th>AICc</th>
<th>( \Delta \text{AICc} )</th>
<th>( w_i \text{AICc} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effort</td>
<td>0.284</td>
<td>294.52</td>
<td>0</td>
<td>0.536</td>
</tr>
<tr>
<td>SSB</td>
<td>0.109</td>
<td>297.13</td>
<td>2.61</td>
<td>0.145</td>
</tr>
<tr>
<td>Effort, SSB</td>
<td>0.386</td>
<td>297.39</td>
<td>2.869</td>
<td>0.128</td>
</tr>
<tr>
<td>SST</td>
<td>0.047</td>
<td>297.94</td>
<td>3.419</td>
<td>0.097</td>
</tr>
<tr>
<td>Effort, SST</td>
<td>0.328</td>
<td>298.46</td>
<td>3.939</td>
<td>0.075</td>
</tr>
<tr>
<td>SSB, SST</td>
<td>0.114</td>
<td>301.78</td>
<td>7.264</td>
<td>0.014</td>
</tr>
<tr>
<td>Effort, SST, SSB</td>
<td>0.390</td>
<td>303.59</td>
<td>9.069</td>
<td>0.006</td>
</tr>
</tbody>
</table>

c) Inertia

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>( r^2 )</th>
<th>AICc</th>
<th>( \Delta \text{AICc} )</th>
<th>( w_i \text{AICc} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effort</td>
<td>0.855</td>
<td>281.53</td>
<td>0</td>
<td>0.639</td>
</tr>
<tr>
<td>Effort, SST</td>
<td>0.883</td>
<td>283.59</td>
<td>2.06</td>
<td>0.228</td>
</tr>
<tr>
<td>Effort, SSB</td>
<td>0.871</td>
<td>284.85</td>
<td>3.32</td>
<td>0.121</td>
</tr>
<tr>
<td>Effort, SSB, SST</td>
<td>0.886</td>
<td>289.56</td>
<td>8.03</td>
<td>0.012</td>
</tr>
<tr>
<td>SSB</td>
<td>0.009</td>
<td>304.57</td>
<td>23.04</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>SST</td>
<td>0.001</td>
<td>304.67</td>
<td>23.14</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>SSB, SST</td>
<td>0.01</td>
<td>309.27</td>
<td>27.73</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

d) Anisotropy ratio

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>( r^2 )</th>
<th>AICc</th>
<th>( \Delta \text{AICc} )</th>
<th>( w_i \text{AICc} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>SST</td>
<td>0.476</td>
<td>102.37</td>
<td>0</td>
<td>0.779</td>
</tr>
<tr>
<td>SSB, SST</td>
<td>0.494</td>
<td>106.67</td>
<td>4.297</td>
<td>0.091</td>
</tr>
<tr>
<td>Effort, SST</td>
<td>0.482</td>
<td>106.96</td>
<td>4.588</td>
<td>0.079</td>
</tr>
<tr>
<td>Effort</td>
<td>0.056</td>
<td>109.44</td>
<td>7.068</td>
<td>0.023</td>
</tr>
<tr>
<td>SSB</td>
<td>0.046</td>
<td>109.56</td>
<td>7.191</td>
<td>0.021</td>
</tr>
<tr>
<td>Effort, SSB, SST</td>
<td>0.494</td>
<td>112.95</td>
<td>10.579</td>
<td>0.004</td>
</tr>
<tr>
<td>Effort, SSB</td>
<td>0.144</td>
<td>112.98</td>
<td>10.605</td>
<td>0.004</td>
</tr>
</tbody>
</table>
The proportion of annual spawning interpolated by the GAM prediction in four areas on the shelf edge has also changed over time (Figure 2.5). The Goban Spur and shelf edge regions southeast of this were initially the main areas of egg production. In more recent surveys, the Porcupine Bank has become the co-dominant area of activity, with some evidence for an increasing proportion of the total egg production along the edge of the Rockall Trough.

The size of the estimated population of reproductively mature mackerel did not seem to affect the spatial patterns observed. Spawning stock biomass (SSB) was not significantly correlated with the proportion of annual spawning in any of the four areas used for figure 2.6.
Figure 2.6 Map showing areas depicting Rockall Trough (RT); Porcupine Bank (PB); Goban Spur (GS) and Bay of Biscay (BB). Histogram relative contribution of each area to total modelled egg production (%) over successive surveys.
2.5 Discussion

The summary spatial statistics indicate that spawning in the NEA-WSC has moved north in association with a regional warming. Results presented in the current study are consistent with the preliminary findings of Beare and Reid (2002). The northward movement in egg production is strongly affected by the direction of expansion in survey effort; however, a multiple regression shows a better model fit when SST is included alongside the survey effect. Despite the adaptive survey design potentially disguising ecological patterns, the result highlights a temperature signal that is influencing the observed movement north in NEAM spawning distribution.

Alongside a northwards movement in egg production in warmer years, the spatial distribution of egg production is also changing. The spatial spread of egg production appears less elongated (changes in anisotropy, Figure 2.6) in warm years. We can therefore reject the hypothesis that the distributional shifts in spawning involve a simple northwards translation of the existing spatial pattern. Distributional shifts in commercially important fish populations such as Atlantic mackerel will have a range of impacts on fishing fleets. For example, populations may move towards or away from main areas of fishing fleet operations, changing the distance required to travel per unit of catch and therefore with cost and profitability implications the fishery. Where populations cross international boundaries there may be consequences for quota allocations. Changes in spawning location may also affect the growth and survival of juveniles, for example if eggs are released into regions with different productivity to what was previously the case.

The effect of moving spawning further north is that mackerel eggs are being released at approximately the same temperature despite the regional warming. As a consequence of moving north, more spawning activity occurs in the topographically convoluted region of the Porcupine Bank (see Figures 2.2 and 2.6, particularly the greater area of seabed between the 200-1000 m contour lines). The pattern of habitat associated with depths around 200m (thought to be the favoured spawning habitat for mackerel, Beare and Reid, 2002) may therefore help explain why spawning activity becomes more isotropic in warmer years. Across the survey years, the estimated spawning stock biomass (SSB) of mackerel has been relatively constant (ICES, 2011), with the exception of a large decrease between 2003 and 2005 with an increase in SSB in 2010 (see Figure 2.4). An increase in density may have changed the structure or number of shoals, influencing the spatial distribution of spawning, but this hypothesis was not supported when SSB was included as a potential predictor for centre of gravity or spatial spread of egg production. Whilst we can conclude that there was little evidence that variation in SSB was associated
with shifts in mackerel spawning distribution, it is possible that greater variability in SSB would have an effect on spatial distribution of the mackerel population.

The similarity between observed northing CoG values and CoG values generated from randomization reflects the adaptive nature of the ICES surveys. The survey planning and execution have succeeded in following the northward movement of spawning. Observed easting CoG locations for spawning were further west than would be expected on the basis of sampling location alone. Plots of egg production as a function of easting are skewed, with more production towards the shelf edge and less on the shelf. This skew is sufficient to render the observed CoG more westerly than is the case when observations are randomized across locations. The same phenomenon does not occur along the north-south axis as there is no directional skew of observed egg production values. The lack of an SST influence on eastings CoG also means that no temperature-influenced mackerel migration onto the shelf was observed (c.f. Overholtz et al. 2011). Lack of a longitudinal migration signal may reflect the absence of a temperature barrier to mackerel along much of the northeast Atlantic shelf, unlike the cooler northwest Atlantic.

Although there is strong evidence that spring SST influences the location of mackerel spawning, this predictor variable is a proxy used as a result on the absence of finer scale sea temperatures. More detail on fine scale temperature variation (including depth variation) may help improve predictions of migratory behaviour. For example, 2010 was a noticeably cold year with a spring average over 1.5 °C cooler than the previous survey year and yet this did not lead to spawning being found dramatically further south. Beare and Reid (2002) suggested that it may be the temperature gradients, rather than the temperature levels, experienced by shoals of mackerel that cue behaviour, including spawning. Therefore, whilst we demonstrate there is a significant association between mackerel spawning distribution and the average spring temperature of the northeast Atlantic Ocean, a more spatially explicit investigation might be warranted to further explore the details of the temperature relationship and to understand the likely fine scale cues for individual shoals.

The links between changes in spawning pattern and mackerel recruitment are not clear. Over the period of the egg survey to date the estimated recruitment for the North East Atlantic mackerel stock (ICES, 2011) has no long term trend. The locations of egg release affect estimates of survival (Bartsch, 2005), with the Porcupine Bank identified as an area of high survivorship. A relative increase in spawning over the Porcupine Bank would perhaps therefore result in higher recruitment. Similarly, a broader spatial spread of spawning may act to reduce variability in recruitment as eggs are not released in the same area.
Linear regression analyses, including combinations of inertia, centre of gravity location and centre of gravity day for spawning were not, however, successful at predicting recruitment (no significant regression fits). While it seems likely that moving spawning into a different oceanographic domain will affect recruitment, the additional variables of food availability and processes such as off-shelf transport may prevent linear relationships.

Considering the apparent relationship between egg production and SST, the estimated northwards movement of NEAM spawning was 37.7 km °C⁻¹. The projected rate of warming for waters in this region is of the order of 3 °C for 2000-2099 (Sheppard, 2004). The calculated rate of warming would imply that the centre of gravity of mackerel spawning could be 113 km further north than its position in 2000 by 2099 which may be a useful first approximation for predicting the effects of changing temperatures. The pattern with mackerel spawning, however, suggests two important constraints. The first is that, while there may be a general relationship with temperature, this is not entirely consistent: in cold years (e.g., 2010) migration was not simply extended southwards until fish reached warmer waters. A second caveat to extrapolation is that the spatial pattern of a species range, or of an activity like spawning, may not simply shift polewards with warming. Features of the habitat that a population moves into may affect the spatial pattern: as may be the case for mackerel spawning in more northern areas. The consequences of such changes in spatial pattern for mackerel are not yet clear. Modelling suggests that recruitment can be affected (Bartsch, 2005), but there may also be effects such as changes in the overlap with other species (such as herring, ICES 2010) leading to changes at an ecosystem level.
Acknowledgements;
We would especially like to thank ICES WGMEGS (working group of the mackerel egg survey) for the provision of the egg data and for their constructive comments on this research. Whilst there are 12 survey years WGECO have met every year and undertaken very careful planning of the surveys and collation and analysis of the results, for which we are tremendously appreciative to everyone involved over the past 36 years. We are enormously grateful for the huge amount of work put in by all crew and scientists to collect and analyse the 11981 plankton samples over 12 years constituting a total of 57 months sampling. We also particularly thank the participants of the survey; IMARES (Netherlands); Instituto Español de Oceanografía (IEO) and Institute of Fisheries Science and Technology AZTI (Basque); Centre for Environment, Fisheries and Aquaculture Science (Cefas) (UK); Marine Scotland Science, Marine Laboratory (Scotland); Thünen-Institute of Sea Fisheries (Germany); Marine Institute (Ireland); Portuguese Institute for the Sea and Atmosphere IPMA (Portugal); Institute of Marine Research (Norway); Marine Research Institute (Iceland); Faroese Marine Research Institute (Faroe Islands); French Research Institute for Exploitation of the Seas (IFREMER) (France). We would also like to thank the anonymous reviewers who made helpful comments with the manuscript. This project (Grant-Aid Agreement No. PhD/FS/07/006) was carried out under the Sea Change strategy with the support of the Marine Institute and the Marine Research Sub-Programme of the National Development Plan 2007–2013, co-financed under the European Regional Development Fund.
References


in fisheries, environmental protection, and in the study of ecosystem response to environmental change. Progress in Oceanography, 58: 175-191.


Tseng, C-T., Sun, C-L., Yeh, S-Z., Chen, S-C., Su, W-C. and Liu, D-C. 2011. Influence of climate driven sea surface temperature increase on potential


Chapter 3: Spatially resolved analysis of Atlantic mackerel (*Scomber scombrus*) distribution using international catch data: Fishery, environment and management effects.
3.1 Abstract

Fishery dependent data are often overlooked as a useful source of spatial information on fish abundance and distribution. Furthermore, catch or landings data are important in their own right, feeding directly into stock assessment to assess fishing mortality. Misinterpretation of fishery dependent data analyses occur when absolute catch is unknown or the relative catch is unstable through time. In this Chapter an empirical orthogonal function analysis (EOF) was applied to northeast Atlantic mackerel (NEAM) international catch data (1977-2010) to identify regions most contributing to changes in mackerel distribution over time. Spatial statistics (centre of gravity (CoG)) were used to weight environmental parameters (sea surface temperature (SST) and bathymetry) by abundance. Results showed that the continental shelf edge (CSE), southern Norwegian Sea and northern North Sea are important fishing grounds for mackerel. Increased catches occurred along the CSE throughout the time series. Nine regions were identified. Three regions did not significantly change in annual catch abundance over time and appeared to represent the majority of the catch trend. Three regions significantly increased in catch over time, of these two significantly increased in mean SST whilst one did not and the catch weighted CoG SST did not change in any of them. The final three regions significantly decreased in annual catch abundance over time and significantly increased in mean SST whilst the COG SST did not change; except for one region on the shelf. The results suggest that where possible, mackerel are changing in distribution and relative abundance within areas that are warming to alleviate the increase in SST. There was a general offshore movement shown by an increase in the CoG bathymetry, although it is unclear whether this was a response to climate or fishing pressure. The NEAM fishing fleet effort has shifted away from the continental shelf in more recent years, demonstrated through a CoG of catch year, and the fishery appears to have to travel larger distance per unit of mackerel catch.
3.2 Introduction

An underlying challenge in fisheries ecology is constructing a comprehensive overview of variables that might affect the distribution and abundance of biological populations, and how environmental and anthropogenic factors might act as an interrelated system to collectively drive said changes (Sissenwine 1984; Cushing 1990). Various factors have been examined in the past, for example it was long assumed that fisheries effects alone controlled the abundance and distribution of exploited fish populations (Fogarty and Murawski 1998; Garrison and Link 2000), including many well documented stock collapses (e.g. North Sea cod *Gadus Morhua* (Cook 1998); Peruvian anchovetta *Engraulis ringens* (Clark 1977); Irish orange roughy *Hoplostethus atlanticus* (Foley 2010)). However, more recent research has demonstrated the impact of climatic variability on the distribution of fish populations (Li *et al.* 2010; Simpson *et al.* 2011), particularly as an interactive rather than additive driver (Hollowed *et al.* 2012; Hiddink and Coleby, 2012; Pitois *et al.* 2012). Alongside these well documented factors, other intrinsic mechanisms have been shown to affect a population. Examples include density dependent regulation (Lorenzen and Enberg 2002), age structure effects (Stevens *et al.* 2000; Hidalgo 2011) and match mis-match occurrences (Fortier *et al.* 1995), as well as less freely observable changes such as evolutionary modifications (Heino and Dieckmann 2009). Bettering the scientific foundation for successful and sustainable ecosystem based management of fisheries and fish populations would therefore benefit from an enhanced understanding of connectivity between climate influence, environmental factors and anthropogenic activities (fishing, pollution, habitat destruction etc.), and the ‘system influence’ on biological distribution and abundance trends.

Data often used in the analysis of fish population dynamics includes fisheries independent or survey data (Stallings 2009; Irwin 2008; Simpfendorfer *et al.* 2002), which have known benefits over fishery-dependent (catch/landings) data (see Rotherham *et al.* 2007). It is becoming more common that scientific surveys are deployed for commercially important species, to provide indications of changes in relative abundance that is not confounded by management regimes, and to monitor distribution and relative abundance in areas that are not covered by commercial fisheries (Mason 2010). Butler *et al.* (1998) assessed blackgill rockfish by regional CPUE which did not reflect the serial depletion of the populations which was a pre-cursor to stock collapse (Yoklavich *et al.* 2007), and therefore survey data may have been a more appropriate assessment measure to interpret patterns of species depletion which would have been seen at higher spatial resolution (Mason 2010). It is important to also consider the limitations of survey data, which depends to
some extent on the research question being asked. As an example, the interpretation of data gathered by studies examining age-structure in fish populations for stock density indices may be affected by seasonal patterns in sampling data, and gear related biases which can affect length frequency data (Willis *et al.* 1993). Very often survey data has inconsistent spatial and temporal coverage, as well as variations in sampling gear and strategy, (Blanchard 2008; Cooper 2012). This is usually as a result of time and resource constraints on data collection or technological improvements, as well as the large amount of time required to process the data for standardisation.

Fisheries dependent data includes catch or landings data, and this type of data is important in its own right, feeding directly into stock assessment and assessing fishing mortality. In general the data span a longer time frame than fisheries independent data, and include market driven signals for socio-economic assessment. Fisheries dependent data have been used extensively in stock assessment (Bishop 2006) and have enabled statistical population modelling (Large 1992; Candy 2004; Lewy and Kristensen 2008; Frisk *et al.* 2010), as well as spatial analysis of fleet pattern dynamics (Vignaux 1996). Difficulties in interpreting catch data arise when you do not know the absolute catch or the relative catch is not stable over time (Rotherham *et al.* 2007). Specifically, weight (catch/landings) or area misreporting is present, potentially leading to an underestimation of fishing induced mortality (through slipping/discarding and illegal landings); spawning stock biomass (SSB) (depending on stock assessment methods), and spatially resolved abundances. Further complicating this is the lack of monitoring to assess the degree of error in the landings data, be it vessel log book or port records.

Previous studies using catch data have focused on describing the spatial distribution of fishing effort in various spatial scales. Jennings *et al.* (1999) used ICES statistical rectangles to examine the beam trawling effort in regions; the northern, central and southern North Sea. Other investigations have used catch data to track the distributions and associated habitats of target species (Vignaux 1995; Zainuddin *et al.* 2006), mostly at the regional scale. Rjinsdorp *et al.* (1996) examined the spatial distribution of fishing effort, to show that patchiness of fishing effort decreased with increasing spatial resolution (from 30x30nm to 1x1nm); indicative that analysing data in varying spatial scales can impact on the interpretation of fisheries catch data. Contemporary high resolution data is becoming more widely available to fisheries scientists, such as vessel monitoring system (VMS) data, which contains information on speed and direction of all EU vessels (>15 m from 2006; >24 m from 2000). Murawski *et al.* (2005) showed how log book records were not spatially resolved enough to identify the effects of an imposed marine protected area and that VMS data were required, along with a cross validation with observer
records, for a more informative analysis. Other investigations have used VMS data for a more spatially resolved analysis of fishing fleet behaviour and anomalies (Fonseca et al. 2008; Mullowney and Dawe, 2009).

A common approach in stock assessment and the scientific ecological analysis of fish population ecology is to use catch or landings data in conjunction with fisheries-independent data to identify and test patterns and trends of total abundance and spatio-temporal relative abundance (Rotherham et al. 2007; Booth 2000; Pecquerie et al. 2010). Recent re-analysis of previously published data has highlighted errors associated from analysing fisheries data in isolation from fleet and market driven influences. Mutsert et al. (2007) re-tested data from two well known papers, demonstrating how the authors reported faulty conclusions regarding the state of the ecosystem. The first example investigated the use of the mean trophic level index (MTLI), where initially it was concluded that a reduction in MTLI was a result of a deterioration of the food web. However, Mutsert et al. attributed the reduction to a shift in market demand for lower trophic species. Essington et al. (2005) also found a similar pattern in 48 worldwide large marine ecosystems, where a reduction in MTLI was not as a result of lower biomass of higher trophic species, but the addition of lower trophic fisheries. In the second example Mutsert et al. examined, numerous fishery collapses that were reported in the Gulf of Mexico. Here they re-analysed the data but included fishery effects such as species targeting, variability in fishing effort and market forces, demonstrating that the authors had made claims of many false cases of fishery collapses. Mutsert et al. (2007) concluded that the inaccuracies in both examples were due to the assumption that commercial landings data, in isolation from market and fleet driven forces, suitably described the fish populations and communities.

Other investigators have used both fisheries and research based data together to understand the dynamics of fish populations through time. Fox and Starr (1996) compared the usefulness in describing the distribution and relative abundance of commercially exploited species, between west coast USA ground fish trawl logbook data with US National Marine Fisheries Service research trawls, which were conducted simultaneously in time and space. They concluded that fisheries dependent and independent data, when analysed synchronously, can improve estimates of the distribution and relative abundance of commercially exploited fish species. Conversely, Abella and Serena (2005) compared elasmobranch catch rates and geographical distribution from research trawl surveys with fisheries landings data. Inconsistencies in the results between the two data sets were accounted for by changes in spatial effort allocation between research and fishery landings, as a result of market demand targeting certain species. Albert and Hoines (2003) were able to distinguish distributional changes in Greenland halibut
(Reinhardtius hippoglossoides) year 1 abundances due to the north Atlantic oscillation index (NAOI), accounting for changes in fishing and research gear. By understanding changes in data collection methods, fisheries management changes and oceanographic indexes, the authors discussed peculiar distributional changes relating to the NAOI in light of climate change and fishery based stock management. In a recent paper, Jansen et al. (2012) reported on the correlations between Atlantic mackerel migration/distribution and temperature, that the continental shelf edge current appeared to guide their southerly migration to spawning grounds. The authors used both mackerel landings data and scientific trawl data. It was reported that whilst there were correlations between mackerel abundance and temperature, the correlations were weak and present only in times where technical and or legislative developments were not substantial – emphasising the influence management effects can have on fisheries dependent data analysis.

Understanding the relative contributions of climate and fishing to fish populations and their distribution, as well as disentangling the responses of each can prove difficult. In a study of European hake in the Mediterranean, Hidalo et al. (2011) showed that mechanisms intrinsic to the population were responsible for a 15 year cycle in CPUE indices during 1940-2007. The cycle broke down in the 1980’s at which point the CPUE was highly correlated with a local environmental index. They concluded that intra-population regulatory mechanisms, in this case, age structure, controlled natural population fluxes. However, when the population biomass was lower other factors took control such as local environmental factors. Whilst examining populations as a whole is one way to extract climate from fishing signals, highly resolved, spatially explicit methods depicting changes in distribution might be another approach. Spatially resolved fisheries data are becoming a prominent factor in the ecosystem approach to fisheries management (EAFM) (Gerritsen and Lordan 2010), and are becoming more important for marine monitoring such as understanding the effects of area closures and other management regimes (Mills et al. 2007).

In this paper, a novel approach for detecting locations that contribute high levels of variation in international mackerel catch data from 1977 to 2010 will be used. Each area isolated by the technique will be examined for catch trend over time, mean environmental conditions (temperature and bathymetric depth). In addition, spatial statistics are applied to determine the most likely environmental condition experienced by mackerel within each area. The aim is to detect changes in distribution and relative abundance and to relate these changes back to causal factors of either the environment, climate change or the fishery. It is also the intent to examine the dynamics of the international
Atlantic mackerel fishing fleet over time to test for changes in the spatial extent and potential cost-benefit of catch between 1977 and 2010.

