Predicting the effects of climate change on south-west UK fisheries

Submitted by Bryony Uglow, to the University of Exeter as a thesis for the degree of Masters by Research in Biological Sciences

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

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Abstract

Climate change, caused predominantly by rising levels of atmospheric carbon dioxide, is changing the function and composition of marine communities. This thesis considers the past and potential future effects of warming seas, on the fish assemblage of the south-west UK. Using fishery-independent data, this research aims to identify trends in the abundance and diversity of key fish species over the past three decades, and predict how these trends may continue over the 21st century, according to forecasted climate scenarios.

The oceans have absorbed over a quarter of anthropogenic carbon dioxide since the Industrial Revolution, as well as over ninety percent of the Earths excess heat which has helped to mitigate the impacts of climate change. However, carbon dioxide emissions, and the subsequent rise in air and sea temperatures, have reached unprecedented levels in recent decades. Consequently, oceans are becoming more acidic, sea levels are rising, and weather events such as storms are increasing in both frequency and severity. Due to the complex and integrated nature of marine ecosystems, climate-induced changes are likely to affect organisms and communities at all levels, both directly and indirectly. This could mean changes to the composition of fish assemblages, which consequently will affect human populations reliant on them for food and income. Whilst fish stocks are prone to natural fluctuations and variability, there is a growing body of literature demonstrating that anthropogenic activity is having a significant, and perhaps irreversible effect on some fish populations.

The first part of the research conducted here demonstrates that since the mid-1980s there has been a significant increase in the species richness and diversity of the south-west UK fish assemblage, likely driven by an increase in the abundance of warm-water adapted species. In addition, some commercially important fish species typically associated with colder waters have decreased in abundance. The second part of the research in this thesis uses a data-driven predictive modelling approach to forecast how key species of the UK fish assemblage may respond (in terms of abundance and spatial distribution) to the latest predicted climate scenario. The results demonstrate that, according to a

“best case scenario” of carbon emissions, many of the warm water species shown to have increased in abundance over the last three decades will continue to do so. Similarly, many cold water species will continue to decline, such that some economically valuable species may be absent from south-west UK waters by the end of the century. The results also suggest that by the end of the century, the fish assemblage is likely to be characterised by species that currently have a lower latitudinal preference, smaller mean body size and lower trophic level.

The ability to predict and anticipate how fish populations may respond to a changing climate will be essential for the successful continuity of the fishing industry. As such, management plans and fishing practices will need to be adaptive and flexible in order to exploit new opportunities, as well as protecting and preserving the stocks most threatened by climate change.

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Abbreviations and Definitions

AIC	Akaike information criterion
CFP	Common fisheries policy
CPUE	Catch per unit effort
FAO	Food and Agriculture Organization
GAM	Generalised additive model
GCV	Generalised cross validation
GDP	Gross domestic product
GLM	Generalised linear model
GOV	Grande Overture Vertical trawl
GVA	Gross value added
HAB	Harmful algal bloom
IBTS	International bottom trawl survey
ICES	International council for the exploration of the seas
LS-mean	Least square mean
MPA	Marine protected areas
MRP	Maximum revenue potential
MSC	Marine stewardship council
NBS	Near bottom salinity
NBT	Near bottom temperature
PSU	Practical salinity units
RCP	Representative concentration pathway
SSB	Spawning stock biomass
SSS	Sea surface salinity
SST	Sea surface temperature
TSD	Temperature sex determination
TSN	Taxonomic serial number
WoRMS	World register of marine species

Chapter 1: Introduction

1. Background

Climate change affects physical, geochemical and biological processes at many levels. Marine-based environmental changes associated with climate change include a rise in sea level and average temperatures, ocean acidification, varying salinity and oxygen concentrations, and alterations to ocean circulation. Studies have demonstrated that climate change, in particular an increase in sea temperature, is linked to changes in fish behaviour, physiology, abundance and distribution. The seas surrounding the UK have experienced particularly intense warming over the last three decades, in some areas up to six times greater than the global average (Dye et al. 2013). The response of marine organisms to warming has led to compositional changes in fish assemblages (Genner et al. 2004; Simpson et al. 2011), which in turn has altered community structure and trophic dynamics (Cheung et al. 2013). There is strong evidence that warm-water adapted (Lusitanian) species such as grey gurnard (*Eutrigla gurnardus*) and red mullet (*Mullus barbatus*) are now found in abundance in the waters surrounding the UK (Beare et al. 2004), whereas some cold-water adapted (boreal) species such as Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) have shown a decrease in abundance (Simpson et al. 2013). These shifts in distribution may dramatically alter the structure of marine ecosystems, and will have consequences for the fishing industry.