3.3 Materials and methods

3.3.1 International catch data

Mackerel international catch data (ICD) 1977-2010 represents total catch (in tonnes) per ICES statistical rectangle (0.5° latitude by 1° longitude: area of rectangle 3720 km² at 53°N (Duplisea et al. 2001)) per fishing quarter (3 month blocks starting from January) and year from official log book records. The data do not represent all participating countries; France currently does not submit catch data to ICES at the spatial resolution of statistical rectangles. Pre-1976, catch contributed approximately 10% of official landings. From 1977 – present the ICD includes 80% or more of the official landings. Further inaccuracies in vessel catch data as well as official landings data occur due to the difficulties of estimating rates of discarding, slipping and misreporting. High grading which targets mackerel > 600 g (ICES 2011) results in smaller but still marketable fish being caught but removed from landings through discarding or ‘slipping’, thus leading to underestimates of catch. The level of discarding and slipping are unknown, although there are reports of unaccounted removals to the extent of 60% underreporting in 95% of the actual landings (ICES 2006). Therefore, landings are only meaningful in relation to population size if unaccounted catch over time is relatively stable (ICES 2006). Estimates of discards have been given (with a few exceptions) for the areas VI, VII/VIIia,b,d,e and III/IV since 1978, although these are considered incomplete by the working group (ICES 2011). The five nations who submit discards data to the mackerel working group are Scotland, the Netherlands, Germany, Ireland and Spain, and total discards sum approximately 7000t from these countries (ICES 2011).

Area misreporting can spatially corrupt the data, a common example being catches from ICES division IVa (northeast of Scotland) being reported in VIa (west of Scotland – see Figure 3.1). Reasons for misreporting include management restrictions in fisheries opening and closing times and locations, to protect juvenile mackerel. Existing regulatory mechanisms for mackerel are described in ICES (2007), and the most recent working group on widely distributed stocks (ICES 2012) report states that total catch related removals are approximately between 1.6 and 3.4 times the catch.
Figure 3.1 Preliminary analysis of quarter one EOF results. (a) Principal component trends 1 (black) and 2 (red). (b) Map highlighting the respective associated loadings to PC2 only, with the most positive loadings in green (left) and most negative loadings in orange (right). The red box on the left hand map represents the area of the southwest mackerel box. (c) The relative catches from the associated loading locations. The left graph corresponds to the locations highlighted in the left map; the right graph corresponds to the locations highlighted on the right hand map.
3.3.2 Spatial and temporal variance

Empirical orthogonal function analysis (EOF, Preisendorfer 1988) has commonly been used in oceanography (Weare et al. 1976; Gallaudet and Simpson 1994) and climate change analysis (Shoshiro, 1997; Smith et al. 1996) to identify spatial and temporal variability from large data matrices. The aim of the present analysis was to determine the principle modes of variation in catch abundance, and to relate these to environmental forcing and fisheries dependent drivers of change. The EOF is a data reduction technique, analogous to a PCA through time, producing independent modes of variation through reducing the dimensions of the initial data matrix, with time (years) as cases, and space (ICES statistical rectangles) as variables. The first principle component (PC) describes the pattern of greatest variability; the following PC provides the pattern of greatest variance not explained by the first, and so on. Each PC has an associated eigenvalue, describing the variance among cases associated with that component. Each spatial location is associated to the trend in each component by a loading, analogous to a correlation (positive or negative) with the overall trend. Locations having a similar relationship to the trend summarized in a particular principal component will have similar loadings. By grouping locations with similar loadings, areas undergoing coherent dynamics can be identified, with the average catch across such groups summarising what the coherent dynamics represent.

Some catch records in the mackerel international catch data set were erroneously recorded on land and so were eliminated from the analysis (0.3% of total data). The ICD include the southern stock which was removed using the boundary agreed on in stock assessments (ICES 1999). The ICD were partitioned, according to the temporal structure of NEAM fisheries management framework, into quarters each representing 3 months. The data were log transformed (Ln+1) with years as columns and catch locations as rows (and filtered so the location that had the most years with catch records was at the top). Where no catch was recorded the entry was zero. A correlation matrix method was used for the PCA, which was performed in Minitab (Minitab 2010). Many ICES statistical rectangles did not contain a complete series of non-zero catches from 1977-2010. This potentially distorts the identification of common trends in the EOF. To investigate the role of zero catches on the patterns identified, an analysis using all locations was compared to one where locations were filtered to include only those rectangles where >75% of years contained non-zero catch. The results using all locations and the filtered locations were not qualitatively different (upon visual inspection) therefore the full data set was used for EOF as using 100% of the data had the advantage of better spatial coverage. Despite containing areas of low and
patchy catch, the full data set provided more scope for analytical interpretation than the sparse but regularly fished locations (14% of the rectangles).

### 3.3.3 Statistical significance of principal components

In order to validate the statistical significance of the components identified by the EOF, a broken stick method (Fronteir, 1976; Jackson, 1993) was carried out in R (R Development Core Team 2008), using the CRAN library package “**BiodiversityR**” (Kindt and Coe 2005), to determine whether the amount of variation represented by each principle component is statistically significantly different (alpha level = 5%), from that which would be allocated by random splitting; as would be the case with non-structured data (i.e. noise). Quarter two PCA analyses had no significant structure according to the broken stick test therefore results for this quarter are not discussed further.

### 3.3.4 Grouping the loadings

A suitable threshold for deciding which covariate locations (catch data records centred on ICES statistical rectangles, see Figure 3.2) were used in the analysis was tested using cumulative distribution frequencies of loadings in order to identify potential natural breaks. However, there was no clear grouping in the loadings themselves so an arbitrary level was decided upon which was 30% of the data. This excluded the majority of data that contributed only a small amount of the variance, whilst keeping those locations that most represented the strongest pattern of the PCA. ICES statistical rectangles (representing catch location) were ranked within each quarter, by their loading to the relevant PCA (one and two); 15% of each of the largest loading, highest (most positive) and lowest (most negative). Therefore there were three quarters and within each of these there were positive and negative loadings for both PC1 and PC2 resulting in 12 separate analyses extracted from the International catch data. Each of the 12 analyses potentially represents a coherent region undergoing similar catch
dynamics over time.

![Figure 3.2 Map showing all ICES catch data records for mackerel in the Atlantic 1977-2010, alongside the current distribution of the southwest mackerel box which can be seen by the red box.](image)

3.3.5 Histogram of loadings

The histogram of loadings (Figure 3.3) illustrates the distribution of associations between the time series at each ICES statistical square, and the trend extracted by the principal component. In general, a large number of locations have a weak or no correlation to the general pattern, shown by peak frequencies around zero. The modal loadings for PC1 were generally close to zero, indicating sites with no association with the pattern identified by the principal component. As there were few strongly negative loadings, sites were generally following the PC1 trend or were not associated with it. There were few cases of sites negatively correlated to the extracted PC1 trends, whereas a small number of sites were strongly positively correlated to the PC pattern. In contrast, the distributions of loadings for PC2 were more symmetric, leptokurtic distributions. This suggested that PC2 identified two patterns of variability that tended to be negatively correlated with each other.
Figure 3.3. EOF outputs and catch trend for the quarter. (a) Quarter one. Top left, PC1 (solid line) and PC2 (broken line) trend over years. Top right, annual sum of catch for the whole
quarter (in tonnes). Bottom left, histogram of loadings for PC1. Bottom right, histogram of loadings for PC2; (b) quarter three; (c) quarter four. The axis
3.3.6 The mackerel southwest box

One of the clearest patterns in the preliminary analysis of catch data was the identification of a steep decline in catch around southwest England in the early 1980’s, accompanied by a relative increase in catch in other areas, including the North Sea (see Figure 3.1). This effect was seen in quarters one, two and four to varying degrees, around the period of the mid 1980’s noted in the second component. These patterns were more clearly seen using 100% of the data, indicating the increased sensitivity with the better spatial coverage. The pattern extracted from the preliminary analysis is consistent with a major management intervention in the fishery: in 1981 an area around the southwest of England was created to protect the overwintering juvenile mackerel nursery ground (CEFAS 1997; ICES 2011) (see Figure 3.2). In 1989 the area was extended to its current boundaries (Figure 3.2). Within this area only gill net and hand line gear are allowed (CEFAS 1997), with no directed trawling for mackerel. The fishery is managed under the EU Common Fisheries Policy, in accordance with an additional EU-Norway-Faroese agreement (MSC 2009). Since 1998 the handline fishery has received a minimum quota of 1750 tonnes so as to protect the rights of the traditional handline fishermen (MSC 2009). The quota is also protected in that the handline fishery may continue, up to the quota level, even if the fishery has been closed to all other sectors (MSC 2009). Mackerel bycatch limits are set for vessels fishing for other species as well (MSC 2009). As a result of this closure, a new fishery opened up around the Great Sole Bank southwest of Ireland and in areas north of the British Isles (ICES 1988). When the catch data for both areas were analysed there was a strong positive correlation with the second principle component for quarters one, two and four. The result demonstrates how the EOF method can identify spatiotemporal patterns of change. As the mackerel box closure had such a clear effect, subsequent analyses did not include data within the area of the southwest mackerel box to increase the scope for identifying other spatiotemporal patterns in the catch data.
3.3.7 Characterisation of location

As a result of the fishery data being collected by quarter, an EOF analysis was performed on each quarter (except quarter 2 due to the lack of statistical significance), resulting in PC’s for each quarter. Each location eigenvalue then represented either a positive or negative correlation to the main trend of the PC’s and therefore, there are 12 separate analyses presented here, positive and negative correlations to PC one and two for each of the three quarters (2x2x3 = 12). The spatial units of the EOF are that of ICES statistical rectangles. Each of the 12 analyses extracted by the EOF were characterised by bottom depth (bathymetry) and sea surface temperature (SST). Bathymetry data were downloaded from GEBCO (www.GEBCO.net) and is derived primarily from ship soundings data, interpolated using satellite gravity data. The catch locations were georeferenced in Arc Map 10 (ArcGIS) using the northwest corner of each ICES statistical rectangle as the coordinates to reference. Using the northwest corner resulted in some coastal catch values being located on land, when the rectangle with catch records overlapped the land. All land values were removed from the bathymetry data set a priori using ArcGIS version 10, however the slight mis-match between a small proportion of the catch and bathymetry data (<0.01% total data set) meant that not all catch locations could be assigned depth value. Due to the variable nature of coastlines, the use of depths from the northwest of each rectangle had no persistent bias on depths in comparison to using the midpoint location of each rectangle, due to the infrequent occurrence (<0.001% total data set). As the mean bathymetry is a fixed statistic through time, which may mask other spatial changes in the environment of the catch within the area over time, it is possible to weight the bathymetric depth by the catch per year to obtain a time series of annual weighted bathymetry for all regions identified. This means that the annual weighted bathymetry shows the most likely bottom depth an individual fish taken at random from the population is most likely to experience, which is variable between years depending on the distribution of the relative abundance.

Sea surface temperature (SST) was downloaded from Hadley (HadSST2) data set (www.BADC.nerc.ac.uk) for the years 1977–2010 and interpolated using ArcMap (ArcGIS) using an inverse distance weighting technique that assumes each value has a local influence that diminishes with distance, before being associated with the catch data. As with the bathymetry, the SST can be weighted by the catch values to obtain a time series of annual weighted temperature for all locations identified. Using a weighted SST will identify patterns that arise from a spatial shift in catch within one area, which would not be identified using the mean SST of the area. It is important to highlight that the temperatures used in this analysis are surface temperatures, which are
not ideal as mackerel are thought to seek depths reflecting their thermal preferences (Reid et al. 1997; Walsh et al. 1995). As catch depth or temperature at depth data are not available, it is not possible to report on in situ temperature so surface temperature is therefore used as a proxy.

3.3.8 Changes in fishery extent and catch intensity over time

The fishery catches were examined for changes in location and extent to test for general and large spatial changes in the fishery catch locations and rates over time. The data were recorded as catch in tonnes per ICES statistical box, for each quarter. Time series were generated for each quarter for: number of boxes with non-zero catch recorded in them, total catch and total catch divided by number of boxes with non-zero catch. The aim of the analysis was to test whether the spatial coverage of the fishery has changed and how. The catch centre of gravity (CoG) year per location (or mean year of catch) was also determined, using the following equation, where \( Y \) = year and \( C \) = catch abundance per location within that year:

\[
\text{Equation 1} \quad \frac{\sum_{i=1}^{n} Y_i \cdot C_i}{\sum_{i=1}^{n} C_i}
\]

This method summarises the distribution of catches over time in each statistical rectangle. The catch CoG is the arithmetical mid-point of all years fished, weighted by the catch in any particular year. For example, a statistical rectangle with roughly the same catch in every year from 1977 to 2010 would have a mean year of catch off 1993.5. In comparison, a statistical rectangle fished only in later years would have a mean year of catch falling later than 1993.5. To display the spatial variation in mean year of catch a colour gradient raster surface was created in ArcGIS using an inverse distance weighting technique, where weights are proportional to the inverse of the distance between sample locations. This shows the spatial distribution of the year the catch most likely came from.

3.4 Results

Only the first two principal components from the EOF analyses were included in the analysis for all three components, as a small amount of variation was represented after the second component, with component three contributing less than 6% variance on average. The percentage variance explained by the first component was generally high (mean 46%; range 10%). The first two
principal components within each quarter represented between 63% (quarter one) and 54% (quarter 4) of the variance in international mackerel catch. The components trend through time (figure 3.3) showed the underlying pattern recognised by that component. The locations most reflecting the pattern represented by a particular component were identified in space using the thresholding at 15% of the most positive and most negative loadings and can be seen in figure 3.4.
Figure 3.4. Locations of the 15% most positive and most negative loadings for each quarter. (a) quarter one. Top to bottom, PC1 positive loading locations with mean annual catch, PC1 negative loading locations with mean annual catch, repeated for PC2. (b) Quarter three. (c) Quarter four.
3.4.1 Patterns in principal component one

The patterns of the loadings are all very similar (see figure 3.3, graph 3 on panels a,b and c) as well as the fact that mean PC1 loading (see figure 3.3 graph 1 in panels a, b and c) is slightly positive in all three quarters and the interannual variation is not very strong, compared to PC2. The negative loadings associated with PC1 represented less than 1% of the total catch, combined. Therefore any patterns from these modes of variation did not have a significant bearing on the majority of the catches. These loadings were scattered over a relatively large area with weak or no relationship between the main component trend. Therefore they are not discussed further as their catches are negligible. Of the positive loadings associated with PC1, highly defined fisheries can be seen (see figure 3.4) in Q1 along the CSE; Q2 along the Norwegian coast in ICES division IVa and again in ICES division IIa but outside of Norways EEZ. The PC was significantly correlated with the main catch trend of the quarter for Q1 and Q4 (<0.05). Avoidance of warming water occurred in Q4 with a decrease in the CoG SST, but an increase in the mean SST (see figure 3.5).
Figure 3.5. Weighted (black line) and mean (red line) of SST (top) and bathymetry (bottom) of each panel which represents a quarter. Quarter 1 (top) to quarter 4 (bottom). Left to right; 15% most positive and most negative scoring loadings, for PC1 and PC2.

3.4.1.1 Quarter one

Component one was positively correlated with total catch for the whole quarter over time ($r = 0.45, P < 0.01$). Highest total catch abundance was in the mid 1990’s (see Figure 3.3a) and the lowest catch levels were during the mid 1980’s. The positive histogram of scores showed that a few locations had a very strong influence on the principal component. The continental shelf edge (CSE) corresponded well to the primary pattern of variation, highlighted by the positive locations (Figure 3.4a). The mean and weighted SST for the locations increased significantly over years ($r = 0.879; 0.442, P < 0.001$, respectively).
both from approximately 8°C to almost 10°C (see Figure 3.5). The mean
bathymetry was -699 m, whilst the weighted bathymetry increased over time
from -200 m in the early 1980’s to over 1 km depths towards the end of the
time series, with the last 2 years showing catch from much shallower waters at
-200 m depths ($r = -0.575$, $P < 0.05$). The histogram of scores showed that most
locations were slightly negatively correlated, or had no relationship (figure
3.3), and the areas picked out here were representative of a much larger area.

3.4.1.2 Quarter three

The first component was slightly positive and increased significantly over time
($r = 0.457$, $P < 0.01$), with a high frequency of slightly negatively correlated
locations in comparison to fewer strongly positively correlated locations
(Figure 3b). The positive loading areas appeared spatially distinct in two areas
in water around the coast of Norway, in ICES sub-areas IVa and in IIa, the
latter being outside the Norwegian EEZ (Figure 4b). The catch trend for the
area did not significantly change over the years and was not significantly
correlated to PC1. The mean and weighted SST did not significantly change
when correlated with year for these locations ($P > 0.05$) (Figure 5). The mean
bathymetry was skewed at -1453 m whilst the weighted bathymetry
significantly increased in depth over time ($r = -0.605$, $P < 0.001$) with a large
range, from -160 m in 1977 to -1400 m in 2007, suggesting the catch came
from deeper waters in more recent years.

3.4.1.3 Quarter four

The first component of quarter four was positively correlated with the total
catch for the whole quarter ($r = 0.431$, $P < 0.02$) and year ($r = 0.682$, $P < 0.001$).
The histogram of scores was slightly negatively skewed with a small number
of locations strongly positively correlated (Figure 3c). The positive loading
locations were spatially clustered around northwest Ireland and north to
northeast Scotland, stretching across the northern boundary of the North Sea
over the Viking Bank, and characterised a highly defined fishery (Figure 4c).
The catch for the most positive loading locations increased over time although
not significantly ($P > 0.05$). The mean SST significantly increased when
correlated with years ($r = 0.361$, $P < 0.05$) (Figure 5), whilst the weighted SST
significantly decreased ($r = -0.489$, $P < 0.005$). The mean bathymetry was -272
m, and the weighted bathymetry had peak depths in 1985; 1986 and 1988.
Patterns in principal component two
The catch weights for the most positive and most negative loadings of component two in all quarters were more similar, compared with the first component positive and negative loading catch weights. The histogram of scores was more centrally distributed in general (Figure 3.3), showing the areas highlighted by the positive and negative loadings were for the most part negatively correlated with each other. In all quarters the catch trends of the second component’s positive and negative loadings were significantly negatively correlated against each other (Q1 \( r = -0.654 \); Q3 \( r = -0.461 \); Q4 \( r = -0.690, P < 0.01 \)), although all increases and decreases in catch between the positive and negative scoring locations were significantly correlated with year (\( P < 0.001 \)), indicative of a temporally synchronous shift in catch between different fisheries. Well defined areas that were highlighted in the present analysis as adding large amounts of variance to the fishery catch data were similar for components one and two and included the continental shelf edge, northern North Sea, southern Norwegian Sea, north Scotland and northwest and southwest Ireland (Figure 3.4). The second principle component increased over time for quarters one and three. Quarter four significantly decreased over time (\( r = -0.829, P < 0.05 \)) and was the only component to do so (Figure 3.3).

### 3.4.1.4 Quarter one

In quarter one there was a large negative tail in the distribution of scores (Figure 3.3a) demonstrating the small number of highly negatively correlated locations to the component, opposed to the greater frequency of positive loading (but to a lesser extent) locations. The positive loading locations for component two lay on the CSE from the northern Bay of Biscay to north of the Shetland Islands (Figure 3.4a), with a significant increase in catch over time (\( r = 0.623, P < 0.001 \)). The mean SST for these locations increased significantly over the years (\( r = 0.846, P < 0.001 \)) alongside the weighted SST (\( r = 0.526, P < 0.001 \)). For the CSE region the mean bathymetry was -850 m, and the weighted bathymetric depth ranged between -200 and -1600 m, with no correlation with years (\( P > 0.05 \)) (Figure 3.5).

The negatively correlated locations were less spatially distinct, although tended to be in more coastal regions (Figure 3.4a). The catch abundance significantly decreased with year (\( r = -0.698, P < 0.001 \)). The mean SST increased over time with years (\( r = 0.867, P < 0.001 \)), although the weighted SST was not changing significantly with years (\( P > 0.05 \)), indicative that the shift in relative abundance of mackerel catch between locations of different temperatures offset the increase in SST. The negative on-shelf areas mean bathymetry was -187 m (Figure 3.5), whilst the weighted bathymetric depth significantly increased over time (\( r = -0.362, P < 0.05 \)) with maximum depths of about -500 m.
m in the mid 1990’s and in 2007. The corresponding increase (positive loading locations) and decrease (negative loading locations) in catch showed a spatial shift in mackerel catch abundance from on-shelf regions (mean bathymetry -187 m) to the CSE (mean bathymetry -850 m).

### 3.4.1.5 Quarter three

In quarter three, the second component significantly increased over time \( (r = 0.942, P < 0.001) \) (Figure 3.3b). The positive loading areas were located in ICES sub-area IIa east of Iceland into the southern Norwegian Sea (Figure 3.4b). Here the catch increased over time, significantly correlated with year \( (r = 0.802, P < 0.001) \). The mean and weighted SST did not change over time \( (P > 0.05) \), whilst the mean bathymetry was -2579 m, and the weighted bathymetry did not significantly change over time \( (P > 0.05) \), characteristic of a fishery in very deep waters (Figure 3.5).

The strongly negative loadings appeared to define pockets of fishing locations that were all declining in catch on the shelf, west of Ireland, northwest of Scotland, in the middle of the North Sea and in the southern Norwegian Sea (Figure 3.3b). The catch for these areas significantly declined over the years \( (r = -0.744, P < 0.001) \). The mean SST increased significantly over the years \( (r = 0.774, P < 0.001) \) as well as the weighed SST \( (r = 0.439, P < 0.05) \). The mean bathymetry was -292 m, whereas the weighted bathymetry, although variable, generally decreased until the 1990’s when it started to increase, although in the last few years there is evidence of the catch coming from deeper waters. The weighted bathymetry was significantly correlated with year suggesting it is becoming shallower over time \( (r = 0.343, P < 0.05) \) (Figure 3.5).

### 3.4.1.6 Quarter four

In quarter four, the second component increased in the mid 1980’s, but has declined since then (Figure 3.3c). The histogram of scores (see graph 4 in panels a,b and c of figure 3.3) suggested there are few locations positively correlated with the decrease in variance, and a slightly higher frequency of locations that are less strongly negatively correlated. The positive loading locations (Figure 3.4c) showed a significantly negative relationship in catch abundance with year \( (r = -0.690, P < 0.001) \), and were located northwest of Scotland and northwest Ireland, with a few locations in the English Channel and the southeast North Sea. The mean SST significantly increased when correlated against year \( (r = 0.480, P < 0.01) \) although the weighted SST did not significantly change over time \( (P > 0.05) \) (Figure 3.5). The mean bathymetry
was approximately -182 m although the weighted bathymetry showed more interannual variability, decreasing until the late 1980’s, then increasing until 2010, and was significantly correlated with year \( (r = -0.441, P < 0.01) \), suggestive of an increase in depth over time.

The negatively scoring locations were predominantly around SW Norway in ICES sub-area IVa (see figure 3.4, panel c), although were also in the southern Celtic Sea/northern Bay of Biscay with small catches west of Ireland. The catch increased over time, (correlation with year, \( r = 0.785, P < 0.001 \)), and was negatively correlated with the increase in catch found in the positive loading locations \( (r = -0.691, P < 0.05) \) (Figure 3.4c). The mean SST significantly increased over time \( (r = 0.526, P < 0.001) \), whilst the weighted SST had no significant trend \( (P > 0.05) \). The mean bathymetry for the negative locations was -255 m, although the weighted bathymetry had two peak depths around 1981 and 1986 of approximately -400 m with no significant trend over time. The weighted bathymetry and SST were significantly correlated \( (r = 0.415, P < 0.05) \) (Figure 3.5).

3.4.2 Summary of EOF analysis

Locations positively associated with PC1 represented the distributions of the main fisheries that is, the continental shelf edge (CSE), northern North Sea and southern Norwegian Sea. Proportionally, the catch for these regions were high (mean 17% of total catch per region mentioned) and catch levels displayed low variability through time although there was no significant relationship with the environmental variables tested. In contrast, the locations negatively correlated to the trend of PC1 represented very low catch levels (<1% combined) and so are not discussed as they do not add to the significant explanation in changes in the NEAM fishery over time.