The UK fishing industry’s contribution to the economy, in terms of gross value added (GVA), was £426 million in 2014; an increase of 14% over the last decade (Marine Management Organisation 2014). In this same year, fishery landings totalled 756,000 tonnes, with a value of £861 million; finfish accounted for 80% of the tonnage, and 66% of the value. The industry currently comprises 6,383 vessels, 27% of which are registered to four ports in south-west England (Newlyn, Plymouth, Brixham and Poole), of which the majority (~80%) are under 10m in length. There has been a steady decrease in the number of operational UK fishing vessels over the last two decades, attributed to a decline in fishing opportunities, as well as the decommissioning of vessels by UK fisheries administrations. This sequence of measures, along with quota restrictions set by the European Commission, were aimed at reducing fishing pressure to enable fish stock recovery. Demersal species in particular have experienced a significant decline in landings; in 2014 landings were less than 20% of the quantity landed in 1970 (Marine Management Organisation 2014). Whilst landings of pelagic species have fluctuated, they have not experienced the same decline as demersal species. Decreasing landings have been attributed to a number of causes, including a reduction in fleet size and restricted opportunities (Marine Management Organisation 2014), rising fuel prices (Abernethy et al. 2010), declining fish stocks (Molfese et al. 2014) and climate change (Simpson et al. 2011).

The increasing trend in sea surface temperature (SST) is expected to continue, with a predicted rise of 1.5–2.5°C in open ocean, shelf edge regions and the Northern North Sea, and a rise of 2.5–4.0°C for the Celtic Sea, Irish Sea and Southern North Sea by the end of the century (Lowe et al. 2009). There is some debate over how much of the observed increase is due to natural climate variability and how much is a direct result of anthropogenic activity and carbon dioxide emissions – some studies have suggested that natural climate variability could account for 50% of the observed warming in recent years (Dye et al. 2013) – but whatever the driver(s) the warming trend is unequivocal.

A number of studies have assessed both the past and anticipated future changes of the North Sea fish assemblage (Beare et al. 2004; Perry et al. 2005; Dulvy et al. 2008; Beaugrand & Kirby 2010; Petitgas et al. 2012; Rutterford et al. 2015), due, in part, to the substantial quantity of standardised data available for this area. In contrast, there is a lack of consistent, standardised data relating to fish abundance in other parts of the UK, particularly around south-west England. Consequently, few studies have considered the possible implications of climate change in this region. This thesis aims to address this knowledge gap. This Introduction chapter will review the effects of climate change on the different trophic and community levels within marine ecosystems around the UK, and explore the implications for commercial fisheries. The subsequent chapters of this study will explore how the fish assemblage in south-west England has changed in recent decades (*Chapter 2*), and how it may continue to change in the future (*Chapter 3*) in response to predicted climate scenarios.

2. Effects of climate change on fisheries and marine ecosystems

Climate data and models are widely used in research to make predictions about the ecological effects of climate change under different climate scenarios. Many predictions of species responses to climate change are based on bioclimate envelope models (also known as ecological niche models), which consider climatic variables as the primary factor influencing a species’ distribution (Pearson & Dawson 2003). Many of these models make the assumption that a species’ observed distribution is the best indicator of its climatic requirements, and that changing climate will directly influence changes in abundance and distribution (Pearson & Dawson 2003; Genner et al. 2004). However, due to the complex nature of marine ecosystems, these models often fail to take into account, or at least underestimate, the effects of other factors such as habitat availability and predator-prey interactions. Whilst these models do not account for dispersal, they predict a species’ potential range based on the predicted climate, which may be inaccurate when habitat availability and biotic interactions are also considered (Pearson & Dawson 2003). More recently, studies have focused on the use of multiple modelling approaches to generate a suite of predictions about the impacts of climate change, which is generally considered a more robust method (Araújo & New 2007; Jones et al. 2012; 2013). The variation between outputs from different models is often due to the characteristics and properties of the models themselves, and so comparing predictions from multiple models allows the uncertainty of each model to be identified, as well as establishing best and worst case scenarios (Jones et al. 2013). Most studies suggest that projections based on model predictions should be applied with caution, since the complexity of marine ecosystems means that individual and population responses to climate change may be counterintuitive (Genner et al. 2004).

2.1 Primary production

In recent decades the North Sea has experienced changes in phytoplankton and zooplankton composition, with many species showing northward distributional shifts (Beaugrand & Reid 2003). Models have predicted a 10% increase in productivity in the Celtic Sea and English Channel in response to climate change, but a 20% decrease in the central and northern North Sea (Simpson et al. 2013). Cheung et al. (2010) estimated that global primary production will increase by 0.7–8.1% by 2050, which has implications for increases in fish production. However, a study by Steinacher et al. (2010) found contradictory results, estimating a reduction in mean global primary production of 2–20% by 2100, compared to pre-industrial conditions. Another study conducted on the largest marine ecosystems found no large scale consistent trend in primary productivity over a 25 year study period, although some regional fluctuations were observed (Sherman et al. 2009). Changes to fish production have been shown to strongly reflect changes in phytoplankton production (Blanchard et al. 2012; Jones et al. 2015), and so an assumption adopted by many predictions is that fish production is proportional to net primary production. Where fish species may disperse and change in abundance in an area due to unfavourable conditions, they will often be replaced by functionally similar species, and so fish production and biomass may remain relatively unchanged, and the effect on trophic structure may not be as significant as expected (Brander 2007). Whilst temperature has been reported to be the main driving force behind many climate induced changes to fish populations, this may be an indirect effect through its impact on primary production; potential fish production has been shown to reflect changes in primary production more so than changes in temperature (Blanchard et al. 2012).

Atlantic cod is one of the most popular and commercially valuable demersal species in the UK; 14,700 tonnes were landed in 2014 with a value of £29.1 million (Marine Management Organisation 2014). Having been heavily exploited by commercially fisheries, Atlantic cod stocks halved between 1980 and 2000, which has generally been assumed to be a result of over fishing. However, studies by Beaugrand et al. (2003) and Beaugrand and Kirby (2010) showed that climate-induced fluctuations in plankton may also be having a significant effect on cod stocks. Beaugrand et al. (2003) showed that plankton fluctuations in the North Sea were significantly correlated to sea surface temperature, and that long-term changes in cod recruitment (the number of individuals surviving to an age at which they can be caught, thus recruit to the fishery) varied significantly with changes in plankton, often despite intense fishing pressure.

An increase in primary production may be expected at higher latitudes in response to climate change, particularly in areas where there is seasonal ice cover. A contraction of sea ice resulting in greater light penetration could enhance primary production (Brander 2007; Hollowed et al. 2013), as well as in other areas where warming of the sea lengthens the appropriate season (Genner et al. 2004). However, at mid latitudes surface warming of the sea may increase stratification of the water column, thereby compressing the mixed layer depth and reducing the nutrient supply required for primary production (Harley et al. 2006). The predicted increase in global primary production could lead to a potential increase in the occurrence of harmful algal blooms (HAB) and range expansions of certain HAB species (Peperzak 2003; Hallegraeff 2010), which could have significant consequences for fish populations.

2.2 Fish distribution, abundance and community structure

Early research suggested that rising sea temperatures due to climate change would result in poleward shifts in species distributions; cold-water species moving further north, and warm-water species expanding their range at the northerly limit to occupy newly available locations (Stebbing et al. 2002; Perry et al. 2005; Dulvy et al. 2008; Hiddink & ter Hofstede 2008). However, many of the studies upon which these predictions are based do not account for non-thermal dependencies, such as habitat requirements, predator-prey interactions and the dispersal abilities of individual species.

Climate induced changes to distribution, abundance and range have been observed in fish populations across the world. As average sea temperatures rise, UK waters will become more favourable for species currently occupying lower latitudes, but in turn will likely lose species to higher latitudes for which the temperatures become less favourable. Stebbing et al. (2002) suggested that the warming of the North Atlantic had resulted in warm water species expanding their ranges northwards, and were therefore occurring in increasing numbers off the Cornish coast. A more recent study by Simpson et al. (2011) showed that