The second PC for quarters one, three and four, highlighted locations positively and negatively associated to the catch trend, and these locations all represented a significant proportion of the total catch. There were three increasing catch trends (Q1 positive; Q3 positive and Q4 negatively; correlated to the PC2 trend) and three decreasing catch trends (Q1 negative; Q3 negative and Q4 positively; correlated to the PC2 trend). Of the regions showing an increase in catch trend, two of them also increased in mean SST for the area representing warming waters (Q1 positive; Q4 negative). However this warming was not seen in the weighted SST (no significant correlation between weighted SST and years), with one of the regions increasing significantly in weighted bathymetric depth over time (Q1 positively correlated to PC2 trend, increase in bathymetric depth over time \( p<0.05 \)). The increase in bathymetric
depth shows a change in the relative distribution of mackerel into areas where the water column in greater. In the regions where the catch decreased (Q1 negative; Q3 negative; Q4 positive) all regions increased in mean SST, and one shelf area increased in weighted SST too (Q3 negative). For the other two areas, weighted SST did not significantly change over time but the weighted bathymetry depth did increase significantly over time (P<0.05) for one of them suggesting a change in relative abundance of catch location to areas with a deeper water column.

3.4.3 Changes in extent and catch yield in the fishery

The NEAM fishery has changed considerably over the time series in size, catch capacity and gear type, alongside distance and duration capabilities. There are an increasing number of ICES statistical squares (boxes) that have non-zero catch, showing an increase in the net area fished over time or an expansion of the fishery (Figure 3.6). In the earlier years a higher proportion of catch came from the fewer boxes that were being fished, and the overall catch trend was not affected by the increase in fishing locations, or by the decrease in average catch per ICES box. Therefore, in more recent years, an increased effort is required to maintain the annual catch weight from previous years. When catch is divided by number of boxes with non-zero catch and plotted against time, all four quarters show a significant decreasing trend (P < 0.01), particularly from the early 1980’s (see Figure 3.6; quarter one r = -0.748; quarter two r = -0.658; quarter three r = -0.761; quarter four r = -0.748). The results indicate that whilst there is an increase in fishing locations, there is also a smaller catch per location. Pre-1980, catch appeared more clumped in space whereas in more recent years the fishery seems to have stretched to a larger effective fishing area.

The spatial change in fisheries is illustrated by the patterns in centre of gravity year of catch for each location (Figure 3.7). This data includes the catch off Cornwall excluded from other analyses. The duration of the fishery is generally longer on the shelf, resulting in early mean catch years. Deeper waters away from the UK coast tend to have later catch years, indicating locations little fished 30 years ago that have become more important to the catch in recent years.
Figure 3.6. Line plots showing the changes to the fishery over time. Each row corresponds to the quarter. The first column shows the number of boxes with non-zero catch in over time. The middle column shows the total catch divided by the number of boxes fished in over time. The right hand column shows the annual trend of total catch over time.
Figure 3.7. Raster images of the centre of gravity of year for the fishery, going clockwise from top left; quarter 1, 2, 4 and 3. Green represents areas where the centre of gravity of catch was from earlier years whilst blue represents areas where the centre of gravity of catch was from more recent years. Red points represent all fishery locations 1977-2010.
Table 3.1 Table of Pearsons correlations for the catch trend of PC analysis. Percentage of catch per region is against total catch per quarter. The dark grey shading illustrates a statistically significant increase (P<0.05) in the catch of the region over time; the light grey shading denotes a statistically significant decrease in the catch of the region over time (P<0.05).

<table>
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<th>Component</th>
<th>Year</th>
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<th>Mean SST</th>
<th>Weighted SST</th>
<th>Weighted Depth</th>
<th>Percentage of Catch</th>
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<td>ns</td>
</tr>
<tr>
<td>Q3PC2+</td>
<td>0.802</td>
<td>0</td>
<td>-0.072</td>
<td>ns</td>
<td>-0.097</td>
<td>ns</td>
</tr>
<tr>
<td>Q3PC2</td>
<td>-0.744</td>
<td>0</td>
<td>0.678</td>
<td>0</td>
<td>-0.609</td>
<td>0</td>
</tr>
<tr>
<td>Q4PC1+</td>
<td>0.336</td>
<td>ns</td>
<td>0.842</td>
<td>0</td>
<td>-0.05</td>
<td>ns</td>
</tr>
<tr>
<td>Q4PC2+</td>
<td>-0.69</td>
<td>0</td>
<td>0.329</td>
<td>ns</td>
<td>-0.451</td>
<td>0.007</td>
</tr>
<tr>
<td>Q4PC2</td>
<td>0.785</td>
<td>0</td>
<td>0.365</td>
<td>0.034</td>
<td>0.447</td>
<td>0.008</td>
</tr>
</tbody>
</table>
3.5 Discussion

In light of recent management requirements, spatially resolved fisheries data are becoming increasingly important for implementing the ecosystem approach to fisheries management (Gerritsen and Lordan 2010). Mackerel are a schooling species and are known to aggregate in high densities over small areas (Petitgas 1993). Such consistent behaviour can have fishery implications with higher vulnerability to overfishing (Lindberg et al. 2006) as fishers target areas of high density schooling fish. The histogram of scores reveals that relatively low number of locations add large amounts of the variation in the catch data for PC1 in all quarters. There are far more locations that correlate very weakly or have no correlation at all to the component trend. As a consequence the fishery is widely distributed, shown through the latitudinal extent of the mackerel catches, but at the same time fisheries are centred on specific locations at certain times of the year. Vulnerability of a population to environmental and anthropogenic stressors can be increased through an uneven or patchy distribution of individuals through optimal habitat selection (Rose and Kulka 1999). The results presented here have identified particular areas of high fishing variability which changes between the quarters, representing the different life history stages of the mackerel annual migratory cycle. In quarter one the CSE represented 18% of the total catch for the quarter, in quarter three the Norwegian coast in the North Sea and the southern part of ICES division II represented 13% of total catch for the quarter, finally in quarter four ICES area IVa represented 19% of the total catch for the quarter. The histogram of scores shows that a great number of rectangles were not associated with the principle mode of variation highlighted by the EOF.

Hyperaggregation is a phenomenon where local densities of fish increase with decreasing population biomass (Rose and Kulka 1999). Hyperaggregation has been speculated to have been responsible for the decline of cod under the misinterpretation of elevated CPUE data (Rose and Kulka 1999). The results presented in this chapter suggest mackerel may exhibit hyperaggregation, shown by the tight configuration of distribution of the majority of the catch. If indeed mackerel do hyperaggregate, this would stress the need to understand local abundance at the scale of the stock and not from a fishery effort perspective (Rose and Kulka 1999). If the areas highlighted as positively correlated to PC1 (the largest proportion of catch) became targeted by a fishery with non-restricted quotas, high catches may persist (under the influence of, for example, a density dependent habitat selection mechanism) until the population suddenly crashes.
Under the current management system for Atlantic mackerel, total allowable catches (TACs) are devised per ICES division. However at present there is no international agreement between coastal state parties: recent catches (from 2010 onwards) have exceeded advice from the long term management plan, to such an extent that a decline in catch has been predicted for 2013 (ICES 2011). The few locations identified as adding high levels of variation in catch data (and relatively high proportions of catch) in this Chapter, emphasises the need for a spatially complex management structure for NEA mackerel, which is not necessarily fixed throughout a year. In particular the peripheral areas where catch is low may be more indicative of a decline in overall population biomass for Atlantic mackerel, than the areas of higher catch or total catch values, and should be investigated further to monitor potential declines in total stock abundance.

The merit of an EOF using mackerel international catch data was demonstrated in the preliminary analysis with the clearly identified spatio-temporal patterns in catch due to the closure of the SW mackerel box (section 1.3.6). Management implications affect catch regimes greatly, which is often cited as a reason against using catch data in statistical analysis to make inferences on abundance. In quarter four, PC2 shows a temporally synchronous shift in catch around the mid 1980’s from ICES division VIa to IVa. The shift in catch abundance has been attributed to both an effect of area misreporting by fishers (as a result of management restrictions for catch in the North Sea) as well as biological changes in mackerel distribution from both the western and northern spawning components (ICES 1978; 1985; ICES 1987). From the 1960’s the northern spawning component (NSC) of mackerel has been greatly reduced whilst the western spawning component (WSC) is in high abundance. Therefore since the mid 1960’s, management effort has focused on protecting the NSC of mackerel, specifically in the North Sea where restrictions were imposed in ICES division IVa (30 cm minimum landing size and restricted TAC (ICES 1987; 1989)), which is a known nursery ground and therefore closed for the first half of the year when the WSC is not present (ICES 1988). From 1990 the western stock TAC was allowed to fish east of the 4°W line (i.e. division IVa and the agreed boundary between the WSC and NSC), which improved the accuracy of landings for division IVa to some extent (as the WSC was at high reproductive capacity and therefore fishery quotas were large). Despite division IVa being open during quarter four there is still evidence of mis-reporting from area IVa to VIa, which continues today (ICES 2011).

It has been stated that there is a growing need to understand climate, environmental and/or fishery induced distributional changes in fish populations (Hidalgo et al. 2011; Hollowed et al. 2012); with a particular focus on
quantifying the relative importance of each variable for the ecosystem approach to fisheries management (IPCC 1996). The results presented here show how fisheries dependent data can be used in an EOF, to identify in relatively high resolution, specific patterns of distributional change. Locations were isolated and examined, however it is less straightforward to fully disentangle the driving mechanisms for changes in distribution and relative abundance, between environmental or climate forces and legislative or fishing fleet effects. It is possible however, to determine relationships between the environment and changes in the relative abundance of mackerel. For example, there appears to be a typical climate signal in seven of the analyses extracted by the EOF method in that the mean SST significantly increased, and yet the weighted SST of mackerel does not act in the same way as the local SST trend, and is not significantly correlated with years. Therefore there is a shift in relative abundance of mackerel catch within the areas, which has appeared to buffer the experience of an increasing SST, and maintained a possible thermal preference. Of the four areas not changing in weighted SST but increasing in mean SST, one shows that the weighted bathymetric depth increased significantly over time, possibly as a result of mackerel seeking greater depths due to warming surface waters. It is important to highlight that an increase in the weighted bathymetric depth presented in this report does not imply that mackerel depth is increasing as in situ catch depth data were not available; but that the water column depth is increasing, thus providing the potential for increased depth, and/or cooler waters. There are some regions (for example locations in Q1 that are negatively correlated to PC2) where it also would not be possible for mackerel to change their weighted bathymetric depth due to their distributions being far from offshore waters or the shelf edge.

In quarter one, PC2 shows a shift in catch distribution between the on-shelf areas and the continental shelf edge, which may be a change in distribution to avoid warmer waters as the wider Atlantic water meets shelf waters at the shelf edge, and is not warming as fast as on-shelf areas (OSPAR 2009). The northern (and off shelf) shift in relative catch abundance in quarter 3 PC2 might also be as a response to warming shelf waters; poleward shifts in distribution as a response to climate warming has been seen in other fish populations (Murawski 1993). Likewise, the shift in quarter 4 PC2 shows an eastern change in distribution towards the deeper areas around the Norwegian Trench, with mean bathymetric depth greater in the eastern than the western area (-255m and -182m respectively).

It is understood that mackerel have strong associations with SST (Reid et al. 1997; Reid et al. 2001; Walsh et al. 1995) with mackerel movements affected by temperature (Neill 1984; Rose and Legget 1998; D’Amours and Castonguay 1992; Castonguay et al. 1992; Reid et al. 1997; Bernier et al. ...
as well as their distribution (Hughes et al. 2012; Reid et al. 2003; Reid et al. 2001). The importance of temperature as a controlling factor for the annual migration of Atlantic mackerel has been demonstrated (Jansen and Gislason 2011), for example mackerel migrate from northern feeding areas to southern spawning areas in slips of water with preferential temperatures (Walsh et al. 1995; Reid et al. 2001). In a recent paper by Jansen et al. (2012) mackerel migration and distribution gathered from fisheries independent and dependent data were correlated with temperature; mackerel are shown to be guided by the warmer shelf edge current along the CSE to the southern spawning locations. Other species in the northeast Atlantic have been shown to elicit spatial changes be it latitude or depth, to alleviate the experience of warming waters (Simpson et al. 2011; Hedger et al. 2004; Perry et al. 2005; Dulvy et al. 2008). The northeast Atlantic Ocean is warming (OSPAR 2009; Dulvy et al. 2008; Brander et al. 2003; Southward et al. 2004); and rates of warming in all areas except for the wider Atlantic have been greater than the global average, since 1994 (OSPAR 2009).

Understanding causal mechanisms for any off shelf movements in mackerel catch is further complicated by the expanding international mackerel fishery which has been shown to have shifted away from the British Isles over the time series. In other fish stocks actual stock biomass has decreased whilst this pattern has not been seen from fisheries catch rates (DG Fisheries 2003) which has led to a stock collapse. Deciphering whether the offshore movement in catch is as a result of fishing pressure, increased stress from warming shelf waters or changes in prey distributions would require a more in-depth investigation, perhaps modelling temperature and mackerel distribution using a climate envelope model, or modelling prey abundance from CPR (continuous plankton recorder) data using generalized additive models (GAMs), to test the likelihood of mackerel tolerance to changing shelf conditions. However, the fact that mackerel are less abundant per unit area; there appears an avoidance of warming shelf waters; there is a current breakdown in mackerel management between the coastal states; unilateral TAC’s are being set higher than the long term management plan, all suggest that the western stock of Atlantic mackerel might be under greater pressure now than it has been in the past.

One line of future research may be to investigate the potential for changes in prey distribution as a causative factor for mackerel distribution. Physical changes in the environment (such as increasing SST’s) may influence productivity. For example changes in weather patterns may alter the amount of nutrients in the water which may in turn affect the strength, timing or community composition of phytoplankton blooms, thus affecting the abundance and distribution of zooplankton (Livingston and Wilderbuer 2004),
and possibly mackerel. Two hypotheses could be tested, first are mackerel following a changing distribution of prey and secondly how might changing mackerel distribution affect prey availability. CPR data would be a useful way to explore changes in zooplankton, particularly copepod abundances and distributions.

The importance of the results presented here is amplified by the fact that relatively little information exists on NEAM population distributional responses to environmental variables, especially climate change, as well as fishery impacts around Ireland. Current international mackerel management regimes have broken down in recent years and therefore the need to understand the impact of increased fishing pressure is essential. These results are of particular importance considering the northeast Atlantic has been described as one of the fastest responding areas to climate change (Drinkwater, 2005; Hughes et al. 2009), alongside mackerel constituting Europe’s largest fishery (Beare and Reid, 2002; Tenningen, 2011). Future research might focus on using survey data (mackerel egg survey or North Sea ground fish survey) alongside catch data to better describe relationships between mackerel distribution, SST, depth and fishery induced drivers of distributional change; as well as testing spatial trophic match/mis-match patterns.
3.6 References


Bishop, J. 2006. Standardizing fishery-dependent catch and effort data in complex fisheries with technology change. Review in Fish Biology and Fisheries. 16 1: 21-38


D’Amours, D., Castonguay, M. 1992. Spring migration of Atlantic mackerel, Scomber scombrus, in relation to water temperature through Cabot Strait (Gulf of St. Lawrence). Environmental Biology of Fishes. 34 4: 393-399


Frisk, M.G., Martell, S.J.D., Miller, T.J. and Sosebee, K. 2010. Exploring the population dynamics of winter skate (Leucoraja ocellata) in the Georges Bank region using a statistical catch-at-age model incorporating length, migration and recruitment process errors. Canadian Journal of Fisheries and Aquatic Sciences. 67: 774-792


Gerritsen, H. and Lordan, C. 2010. Integrating vessel monitoring systems (VMS) data with daily catch data from logbooks to explore the spatial distribution of catch and effort at high resolution. ICES Journal of Marine Science. doi:10.1093/icesjms/fsq137


Hidalgo, M., Rouyer, T., Molinero, J.C., Massuti, E., Moranta, J., Guijarro, B. and Steneth, N.C. 2011. Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. Marine Ecology Progress Series. 426: 1-12


Jansen, T. and Gislason, H. 2011. Temperature affects the timing of spawning and migration of North Sea mackerel. Continental Shelf Research. 31: 64-72


Large, P.A. 1992. Use of a multiplicative model to estimate relative abundance from commercial CPUE data. ICES Journal of Marine Science. 49 3: 253-262


Mutsert, K., Cowan, Jr., J.H., Essington, T.E. and Hilborn, R. 2008. Reanalyses of Gulf of Mexico fisheries data: Landings can be misleading in assessments of fisheries and fisheries ecosystems. PNAS 105 7: 2740-2744


Petitgas, P. 1993. Use of a disjunctive kriging to model areas of high pelagic fish density in acoustic fisheries surveys. Aquatic Living Resources. 6: 201-209


Reid, D.G., Eltink, A., Kelly, C.J. 2003. Inferences on the changes in pattern in the prespawning migration of the western mackerel (Scomber scombrus) from commercial vessel data. ICES CM2003/Q:19


Vignaux, M. 1996. Analysis of vessel movements and strategies using commercial catch and effort data from the New Zealand hoki fishery. Canadian Journal of Fisheries and Aquatic Sciences. 53: 2126-2136


Chapter 4: The role of local habitat on large and small spatial scale abundance fluctuations of cod (*Gadus morhua*) in the North Sea and Celtic Sea
4.1 Abstract

The ability to describe a fish population in space is necessary for its effective management. Patterns of fish distribution have been linked to environmental parameters. Results presented in this Chapter examines two cod (*Gadus morhua*) stocks in the northeast Atlantic using data from the International Bottom Trawl Survey (IBTS); North Sea cod (1977-2010), and a sub sample of the Celtic and Western Channel cod (2003-2011) (ICES divisions VIIj&g). Spatial statistics showed a significant northwest shift in the mean catch location (Centre of Gravity (CoG)) in the North Sea over time (1977-2010). However, an empirical orthogonal function (EOF) revealed that rather than a simple increase in relative abundance in the northwest and a decrease in the southeast, cod abundance variations per ICES statistical rectangle were highly spatially heterogeneous, and the observed change in CoG was from a blend of small-scale changes. A regression between the degree of correlation in North Sea cod abundance variations through time per site, and distance between each site demonstrated that locations in closer proximity to each other responded more similarly, whilst remote locations had no significant relationship (distance-decay pattern), opposed to locations at greater distances acting dichotomously (increasing and decreasing). The Celtic Sea and western Channel cod did not significantly change in average catch location (2003-2011) neither did they appear to display density dependent habitat selection, a pattern of distribution which has been shown with other cod stocks; however these conclusions may reflect the fact that only a small proportion of the stock was represented by the data. Results are discussed in light of local and regional habitat differences.
4.2 Introduction

Real populations are rarely well circumscribed in space, and are one of the many factors that make it difficult for an ecologist to describe a population’s relative abundance changes in space and time (Walker 2011). Individuals move around and experience different local environmental conditions that can affect growth, survival and reproduction. Spatial variation in a population’s local density patterns is often a result of gradients in resource availability (MacCall 1990). Habitat requirements can change within a year depending on the life history characteristics of a species, such as migratory populations who spawn and feed in different areas e.g. blue fin tuna (Muhling et al. 2011), Atlantic mackerel (Reid et al. 1997), and Salmon (Peyronnet et al. 2007). As well, habitats themselves change throughout time on differing scales for example annual and inter-annual cycles of change in, sea temperature in the Pacific (Holland and Mitchum 2005), spring phytoplankton bloom timing and stratification in the North Sea (Sharples et al. 2006) and salinity and temperature in the northeast Atlantic (Hatun et al. 2005).

Intra-population dynamics can also modify habitat choice when resources are affected by a population, for example density dependent habitat selection has often been used to explain distribution-abundance relationships (Fretwell and Lucas, 1970; Blanchard et al. 2005). Intra-specific competition for food or other resources is increased in higher densities thereby reducing the quality of the habitat (Fretwell 1972; Partridge 1978). Based on the theory of the ideal free distribution (IFD, Fretwell and Lucas 1970), optimal habitat is selected for by individuals of a population where each individual has an equal correlate of fitness (Quijano and Passino, 2007) until spatial saturation occurs, at which point a trade off between density (competition), and availability of resources, results in occupation of marginal habitat (Persohn et al. 2009; Kawecki 2008). This results in equilibrium of an individual’s fitness across the occupied habitat (Shepherd and Litvak 2004). The IFD assumes that; all individuals are equal in food acquisition ability, individuals can move freely between patches and have accurate knowledge regarding the distribution of both the resource supply and competitors – and therefore will move to the patch that offers the highest gain (Smith 1982).

Therefore abundance fluctuations can lead to temporally dynamic spatial patterns in a population’s distribution without the characteristics or availability of habitats changing (Laurel et al. 2007). The theory of ideal free distribution (IFD) summarises density-dependent habitat selection by stating that when populations are free to move and have a perfect and full knowledge of their environment, they will be attracted to areas that will maximise their fitness...
The IFD has been demonstrated as occurring in a variety of different fish, such as, haddock in the Scotian Shelf (Marshall and Frank 1995); Atlantic salmon (Gibson et al. 2008) and juvenile cod in the North Sea (Blanchard et al. 2005) and western Atlantic (Swain and Wade 1993). Density dependent habitat selection has often been used to describe the variation of spatial distributions of marine fish that undergo large abundance fluctuations as a result of recruitment variability, fishing mortality and latitudinal shifts from climate change (Laurel et al. 2007).

Spatial inhomogeneity of fish populations can cause problems for fisheries scientists and managers as there is a practical need for coherent stock identification in order for effective management (Ricker 1958; Sinclair, 1988; NRC 1994). Where spatial data on fish stocks are available, it is possible to examine temporal and spatial changes in distribution, and identify local changes in dynamics within a population (Petitgas 1998; Berkeley et al. 2004). These local variations in dynamics could represent: responses to different habitats at a small scale for increased fitness or reproductive potential (Levy 1991), the movement of populations at large scales (Batchelder et al. 2011; Overland et al. 2010), or both (Holland et al. 2004). For example, a population may track a broad thermal niche resulting in a distributional shift from optimal habitat to suboptimal habitat (Parmesan and Yohe, 2003; Yara et al. 2012). Such habitat ‘trade-offs’ have been seen in a number of fish species, such as minnows that changed location on a small scale to maximise profitability between favourable temperature but low food abundance, and sub-optimal temperatures but high prey availability (Garner et al. 1998).

Other populations are confined in their dispersal ability, such as fish in land locked lakes (DeStasio et al. 1996), or philopatric females seeking natal spawning grounds (Weishampel et al. 2008). In cases of local environmental change, individuals may not move therefore local abundances or densities may fluctuate depending on survival rates as a factor of the environment thus affecting the population dynamics as a whole over a broader spatial area. Figure 4.1 summarises potential spatial abundance responses a population might display to changing environmental conditions. In this example populations are reacting through (A) sporadic and non-structured variations in abundance with no average change in population distribution; (B) some heterogeneous fluctuations but a general trend of a directional movement for the population as a whole; and (C) the within population structure responds to environmental forcing in the same way therefore the population as a whole shifts in distribution to a new niche/habitat. Affecting movements between these three patterns are a population’s requirements for energy, growth and reproduction as an interaction between the individual fish and conspecifics and other biotic and abiotic environments.
Figure 4.1. A schematic diagram showing the effect of relative abundance fluxes in local or sub populations as a result of spatial heterogeneity, on the entire or meta-population. Large arrows depict local population fluxes (up is an increase, down is a decrease), small arrows depict relative abundance spatial changes of entire population, and circle represents 95% of the population distribution. (A) Independent local abundance variations with no spatial pattern which has no net effect on the whole population. (B) Local abundance variations that are more similar when in closer proximity, and more contrasting with increasing distance which results in a general decrease in one region and a general increase in another region, thereby the whole population changes in mean distribution in one direction. (C) All local populations respond in abundance and distribution in the same way, shifting the population as a whole.