72% of common UK demersal fish species were responding in abundance to warming seas, with the number of species increasing in abundance with warming seas being three times greater than those showing a decline. In addition to latitudinal shifts in distribution, some studies have reported fish species moving into areas of deeper water in response to temperature change (Dulvy et al. 2008; Rijnsdorp et al. 2009). Many fish species are constrained to a particular depth by factors such as oxygen requirement, prey availability and temperature. A study conducted on the fish assemblage in the North Sea found species had deepened by an average of 3.6 m decade^{-1}, with certain species (megrim; *Lepidorhombus whiffiagonis,* and angler; *Lophius piscatorius*) deepening by up to 10 m decade^{-1} (Dulvy et al. 2008). Where suitable deeper environments are available it may not be necessary for fish to move polewards to track suitable thermal niches, as they may instead remain at the same latitude by moving in to deeper water (Dulvy et al. 2008). Some research has suggested that North Sea fish occupying deeper water are likely to be less affected by changing sea temperatures (Rijnsdorp et al. 2009), whilst other research suggests that these species may be at greater risk, due to the limited availability of deep water (>80 m) habitats in the North Sea (Dulvy et al. 2008).

A fish species' reliance on specific habitats has been shown to greatly influence their ability to respond to climate variation; many species require certain habitats for feeding, spawning and nursery grounds (Simpson et al. 2013). For some species, the dependence on specific habitats may limit the potential for a latitudinal shift (Rutterford et al. 2015). Different life stages of a species may also require spatially separated habitats, and so the availability of suitable, well connected essential habitat is vital to the success of the species (McHugh et al. 2011; Hollowed et al. 2013; discussed further in *Section 2.3*). Demersal and pelagic fish species will differ in their responses to climate change; for example, demersal species such as cod, haddock and whiting (*Merlangius merlangus*) may be less likely to show a rapid range shift as a result of climate change due to their habitat requirements (Rijnsdorp et al. 2009). Pelagic species, which do not have the same reliance on benthic habitats and, as adults, have high motility, may have greater capacity for range shifts (Montero-Serra et al. 2015). Fish occupying semi-enclosed seas are likely to be more greatly affected by climatic variation due to the physical barriers preventing them from dispersing to more thermally suitable areas (Cheung et al. 2009). The response of a population to climate change will also vary according to whether they are within the centre of their latitudinal range and optimum environmental conditions, or towards the range limits (Hollowed et al. 2013). It is generally accepted that species at the limits of their latitudinal distribution will show a stronger response to climate variability (Rijnsdorp et al. 2009); Robinson et al. (2015) suggest that species at the trailing edge of their distribution will respond faster to climate change than species at the centre or leading edge of their distribution. High latitudes generally experience the greatest rates of warming, so species in these environments will have limited time in which to adapt, and may be unable to do so if they are already occupying an environment close to their thermal maximum (Somero 2010).

All of the possible impacts of climate change detailed above could be considered direct effects of climate change on individual fish species. These in turn will filter through to the community level, and are likely to dramatically alter community structure and richness, through the arrival of novel and loss of traditional species, predator-prey interactions and trophic dynamics (Montero-Serra et al. 2015). Ecosystems with a simple trophic structure are likely to display a more rapid responses to climate change than those with a complex trophic structure and associated functional redundancy (Rijnsdorp et al. 2009).

A number of studies have investigated changes in species richness in response to climate change. Hiddink & ter Hofstede (2008) found that richness of benthic and small pelagic species was positively correlated to average winter bottom temperatures, and that whilst the ranges of many species expanded, the ranges of some commercially important species had retracted. The observed increase in richness was greater than could be predicted by temperature alone; the authors suggest this could be due to the exploitation of larger species, releasing smaller ones from the pressure of predation, and also that the southern species could be expanding northwards at a greater rate than northern species retracted further north. It is likely that where large-scale distributional changes are occurring, there will be a lag between the influx of warm water species and the departure of cold water species; this unbalanced ecosystem could have significant impacts on community structure and trophic dynamics. It is likely that species richness will only increase where suitable habitat is available, and where a species is constrained by dispersal capabilities or habitat requirements, climate change could pose a serious threat (Perry et al. 2005; Hiddink & ter Hofstede 2008).

McHugh et al. (2011) showed that over a period of almost a century there were significant changes to the structure and composition of a fish assemblage occupying the English Channel, although changes were not consistent between taxonomic groups. In general there were significant declines in all elasmobranchs, though less evidence of changes to abundances of flatfish. A study by Genner et al. (2004) demonstrated that the same species showed different responses between geographically separated sites, and suggested that local environmental factors and interactions had a significant impact on a species' response to climate change. This will make applying blanket predictions to fish assemblages difficult. For many species, the ecological mechanisms driving the response are poorly understood (Blanchard et al. 2012), and whilst statistical correlations may allow inferences to be drawn from data, they do not indicate the underlying process behind the correlation (Rijnsdorp et al. 2009).