By comparing two different stocks of the same species, in different areas over the same broad region, it is possible to obtain a better understanding of the effect of local and regional environmental forcing, as well as stochastic abundance variations, on the spatial structure of each stock. Within the northeast Atlantic there are well defined cod stocks around the British Isles. In this report groundfish survey data from the North Sea (1977 – 2010) and a sub-area of the Celtic Sea and western Channel cod stock (2003-2010), as well as ICES working group virtual population analysis (VPA) outputs on biological indices (spawning stock biomass (SSB), and recruitment) is used to investigate changes in total stock biomass as well as spatial changes in distribution.

4.2.1 Cod (*Gadus morhua*)

Cod are an important species in the marine ecosystem as essential components in the marine food web (Frank *et al.* 2005; Köster and Schnack 1994), with a far reaching distribution in the northeast Atlantic (Drinkwater *et al.* 2005), particularly on shelf areas (Sundby 2000). They are an important species to study considering their distribution, strong historical fishing record (Rosenberg *et al.* 2005), current high economic value (estimated EU TAC value for 2012 is €57,300,323, and for Ireland is €4,210,055 (The Stock Book 2012)), previous stock collapses (Walters and Maguire 1996), and low resilience to overfishing (Fleming 1960; Ottersen *et al.* 2006). Due to the longevity of fishing pressure on cod, evidence from northwest Atlantic cod suggests overfishing has caused evolutionary modifications increasing natural mortality rates and reducing
overall population growth capacity (Hutchings 2011). The northeast Atlantic is an important area to study cod as it contains the latitudinal extremes of Atlantic cod distribution (where the southern North Sea and Celtic Sea represents the southern boundary (Myers and Mertz 1997)), with potential increased recruitment variability at these range boundaries (Myers 1991). In this report data from the International Bottom Trawl Survey from the North Sea cod stock (1977-2010) and the Celtic and western Channel cod stock (2003-2011) will be used to examine spatial changes in abundance over time.

4.2.2 North Sea cod

There is substantial evidence to suggest North Sea cod is a metapopulation of smaller genetically distinguished sub populations (occurring in the Bergen Bank, Moray Firth, Flamborough Head and Southern Bight) with the degree of genetic similarity decaying with distance (Hutchinson et al. 2001). There is also evidence of age structured distribution (ICES 2012b), distinct spawning aggregations (which occurs January – April, in the southern and eastern edge of the Dogger Bank, the German Bight, the Moray Forth and east of the Shetland Isles (Fox et al. 2008)), with a general accord around the British Isles for a tendency for later spawning at higher latitudes (ICES 2005), but mixed feeding areas (Metcalfe 2006; Robichaud and Rose 2004; Heath et al. 2008). The abundance fluctuations between the SSB of sub-populations in different spawning grounds appear asynchronous across areas (Holmes et al. 2008). ICES conclude that there are two stocks with long-term differences in recruitment trends; one is located in the deeper water in the northern North Sea, and are not expected to re-colonize diminishing areas in the southern North Sea (ICES 2012b).

As there are few physical and environmental barriers within the North Sea to influence population structure, behavioural aspects have been proposed as a mechanism for the observed autonomous distribution and abundance patterns in genetically distinct sub-populations. However there appear several hypotheses as to the behaviours responsible for the structure of the observed sub-populations. For example, Robichaud and Rose (2004) described cod in the North Sea as showing four different dispersal behaviours for cod in the North Sea; from year round site fidelity, to decidedly mobile individuals with high distribution rates within a large geographical area. Heath et al. (2008) goes on to suggest that these behavioural types are not categorical and apply in various degrees throughout regions in the North Sea. Models have been applied to test theories on abundance and distribution, as well as active homing although they have not been able to explain all the patterns observed for cod the European Shelf or in the North Sea (Andrews et al. 2006; Heath et al.
As well as behavioural aspects, different preferences for environmental conditions have been hypothesised as the reason for disaggregated southern and northern sub populations. Hedger et al. (2004) showed cod in the southern North Sea were associated with shallow (<50 m), cooler and less saline waters, however cod in the northern North Sea favoured deeper (>100 m), warmer and more saline waters. Righton et al (2008) also found migratory individuals sometimes used deep topographic channels in the North Sea as “highways”.

Reports suggest there has been a significant northern shift in mean distribution of North Sea cod as a result of increasing water temperatures (Perry et al. 2005). Hedger et al. (2004) found a similar trend but suggested the change in mean latitude of the metapopulation is as a result of warming waters resulting in the southern cod sub-population unable to support itself, and either moving north or reducing in biomass. Other reports propose the change is from more intense fishing pressure in the southern North Sea removing a larger proportion of the North Sea cod biomass than in the north (STECF-SGRST-07-01). Rindorf and Lewy (2006) ascribed the northward shift to be as a result of warmer and windier winters influencing the advection of cod larvae towards the north where they settle, and remain, as well as a northern shift in distribution of older age groups of cod. Neat and Righton (2007) suggested warming in the North Sea was not sufficient to cause adult cod to move to cooler waters, as individuals in the south were present in temperatures considered super optimal for growth. However, Righton et al. (2009) showed from tagging studies that dispersal occurred from the Channel to the southern North Sea and not vice versa, and from the southern to the northern North Sea.

Blanchard et al. (2005) demonstrated that a reduction in the metapopulation abundance of juveniles of North Sea cod in Q3 was linked with warmer temperatures, in addition to a reduction in range; suggesting a density dependent habitat selection method for distribution. In contrast, Lewy and Kristensen (2009) reported that Q1 IBTS spatial correlation and dispersion of survey catches remained unchanged (1983-2006), and therefore the stock does not follow the theory of density dependent habitat selection despite demonstrating a northern shift in centre of gravity of distribution.

Cod are caught by almost every demersal gear in the North Sea including bean trawls, otter trawls, seine nets, gill nets and lines, as a target species and as bycatch (ICES 2012b). There has been a gradual improvement in the status of the stock over the previous few years, with the spawning stock biomass (SSB) having increased from a historical low in 2006, although it currently remains just below the lower limit reference point for SSB (Blim) (ICES 2012b). Fishing mortality has been increasing since the 1960’s until the turn of the
century where it started to decline, current levels are below a precautionary reference point ($F_{pa}$), but above the level considered consistent with obtaining maximum sustainable yield ($F_{MSY}$) (ICES 2012b). The management plans for this stock includes the EU-Norway plan (Annex 6.4.2), and the EU has adopted a long term management plan with the same aims (Council Regulation (EC) 1342/2008); both plans are in accordance with the precautionary approach (ICES 2012b). The primary sources of uncertainty in quality stock assessment lie in the estimation of unallocated removals and the assumption of fishing mortality for the 2012 advice forecast (ICES 2012b).

### 4.2.3 Celtic Sea cod

There appears far less information in the scientific literature regarding the Celtic Sea cod genetic stock structure and spatial ecology, in comparison to North Sea cod. However, from tagging studies evidence suggests there is more of a consensus pattern with homogenous migratory movements between the spring spawning areas north of Cornwall (ICES 2012a) to the summer feeding grounds in the east (The Smalls), which is complimentary to fishers reports (ICES 2012a). Additionally, there is a movement of cod between the estuaries in the southern region of Ireland, (ICES division VIIa) and offshore feeding grounds in the Celtic Sea (mostly Division VIIg) (ICES 2012a). The Celtic Sea cod population is at the southern range of cod distribution in the northeast Atlantic, with recruitment said to decrease in the warmer waters (above 8.5°C) with the upper thermal tolerance limit at 12°C (ICES 2012a). The growth rate for this stock is thought to be the fastest observed for cod (ICES 2012a). There is some evidence that there is some dispersal between the Irish Sea and Celtic Sea but this is reported to be slight. Recent reports also suggest the Celtic cod stock also reside in the southern area of the Irish Sea (ICES division VIIa) (ICES 2012a), and therefore recent landings have been revised to include this area. The stock was considered to have contracted by a significant amount according to landings data although area occupied by the stock can expand considerably when recruitment is strong, as with for example the 2009 year class (ICES 2012). Currently, age structure of Celtic Sea cod is truncated with age 2 cod being the most abundant catch. This is as a result of particularly strong recruitment events in 2009 and 2010, demonstrating how cod recruitment has a large impact on the total biomass of the population (ICES 2012).

Spawning stock biomass (SSB) for Celtic and western Channel cod is currently above the level where cautious management would be applied (MSY $B_{trigger}$). Fishing mortality ($F$), which is calculated by the instantaneous total mortality rate ($Z$) multiplied by the ratio of fishing deaths to all deaths (ICES 2012d),
increased from approximately 0.5 in the early 1970’s to 0.8 in the early 1980’s and has remained around this level with no significant trend, until it declined to the maximum sustainable yield (0.4) in 2011 (ICES 2012a). Current management plans for this stock are under construction by north western waters regional advice committee (NWWRAC) and the scientific technical and economic committee for fisheries (STECF) (ICES 2012a). Celtic Sea cod are taken in mixed demersal trawl fisheries (including Nephrops trawlers, gadoid trawlers, otter trawlers, beam trawlers and gillnetters) with a peak in landings during the winter months, especially February to March, and peak landings from French fleets (~70%) (ICES 2012a). Total allowable catches have been reduced since 2003. Misreporting, discarding and highgrading are the main threats to the quality of the ICES stock assessment, which is particularly relevant when quotas are restricted (2003-2008, 2011) (ICES 2012a).

In summary, this Chapter aims to i) assess broad scale changes in North Sea and Celtic Sea and western Channel cod, and to examine the relationship between spatial change and the environment (sea surface temperature (SST) and sea bottom temperature (SBT - North Sea only) and bathymetry); ii) identify spatial patterns of cod abundance in high resolution (ICES statistical squares) in the North Sea and to relate this to environmental variability including characterising the environment of high and low abundance iii) investigate the relationship of distance between sites and degree of correlation in cod abundance patterns over time in North Sea cod, and iv) determine whether Celtic Sea and western Channel cod display density dependent habitat selection characteristics.

4.3 Materials and methods

4.3.1 Survey Data

4.3.1.1 North Sea cod stock

The North Sea cod relative abundances were taken from the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) North Sea ground fish survey (NSGFS), which has been in place since the 1960’s but only since 1991 has it been part of the international bottom trawl survey (IBTS) coordinated by the International Council for the Exploration of the Seas (ICES). The aim of the survey is to provide recruitment indices for commercially important species, as well as to collect information regarding the abundance and distribution of non-commercial species for an overview of ecosystem health in the North Sea (ICES 2007). Biological indices (weight,
length, sex) and hydrographical data are collected and recorded during the survey, although these were not available for the analysis presented here. The survey is conducted in the first and third quarters since 1997, and on a quarterly basis since 1991 (ICES 2010), the restriction in number of surveys per annum comes as a result of resource limitations. For the purposes of this investigation, data used are from the third quarter (August and September) 1977 – 2010. The area included the North Sea, from 62º to 51ºN (see Figure 4.2). The survey was based on ICES statistical rectangles (1º longitude x 0.5º latitude = ca. 3720 km² at 53ºN, Duplisea et al. 2001), with a standard haul duration of 30 or 60 minutes and a standard fishing speed of 4 knots (ICES 2007). Prior to 1977 various bottom trawls were used with a small mesh cover, in 1977 ICES recommended that all ships should use a Granton Overture Verticale (GOV) trawl, which was phased in although this took a few years for example in 1977 only 3 nations used the GOV trawl, but by 1992 all nations used the gear (for Q3 surveys) (ICES 2010). Whilst the gear is standard, there remain differences in the rigging (ICES 2013). Relative abundance indices were expressed as mean numbers per standardized tow (per hour) for each ICES statistical rectangle. Since the abundances are standardized for the whole time series and areas (for details on the standardization see ICES 2006), the gear change should not have any significant influence on the analyses performed in this investigation, alongside any effect being applied to all locations simultaneously (Blanchard et al. 2005), although temporal changes cannot be ruled out. The survey (assessment) area is within the range of the management area which can be seen in Figure 4.2.
Figure 4.2. Survey locations of the Celtic Sea and western Channel cod stock, and North Sea cod stock. Yellow points represent locations where Celtic Sea and western Channel cod stock were present in the Irish Groundfish Survey (IGFS) 2003-2010. Red points represent locations where North Sea cod were present in the North Sea groundfish survey (NSGFS) 1977-2010. Red lines depict the ICES North Sea cod stock management area.

4.3.1.2 Celtic Sea and western Channel cod stock

The data for Celtic Sea and western Channel cod were obtained from the IGFS which is part of the western IBTS and data are collected during November-December (Marine Institute 2012). The purpose of the survey is to collect information to help determine the distribution and abundance of commercial fish around Ireland, and has been undertaken since 1990 (The Marine Institute 2012), although data available for the research presented in this paper is only from 2003. The survey uses a semi-random depth stratified survey design (The Marine Institute 2012). Stations are stratified by depth band and ICES division resulting in 17 strata (The Marine Institute 2012). The numbers of hauls per strata are proportional to the area of the strata, and abundances indices used in this analysis are mean numbers per standardised tow (per hour). The IGFS uses trawls at 30 minute duration at a standard speed of 3.5 – 4 knots, using a GOV trawl gear (The Marine Institute 2012). The current stratification scheme can be seen in figure 1.2 of Chapter 1. The stratification has developed over time with changes in the effort allocation and area surveyed, for example from 2005 ICES division VIIa (the Irish Sea) effort was reallocated to new slope strata.
(200 m – 600 m) for areas VIa, VIIb and VIIj. As a result all data from these areas have been removed from (Irish Sea and Slope Strata) the data presented in this Chapter for consistent sample locations over time.

It should be highlighted that the survey data from this analysis includes only ICES divisions VIIg&j and misses VIIe,f,g&k. Landings data are not split in such a way as to ascertain the proportional abundances from ICES division VIIg&j and therefore it is not possible to estimate the proportion of the population that the data presented here represents. The limitation of data will therefore be taken into account when discussing the results. It is also important to note that the management area is larger than the assessment area (see Figure 4.3)

![Figure 4.3. ICES management areas (red boxes) of Celtic Sea and Western Channel cod, along with the assessment area (blue hatched box) for the Celtic Sea and Western Channel cod. Figure taken from Marine Institute (2012a).](image)

### 4.3.2 Biological indices

Indices of spawning stock biomass (SSB) and population recruitment were obtained from the most current ICES virtual population analysis (VPA) taken from the relevant ICES working groups. Cod in the North Sea is assessed by the ICES working group on the assessment of demersal stocks in the North Sea and Skagerrak (ICES 2012b). The stock extends slightly further than the North Sea groundfish survey area as the survey misses the eastern English Channel, Skagerrak (between Norway and Sweden), and the Kattegat (between Denmark and Sweden), however there is adequate coverage of the North Sea cod stock (see Figure 4.2). The Celtic Sea cod population indices were taken from ICES working group on the Celtic Seas Ecoregion (ICES 2012) for cod in Divisions VIIe-k, the Celtic Sea and western Channel cod stock. The IGFS
covers most of the Celtic cod stock although it misses area VIIe,f,h, and most of area VIIk (see Figure 4.2).

### 4.3.3 Environmental data

Temperature data were obtained *in situ* from the North Sea groundfish survey data, and included SBT and SST. Significant gaps in the temperature data (both SST and SBT) exist after 1998, therefore only the time series 1977–1998 was used in the present analysis; of the remaining data, missing values comprised a maximum of 3.13% for SBT, and 3.67% for SST. To obtain a full time series between sea SST and survey data, the Hadley (HadSST2; Rayner *et al.* 2006) data set ([www.BADC.nerc.ac.uk](http://www.BADC.nerc.ac.uk)) for the years 1977–2010 was downloaded and georeferenced in ArcGIS (ArcMap v10). The survey SST and Hadley SST were tested for similarity using Pearson's correlation and were found to be highly significantly correlated ($r = 0.788$, $P < 0.001$). As the Hadley SST provided a full time series, it was used in place of the *in situ* SST data for all subsequent analysis. In order to associate the Hadley SST data with cod abundance data in space (to join satellite derived data to survey data), the Hadley data set was interpolated using a raster creation technique in ArcGIS, through an inverse distance weighting method that assumed each value had a local influence that diminished with distance, as was carried out in Chapter 2. Bathymetry data were downloaded from GEBCO ([www.GEBCO.net](http://www.GEBCO.net), GEBCO 2003) and are derived primarily from ship soundings data, interpolated using satellite gravity data. The data were georeferenced in ArcGIS as a raster layer.

### 4.3.4 Characterising population scale distributional changes and the associated environment

The centre of gravity (CoG) was used as a summary spatial statistic to test changes in abundance distribution of cod (see Chapter 2 Section 2.2 for methods). The CoG characterises the mean location of the population (Wolliez *et al.* 2007), and is a useful technique to measure changes in population distribution over time. The CoG of the North Sea and the Celtic Sea cod stock was determined for each year to test for spatial changes of the whole population over time. Rather than using latitude and longitude which are not uniform in the distances they represent, universal transverse Mercator (UTM) coordinates were used which are in meters from the equator (Northings) and from Greenwich meridian (Eastings).

To test how changes in relative abundance and distribution might affect the immediate environment of cod, two methods were employed in the form of the
mean and weighted (or CoG) values of environmental variables. The CoG of an environmental variable is described in Bez and Rivoirard (2000) as the probability of an individual being within a particular temperature class being determined by the relative abundance of individuals within that class. Therefore, if an individual is pulled from the population at random, the weighted temperature represents the most likely temperature that individual would experience.

The SBT data were taken over all haul locations per annum in the North Sea. As SBT was in situ data, it was already associated to the cod abundance in time and space. The Hadley SST and bathymetry data were coupled with the haul location in ArcGIS (ESRI 2011) using a bi-linear interpolation technique which was appropriate considering the haul was a 30 or 60 minute transect over an area centred on each ICES statistical rectangle. To test for changes in environment as a result of changes in abundance and distribution, the weighted COG technique was used for the SST, SBT and bathymetry for the North Sea and SST and bathymetry for the Celtic Sea cod (as no SBT data were available), where the environmental variable is multiplied by the cod abundance, per haul, summed and divided by the total abundance.

4.3.5 Spatially resolved North Sea cod abundance variations

Empirical orthogonal function (EOF, Preisendorfer, 1988) has been used as a successful technique to decompose spatial and temporal patterns in large data matrices, particularly in the field of meteorology (Palanisamy et al. 2012; Hannachi et al. 2007; Kaihatu et al. 1998) (see Chapter 3 Section 2.10 for more details). In this study an EOF was used as a method for assessing the dynamics and spatial patterns of abundance trends per location through time in high resolution. The aim was to identify specific areas that have added large amounts of variation to the data set, to determine the associated environmental conditions that might be driving said patterns of change.

The whole data set was used in the EOF and was log transformed a priori. The EOF was executed using Minitab, with missing values left as blank. Based on the previous methods of EOF analysis with mackerel catch data, (see Chapter 3 Section 2.4), the data were tested for any natural groupings using cumulative distribution frequency graphs, although there appeared no natural threshold. As a result it was decided upon a priori that 30% of each of the largest loadings were used (15% most positive loadings; 15% most negative loadings) to test for spatially defined patterns in high variance abundance trends. This appeared to be an intuitive amount to represent the more extreme patterns of variation whilst still including a sensible amount of the data in the analyses.
The statistical significance of the components identified by the EOF were validated using a broken stick method (Fronteir, 1976; Jackson, 1993) carried out in R (R Development Core Team 2008), using the CRAN library package “BiodiversityR” (Kindt and Coe 2005), to test the significance of the principal components (see Chapter 3 Section 2.3). Whilst the first principal component was statistically significant, the second was not. The spatial patterns of both components are not discussed or analysed in detail; however both are presented as maps (see Figure 4.4) to visually illustrate the spatial heterogeneity associated with the locations of highest variation.
Figure 4.4. EOF maps showing the 15% highest (black) and 15% lowest (red) loadings associated with PC1 (a) and PC2 (b). Symbols are proportional to the size of the loading. (c) catch associated with 15% highest (black) and lowest (red) loadings, solid line is PC1 and broken line is PC2.
4.3.6 North Sea cod abundance variations versus distance

As a method to examine the relationship between the degree of correlation in North Sea cod abundance variations through time per site, and distance between each site, distance correlation matrices were computed. Cod abundance was log transformed (Ln+1) prior to analysis and survey locations were projected from decimal degrees into Universal Transverse Mercator (UTM) coordinates; Eastings and Northings in ArcMap (ESRI 2011). The time series of cod abundance for each location was correlated against every other location, with missing values left as blank, to obtain a correlation matrix of abundance fluxes through time between each site. The distance between each location was determined using Pythagoras theorem on eastings (x) and northings (y);

\[
\text{Distance} = \sqrt{(x_1 - x)^2 + (y_1 - y)^2}
\]

(1)

The distance between all locations was determined using a matrix format using Universal Transverse Mercator (UTM) coordinate system which gives the distances in meters. The two matrices (correlation matrix and distance matrix) were aligned into two vectors and distances plotted against correlation coefficients. A mantel test of significance was performed. This was not repeated for the Celtic Sea and western Channel cod as only a small proportion of the stock was covered by the survey.

4.3.7 Distribution-abundance relationships for cod in ICES divisions VIIg&j

The effect the ideal free distribution (IFD) has on the relationship between abundance and the total area occupied by the population means that at higher densities, 95% of the population will occupy a smaller proportion of the total area occupied by the population. If a population simply increases the area it occupies directly as a function of its abundance, a linear relationship between area occupied and total abundance should occur (see Figure 4.5). In the North Sea there is a positive curvilinear relationship between the distribution and abundance of juvenile North Sea cod, which was reported as consistent with other cod stocks (Blanchard et al. 2005).
Figure 4.5. Schematic diagram showing distribution (A-C) and graphical representation (D) of (i) density dependent habitat selection, where distribution is a factor of optimal versus marginal habitat quality and abundance, and (ii) density independent distribution where total area occupied is directly proportional to total population abundance. The graphs (i&ii D) show the relationship between population abundance, and the proportion of area occupied by the whole population, that represents 95% of the total abundance of the population.

To resolve the relationship between total abundance and distribution for the Celtic Sea cod stock, the minimum area occupied by >95% age 1 and 2 year old cod was plotted against the abundance of age 1 and 2 cod. Abundance versus distribution was therefore calculated as a proportion of the total area of the survey, by ranking ICES statistical squares by their abundance in decreasing order, and taking the minimum area that accounts for 95% of the population. Total abundance was taken from the working group of Celtic Shelf ecosystem (ICES 2012) age disaggregated virtual population analysis (VPA) output. Following methods from Blanchard et al. (2005), only years 1 and 2 cod were included in the analysis to avoid bias from fishing patterns and mortality that might be included with the older individuals that experience higher fishing mortality; as a result, the higher abundance of the ages 1 and 2 cod gives greater statistical power to the survey (Blanchard et al. 2005). Ages 1 and 2 cod were isolated from the data and data were sorted from highest to lowest abundance per annum to create a cumulative distribution frequency (CDF) where the minimum number of ICES statistical squares was used to include 95% of the total population abundance. As 95% was never exactly included, the nearest lower percentage was used.
4.4 Results

4.4.1 Biological and spatial population trends

4.4.1.1 Spawning stock biomass and recruitment

There has been a decrease over time (1977-2010), of North Sea cod spawning stock biomass (SSB) (correlation with year, \( r = -0.918, \ P<0.001 \)) and recruitment (\( r = -0.761, \ P < 0.001 \)) (see Figure 4.6). The annual sum of abundance of cod from the North Sea groundfish survey has also decreased over time (correlation with year, \( r = -0.750, \ P < 0.001 \)) which likely represents a true biological trend as the survey effort has remained relatively stable with only slight interannual variability (average of 76 stations per year; range of 18, correlation with years \( P > 0.05 \)) (see Figure 4.7c). The recruitment index of North Sea cod shows that there is relatively high interannual variability pre 2000 however in the last decade recruitment is less variable and slightly below average for the whole time series. The Celtic Sea and western Channel cod are far more variable and show no significant change over time (1977-2010) in spawning stock biomass or recruitment (\( P > 0.05 \)) (see Figure 4.6).

![Figure 4.6: Annual spawning stock biomass (solid line) and recruitment (broken line) of North Sea cod (red lines) taken from WGNSSK (2012), and Celtic Sea cod (black lines) taken from WGCSE (2012), 1977-2011. Both standardised to a mean of zero and standard deviation of one.](image-url)
Figure 4.7. Associated environmental conditions and survey dynamics of Irish and North Sea cod. (A) Survey data cod abundance from areas VIIg&j: black lines represent sea surface temperature (HadSST2), grey lines represent bathymetry; broken lines represent annual centre of gravity and solid line represents the annual mean. (B) Survey data North Sea cod abundance: solid lines represent the mean and broken lines represent the centre of gravity. Black line shows the sea surface temperature data (HadSST2); dark grey line shows the in situ sea bottom temperature (SBT); light grey line shows the bathymetry. (C) North Sea cod survey
data; the annual sum of cod survey abundance of cod over time for the NSGFS (solid line) with the corresponding annual number of stations (broken line).

During the late 1980’s there was a large increase in both spawning stock biomass and recruitment, in the mid 1990’s they levelled off to slightly above average before declining sharply between 2000 and 2005, and since 2006 have increased. 2009 and 2010 were highly successful recruitment years with large year classes which have dominated the fishery and can be seen through the increased recruitment and spawning stock biomass.

4.4.1.2 Characterising population scale distribution and environmental changes – the centre of gravity

The annual CoG of latitude (UTM northings) and longitude (UTM eastings) for the metapopulation of North Sea cod reveal a northwest movement in general abundance, over time with northings being significantly correlated with year ($r=0.578$, $P<0.001$) and eastings being negatively correlated with year ($r = -0.614$, $P < 0.001$), showing a western shift (see figure 4.8 A&B). However, the same pattern can be observed for the mean annual survey effort location, which also displayed a significant northward ($r = 0.549$, $P<0.001$) and western shift (correlation with eastings $r = -0.599$, $P<0.001$), over time. Using a best subset analysis with: mean annual survey effort location, mean annual Hadley SST, mean annual bathymetry and years as predictor variables and the annual CoG of northings of abundance as the response variable, the best two models (based on $R^2$ (adj) and mallows CP) included year, SST and bathymetry and did not include mean annual survey effort location. For the Celtic Sea and western Channel cod stock in ICES divisions VIIg&j there was no significant directional movement for either northings or eastings ($P>0.05$) (see figure 9).
Figure 4.8. North Sea cod stock distribution from 1977-2010. Points represent the annual centre of gravity of North Sea cod abundance, with the labels representing the last two digits of the corresponding year. The background colour represents the mean SST taken from the Hadley (HadSST2) SST data set (see inset temperature key) with colder regions represented by dark blue stretching to red which represents warmer areas. Inset map shows the region selected from the North Sea. Graph (A) shows northings (UTM) increasing in hundreds of kilometres, (B) shows eastings with the y axis in hundreds of kilometres.
The annual centre of gravity analysis representing the Celtic Sea and western Channel cod, taken from the Irish ground fish survey data in ICES divisions VIIg&j. Each point is labelled with the corresponding year. The figure is labelled with degrees of latitude and longitude, and the inset map in the lower right corner shows the selected area in relation to Ireland.

The annual SST from the Hadley data set showed the mean, and CoG of North Sea cod temperature increased significantly when correlated against year ($r = 0.799$, $r = 0.596$, respectively $P < 0.001$) (See Figure 4.7b). The in situ CoG of SBT data, decreased over time ($r = -0.567$, $P < 0.001$), and the CoG of bathymetric depth increased over time (became deeper) (correlation with years $r = -0.752$, $P < 0.001$) (see Figure 4.7b).

In the Celtic Sea the mean SST of the survey locations correlated significantly with the CoG SST ($r = 0.976$, $P < 0.001$) and showed no trend over time (correlation with year, mean $r = -0.179$; CoG $r = -0.310$, $P > 0.05$) (see Figure 4.7a). The survey mean bathymetry and CoG bathymetry were not significantly correlated with year ($P > 0.05$) although were significantly correlated with each other ($r = 0.861$, $P < 0.01$) (see Figure 4.7a).
4.4.2 High spatial resolution analysis of North Sea cod abundance variability

The first two principle components from the EOF on the whole data set were both significantly correlated to the sum of annual cod abundance, PC1 was negatively correlated ($r = -0.598$, $P < 0.001$) and showed an increase over time; and PC2 was positively correlated ($r = 0.743$, $P < 0.001$) and decreased in variance over time. PC1 contributed 23.5% variance of the data set and PC2 contributed 9.3% variance. According to the broken stick method of significance testing; only PC1 was significant. Both PC’s are presented in figure 4.9 to illustrate the similarity in the patterns produced by the EOF method, despite only PC1 being similar (see Figure 4.4 a&b).

Cod abundance in the positively correlated locations for the first PC (see Figure 4.4c), shows a gradual increase over time (correlation with years $r = 0.641$, $P < 0.001$). The time series increases from 1977 – 1991 at which point there is a large increase in biomass which remains until 1998 when the level of abundance drops slightly, showing small levels of intra-annual variation until the end of the time series. This is also the time when the gear change occurred in the survey methodology. In contrast, the lowest associated loadings show a large decline at the beginning of the time series (correlation with year, $r = -0.592$, $P < 0.001$), falling from very high abundance of cod, to almost negligible levels of cod within 5 years. From 1981 onwards there is little to no abundance of cod in these areas.

4.4.3 High spatial resolution environmental associations of North Sea cod abundance

In all of the locations extracted from PC one and two (15% highest and lowest loadings), a significant increase in mean and CoG of SST was seen (mean $r = 0.760$; mean $r = 0.764$, $P < 0.001$, respectively) (see figure 4.10). The increases in SST within PC1 and PC2 were all highly significantly correlated with each other (see figure 4.10). However, the mean SBTs (1977 – 1998) appeared not to be changing (correlation with years, $P > 0.05$) in both PCs, highest and lowest loadings. For the CoG of SBT (1977-1998), the highest associated loading locations to PC1 and two did not change over time ($P > 0.05$), however the lowest associated loading locations significantly increased throughout the time series (correlation with year of PC1 lowest loadings $r = 0.517$, $P < 0.05$; PC2 lowest loadings $r = 0.685$, $P < 0.001$). The centre of gravity of bathymetric depth for the highest loadings did not change over time (correlation with year, $P > 0.05$), and the lowest loadings significantly decreased (becoming shallower) over time (PC1 lowest $r = 0.639$; PC2 lowest $r = 0.4$, $P < 0.05$). The
mean bathymetry for all modes of variation was similar, between -74 and -95m with an overall mean of -84.9m.

**Figure 4.10.** Environmental associations to extracted EOF loadings. Black lines represent 15% highest loadings; Red lines represent 15% lowest loadings. Broken lines represent the mean and solid lines represent the centre of gravity. Years are along the x axis. Boxes located at the top left show the correlations between the CoG and mean SST correlations for the respective graph (all significant correlations (P < 0.05).
4.4.4 North Sea cod: Abundance variation versus distance

The linear regression of distance versus correlations between locations significantly decreased with distance between locations (Mantels test, correlation $r = -0.049$, $P < 0.001$, see figure 4.11). The regression line approached but did not intercept zero, even at higher abundances. This implies that at greater distances locations were not significantly acting in opposition in abundance dynamics (as would be the case with a simple increase in the north and decrease in the south). In most cases the relationship breaks down at greater distance, with independent cod abundance patterns at large distances. Overall there were more positive correlations than negative (1818 positive correlations, 640 negative correlations), and the mean correlation over all locations was 0.30 (SE±0.01), therefore in general the locations are acting in a more similar way particularly when in closer proximity, and at greater distances abundance trends over time are independent.
Figure 4.11. Regression of distance against correlation coefficient of abundance variations over time per survey location from NSGFS trawl sites in North Sea. Red line symbolises the average correlation coefficient, grey line represents linear regression

4.4.5 Distribution –abundance relationships for the cod in ICES divisions VIIg&j

There does not appear to be any relationship between the minimum areas occupied by 95% of ages one and two cod, and the estimated numbers at age from the cod VPA (see Figure 4.12). For age one it appears 2010 is anomalous, probably due to the large cohort of 2009 coming through the fishery. When 2010 is removed the pattern is more similar to that shown in age 2 with no significant relationships and no clear pattern in abundance distribution relationships.
Figure 4.12. The minimum proportion of area containing c.95% of Celtic Sea and western Channel cod stock population taken from ICES areas VIIg&j only, against respective abundance from ICES working group (WGCSE 2012) VPA estimation output for ages 1 (left) and 2 (right). Points are labelled with years.
4.5 Discussion.

4.5.1 Population indices and fishing impacts

The SSB and recruitment indices of the North Sea and the Celtic Sea and western Channel cod stock show very different dynamics to each other over time. Probably the most important influence acting on the biomass of each of the stocks is fishing. Since the early 1970’s North Sea cod has been overfished (O’Brien et al. 2000; Alheit et al. 2005). In 1992 the ICES advice for the North Sea cod stock was to drastically curb or entirely halt fishing (ICES 1992). From the early 1970’s the mature cod stock the SSB was approximately 250000 t (Horwood et al. 2006) and from then there has been a steep decline to a historical low in 2006 at under 40000 t (ICES 2012c). Currently the North Sea cod stock SSB is just below B_{lim} which is the limit reference point, although fishing mortality has been declining since 2000 and is now just below F_{pa} (the precautionary reference point for fishing mortality), but well above F_{MSY} (fishing mortality is consistent with achieving maximum sustainable yield (MSY)) (ICES 2012c). For Celtic Sea cod, fishing mortality has also been very high from the mid 1970’s, and the SSB has been highly variable. Since 2005 fishing mortality has declined, although from 2000 the SSB also declined to well below B_{lim}. Occasional very high recruitment (1987 and 2010) has dominated the SSB trend, and currently the SSB is well above the MSY B_{trigger} (ICES 2012a).

4.5.2 Population indices and environmental impacts

As well as overfishing, other ecological factors have been hypothesised to have had an effect on North Sea cod productivity such as cod recruitment declining in response to a reduction in quantity and quality of larval food around 1987 (Beaugrand et al. 2003). The high NAO index from the late 1980’s was also reported to have had a negative effect on North Sea cod recruitment (Alheit et al. 2005), through upper water layer temperatures having an effect on trophic pathways (Alheit et al. 2005). Predictions made from Global Circulation Models (GCM) state that cod stocks in the Celtic and Irish Seas are likely to disappear by 2100 (Drinkwater 2005). Lauria et al. (2012) shows that there is climate warming in the Celtic Sea although the trophic food web interactions are complex and ecosystem responses to possible climate change scenarios might not be as marked as, for example, the North Sea therefore necessitating more regional studies in population dynamics. Because of the heavy influence of fishing on both cod stocks in this study, other environmental or local habitat derived signals might not be apparent in the biomass or recruitment response therefore it is problematic to speculate on possible relationships (based on the methods used in this study). A far more detailed study would be required,
probably using multiple trophic levels, at varying spatial scales to attempt to identify ecological patterns, rather than a ‘predictor and response’ type of analysis.

4.5.3 North Sea cod spatial structuring

The significant results from the EOF analysis (PC1) show that there is very little spatial structure in the abundance variation over time in the North Sea. The results do not show patterns identified from previous research that says there are distinct subpopulations in terms of coherent geographic areas of asynchronous trends in abundance over time. There is an overwhelming amount of evidence from tagging studies (Metcalfe 2006; Righton 2007), ichthyoplankton surveys (Fox et al. 2008) and genetic studies (Hutchinson et al. 2001) on stock structure in the North Sea and compelling evidence that there are distinctive sub-populations (Horwood et al. 2006). These encompass spatial studies in the macro and meso scale. There does seem to be consensus that population structure is more apparent during the spawning season and at spawning sites (Fox et al. 2008), with differential mixing between sub populations at different times of the year (Metcalfe 2006; Robichaud and Rose 2004; Heath et al. 2008). Data used in this analysis is from Q3 (August and September), which is outside of the spawning season (January – April) (Riley and Parnell 1984; Brander 1994). Thus discrete abundance patterns between sub populations might be better identified (using the EOF method) with Q1 IBTS data. If the population is mixed outside of the spawning season with different levels of dispersal between individuals and subpopulations, then one may not necessarily expect to see any spatial structure from an EOF analysis, and the results presented here support the idea that abundance variations through time is locally mixed during Q3 in the North Sea. The analysis does support the need for distribution abundance analysis to be conducted at a fine spatial resolution considering the spatial complexity of population structure of cod in the North Sea.

The significant regression between the degree of correlation in North Sea cod abundance variations through time per site, and distance between each site show that abundance trends are more similar when in closer proximity, suggesting there is some coherence in local abundance patterns through time. In the North Sea the morphology of the sea floor is relatively homogenous with southeast areas being less than 50m depth, a central area running north along the British coastline which is slightly deeper (50-100m) (ICES 2008) and the Norwegian Trench which reaches depths of 500m (Judd and Hovland 2007). Because of the lack of physical features it is unlikely that structural habitat affects temporal abundance trends in space, additionally sediment type which is known to affect cod distribution (Gotceitas and Brown 1993) is
similar within regions in the North Sea (ICES 2008). Fishing has already been acknowledged as a primary influence on abundance, and the level of fishing mortality differs spatially (Horwood et al. 2006). Therefore similar close proximity abundance trends through time might be as a result of local fishing effort patterns, as well as mixing of sub populations. Interestingly, the results show that at greater distances the correlation in abundance variations through time breaks down; rather than locations in the north increasing in abundance and locations in the south decreasing, there is no opposing abundance trend relationship. Whilst there is considerable evidence to suggest that there has been a shift in the centre of distribution in the North Sea cod population (Hedger et al. 2004; Perry et al. 2005), there is far less data to support whether this shift is from the metapopulation shifting distribution in response to, for example, warming waters, or whether it is as a result of a relative decrease in abundance in the south and an increase in the north. The linear regression presented here supports the idea that there is not a relative change in abundance (decrease in the south and increase in the north), but that any shift in the metapopulation is due to a combination of smaller local changes in abundance throughout the North Sea.

It is worth noting that an assumption of the North Sea IBTS data was that the gear change introduced in 1981 (from various trawl gear to the GOV trawl) did not have an effect on the standardised data. In the EOF analysis there were abundance changes in that the negative loadings associated with PC1 decreased around 1981 and the positive loadings associated with PC1 increased in the early 1990’s. The GOV was introduced in 1981 and gradually phased in, but only by 1991 were all participating countries using the gear. The catchability of the gears (and therefore the survey) may be different pre-1981 and post 1991. Therefore a bias in this analysis is that the EOF is picking up an effect in abundance that occurred at the beginning and end of the change. It therefore should not be assumed that the gear change does not have a temporal effect on the abundance dynamics of the data set, despite the change unlikely to have a spatial effect.

The apparent northwest shift in the centre of gravity of abundance was likely influenced by the change in survey effort, where average annual survey location also shifted significantly northwest. However, best subset analysis indicates that mean survey location was not sufficient to explain the shift in the CoG of cod abundance. The predictors used in the models with the best fit were years, mean Hadley SST and mean bathymetry. The result supports previous evidence. Hedger et al. (2004) used fisheries CPUE age and length disaggregated data between 1980 and 1999, and found a significant northern shift in North Sea cod distribution (based on a two-sample Cramer-von Mises test for differences between two unimodal probability distributions (Syrjala
between two decades. Perry et al. (2005) also found a northern shift in North Sea cod distribution, using IBTS data converted into CPUE data, and showed the relationship between the shift and mean winter temperature.

In the North Sea the mean and CoG SST both increased, in opposition to the in situ CoG SBT which decreased over time. The CoG bathymetric depth also increased (became deeper) over time and considering the close association of water column depth and temperature, SST may not a good proxy for characterising the environmental temperatures of groundfish species distribution. In the North Sea there appears to be a typical climate response of an increase in latitude and depth which has been seen with other groundfish species in the North Sea (Perry et al. 2005; Simpson et al. 2011). There is ample evidence to show the North Sea is warming (Beaugrand 2004; Cook and Heath 2005), that cod are at the southern boundary of their range (O’Brien et al. 2004), and there appears a northern shift in average distribution of North Sea cod (Hedger et al. 2004; Perry et al. 2005) whilst depth is increasing (Dulvy et al. 2008). The spatial statistics presented here on distribution and environmental characterisation support previous evidence of a response in cod distribution to warming waters in the North Sea. In contrast, in the Celtic Sea there is no trend in the mean and CoG of SST or bathymetry. The survey data used for the analysis does not cover the whole stock and therefore might not represent the true distribution pattern of the whole population. The time series for the survey is very short and might not capture low frequency information for distributional changes. Other factors that may disguise distributional responses to a changing climate are intense fishing pressure, as well as recruitment dynamics which have a big effect on the SSB (for example the exceptional recruitment in 1987 and 2010), as in general the stock biomass is low. There is also evidence over 20 years that whilst the Celtic Sea is increasing in temperature, only a weak climate signal in the marine food web exists, which is not as pronounced as in nearby regions, although cod dynamics were not examined directly (Lauria et al. 2012). The morphology of the Celtic Sea should also be mentioned however, as very different in structure to the North Sea, with sharper contrasts in slope and depth and therefore a wider range of habitat types as the relatively homogenous and shallow North Sea which may allow for the alleviation of warming waters through much shorter distributional changes. There is scope for extending the time series, which would be worth examining considering Celtic Sea and western Channel cod are considered to reside at the very southern distribution of their range. It would also be useful to obtain SBT for this stock to consider temperature associations that are not identified when using SST.

4.5.4 Density dependent habitat selection
In the North Sea, juvenile cod have been shown to display a curvilinear response with proportion of habitat occupied by 95% of the population (Blanchard et al. 2005) as well as cod in the western Atlantic (Swain and Sinclair 1994). The results presented here do not suggest the same pattern although this might be to do with monitoring only part of the CSWC cod stock. In cases where cod populations are not near the carrying capacity of the ecosystem, a linear relationship between abundance and optimal habitat will ensue, in the sense that only the first linear section of an otherwise curvilinear response will be seen (else no linear pattern at all). Likewise, if the time series is not long enough, an established pattern may not be recognised due to stochasticity. The time series presented here was 7 years compared to over 20 years for other investigations with the North Sea stock. The spatial frame used to calculate proportion of area covered by 95% of the population was ICES statistical squares, although this does not reflect the survey strategy in the sense that 3 trawls may have been made in one rectangle, whilst there were no trawls in the adjacent rectangle. The semi-random depth stratified survey design meant that samples were not spatially homogenous and defining a useful scale to measure area covered was difficult. The standardised numbers per hour trawl could potentially be worked up to density values and then combined with ICES statistical rectangle for a better measure of spatial allocation of stock.
4.6 References


Metcalfe, J.D. 2006. Fish population structuring in the North Sea: understanding processes and mechanisms from studies of the movements of adults. Journal of Fish Biology. 69 (Supplement C): 48-65


Walters, C. and Maguire, J-J. 1996. Lessons for stock assessment from the northern cod collapse. Reviews in Fish Biology and Fisheries. 6: 125-137


Chapter 5: Comparative study on the recruitment variability of three northeast Atlantic pelagic fish species: Atlantic mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*) and blue whiting (*Micromesistius poutassou*).
5.1 Abstract

A multispecies comparative approach was used to test the recruitment variation in three northeast Atlantic pelagic fish species. The aim was to test whether using multiple environmental indices and multiple species recruitment time series would render a better description of the marine ‘system’ than a single species, single environmental variable comparison. Blue whiting (*Micromesistius poutassou*), Atlantic mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*) were used in conjunction with sea surface temperature (SST) data, the gyre index (GI), the north Atlantic oscillation index (NAO) and turbulence. A significant positive correlation was found between horse mackerel recruitment and the NAO whilst blue whiting SSB is positively correlated with SST but negatively with the GI; an environmental principle component analysis (PCA) of all environmental data support the finding. Significant negative biological interactions exist between mackerel SSB, and blue whiting and horse mackerel SSB as well as between horse mackerel and blue whiting SSB. Distributional patterns over time do not appear to be similar between the three species and as a results experience different environments. For both mackerel and horse mackerel, egg mortality is highest between stages 1 and 2, and lowest for stages 2 and 3, whilst the mortality ratio between stages 4 and 5 in mackerel is significantly positively correlated to recruitment.
5.2 Introduction

Understanding recruitment-environmental correlations is of considerable interest to fisheries scientists and fisheries managers; to reduce uncertainty in assessing the past and in predicting future recruitment to a stock (Francis 2006). Approaches to understanding recruitment dynamics in fish populations have included a wide range of techniques aimed at explaining the greatest amount of recruitment variation in the simplest way. Previous studies have focused on relationships such as multiple species association with an isolated independent variable (larval supply to various coral reef fish (Milicich et al. 1992)); single species associations with multiple environmental predictors (cod in the North Sea (Lindley et al. 2003)); early life stage mortality and environmental indices (anchovy in the Adriatic Sea (Regner 1996)) while some studies have combined two or more explanatory and response variables (Köster et al. 2011; Lett and Kohler 1976).

Although many research articles have found evidence of environment-recruitment relationships, these relationships have often broken down when repeated with newly acquired data or longer time series data (Myers 1998). In some cases this has been due to; changes in the dynamics relating a fish population to its environment, or false conclusions being drawn from an original analysis where processes were not fully validated (Francis 2006). Shorter time series data may be more likely to produce one or more spurious correlations if the variables are also cycling with an unrecognised longer frequency process. This leads on to one of the major problems in time series data. Variables of disparate frequencies can often disguise patterns between each other, depending on the temporal scale of the data. For example, a short time series including large amounts of variation derived from localised weather or climatic patterns might not show the typical dynamics of a longer cyclic variation, thus disguising a pattern. Likewise, a study of low frequency forcing is likely to smooth over interannual fluxes that might exert large control over the recruitment process between years. Often data is limited in spatial and temporal extent making it difficult to summarise associations between long term driving forces, and shorter term interannual changes.