The observed rise in sea temperature and changes in fish distributions has enabled the spread and establishment of new species. An increase in sea temperature means that many environments can now support species that they may previously not have been suitable for. Warming in the North Sea, Baltic Sea and north-east Atlantic has prompted an increase in warm water species such as red mullet and anchovy (*Engraulis encrasicolus*), where previously the fish assemblage was characterised by cold water species such as cod and herring (*Clupea harengus*) (Rijnsdorp et al. 2009; Montero-Serra et al. 2015). Anchovy populations have historically occurred in the North Sea, but have increased in abundance and distribution in recent decades (Petitgas et al. 2012). Warmer summer temperatures and a lack of severe winters have improved survival rates. The study by Petitgas et al. (2012) demonstrates that range expansions of remnant populations can occur due to increased productivity at the edge of a species distribution, and are not necessarily a result of a latitudinal shift.

2.3 Fish physiology, phenology and behaviour

Several studies have linked variable sea temperature with the timing of spawning events in species such as sole (*Solea solea*) and plaice (*Pleuronectes platessa*) (Rijnsdorp et al. 2009; McHugh et al. 2011; Pinnegar et al. 2013). Genner et al. (2010a) found that for spring spawning fish, appearance of larvae was significantly dependent on sea temperatures the previous November and December (cooler temperatures result in earlier spawning), whereas summer spawning fish were affected by sea temperatures during the preceding March (warm temperatures result in earlier spawning). The study suggests that for spring spawning fish, the cooler temperatures trigger an earlier winter migration of adults, to warm over-wintering habitat, where the increase in temperature promotes gonad maturation and earlier spawning. For summer spawning fish, it is likely that warm temperatures alone enhance the growth and maturation of fish gonads, causing the observed earlier spawning (Genner et al. 2010a). Whilst warmer seas have been linked to earlier spawning, this does not always coincide with earlier phytoplankton blooms (which is generally mediated by levels of solar radiation), which in some areas has resulted in mismatch between larval appearance and food supply (Harley et al. 2006). This is likely to affect larval survival and recruitment success, and therefore the strength and viability of the fish stock. The larvae of many south-west fish species feed on a varied diet, which primarily consists of the nauplii and copepodite stages of copepods (Last 1978a; Last 1978b), and so may be affected indirectly by temperature-induced changes in phytoplankton abundance. There is also the potential for an increased risk of predation, as warmer temperatures may increase metabolism and therefore feeding rates in predator species (McHugh et al. 2011). Earlier spawning coupled with an increase in average sea temperature could prolong the growing season for many species, which, providing temperatures do not exceed the thermal limits of the species, may have a positive impact on the population. For many fish, winter survival rates are linked to body size; thus, faster growth as a result of prolonged growing season could produce more resilient populations (Pinnegar et al. 2013).

The likelihood of expansion of a species range in response to climate change has been linked by many studies to body size and life cycle. Fish species with a smaller body size and faster life cycle (short generation time) have shown rapid distributional responses to warming seas (Beare et al. 2004; Perry et al. 2005; Hiddink & ter Hofstede 2008; Simpson et al. 2011). Species with slower life cycles, which are naturally more vulnerable to overfishing, may not have such capacity to shift. Fish body size generally increases with increasing latitude, and so some studies have suggested that an increase in average sea temperatures may be coupled with a decrease in average fish body size, which may also be a result of smaller species being released from predation by removal of larger species as a result of exploitation (Hiddink & ter Hofstede 2008; Rijnsdorp et al. 2009).

The dependence on specific habitats varies throughout the life cycle of many species (Harley et al. 2006; McHugh et al. 2011) and can be linked to a shift in temperature tolerance. Earlier life stages of many species occupy shallow and surface waters, whereas the adults of the same species may occupy much deeper water. As body size increases, the optimum temperature for growth decreases, and in some species eggs and larvae have a narrower thermal tolerance range, potentially making them more vulnerable to climatic fluctuations (Rijnsdorp et al. 2009). Where habitat requirements are very specific, bottlenecks can occur in the life cycle, and if habitats are poorly connected, the species may not complete its life cycle (Petitgas et al. 2013). Where ocean circulation aids larval dispersion, it is likely that climate induced changes to circulation will have a significant impact on the success of the species, especially if habitat connectivity is disrupted, which in turn may disrupt population dynamics (Harley et al. 2006). Some species have been shown to occupy suboptimal thermal habitats, even when optimal ones are accessible, possibly due to food availability or other environmental factors (Neat & Righton 2007). Over a prolonged period of time, this is likely to impact growth and metabolism (Rutterford et al. 2015).

A study by Koumoundouros et al. (2002) investigated temperature sex determination (TSD) in European seabass (*Dicentrarchus labrax*); a species of growing importance and economic value to the UK fishing industry. This study demonstrated that warmer temperatures during egg development resulted in a more heavily male dominated population. A more recent study by Ospina-Álvarez & Piferrer (2008) suggests that TSD is far less widespread than originally believed. For certain species however, the authors predict that warmer sea temperature may skew the ratio of male to female from 1:1, to a heavily male dominated population, as much as 3:1 in some species, such as the Argentinian silverside (*Odontesthes bonariensis*).

In addition to the possible climate induced behavioural and physiological changes, fish populations may also have to contend with higher prevalence of diseases. It is likely that continued rising sea temperatures will facilitate the spread and establishment of parasites and pathogens (Harvell et al. 2002; Brander 2007), and may also increase the severity of disease; pathogens generally have a higher optimum temperature than their host (Harley et al. 2006).

The majority of studies have focused on the effects of rising sea temperature, as a result of climate change. However, this is likely to be accompanied by a wealth of other environmental changes. The main factor causing concern other than a rise in sea temperature is a reduction in ocean pH, due to increasing atmospheric carbon dioxide (Simpson et al. 2013). For some species, a change in ocean chemistry may have greater implications than fluctuating temperature. Salinity fluctuations on global and regional scales are likely to be observed, due to sea ice melting and changes to precipitation, which will impact fish species, particularly those with a narrow tolerance range. Beaugrand et al. (2011) report that Atlantic cod cannot reproduce successfully in salinity lower than 11 psu, as eggs sink and sperm becomes immobile. A reduction in salinity of ~0.2 psu has been predicted for the Northeast Atlantic and the North Sea by the end of the century, and a reduction of ~0.1 for the Celtic and Irish Seas (Lowe et al. 2009). In addition to salinity fluctuations, oxygen concentration may also vary, particularly with increased stratification of the water column, associated with a rise in temperature. Whilst low oxygen environments do occur naturally, the presence of reduced-oxygen and hypoxic environments are predicted to increase in both frequency and duration as a result of climate change (Townhill et al. 2017). A reduction in oxygen saturation and expansion of the oxygen minimum zone is likely to impact metabolism and behaviour; some species may aggregate closer to the surface, making them more vulnerable to predation or surface fishing gears, and thus giving false indications of high abundance (Stramma et al. 2011). Similarly, a shallowing of the mixed layer depth, due to the rise in temperature and increased thermal stratification, may cause vertical habitat compression, resulting in behavioural changes. Prolonged exposure to low levels of oxygen may affect egg development, recruitment, body size and predator–prey interactions. The varying responses and tolerances of different species to low oxygen levels will mean it is difficult to anticipate how communities and therefore whole ecosystems will fare in reduced oxygen environments (Townhill et al. 2017).

An increase in sea temperature can affect a number of physiological processes within an organism, including organ function and protein synthesis (Harley et al. 2006). A factor which may affect a species capacity to withstand climate change is the potential for genetic adaptation, though there is a paucity of studies reporting evidence of this (Pearson & Dawson 2003; Crozier & Hutchings 2014). Somero (2010) reported that temperature-adaptive alterations to proteins can take place with a substitution of a single amino acid, and so the possibility of this seems highly plausible, particularly in species with rapid generation times. Population size and the amount of genetic variation within the population will determine how likely it is that evolutionary changes will occur (Crozier & Hutchings 2014), however for many species it is unlikely that adaptation will occur quickly enough to counter the effects of predicted climate scenarios (Hoffmann & Sgrò 2011). Some species may have irreversibly lost the capacity to adapt to warmer temperatures; due to long periods of highly stable low temperatures, some stenothermic species may have lost protein coding genes and gene regulatory mechanisms that would be required for coping with a rise in temperature (Somero 2010).

2.4 Commercial fisheries

Fishing targets individuals of a certain size within a population and selectively removes them, thereby often reducing the number of mature spawning individuals, and skewing the age distribution of the population towards younger fish (Brander 2007; Beaugrand and Kirby 2010). Intensive fishing can therefore make populations more vulnerable to the effects of climate change, by reducing its capacity to buffer against added stressors or the occasional poor year class

(Rijnsdorp et al. 2009; Pinnegar et al. 2013). Cold water environments, or those with low primary productivity, are perhaps more susceptible to the detrimental effects of heavy fishing due to relatively low growth rates of the organisms within them (Blanchard et al. 2012).