There are a number of weaknesses with the conventional approach in testing environment-recruitment relationships that go beyond the basic issue of the length of the data series. The first is that the system may be summarised in a number of ways. As species interact, it may be more appropriate to consider the combined recruitment of several species rather than take an individual species approach. Similarly, the environmental variables used are typically not entirely comprehensive, but represent a set of associations with other variables.
Most well known is the NAO: this index is associated with a variety of phenomena, but is treated as a single entity in many correlational studies. Similarly, sea surface temperature (SST) is a variable which contains direct effects, alongside unstated correlations with possible variables of interest such as stratification depth and timing of the spring phytoplankton bloom. Given the hidden variables inherent in most predictor variables, it may be that different combinations of these variables may be more informative. Similarly, correlational studies often assume a linear relationship, when a non linear function may be more appropriate. Unfortunately, the use of non linear relationships and multiple combinations of predictors present problems of model selection. Potential paths around this issue are to define linear combinations of predictors \textit{a priori} using a scaling like principal component analysis. For the response variable, a first step may be to attempt to define conditions associated with outliers (peak recruitment or recruitment failure) without attempting to identify a functional relationship for all environmental conditions.

In the northeast Atlantic there have been very few studies which have used a comparative approach between species (Web of Science search for key words; comparative, recruitment and Atlantic, returned two hits: Fogarty et al. 2001 and Legget and Frank 1997). The northeast Atlantic is a complex and dynamic ecosystem with hydro-meteorological and climatic events that vary across different time scales. The northeast Atlantic supports a valuable fishery, for which the ecosystem approach of fisheries management (EAFM) is becoming ever more relevant. The EAFM is generally defined amongst fisheries scientists as an approach towards considering the most important driving forces on, and the processes within, the ecosystem (Svendsen \textit{et al.} 2007), as well as examining ecosystem effects of fishing thereby moving away from single stock fisheries management (Beaufort 2012). Understanding the most important variables for the environment-recruit relationship is in accordance with the EAFM.

The aim of the study was to adopt a number of approaches to understand the driving forces behind the recruitment dynamics of three commercially important pelagic northeast Atlantic fish species. Specifically, the aim was to test i) whether the recruitment dynamics of the three species respond differently to broad scale environmental forcing either singly or in multivariate combinations, independently of their spawning stock biomass, ii) to what extent the spatial distribution of the adult (blue whiting) and early life history stages (mackerel and horse mackerel) of fish might affect recruitment of the species, including the links of spatial variables to environmental predictors (NAO, GI, turbulence and SST); and finally iii) if there are common
environmental features associated with extreme recruitment events (high and low) for the different species.

5.3 Materials and Methods

5.3.1 Study species

5.3.1.1 Mackerel

Mackerel (Scomber scombrus L.) is a migratory pelagic species ranging from the southern Iberian peninsula to the Norwegian Sea, North Sea and as far west as -20ºW (ICES 2001; Molloy 2004). The northeast Atlantic mackerel (NEAM) population is divided into three spawning components, western, southern and northern although they are all part of one stock. The spawning components mix at certain times of the year although during spawning they are understood to be spatially distinct (Molloy 2004). The annual migration pattern of the western spawning component is from the winter feeding grounds in the North and Norwegian Seas to the spawning areas which are located from the Bay of Biscay to west of Ireland and Scotland between January and July (Reid et al. 2001). Spawning takes place between February and July throughout a large area concentrated primarily along the continental slope with spawning hotspots in the southeast Bay of Biscay and the Porcupine Bank. NEAM supports one of the most important EU fisheries and currently no international agreement for quotas is in place within the coastal states agreement (ICES 2012). The timing and distribution of mackerel spawning has been linked to SST in the past (Walsh et al. 1995; Reid et al. 1997; Bernier et al. 2000; Jansen et al. 2012a; 2012b). Evidence from more northern areas have shown a change in the latitude of their distribution in more recent years (Nøttestad et al. 2012), with hypotheses as to why being as a result of an increase in SSB, new feeding niche’s and increased water temperatures. There have also been links between mackerel and blue whiting SSB (Payne et al. 2012).

5.3.1.2 Horse mackerel

In the northeast Atlantic, horse mackerel (Trachurus trachurus) is divided into three separate management stocks for management purposes, by ICES (ICES 2011). The species lives up to 30 years old therefore a strong year class can lead to high abundance for extended periods of time, as seen with the extraordinarily high 1982 year class. As a result of the strong 1982 year class, a substantial horse mackerel fishery continued for more than a decade; consequently horse mackerel became one of the three most important pelagic
fisheries in Europe (Abaunza et al. 2003). Horse mackerel is a pelagic migratory species, adopting similar migration patterns to Atlantic mackerel (Iversen 2002). Temperature has been shown to influence horse mackerel migration, for example there is a reported lower threshold in the feeding areas in the Norwegian Sea and North Sea of \(10^\circ\)C which, when experienced, triggers the start of migration to the overwintering areas further south, namely around the British Isles and Bay of Biscay along the continental shelf edge (CSE) (Macer 1977; Eaton 1983). The spawning period is as long as eight months, taking place along the continental shelf edge for the western stock (Macer, 1977; Eaton 1989; Porteiro et al. 1993), starting in the southern regions and moving north (Abaunza et al. 2003) and thought to be in synchrony with increasing spring sea temperatures (Chuskin and Nazarov 1989). The recruitment of horse mackerel has been reported as being more dependent on environmental factors than on the size of the stock (Abaunza et al. 2003). Temperature not only elicits controls in the development time of horse mackerel eggs (as with all fish eggs) and larvae as but has also been reported to regulate adult appetite (Abaunza et al. 2003). There is evidence to suggest that density dependent mechanisms occur within this species; for the particularly large year class of 1982 it has been shown that growth rates were affected, as well as for subsequent cohorts whilst the 1982 class were still in the fishery (Abaunza et al. 2003).

5.3.1.3 Blue Whiting

Blue whiting (*Micromesistius poutassou*) is a small pelagic planktivorous gadoid species widely distributed throughout the northeast Atlantic (ICES 2011). Distribution is focused along the edge of the continental shelf edge west of the British Isles, Rockall Plateau and Rockall Trough (Bailey 1982; Hatun et al. 2009a), although the species is present in all ICES management areas (ICES 2011), and has been recorded as far as the west coast of North America (Payne 2012). Despite this, blue whiting is managed as one population centred along the continental shelf edge (ICES 2010a). Blue Whiting are found in depths of 300 to 600 meters, and nursery areas are thought to be found mostly in the Norwegian Sea (ICES 2011). Adult blue whiting carry out similar feeding and spawning migrations as adult mackerel and herring, and are an integral part of the pelagic ecosystem (ICES 2011). Early life stage survivorship are said to have an important impact on the reproductive capability of the stock, oceanographic factors controlling the advection and retention of eggs play a big part (ICES 2011). Also there is thought to be a strong relationship between mackerel feeding in the spawning ground of the blue whiting, and the successful recruitment of blue whiting, in fact mackerel are thought to have contributed to the recruitment failure of the blue whiting (Payne et al. 2012). Other factors such as the sub pub polar gyre (SPG) are
thought to affect the recruitment of blue whiting to such an extent that recruitment forecasting may be possible (Hatun et al. 2009a; Lohman et al. 2009). The stock has undergone some dramatic changes in the past, with unusually high year classes after 1996 to peaks in the mid 2000s which meant the Atlantic blue whiting fishery was one of the largest fisheries in the world at the time (Payne et al. 2012). In recent years however the stock has declined with a mix of poor recruitment years and high catches (ICES 2010a). The international fishery which is comprised of 10 different countries reported total catch landings in 2010 to be 524 000 tonnes (ICES 2011).

5.3.2 Biological spatial abundance data

To test for any spatial changes in mackerel and horse mackerel stocks, egg data from the ICES triennial mackerel and horse mackerel egg survey were used from 1977 – 2010. The survey covered the majority of the western (spawning/management) stock of both species. The aim of the survey is slightly different for each species owing to the biological variations between the species. As mackerel is assumed to be a determinate spawner, egg counts can be used with fecundity and atresia values (from biological sampling) to ascertain an estimate of the spawning stock biomass based on egg production rates per female with a sex ratio of 1:1. However horse mackerel is thought to be an indeterminate spawner which means fecundity is unknown and therefore the survey aims to produce an estimate of the index of egg production. Samples of the water column are taken from a plankton tow, a Gulf VII sampler, or similar, and towed for 30 minutes to a maximum depth of 200m or the seabed, whichever is shallower. Eggs are then identified and counted and staged to a development stage, 1-5 for mackerel and 1-4 for horse mackerel. For more details on the survey and problems associated with sampling in high egg density regions, refer to Chapter 2 section 2.1 “Survey background”. For all calculations of egg stages, surface density is the unit, which is the calculated measure of density of eggs below one metre square (M²) of surface water.

Blue whiting abundance data were taken from the international blue whiting spawning stock survey (Working Group on Northeast Atlantic Pelagic Ecosystems Surveys (WGNAPES)) which is carried out on the spawning grounds to the west of the British Isles in March-April. The survey started in the 1970s by Norway, although the times series for the research presented here is from 2006 to 2010 only. In 2004, an internationally coordinated survey program has expanded to include Norway, Russia, the Faroe Islands and the EU, and is coordinated by WGNAPES (ICES 2011a). The aims of the survey are to collect acoustic data on spawning and post spawning aggregations along
the northern migration pathway from key spawning areas, to obtain biological samples from trawling and to determine age stratified estimates of relative abundances and biomass.

5.3.3 Biological population indices data

Fish population data including spawning stock biomass (SSB) and recruitment were collected from the WGWIDE (working group on widely distributed stocks, ICES 2012). The data were calculated using a virtual population analysis (VPA), which is based on catch processes such as fishing mortality at age from catch at age data to simulate year to year cohort survival. The data is tuned using abundance indices from fisheries independent surveys and commercial fleets. The recruitment age is generally the minimum age an individual fish becomes part of the fishery, although for mackerel and horse mackerel the recruitment is based on zero age whilst the blue whiting is age one (due to differences in biological maturation rates) and has therefore been time lagged by one year so hatching year corresponds to the environmental indices and other species recruitment data. Despite well known inaccuracies within the VPA data (Lapointe et al. 1989), it is considered the most accurate estimate, has been used in recruitment variability investigations in the past and in the current stock management (Myers and Pepin 1994; Lassen and Medley 2000).

The time series used for the population data correlation analysis was 1972-2010 for mackerel and 1982-2010 for horse mackerel, and 1981-2010 for blue whiting to include the most complete time series for each of the three species. The population data for mackerel includes the three spawning components (southern, western and northern) whilst the horse mackerel recruitment index includes the western stock only as the southern time series starts at 1992. The horse mackerel recruitment data were logged due to the strong 1982 year class, while the mackerel and blue whiting data were normally distributed. The recruitment data were all standardised to a mean of zero, standard deviation of one, for the analysis of extreme recruitment years.

5.3.4 Environmental data

The environmental data sets used in the analysis included the North Atlantic oscillation index (NAOI, defined as the pressure difference between the Azores high and the Icelandic low), the Gyre Index (GI), mean sea surface temperature (SST) and turbulence (defined as the cube of geostrophic wind speed (Borja et al. 2002)). The NAO is a well recognized feature of the global
climate system in the north Atlantic, defined by the pressure between two stations located close to the centres of action that make up the NAO dynamics (Jones et al. 1997) one in Iceland (low) and the other in the Azores. Hurrell (1995) has shown that during the winter season of the year, the oscillation provides a simple means of explaining much of the variability of weather all over Europe (storm track, precipitation, strength of westerly winds), and they are strongly associated with oceanic conditions (sea temperature and salinity, Gulf Stream intensity and wave height (Brunel and Boucher 2007)). In this investigation the annual NAO index was derived from the difference of normalized sea-level pressure between Lisbon, Portugal and Reykjavik, Iceland (Hurrell 1995). SST values are averaged over April – June, which is the spawning season to correlate with the period of the mackerel and horse mackerel egg surveys, the NAO, turbulence and SPG index were all averaged over the year from monthly means.

Water column salinities and temperature around the west of the British Isles depend largely on the strength of the subpolar gyre and the subtropical gyre, as these are the waters that feed the northeast Atlantic and Nordic seas (Hatun et al. 2005). The gyre index is a measure of the strength of the subpolar gyre, so in high index years the subpolar gyre is strong and pushes east towards the British Isles which increases the proportion of cooler fresher water dominating the waters around Britain. In low index years the subpolar gyre is weak which allows a greater influx of water from the subtropical gyre to influence the waters around the British Isles resulting in warmer more saline waters pushing north. The gyre index was obtained for the time series 1977 – 2010 from two different indices. Time series data between 1977–2003 were from the simulated output of the combined ocean general circulation model (OGCM) from the Miami isopycnal coordinate ocean model (MIRCOM), with the daily mean National Centre for Environmental Prediction/National Centre for Atmospheric Research (NCEP/NCAR) for fresh water, heat and momentum fluxes during the period from 1948 to 2003 (Hatun 2005). From 1993-2011 the index was based on satellite altimetry data (AVISO) using the example from Häkkinen and Rhines (2004), where the first principle component from an empirical orthogonal function analysis characterises the increasing salinities in the northeastern Atlantic, representative of the gyre index. The altimetry data picks up changes in sea surface height caused from changes in the density of the water between the cool fresh, and the warm saline waters. The two data sets are scaled differently but the values are not physical therefore they can be combined by standardising each data set to a mean of zero and a standard deviation of one, and then using the difference between the standardized values and the mean from each data set, forcing the regression between the overlapping years to intercept zero. Each respective time series index was obtained from Hatun (pers comm.) 2012.
Sea surface temperature was taken from the Hadley data set (HadSST2) (Raynor et al. 2006), which is a 5° by 5° monthly grid of in situ SST measurements from ships and buoys, available from the UK Met Office (www.metoffice.gov.uk/hadobs/hadsst2/index.html). SST data were added as a layer in ArcMap (ArcGIS) and monthly values (April – June) were interpolated using an inverse distance weighting technique where weights are proportional to the inverse distance, to create a raster layer. The SST was then associated with and extracted from a grid of 0.5 latitude x 1 longitude spanning from -5° to -15° West and 60° to 40° north to calculate mean spring sea temperatures.

Mean monthly wind speeds were downloaded from the cross-calibrated multi-platform (CCMP) ocean surface wind vector L3.5A (Atlas et al. 2011), from the physical oceanography distributed active archive centre (PO.DAAC) of NASA’s Jet Propulsion Laboratory (http://www.podaac.jpl.nasa.gov), at the spatial resolution of 0.25 degree cylindrical coordinate grid, referenced to 10m above the sea surface. Data were downloaded as NetCDF files and georeferenced and converted to raster layers using the Multidimension Toolbox programme in ArcGIS ArcToolbox (ESRI 2011). Data were available from January-December 1988-2011, however for this analysis only data up to and including 2010 were required. Following on from Borja et al. (2002), turbulence was calculated as the cube of the monthly wind speed (m/s^3), and was extracted using the same 10 locations extending from Galicia in the south to southern Norway in the north, using a bilinear technique in Spatial Analyst Tools in the ArcToolbox of ArcGIS.

The mean values for all 10 stations for the annual spawning period (March – July) were used for comparison. The two indices (Borja et al. 2002) and the present data) were standardised to a mean of zero and standard deviation of one. Each index was then standardised again by the mean value for the common years (i.e. 1988-1997), to ensure the intercept of the regression between the overlapping years was at zero. The data were then combined using Borja et al. (2002) index from 1969-1987, and the CCMP model output turbulence data for 1988-2010.

5.3.5 Multi combination data analysis versus recruitment

5.3.5.1 Multivariate analysis

Examining potential relationships between recruitment patterns and other biological and environmental data available required various combinations of
data analysis. Recruitment data were correlated with individual and grouped environmental data, to test whether the environmental data explained recruitment variability better when combined or individually. A number of combinations were tested. First, all environmental variables (1977-2010) were combined using a principle component analysis (PCA) through time. The resultant loadings were correlated with species recruitment data to test for significant relationships. To test whether an improved relationship existed for recruitment and environmental data with SSB data, the environmental variables and stock size in the form of SSB were combined through a temporal PCA, and the resulting loadings were correlated against recruitment of the individual species. Finally, the recruitment indices were combined (for the years 1982-2010) using a temporal PCA (empirical orthogonal function analysis) to assess whether multispecies analysis with single environmental data approach, was better than using multi environmental data analysis to a single species recruitment approach. All multivariate analysis was performed using Minitab.

5.3.5.2 Common threshold response

Recruitment data were analysed by testing for common patterns in extreme recruitment years (good and bad recruitment levels) and environmental data. Recruitment data were log transformed *a priori* and extreme years were identified as being outside 1 standard deviation of the mean of the time series. For a year to be considered ‘extreme’ in recruitment, at least two species required their recruitment value to be outside 1 standard deviation of the mean.

A PCA was then carried out using the four indices of environmental data. The environmental principle components (one and two) were then plotted against each other and ‘extreme’ recruitment years identified to identify associations.

5.3.6 Within species analysis - egg transition stage mortality

Paulik diagrams (Paulik 1973) were constructed using annual sums of egg density data for each development stage. All records that did not have a complete identification of all stages were excluded from the analysis. This equates to a total exclusion percentage of 5.21% of mackerel data, and 9.8% of horse mackerel data. Annual average abundance of each development stage of mackerel and horse mackerel was plotted against each other in the context of Paulik diagrams (Paulik 1973). Before hatching into larvae, there are five development stages of mackerel, whilst there are four for horse mackerel. By looking at the adjacent life history stages of growth and development of each
species, the Paulik diagram graphically represents the transition between each stage. Each point represents a year for which the survey was conducted in. Whilst the total egg production would be expected to increase throughout the years, due to an increase in survey effort, the Paulik diagram can identify levels of egg mortality within the survey years.

Egg stage transition mortality rates were also determined using the ratio between development stages by dividing each development stage by the previous stage (i.e. mackerel egg stage 2/mackerel egg stage 1 etc.) and then correlate the ‘mortality ratio’ time series with the recruitment index for the relative species.

5.3.7 Between species analysis - spatio-temporal distribution dynamics

Spatial statistics in the form of the annual centre of gravity (CoG) and associated inertia (spatial variance around the CoG) were determined for mackerel and horse mackerel eggs (all stages), and blue whiting spawning biomass (see Chapter 2 section 2.2 for more details on calculations). The centre of gravity is a summary statistic describing the mean distribution of the population in space. The centre of gravity was determined for each development stage for mackerel and horse mackerel, using egg surface density (m$^2$) 1977–2010. Blue whiting spatial data came from acoustic surveys (2006 - 2010) which measures stock biomass in acoustic density (sA/m$^2$/nm$^2$ – a measure of the fish population density according to the backscatter coefficient).

The CoG was used to determine the rate of spatial displacement between only the first development stage (as later development stage abundance and distribution is a factor of temperature) of mackerel and horse mackerel by subtracting horse mackerel X and Y coordinates from mackerel X and Y coordinates. The difference between locations was then compared with a recruitment ratio between the two species to test if spatial differences between mackerel and horse mackerel distribution have an effect on recruitment between the species.
5.4 Results

5.4.1 Dynamics of biological indices and environmental forcing

Only horse mackerel recruitment was significantly correlated against year ($r = -0.418$, $P < 0.05$) with no significant correlations between the recruitment indices of each species ($P > 0.05$) (see Figure 5.1). The SSB of blue whiting increased over time ($r = 0.679$, $P < 0.001$) but there is no significant correlation observed for the other species. Horse mackerel recruitment is negatively correlated with the SSB of mackerel ($r = -0.509$, $P < 0.01$), as well as blue whiting SSB negatively correlated with mackerel SSB ($r = -0.412$, $P < 0.024$). Both the time lagged (-1 year) recruitment and SSB of blue whiting is negatively correlated with the SSB of horse mackerel ($r = -0.621$, -0.402, $P < 0.05$) (see Figure 5.1).
Figure 5.1  Biological indices for (A) mackerel, (B) horse mackerel (note the high recruitment year of 1982) and (C) blue whiting. Solid line represents recruitment and broken line represents spawning stock biomass (SSB). Indices from most recent VPA (2012) output from ICES working groups.
The gyre index and the NAO are significantly positively correlated with each other between the years 1982–2010 ($r = 0.451$, $P<0.05$) with the NAO having a much higher variance than the gyre index (see Figure 5.2). The NAO is dominated by interannual variability although interdecadal periods of increase can be seen between 1900 and 1930, and from 1980 to the present, as well as decreasing periods e.g. 1960 to 1975. During the time frame for the biological data presented here, the NAO generally increases although interannual high frequency variations still exist. The gyre index follows a similar long term pattern with an increase in the index from 1980 to 1993 (representing cold fresh water) and then a decrease to a low index values in 1998 (representing warmer more saline water) (see Figure 5.2). It is important to note that an increase in the gyre index (and NAO) has differential consequences north and south of 54°N due to the unique hydrography of the area and the North Atlantic current (Marshall et al. 2000; Jansen et al. 2013). The gyre index is negatively correlated with blue whiting SSB ($r = -0.711$, $P<0.001$) and horse mackerel SSB ($r = 0.4133$, $P < 0.05$). There is a significant positive relationship with horse mackerel recruitment and the NAO ($r = 0.367$, $P < 0.05$). The SST is far less variable, although mean temperature (April – June 1977-2010) have been increasing significantly over time ($r = 0.913$, $P<0.001$), and mean SST is significantly correlated with blue whiting SSB ($r = 0.5$, $P<0.05$). Turbulence is significantly correlated with the NAO index only ($r = 0.645$, $P<0.001$), and the GI is significantly negatively correlated with the mean SST ($r = -0.544$, $P < 0.01$). Mackerel have no significant correlations with the environmental indices.
The primary trend of variation in the environmental data were summarised by the first principle component (PC) of the PCA of environmental variables (SST, NAO, turbulence and GI), which explained 49.3% of the variance. The loadings of the first PC characterised a long term decline (correlation with year, $r = -0.455$, $P < 0.01$), with a switch between 1994 and 1996 from positive values to negative values coinciding with a switch in the gyre index at around the same time (see Figure 5.3). The first component was highly correlated with all four environmental variables, positively with the gyre index, turbulence and the NAO ($r = 0.740$, $0.618$, $0.844$, $P < 0.001$, respectively) and negatively with SST and year ($r = -0.576$; -0.455, $P < 0.01$). There was a significant relationship between the logged horse mackerel recruitment and the first principle component loadings ($r = 0.385$, $P < 0.05$), and blue whiting SSB ($r = -0.402$, $P<0.05$).
Figure 5.3 Principle component trends over time from the temporal PCA using the 4 environmental data sets. The black line represents PC1 and the red line represents PC2.

PC2 explained 32.6% of the variance in the environmental data, the loading trends were significantly correlated with all four environmental variables again, positively with SST, NAO and turbulence \( (r = 0.677, 0.368, 0.697, P<0.05) \) and negatively with GI \( (r = -0.475, P<0.01) \). Only blue whiting SSB is significantly correlated with the second principle component.

A PCA of all recruitment indices together \( (1977-2010) \) showed PC1 represented 50.7% of the variance of the data, with the loadings to the first component not significantly changing over time. PC1 loadings trend over time was not significantly correlated with any of the environmental variables \( (P>0.05) \). PC2 loadings significantly decreased over time (correlation with year, \( r = -0.416, P<0.025 \)) and was significantly correlated only with the GI \( (r = 0.372, P < 0.05) \).