Whilst many studies have reported an increase in species richness around the UK and suggested that species are expanding their ranges, some of those that have shown a decrease in abundance and range are among the most commercially valuable (Hiddink & ter Hofstede 2008; Simpson et al. 2011). Large bodied, cold water species such as Atlantic cod and haddock have shown declines in abundance, threatening the sustainability of the stock and reducing the value of the fishery. Furthermore, there is mounting evidence that these large, slow maturing fish are being replaced by small-bodied species (Hiddink & ter Hofstede 2008; McHugh et al. 2011). The observed changes to fish populations as a result of climate change have been reflected in landings data, and may result in a redistribution of fish production on a global scale. Landings of boreal species halved between 1980–2007, whereas landings of Lusitanian species increased by 250% (Simpson et al. 2011). Cheung et al. (2010) predicted an increase in global catch potential of 30–70% at higher latitudes, and a reduction of up to 40% in the tropics; other studies have reported similar predictions (see Blanchard et al. 2012 and Barange et al. 2014). As a result, catches of warm-water species are likely to increase together with a decrease in catches of cold water species (Cheung et al. 2013).

It is likely that global trends in productivity will mask local and regional fluctuations (Worm et al. 2009), influenced by the present environmental conditions. Inconsistencies between the responses of different fish populations to climate change mean that applying generalised predictions will be difficult. The North Sea experienced a rise in sea surface temperature of 0.55°C decade^{-1} between 1982 and 2006, which was coupled with a decline in fisheries biomass yield, contrary to other large marine ecosystems where an increase in yield occurred with warming (Sherman et al. 2009). The authors suggest this is a result of heavy exploitation and distributional shifts of target species due to the rise in temperature.

The observed redistribution of fish populations has, in some areas, allowed for new fish stocks to be exploited, where previously a fishery may not have been viable (Brander 2007). The change in environmental conditions, primarily warming, means that many warm-water adapted species, such as red mullet, anchovy, and boarfish (*Capros aper*) are now found in UK waters in increasing abundance (Dulvy et al. 2008; McHugh et al. 2011; Pinnegar et al. 2013). It may be that some species have always been present at low abundance, but are now benefitting from more favourable environmental conditions, and their presence may not necessarily be a result of dispersal; this appears to be the case for the recent increase in anchovy around the UK (Petitgas et al. 2012).

3. Future predictions and socio-economic impacts

Recent research has predicted many possible impacts on fish communities as a result of changing climate. These range from widespread extinctions (Harley et al. 2006), an increase in disease prevalence and severity (Perry et al. 2005), a loss in functional diversity (Buisson et al. 2013) and alterations to migration routes (Rijnsdorp et al. 2009). There is a wealth of literature describing distributional changes of fish species, generally moving towards the poles, coupled with an increase in species richness at higher latitudes (Hiddink & ter Hofstede 2008). However, applying general predictions may be difficult due to local and regional variations. A reduction in species richness, particularly of large cold water species, has been observed in northwest Scotland (Simpson et al. 2013). Perry et al. (2005) discuss the unusual temperature patterns of the North Sea, where at high latitude, an influx of warmer North Atlantic water could account for the loss of large cold water species described.