Best subset analysis was performed using combinations of: the four environmental data sets together, SSB data from all three species and environmental data sets together, and principle components one and two from the environmental PCA analysis. In general, the model fits were poor, the best model included blue whiting as the response variable and included SST,
turbulence, and mackerel and horse mackerel SSB, with an adjusted $R^2$ value of 60.2.

### 5.4.2 Recruitment threshold responses

To test for common modes of variation between environmental variables and extreme recruitment years, a temporal PCA using four environmental variables was carried out and the loadings were plotted and grouped into categories according to extreme recruitment years (defined as outside of 1 standard deviation from the mean for at least two of the species recruitment indices) and average recruitment years. The ordination of environmental variables loadings can be seen in Figure 5.4. There appears to be little structure in groupings of extreme recruitment years according to the association of the recruitment event year to the 2D ordination of the environmental PCA. However, the majority (eight out of ten) extreme recruitment years appear in the positive region of PC2 loadings. PC2 loadings are significantly correlated with SST, NAO and turbulence, and negatively with the GI. Therefore more extreme recruitment events occur in years where there is strong turbulence, higher SST values and a more positive NAO index, and also when there is a weak GI.
Figure 5.4 Environmental PCA analysis – Principle components 1 (x axis) and 2 (y axis) – identified by average recruitment years (black circles) and extreme recruitment years (red circles – years in which at least 2 species recruitment values are outside 1 standard deviation from the mean of the individual time series).

5.4.3 Within population spatial analysis to environmental forcing

5.4.3.1 Mortality rates

The Paulik diagrams (Figures 5.5 and 5.6) show the total annual abundance of stages plotted against each successive stage in order to identify anomalous years of high or low egg stage transition mortality rates, as well as general abundance levels. The Paulik diagram for mackerel identifies 1977 and 1998 as very low total egg abundance, whereas 2007 was a year of exceptionally high egg abundance with 1983, 1986 and 1989 being relatively high, compared to other years. The ‘extreme’ abundance years such as 1977 (low) and 2007 (high) were the same for both horse mackerel and mackerel. Horse mackerel had low total egg abundance for 1983 and 1986, and a slightly lower abundance for 1992 and 1995. The residuals of abundance per stage transition

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were tested for correlations within and between species but no significant relationships were identified, except with mackerel (stage 2-3 and 3-4, \( r = -0.616, P < 0.05 \)).

There is a clear relationship between the difference in relative abundance of the first and last development stage, (which is characterising mortality) for mackerel and horse mackerel (mackerel annual mortality correlated against horse mackerel annual mortality, \( r = 0.801, P < 0.002 \)). Egg transition stage mortality is positively correlated with initial egg density for stage one to stage two eggs in mackerel \( r = 0.981, P < 0.001 \)) and horse mackerel \( r = 0.985, P < 0.001 \)). Also the slope of the regression line is representative of the average mortality between stages. Although the slope appears relatively similar in all cases, there is a similar pattern between egg stage mortality of mackerel and horse mackerel with stages one-two transition having a shallower slope (higher mortality), compared to the steepest slope of stage two-three (lower mortality). The 'mortality ratio' showed a significant correlation between stages four and five (mackerel stage 5/mackerel stage 4) and recruitment \( r = 0.742, P < 0.05 \), however none of the other development stage fractions were significantly correlated with recruitment.
Figure 5.5. Paulik diagrams showing the annual mean of western stock of Atlantic mackerel egg surface density for stages 1-4 plotted against each other
Figure 5.6. Paulik diagrams showing the annual mean of western stock of horse mackerel egg surface density for stages 1-4 plotted against each other, and time series of first egg development stage minus final egg development stage for mean annual egg surface density for mackerel and horse mackerel.
5.4.4 Between Species Analysis

5.4.4.1 Spatial patterns over Time

The spatial dynamics of mackerel, horse mackerel and blue whiting showed different responses to environmental conditions (see table 5.1). The centre of gravity of northings for Atlantic mackerel stage1 eggs increased significantly over time (correlation with year, mean $r = 0.834$, $p < 0.01$) (Figure 5.7, Table 5.1), although eastings were only significantly correlated with year for stage four ($r = -0.723$, $P < 0.001$). The inertia increased significantly for all egg stages (mean $r = 0.723$, $P < 0.05$). In contrast the western stock of Atlantic horse mackerel egg density abundance centre of gravity does not change significantly over time for eastings or northings stages 1-4 (correlation with year, $P > 0.05$) (Figure 5.7), however the spatial variance associated with the centre of gravity significantly increased over time for all stages (correlation with year, mean $r = 0.755$, $p < 0.05$). The blue whiting centre of gravity is increasing significantly with year for eastings only ($r = 0.962$, $P < 0.01$) (Figure 5.7), but the inertia does not increase or decrease.
Figure 5.7. Centre of gravity (northings and eastings) for mackerel (stages 1-5), horse mackerel (stages 1-4), and blue whiting.
5.4.4.2 Environmental CoG and recruitment

The centre of gravity of SST was determined for each stage of the mackerel and horse mackerel for each of the survey years. The centre of gravity of mackerel egg stages SST did not significantly change for any stage, although the mean temperature of the northeast Atlantic (NEA) (63° to 40°N and 0° to -20°W) for the survey years did significantly increase over time (correlation with years, r = 0.913, P<0.0001), with the CoG of bathymetry becoming deeper (mean r = -0.774, P < 0.01). For horse mackerel the SST CoG for all stages increased over time (mean correlation with years r=0.744, P<0.05), and were all significantly correlated with mean SST for the NEA (mean r=0.784, P<0.01). The horse mackerel CoG of bathymetry did not change over time (P>0.05) (see table 5.2). Blue whiting CoG of environment did not change over time for any of the variables.

5.4.5 Early life stage distribution patterns with recruitment

To test the associations with mackerel and horse mackerel egg stage distribution and the environment, northings, eastings and inertia were plotted against SST, NAO and GI (See Figure 5.8) and correlations were performed. All egg stages were tested although only stage 1 eggs are shown, as they are representative of subsequent stages relationship trends (although relationships are not necessarily statistically significant). Mackerel northings were significantly associated with mean SST (r = 0.662, P < 0.05), although horse mackerel was not. Mackerel inertia was also significantly correlated with mean SST (r = 0.851, P < 0.01), as well as horse mackerel inertia and SST (r = 0.718, P < 0.05). The inertias of both mackerel and horse mackerel were also significantly correlated with the GI (r = -0.618; -0.663, P < 0.05, respectively).
Figure 5.8 Plots of the distribution against environmental index. Black points = mackerel; red points = horse mackerel.
Mackerel and horse mackerel distributional response to the environmental forcing of the mean SST of the NE Atlantic, NAO, turbulence and GI are inconsistent. The mean SST of the NE Atlantic show that mackerel eggs are spawned further north in warmer years ($r=0.662$, $P<0.02$), and further north in years of a low GI ($r=-0.879$, $P<0.05$). The NAO is not significantly related to either species estimates of northings, although this may be due to the spatial heterogeneity of the effects of the NAO north and south of the zero curl and could be addressed by spatially splitting the data at $54^\circ$ north and looking at the two regions individually. The inertia of mackerel is significantly related to mean SST (mean $r=0.853$, $P<0.002$) and GI (mean $r=-0.629$, $P<0.05$), although not to the NAO and turbulence. In contrast horse mackerel has no significant correlation between northings and SST or the GI ($P>0.05$) but is significantly correlated to the NAO ($r = 0.693$, $P<0.05$). The inertia of horse mackerel egg stages (1-4) has a significant relationship with the SST (mean $r = 0.676$, $P<0.05$) and GI (mean $r = -0.726$, $P < 0.05$), whilst turbulence is not significantly correlated with inertia and the NAO is significantly negatively correlated only with inertia trends in stage 4 ($-0.714$, $P<0.05$).

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*** \( P<0.05 \)  
** \( P<0.01 \)  
* \( P<0.001 \)
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* *** P<0.001  
** P<0.01  
* P<0.05  
* P<0.001

**Table 5.2** Correlations between the biological indices for mackerel, horse mackerel, and blue whiting and environmental indices.
5.5 Discussion

There is an underlying drive in stock assessment to focus on describing interannual variability in recruitment dynamics for the purposes of allocating total allowable catch (TAC) which is highly dependent on stock-recruit relationships (Myers et al. 1994). The results presented here indicate the difficulties in picking out coherent trends in space and time between environmental patterns (sea surface temperature (SST), north Atlantic oscillation (NAO), gyre index (GI) and turbulence), and biological responses (recruitment and spawning stock biomass (SSB)), of pelagic fish species in the northeast Atlantic. However patterns did emerge between individual stock parameters over time, and environmental variables, as well as between the stock dynamics of different species.

The principle component analysis (PCA) of environmental data illustrated associations between the four environmental indices used in this analysis. SST, NAO, turbulence and GI were all significantly correlated to principle component (PC) 1, suggesting the primary mode of variation within all datasets combined, is representative of each individual pattern. PC1 was positively correlated with the NAO, GI and turbulence, whilst it was negatively correlated with SST and year. PC1 was also significantly correlated with horse mackerel recruitment (which on its own was positively correlated with the NAO), and blue whiting SSB (which on its own was significantly positively correlated with the SST and negatively with the GI) suggesting that analysing environmental data synchronously using a multivariate technique is a useful way to summarise dynamic environmental information. PC2 indicates that whilst SST, turbulence and the NAO were similar (positively correlated with PC2) the GI is negatively correlated, suggesting the GI has some unique influence over the region, being different in its trend to the other environmental indices used here. PC2 of the environmental PCA was significantly positively correlated with blue whiting SSB alone.

There is relatively substantial evidence for the links between blue whiting distribution and the strength of the GI (Hatun et al. 2009a; 2009b). It has been speculated that blue whiting recruitment may be affected by the strength of the sub polar gyre (Hatun et al. 2009a), due to the known associations between early life stage survival and recruitment (Hatun et al. 2009a). Payne et al. (2012) demonstrated a synchronous (but not statistically significant) change in the GI and blue whiting recruitment in the 1990’s, although the results presented here show no significant relationship. Atlantic mackerel SSB and recruitment were not significantly correlated with any of the environmental indices neither with the environmental PCA outputs. The PCA of the
recruitment data showed a significant positive relationship between PC2 and the gyre index. The relationship between the gyre index and the biological outputs appears to be clear, possibly as a result of the strong positive correlation between the SSB’s of blue whiting and horse mackerel.

The biological stock dynamics between the species are very different. Whilst blue whiting have not changed in their CoG of northings, the CoG eastings has significantly shifted over time, although the time series is very short thereby increasing the chances of a spurious correlation; however the result does support previous research that adult spawning distribution is affected by the GI (Hatun et al. 2009a). The SSB of blue whiting is significantly related to mean SST of the area possibly indicative of a positive direct or indirect effect. Direct effects might be increased growth rate which has been seen with increased temperatures in a number of studies (Egglishaw and Shackley 1973; Finstad and Jonsson 2012); indirect effects might be trophic interactions of increased prey availability (Lauria et al. 2012; Trueman et al. 2012). The fact that their CoG of SST did not significantly change over time, might suggest the relationship with mean area SST is not a direct, but an indirect effect, or perhaps a unauthentic correlation rather than a mechanistic one. The blue whiting time series for distribution is relatively short and therefore a longer time series would produce more robust relationships.

In contrast mackerel have undergone a latitudinal shift in their CoG in response to ambient water temperature significantly warming, which supports previous research (Walsh et al. 1995; D’Amours and Castonguay 1992; Jansen et al. 2012a; 2012b). However their CoG SST has remained unchanged and neither their SSB nor recruitment has a significant relationship with any of the environmental variables tested here, despite previous links between, for example, recruitment and storminess in the southern Bay of Biscay (Villamor et al. 2011), although this was only examining one year and not time series data. Thus a factor in the degree of relatedness between SSB and recruitment and environmental forcing may be a population’s ability to acquire favourable environmental conditions through changes in distribution. This result is also supported by the significant correlation between horse mackerel SSB and the GI, and horse mackerel recruitment and the NAO, and the general stable distribution over time, of horse mackerel. In contrast, past research has linked horse mackerel distribution to the NAO (Reid et al. 2001) and upwelling (Santos et al. 2001). It is worth noting that the inertia of mackerel and horse mackerel is increasing over time, however as discussed in Chapter 2 this may be an effect of the increase in survey effort and area. However it does strengthen the southerly distribution of horse mackerel in comparison to the northward shift in mackerel distribution, as despite the survey effort increasing
in northwest extent, horse mackerel remains unchanged in average spawning distribution.

Whilst independent relationships exist between the recruitment and/or SSB of the stocks and environmental variables, there is evidence to suggest that some degree of interaction between the species occurs. For example, mackerel SSB has a significant negative relationship with blue whiting and horse mackerel SSB. Furthermore blue whiting SSB and recruitment is significantly negatively correlated with horse mackerel spawning stock biomass. There is evidence to suggest that mackerel is a top predator around Portugal and blue whiting is the main fish prey of mackerel (Cabrel and Muta 2002). The negative interactions between species found in these results are one of the key findings of this chapter. Payne et al. (2012) hypothesised that mackerel predation on blue whiting may affect blue whiting SSB and the degree of spatial overlap of the two stocks is governed by the sub polar gyre. Predation has been accepted as one of the most important causes of egg mortality and mackerel juveniles have been reported as feeding almost exclusively on zooplankton and fish eggs which includes cannibalistic tendencies of feeding on their own species, with density dependence often a factor in recruitment investigations (Lorenzen and Enberg 2002). Therefore if there is heavy feeding by mackerel when there is a spatial overlap with blue whiting there may be a negative interaction. As a result, the interaction between mackerel and blue whiting may oscillate according to the degree of spatial and temporal overlap. The opportunistic feeding of mackerel means that if there is little or no coherence in the timing and geographic distribution of the two species then there is likely to be little interaction. Since Atlantic mackerel are moving further north, it may be postulated that there might be an increased spatial overlap between the two species in the future, and therefore an increase in the degree of negative interactions, although the temporal frame would also at as an influencing factor for this.

The results in the best subset analysis presented in this Chapter also support the influence the SSB of mackerel and horse mackerel have on blue whiting recruitment. Food availability has been shown to have a large effect on the survivorship of early life history stages of fish species (Bartsch and Coombs 2004) as well as the timing of egg production (Bartsch 2005), which was not examined here. Past studies have shown how one species abundance and distribution can influence another species abundance and distribution (Yan et al. 2001; Genner et al. 2001). The links between blue whiting SSB and recruitment, and horse mackerel and mackerel SSB presented here suggest it would be worthwhile to test spatial overlap alongside SSB and recruitment links between all three species, perhaps using niche overlap models or index’ (Pianka 1974; Hurlbert 1978; Wissinger 1992). It will also be interesting to see
whether the relationship between horse mackerel recruitment and mackerel SSB will remain over time, considering the increasing spatial divergence between the CoG of northing in the two species.

Mackerel are spawning further north and in deeper waters appearing to mitigate an increase of general warming in ambient temperature (maintaining a CoG SST) which is a theme discussed throughout this thesis (see Chapter 2 and 3), whilst horse mackerel are not significantly changing in latitude, or spawning depth and are increasing in their CoG of SST. The changes in distribution will have an effect on: the respective oceanographic environments each population will experience (Hatun et al. 2005; Bartsch 2005), food availability (McGinty et al. 2001; Hillgruber and Kloppmann 2001) and temperatures (Bartsch 2005). In particular, temperature has been shown to affect mackerel and horse mackerel growth rates (Lockwood and Nichols 1977; Bartsch and Coombs 2002; Portilla et al. 2007), which in turn has been shown to affect mortality, with faster growing individuals surviving better (Anderson 1988).

The analysis of egg mortality supports previous work presented by Portilla et al. (2007). Here, it is shown that annual egg mortality rates are related to initial egg production for both mackerel and horse mackerel (as shown by Portilla et al. 2004), as well as a higher mortality rates between stages 1 and 2 (Portilla et al. 2007), and a lower mortality in stages 2 and 3. An interesting relationship with mackerel ‘mortality ratio’ (stages 4 and 5) and recruitment was also present, although the mechanism as to how this might be related would require further analysis, perhaps examining growth rates (temperature), predation, or perhaps oceanographic features such as advection/retention.

The temporal extension of the index of turbulence suggests a break down in the relationship found between surface water mixing, and mackerel recruitment, as put forward by Borja et al. (2002). Using the same temporal window, but the latest recruitment VPA estimate, the relationship Borja et al. (2002) reported was still present. Environment recruit relationships have been shown to break down when tested with longer time series analysis (Myers 1998). Whilst the index was determined from different sources (as is often the case with oceanographic or hydrometeorological data), the overlapping period within the turbulence data had a strong correlation which suggests co-linearity and supports the relationship reported on in this Chapter between Atlantic mackerel recruitment and turbulence. Interestingly, turbulence featured in the best subset analysis, suggesting the inclusion of an environmental variable that is not directly correlated with recruitment (although an interplay might still be present), might help explain interrelated processes between multiple variables.
Perhaps investigating turbulence in concurrence with the timing and onset of seasonal stratification would be more informative as to the actual strength of the relationship as mackerel eggs are evenly distributed in the upper 200 m of the water column with no stratification; however mackerel eggs become shallower (<25 m) with the onset of seasonal stratification (Bartsch 2005), which would increase the effect turbulence has on the potential survivorship of the eggs.

I aimed to explore whether any common threshold responses are masked by the near independence of recruitment dynamics of the different species. Using extreme recruitment years (outliers) between three different species in the northeast Atlantic provides a novel approach to ascertaining commonalities between very high or very poor survivorship of different species, and the environmental influences that might contribute to recruitment strength. There did not appear to be any clear common relationship between years of extreme recruitment and the temporal pattern of variation in the environmental dataset. There did however, appear to be less extreme recruit events in the negative scale of PC2 which suggests a potential relationship between higher SST values, positive NAO phases and high turbulence values, whilst the GI is relatively low. The NAO positive phase represents a cold and dry climate whilst a negative phase is warmer and wetter (Visbeck et al. 2001). Whilst the effects of the NAO can be summarised briefly, the dynamics of the changes over a large area are highly variable and have been shown to significantly affect distributions of marine species (Fromentin and Planque 1996) and growth seasons (Post and Stenseth 1999), including fish population fluctuations (Lehodey et al. 2005). Wind has also been shown to have an effect on recruitment, although in a complex interaction (Roy and Reason 2001). Therefore there is evidence to suggest that this method of identifying more ‘extreme’ relationships might be a good way to start investigating environment/biological coupling.

The ability to detect changes in recruitment as a function of environmental characteristics is heavily reliant on the time scale of the environmental and recruitment data. Large fluctuations in interannual recruitment are widespread in pelagic fish, but the lower frequency persistent dynamics have also been documented, e.g., the sub polar gyre index (Hatun et al. 2005). Such longer term dynamics can be obscured by the higher frequency shorter term irregularities and require a long time series of biological data spanning decades (Payne et al. 2009). Therefore long time series data would be a useful start point, with already substantial records for a number of different species. Including more species into an analysis such as this, and perhaps increasing the level of ‘extreme’ (i.e. to perhaps 2 standard deviations) might better represent some of the ecological patterns at play.
The near independent recruitment dynamics of the 3 species suggest different scenarios may be occurring. Firstly, different biological responses may arise from the same or similar environmental forces between species, as a consequence of varying life history characteristics and niche requirements (Nyberg et al. 2001). Alternatively, local mechanisms specific to each species habitat, act in some way, to mediate the environmental impact on the biology of the species, through distorting, amplifying or reducing the broad scale forcing. A combination of these might be the case, to some extent. Whilst there are independent patterns between the three species, the results presented here suggest that in fact, there are relationships that are worth exploring further, and that a multi-species, multivariate approach has been useful in deriving significant relationships between inter-stock dynamics and the environment. In particular, the relationships between spatial overlap and trophic interactions (or resource competition) between mackerel, horse mackerel and blue whiting would be a logical next step for research. Perhaps (considering the differences in spatial distribution and the heterogeneous landscape of the northeast Atlantic) a varying spatial scale analysis would be suitable, to capture local as well as broad scale interactions: as well as a dietary analysis. Also, considering the interesting dynamics regarding the mackerel and horse mackerel egg stage mortality results, and the same/similar patterns have been found previously – it would be beneficial to bridge the gap between egg mortality and spatial dynamics, and mackerel and horse mackerel SSB, by attempting to obtain CPR samples of larvae to test links between abundance and distribution, and recruitment.
5.6 References


D’Amours, D. and Castonguay, M. 1992. Spring migration of mackerel, Scomber scombrus, in relation to water temperature through Cabot Strait (Gulf of St. Lawrence). Environmental Biology of Fishes. 34 4: 393-399

Eaton, D.R. 1989. Spawning stock biomass of scad (Trachurus trachurus L.) to the west of the British Isles, as indicated by egg surveys. Journal du conseil Conseil international pour l’exploration de la mer. 45: 231-247


Häkkinen, S., Rhines, P.B. 2004 Decline of the subpolar north Atlantic circulation during the 1990s. Science 304 5670 555-559


Lapointe, M.F., Peterman, R.M. and MacCall, A.D. 1989. Trends in Fishing Mortality Rate with errors in natural mortality rate can cause spurious time trends in fish stock abundances estimated by virtual population analysis (VPA. Canadian Journal of Fisheries and Aquatic Sciences. 46: 2129-2139


Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., Fromentin, J-M., Hare, S.R., Ottersen, G., Perry, R.I.,


Lockwood, S.J. and Nichols, J.H. 1977. The development rates of mackerel (Scomber scombrus L) eggs over a range of temperatures. ICES CM 1977/J:13


Myers, R.A. 1998. When do environment-recruitment correlations work? Reviews in Fish Biology and Fisheries. 8: 283-305


Chapter 6: Thesis Discussion
6.1 Summary

The aims of this thesis were met succinctly using the methods applied in this piece of novel research. The aims were four fold:

1) Identify spatial changes in northeast Atlantic mackerel (NEAM) spawning distribution taking into account the survey effort. As well as a general change the aim was to identify finer spatial resolution changes in the mechanisms of the changes in distribution in the form of the variance of spread and the direction of spread.

2) To determine whether useful information could be gained from international mackerel catch data (ICD), for example whether management regimes could be identified, whether the main fisheries could be identified and what habitat associations come from the distribution of the fishery throughout the year, not just the spawning season.

3) To identify changes in the distribution of North Sea cod in varying spatial scales to assess whether changes are site specific or relatively homogenous over all sites. Also density dependent habitat selection was tested for Celtic Sea cod as well as general changes in distribution.

4) To assess how similar are the responses of fish populations living in a spatially overlapping area of the northeast Atlantic. To ascertain whether a ‘system’ approach using multiple species or environmental variables would be more informative than a single variable approach.

Two particularly important and novel results came from the thesis presented here. Whilst there have been a number of studies that have examined changes in populations distribution (Rose 2005; Simpson et al. 2011), few have investigated the role of the data collection from the survey effort. Although this is not usually examined when looking at changes in a populations distribution, we show in chapter 2 that it is very important to examine the influence of the survey effort. The results highlight the need within the survey to delineate the peripheral spawning areas and to maintain consistency in the southern regions. By looking at the survey effort, it was also possible to attempt to separate the relative effect of the survey effort using a randomizing procedure. This method is highly repeatable and could be adopted by other surveys such as trawl surveys and other pelagic surveys for eggs and adult fish. There are other methods that might also be employed which were also tested for the purposes of the aims of this thesis, such as examining a ‘core’ sampled area, however the integrity of the data was such that this did not allow conclusive results to be determined.

Another important and novel finding was in Chapter 3 when the mackerel fishery was identified in space for all quarters of the year. Whilst the mackerel
egg survey allows an temporally and spatially explicit analysis of the spawning season, the rest of the year is less well known about in terms of the distribution of mackerel. Some tagging studies have shown spot distributional changes however by using the catch data we show how informative this source is. Identifying the main fisheries from 1977 to 2010 however, shows a far more comprehensive way to method for examining changes in distribution over time, which is imperative for the successful management of the stock. Heterogeneity in space and time of different stock components such as eggs, larvae and juveniles is common in fish populations and for successful management it is important to protect the early life history stages of the stock. This is because recruitment of a fish to the fishery is often dependent on surviving the early life stages. It is particularly important for mackerel who have shown to have nursery areas around the south west of England in the ‘Cornish box’ or ‘mackerel south west box’. Indeed management effects such as the closure of this box in the early 1980’s was picked up by the analysis presented in Chapter 3 demonstrating its sensitivity to changes in the distribution of the catches.

In both of the findings mentioned above, there appeared to be a climate signal in that northeast Atlantic mackerel adjust their distribution to maintain a preferred thermal window. The information relating climate to the distribution of NEAM is important considering the predicted changes that are expected to happen in the northeast Atlantic in terms of temperature rises.

One data source pertinent to all study species of the present analyses would be sea temperature at depths specific to each species distribution in the water column. A number of studies have shown the importance of temperature as a controlling factor in the distribution of mackerel (Beare and Reid 2002) as well as the speed and direction of migratory pathways (Walsh et al. 1995; Reid et al. 2001), the timing of migration and the initiation of spawning (Lockwood 1977; Reid 2001; Reid et al. 2001; Jansen and Gislason 2011; Jansen et al. 2012; Radlinski et al. 2013; Jansen et al. 2013) and for the timing of egg development (Lockwood 1977; 1981), including the results presented here. Horse mackerel egg development is dependent on temperature (Lockwood and Johnson 1977)

Whilst in situ temperature data was obtained for the mackerel ichthyoplankton surveys, the data set was broken with significant levels of missing values due to some countries not recording temperature towards the beginning of time series. One possible way around this would be to use modelled sea temperature data at depth such as the “Subsurface temperature and salinity analyses by Ishii et al.” data set (Frontier research system for global change 2005). By superimposing the temperature data from each survey year at varying depths onto the distribution of spawned stage 1 mackerel eggs, it may be possible to gauge a more accurate record of the temperature the mackerel are likely to be
experiencing within and between years. The analysis for the CoG of sea temperature for cod in the North Sea stressed the difference that exists between the SST and SBT. For mackerel who are generally found at the location of the 200m contour at the CSE, the temperature experienced is likely to be different from the SST used in the analysis for Chapters two and three, warranting the need to understand in situ temperatures.

Furthermore an analysis of the onset and development of the thermocline at specific latitudes would be useful as the distribution of mackerel eggs within the water column can change according to the thermal stratification of water (Reid et al. 2001). The latter analysis would be useful to bridge mackerel spawning distribution to potential patterns in recruitment success which may be related to development rates of eggs.

A second method for ascertaining in situ temperature data would be through electronic tags such as satellite or archival pop up tags. Block et al. (2001) showed differences between in situ temperature of blue fin tuna (Thunnus thynnus) and the SST record for the same region, the authors also described specific depth profiles which acted to indicate episodes of spawning behaviour, leading to conclusions about the maturation of individuals of various sizes. Atlantic mackerel have been previously tagged for discerning stock structure between the western and southern spawning components (Uriarte and Lucio 2001), as well as studying migration pathways (Uriarte et al. 2001), on a tag, release, recapture method. Whether the technology (i.e. size) of electronic tags would be suitable for a smaller fish such as mackerel may be the limiting factor at this stage although this method should not be ruled out for future study.

Overall, the main findings of this thesis include, a northward movement of Atlantic mackerel spawning distribution, associated with a change in survey effort and warming waters, with a greater proportion of mackerel spawning over the Porcupine Bank and Goban Spur. Multivariate analysis using mackerel catch data highlighted the European continental shelf edge (CSE), southern Norwegian Sea and northern North Sea as important fishing areas for the international mackerel fleet. In general, relative abundance of catch avoided warming waters through an offshore or northern shift in distribution, and the fishery was shown to have expanded which is indicative of a reduction in catch per unit cost of fuel. The North Sea cod metapopulation changed in average distribution (CoG) with a north-west movement from 1977-2010. However high resolution spatial analysis demonstrated highly heterogeneous site specific abundance variations in survey locations, with most locations responding in a similar fashion, a pattern which was weakly significant and broke down with increased distance, rather than locations at greater distances acting in opposition in abundance trends over time. Although only a sub sample of Celtic and western Channel cod were analysed there was no
significant directional movement of the population, and density dependent habitat selection was not apparent, as has been shown for North Sea cod and cod in the western Atlantic.

Finally, Atlantic mackerel SSB was shown to have a significant relationship with the SSB’s of blue whiting and horse mackerel, with previous evidence suggesting a trophic effect between the species, also the SSB or blue whiting and horse mackerel were negatively correlated. Significant relationships were also found between horse mackerel recruitment and the NAO, and blue whiting SSB was positively related to the mean SST of the north east Atlantic (NEA) but negatively correlated with the GI. The relationships were supported through a multivariate analysis with all environmental variables. Extreme recruitment events tended to be more related with high SST, NAO (positive) and stronger turbulence events, and a weak GI. However, the previously established relationship between turbulence and mackerel recruitment (Borja et al. 2002) broke down over the longer time period. Similar patterns emerged between the mortality estimates of egg development stages of mackerel and horse mackerel with mortality rates between stages 4 and 5 of mackerel positively related to mackerel recruitment. Differences in distribution of mackerel, horse mackerel and blue whiting suggested species specific responses to particular niches or ecological habitats.

The methods used in this thesis can be broadly defined into two research areas; spatial statistics and multivariate statistics with the incorporation of temporal aspects. Both these approaches were within the theme of obtaining science that would be used to underpin an ecosystem approach to fisheries analysis. Spatial statistics were used to summarise mackerel, cod, horse mackerel and blue whiting population distributions through time as well as the most likely environment experienced by the individuals within the population (mackerel and cod), or a sub-unit of the population. The EAFM (FAO 2008) is particularly relevant to current management and scientific research focus and is represented by the methods used in Chapter 2 where mackerel catch data were analysed with respect to both fishing and environmental effects, and again in Chapter 5 where a multi species comparative approach for describing recruitment variations and broad scale environmental forcing was performed using mackerel, horse mackerel and blue whiting. High resolution spatial analysis was used to describe specific locations of change in mackerel egg distribution, mackerel catch and cod survey abundance data, which allowed spatially resolved, local environmental, climate and anthropogenic factors to be associated and discussed. Through these broad-spectrum approaches, relative impacts of change on pelagic and groundfish populations in the northeast Atlantic were discussed.
6.2 Describing broad scale spatial changes and associated environment

Atlantic mackerel annual centre of gravity (CoG) during the spawning season, was shown to move north in association with a preferred thermal niche in water temperature, and by doing so have avoided warmer waters further south. Recent research has reported on a northwest trend in NEAM Summer/Autumn feeding grounds (Nøttestad et al. 2012; Óskarsson et al. 2012), supporting the increased latitude reported on in the research presented here. As well, in a recent publication by Heath et al. (2012) a northern shift in NEAM landings, particularly between the 1970’s and 1980’s was reported, although it was speculated that this shift was possibly more related to changes in migration patterns and temperature (Walsh and Martin 1986; Walsh et al. 1995). A similar focus of research has also been adopted with western Atlantic mackerel by Overholtz et al. (2011), who estimated a northeast shift in distribution of approximately 250km over the last 40 years, which correlated with interannual variability in temperature and gradual warming. In contrast to the western mackerel stock which displayed an on-shelf movement, results in this thesis showed that NEA mackerel catch is moving offshore. These differences can be attributed to the unique current systems of each region with involves peculiar hydrographic features associated with the east and west North Atlantic.

Previous analysis into NEAM distribution patterns and environmental associations has aimed at the characterisation of separate stock units (Lockwood 1978, 1988; Lockwood and Shepherd 1984; Lockwood et al. 1980), describe migratory pathways using tagging studies (Uriarte and Lucio 2001; Uriarte et al. 2001), characterise environmental (depth, salinity and SST) associations to pre-spawning aggregations (Reid et al. 1997; Reid et al. 2001; Reid et al. 2003), however for each of these studies no more than two years of data were included in the analysis. Time series data examining distribution of Atlantic mackerel has been used in the analysis of migration route from 1973-1998 (Iversen and Skagen 1989) the timing of spawning and migration in the North Sea 1948-2008 (Jansen et al. 2011) and spawning distribution in NEA 1977-1998 (Beare and Reid 2002), migration and distribution in the North Sea 1985-2011 (Jansen et al. 2012a) and spawning distribution in the North Sea 1948-2005 (Jansen et al. 2012b). In this research the time series spans over 30 years which is unique to this data set, being the longest time series analysis using Atlantic mackerel western spawning component (WSC) egg survey data. These results are a timely update to Beare and Reid (2002) and are aligned with the EAFM by utilising the full extent of the mackerel egg survey data.
International policy in mackerel quotas has broken down in recent years, as from 2010 (The Stock Book 2010) Iceland and the Faroes have declared unilateral ‘total allowable catches’ (TAC’s) after speculation that mackerel are becoming more abundant in Icelandic and other northern waters (Rose 2005; Astthorsson and Palsson 2006), giving rise to Iceland claiming a larger portion of the catch – thereby reducing the catch of other mackerel fishing nations. A novel technique was employed to establish the relative effect of survey effort and temperature on the northward shift of mackerel spawning CoG, which could be summarised as a northward movement of 37.5km per °C increase. The characteristics of changes in location of Atlantic mackerel between 1977 and 2010 were tested using the spatial spread of the population around the CoG. Changes in the spread of the population were characterised not as a linear poleward shifts, but described in relation to the unique hydrography of the northeast Atlantic, to show the region of the Porcupine Bank as receiving a larger relative abundance of spawning mackerel at the end of the time series, than was the case in the late 1970’s and early 1980’s. One aspect not tested which has been investigated on the western Atlantic mackerel (Overholtz et al. 2010) and eastern Atlantic mackerel (Beare and Reid 2002), is distance along and across (or from) the CSE, which is an important spawning area of Atlantic mackerel. This would be appropriate considering the association shown between the morphology of the marine shelf area west of the British Isles and the distribution of annual spawning. It would improve the estimates of the northward shift considering the increase in topographic features in higher latitudes (e.g. Rockall Bank), and the results presented here suggest this may affect the rate and shape of the latitudinal increase in spawning events.

The CoG was also tested with North Sea cod, a proportion of the Celtic Sea and western Channel cod, horse mackerel egg stages (1-4), mackerel egg stages (1-5) and blue whiting biomass from acoustic surveys. This method proved a very useful summary statistic for population/stock scale distributional characterisation over time, especially when used in conjunction with higher spatial resolution techniques (EOF analysis). Throughout the research the CoG was also used to summarise environmental associations. In Chapter 3, this method was used to weight environmental indices by catch/abundance for isolated regions of high catch variability in Atlantic mackerel international catch data. The CoG of the environment described the most likely environment experienced by the stock using changes in relative abundance over the area. These changes were associated with fisheries management impacts, fleet and fishery changes through time and possible climate variability. Within isolated pockets of high variability in the mackerel catch data, the mean trend of the area SST and bathymetric depth was extracted and directly compared to the weighted trend. The results showed regions of warming associated with a decrease in mackerel catch abundance and an offshore movement, although the
driver of this change could not be separated from climate and/or fleet expansion patterns. Adaptation to climate signals could be identified, when the mean SST increased yet the CoG SST was not significantly increasing or decreasing. The analysis was also able to highlight highly resolved areas of high fishing intensity which can be useful in assessing density dependent effects of habitat selection of adult mackerel, and fishery impacts of these regions.

Behaviours such as hyperaggregation were speculated on for mackerel, and these could be readily tested by methods of density dependent habitat selection (as tested for Celtic Sea and western Channel cod), or perhaps analysis of lower catch abundance periphery locations (i.e. the outer locations of the fishery). This would be an opportune investigation as the western mackerel stock fishing mortality is above the maximum sustainable yield, and the results presented here demonstrate the mackerel international fishing fleet is having to fish further away from the European shelf to maintain catch levels.

6.3 Spatial aspects of fisheries analysis

Analysing fisheries data in high spatial resolution is important because of the complex heterogeneous marine habitat (Bormann 2006; Horne et al. 1996), localities of which may become more or less appealing to an individual, population or species within or between years or a life cycle (Tyler and Brandt 2001; Beamish et al. 2005). This is particularly true for mobile migratory species (Moustakas et al. 2006) such as mackerel, and groundfish species such as cod that have a strong association with local environmental factors (Methratta and Link 2007). Small scale non-random movements of individuals within populations may be masked within a large population (Sibert et al. 1998), as well as robust conclusions being dependent on the spatial (and temporal) resolution of the data (Dunn et al. 2009). The spatial aspect of this was seen quite clearly with North Sea cod; the metapopulation annual CoG results showed a simple northwest shift in distribution however the higher spatial resolution of the empirical orthogonal function (EOF) showed the spatial pattern was far more complex. The advantage of fishery dependent over independent data is the generally more continuous temporal collection over a large spatial area (e.g. mackerel international catch data), which potentially allows for more robust elucidation of species-habitat coupling by covering different aspects of life history (e.g. spawning/feeding). However, the disadvantage is that it is not independent of fisher’s behaviour and therefore should be analysed accordingly. Therefore the use of multiple data sets (fisheries dependent and independent, as well as vessel monitoring system (VMS) data for higher spatial resolutions) would render a comprehensive
overview of the biological stock, and the fleet behaviour, both of which is important in stock assessment and understanding ecological interactions between the environment and the stock.

The drive in demand for high resolution fisheries data analysis is recognised by the appreciation of the impacts of small scale local environmental forcings which can have a large impact on the population. For example mackerel have been shown to regulate position of prespawning aggregation as a response to depth specific slips of warm water (Reid et al. 2001); complex bathymetric features often appeal to deep water species such as shelf edge canyons (Brodeur 2001); salinity fronts at the shelf-slope interface on continental shelves and larval fish distributions (Sabatés and Olivar 1996). Recent management frameworks such as the Marine Strategy Framework Directive (EU, 2008), and the EAFM (FAO 2008) have driven a demand for fisheries data at a high resolution scales. The use of fine scale fisheries data can be used to evaluate and monitor reserves or marine protected areas, control small scale real time fisheries closures (Needle and Catariono 2011), especially with respect to contemporary ocean uses (aside from fisheries), such as renewable energy sources (wind and wave power), mining, fish farms, shipping etc.

The results presented in Chapter 2 shows how fisheries data can be useful for relatively high resolution spatial analysis. Whilst other data sources have a higher spatial resolution within the northeast Atlantic (VMS data (Gerrtisen et al. 2011); acoustic data (Reid et al. 2001)), drawbacks such as availability restrictions, short time periods (generally just a few years), computational requirements and data storage limit the useful application to pelagic fisheries spatial analysis when it is intended to relate longer term climate variability to stock distribution. Despite the fisheries dependent data source having management biases and fleet foraging aspects associated with it, it is possible to isolate areas of high catch abundance variation, characterise areas important to the international fishing fleet and differentiate between relative catch abundance changes due to legislation, and the environment/climate. Some changes in mackerel relative abundance distribution are very slight and within management areas which makes management regimes an unlikely causative affect. Coupling the high spatial resolution analysis with the environmental CoG analysis means that changes in relative abundance within an area can be identified as well as the difference between the mean environment of the area and the environment most likely experienced by the individual fish. In effect this increases the spatial resolution of the analysis within the regions identified using the empirical orthogonal function analysis (EOF).
In the North Sea, the cod population is shown to be moving northwest over time (1977-2010) in accordance with previous results (Hedger et al. 2004; Perry et al. 2005) however using a higher spatial resolution, the habitat specific abundance variations show how small scale changes are affecting the metapopulation. Despite the general population shift it is possible to conclude that most locations are responding in a similar way, although this pattern breaks down at larger distances, with no opposing phases in abundance patterns over time. The northwest shift in metapopulation distribution is not as a result of an increase in abundance in the north and a decrease in the south but a more complex array of environmental controls and biological preferences. The benefits of these results are synchronous with recent analysis in the North Sea cod population studies that shows that genetic and spatial structuring of cod within the North Sea is complex ranging across all locations (Hutchinson et al. 2001). Habitat specificity with cod distribution has been described in the past (Keats et al. 1987; Scott 1982; Clark and Green 1990), as well as predation risk (Gjosaeter 1987). Therefore the level of spatial resolution presented for the North Sea with the EOF analysis, coupled with the CoG analysis, involving more environmental data such as substrate type, predator and perhaps prey abundance, might offer a comprehensive insight into habitat selection, preferences and tradeoffs.

The current spawning stock biomass (SSB) trends of the stock however, and the historical association with high fishing pressure mean that information on ecological or habitat preferences may not be present in the data, to the same extent as if the stock was at the carrying capacity of the environment. Both the North Sea cod stock and the Celtic Sea and western channel cod stock are heavily fished and the relatively low SSB’s of the respective stocks may influence the amount of information that can be gathered about spatial patterns of distribution, as well as environmental relationships with long term population abundances.

6.4 Science supporting the ecosystem approach to fisheries management

The EAFM overall goal is for sustainability in the ecosystem as a whole, and not just the targeted species of the fishery (FAO 2008), it can be defined as “a balance (between) diverse societal objectives, by taking account of the knowledge and uncertainties of biotic, abiotic and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries” (FAO 2003). In Ireland the EAFM has been adopted by a number of research strategies (Beauford Marine research award project; Sea Change strategy; strategy for science
technology and innovation (see http://www.marine.ie/home/research/ProjectsDatabase/CurrentProjects/EAFM). The wide acceptance of the EAFM as a way to successfully manage fisheries drives the need to better understand the ecosystem and the connectivity between biotic components therein, so as to focus research interests in this area and therefore funding.

The results of Chapter 2 were analysed in the context of science to underpin the EAFM through understanding patterns of change, in terms of the environment (SST and Bathymetry) and anthropogenic influences (fishery management regimes) over time. This led to conclusions based on the effects of both impacts. Specifically, cases where a northern or eastern shift in relative abundance of catch within a local area has offset the impact of local warming of sea temperatures are highlighted. However, the fishery is expanding over time and the CoG of catch is moving away from the continental shelf and is coming from deeper water in more recent years, which may also impact the offshore, eastern or northern shift in relative catch abundance. Changes in relative catch abundance in some cases could be attributed to either management legislation or climate warming. Understanding the driving mechanisms of the change is important to as to predict potential future distributional configurations. This might also be important for ascertaining potential overlap with other species whether there may be an interaction such as blue whiting.

An approach to better understand recruitment dynamics of three pelagic species in the northeast Atlantic, in response to cyclic hydrometeorological forcing including the NAO, GI, turbulence and SST was carried out. A novel approach was developed in light of the independence of recruitment time series between the species to examine threshold responses to common environmental features. The approach included examining the ecosystem as an interrelated structure of variable factors, that act together to elicit particular responses in the biology of different species. For this a multivariate approach used numerous combinations of different data sets to attempt to identify patterns in the ‘ecosystem’ rather than a single predictor/response approach (which is often not temporally robust). Results were successful at identifying the role Atlantic mackerel SSB has on the SSB of blue whiting and horse mackerel. The relationship between the success of blue whiting recruitment and the degree of spatial overlap with Atlantic mackerel has been speculated on in the past (Payne et al. 2012), and to investigate the relationship further would fill a current gap in the scientific knowledge. Future research for this may include developing an index of overlap which can be used to predict future overlap and therefore the degree of possible negative interactions. Also, the use of a principle component analysis to reduce the number of significant
environmental variables that link between biological indices (SSB and recruitment) would be a useful method before, for example, attempting to model certain aspects of an ecosystem. For example, modelling early life history stages has been done in the past (Bartsch 2005; Bartsch and Coombs 2004) although the results presented in Chapter 5 suggest indicate particularly important environmental and biological factors that could provide useful information if included in the model (e.g. horse mackerel recruitment, the NAO and mackerel SSB).

The comparative study between the three species and the environmental data is unique to the northeast Atlantic wider Ocean although has been done in the Baltic Sea, as well as the approach of characterising extreme recruitment years as a novel approach. Considering multi-species responses to common environmental influences can help with understanding interactions between the species, which can be fed into management systems for greater certainties in stock assessments and a better understanding of fisheries impacts (Hollowed et al. 2000). In the Baltic one study showed the differences between using a multispecies approach compared to a single species approach (Gislason 1999). The author compared estimates of the biological reference points between using a multispecies versus a single species approach. The differences come when there appear to be biological interactions between predator and prey but the degree of interaction cannot be quantified (Gislason 1999). Other studies have compared different multispecies model types for the best model to explain productivity in fish stocks (Hollowed et al. 2000). Perhaps for the species used in this thesis it would be sensible for the next step to test the usefulness of structural equation modelling to take into account the interactions between Atlantic mackerel, and blue whiting and horse mackerel.

The same can be said for the comparative study in population abundance dynamics between North Sea and Celtic Sea and western Channel cod. Species distributions can depend on a number of different variables including habitat preferences such as depth, bottom type, hydrological conditions and also interactions with fishers, predators, prey and competitors (e.g. Mitamura et al. 2012; Thorrold et al. 2001). However, without the inclusion of fishing pressure which is one of the more significant impacts on the heavily fished stocks, false relationships may occur and real relationships may not be made clear. It is important to identify the ‘high impact’ variables before analysing data, and in the context of a multi-species, multi-environment approach – multivariate statistics (such as principle component analyses) can identify such factors.

Overall the thesis presented here has added significantly to the current scientific literature about fish stock distributions. The results presented here
are critical to better understand fisheries ecology and improve fisheries management. Whilst the results answer many questions, knowledge gaps are also identified which if addressed successfully may provide a more comprehensive insight to the causes of distributional patterns and changes.
6.5 References


FAO, 2008. Fisheries management. 2. The ecosystem approach to fisheries. 2.1 Best practices in ecosystem modelling for informing an ecosystem approach to fisheries. Supplement 2.1

Gerritsen, H. And Lordan, C. 2011. Integrating vessel monitoring system (VMS) data with daily catch data from logbooks to explore the spatial distribution of catch and effort at high resolution. ICES Journal of Marine Science. 68 1: 245-252


Jansen, T. and Gislason, H. 2011. Temperature affects the timing of spawning and migration of North Sea mackerel. Continental Shelf Research. 31: 64-72


ICES/ESSAS/PICES/AOSB Session – Subarctic-Arctic interactions: ecological consequences. ICES Abstracts – Theme Session M. ICES CM 2012/M:03


Reid, D.G., Eltink, A. and Kelly, C.J. 2003. Inferences on the changes in pattern in the prespawning migration of the western mackerel (Scomber scombrus) from commercial vessel data. ICES Cm 2003/Q:19


Uriarte, A. And Lucio, P. 2001. Migration of adult mackerel along the Atlantic European shelf edge from a tagging experiment in the south of the Bay of Biscay in 1994. Fisheries Research. 50 1-2: 129-139


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