The predicted effects of climate change will have profound consequences for the UK fishing industry. The decrease of traditional, commercially valuable species such as cod and haddock will be detrimental to the industry, but may be coupled with new exploitation possibilities; warm water species such as boarfish and anchovy are now abundant enough in UK waters to sustain a viable fishery (Pinnegar et al. 2013). Vessels operating out of Brixham, one the key south-west UK ports, are already landing large numbers of emerging warm-water species (Defra 2013), but adapting to new exploitation possibilities may require changing or adapting fishing gear and practices, as well as fishing locations, all of which could require substantial financial investment. In order to target new species, fishers would also need to obtain the necessary quota. Some commercially valuable species are associated with coastal and inshore environments, and as many of these species are predicted to move offshore into deeper cooler water (Cheung et al. 2010), it may no longer be practical to fish for them, again, requiring a change in fishing tactics and locations. One advantage for inshore fishing vessels is being able to provide fresh fish, by returning to port generally within 24 hours; this advantage would be lost if they were to target areas further offshore (Defra 2013). Redistribution of fish stocks has led to, and will continue to cause, disagreements over fishing quotas (Pinnegar et al. 2013), and such redistribution is likely to prove difficult for fisheries management. Where fish move between fishing areas and across boundaries there have been disagreements between different nations regarding permissible catches and quotas. One notable recent example is the “Mackerel Wars” between Iceland, the Faroe Islands, Norway and the EU. Atlantic Mackerel (*Scomber scombrus*) are now found in abundance around Iceland and the Faroe Islands (Pinnegar et al. 2013), where stocks of blue whiting (*Micromesistius poutassou*) have greatly diminished. As a result, mackerel have been heavily exploited by Icelandic and Faroese fishing vessels, who are not governed by the Common Fisheries Policy (CFP), and can therefore set their own quotas (Simpson et al. 2013). The increase in quotas set by these countries meant that total landings of mackerel were in excess of the total quota advised by ICES, and so in 2012 Atlantic Mackerel lost its Marine Stewardship Council (MSC) accreditation, as the stock was no longer deemed to be sustainably exploited (British Sea Fishing, 2014). In March 2014 an agreement was reached between the EU, the Faroe Islands and Norway, which split quotas for mackerel in the North East Atlantic. The MSC status has since been re-instated (Marine Stewardship Council, 2016). Another example is the increase in abundance of anchovy in UK waters; fishing vessels from southern Europe where anchovy stocks have been depleted will not automatically be given fishing rights in newly exploitable areas, as the fish are from a genetically different stock (Petitgas et al. 2012).

There is a consensus throughout the literature that globally, most fish stocks are currently fully or over exploited (Brander 2007; Cheung et al. 2010; Blanchard et al. 2012). However, recent years have seen a partial recovery in certain fish stocks surrounding the UK (European Environment Agency 2015), in particular haddock and hake, largely due to reduced fishing mortality, contributing to an increase in spawning stock biomass (SSB) (see ICES Stock Assessment Database, 2014). Despite in many cases, effective precautionary measures, natural factors still have a strong influence on recruitment and SSB for some fish stocks. As such, the varying predicted effects of climate change are likely to exacerbate an already distressed ecosystem, and as fish stocks are prone to natural variability and unexpected fluctuations (Beaugrand & Kirby 2010), there is a need for effective, cautionary and adaptable fisheries management, that considers more than just the most commercially valuable species, and aims to sustain the age and geographic structure of the population (Brander 2007). Some studies suggest that current ecosystem based fisheries management does not consider the effects of climate changes on the ecosystem (Beaugrand & Kirby 2010), and that it is unclear how distributional changes of fish are accounted for in management plans (Link et al. 2011). However, the difficulty in teasing apart the effects of fishing on an ecosystem from the effects of climate change suggests that the two should be considered in conjunction with one another. This requires an understanding of the different variables affecting the response of a fish populations to exploitation and climate variability; some studies have suggested strategies for managing fisheries in line with the predictions made for future changes (e.g. Link et al. 2011). Climate change is likely to have a significant impact on marine global food supply (Cheung et al. 2010), and aquaculture has been suggested as a viable solution to meeting global food demand. Global production from capture fisheries has plateaued since the mid-1980s, whereas global aquaculture production has continued to rise. In 2014, aquaculture accounted for ~44% of total global fish production, almost equalling that of capture fisheries (FAO 2016). However, removing small fish from natural ecosystems for fishmeal in aquaculture will affect trophic dynamics and could disrupt natural ecosystems if those smaller species are heavily exploited (Brander 2007).

Conservation efforts in the form of Marine Protected Areas (MPA) and no-take zones are intended to aid the recovery of fish stocks, increase biodiversity and improve ecosystem health and resilience, and have been shown to be successful in doing so (Roberts et al. 2001; Micheli et al. 2012). However, these measures may be compromised if climatic changes mean that they are no longer an optimum environment for the species they aim to protect or restore (Rijnsdorp et al. 2009; Jones et al. 2013). Distributional shifts have been observed in many species as a result of climate change. van Keeken et al. (2007) reported an offshore shift in distribution of plaice in the North Sea, thereby reducing the effectiveness of the ‘Plaice Box’, an area of no-take designed to allow juvenile plaice some protection from larger trawling vessels. The authors attributed this distributional shift to a rise in water temperatures. As such, the designation of MPA status should be flexible and adaptive in order to be most effective (Cheung et al. 2012; Pinnegar et al. 2013).

5. Conclusion

Natural fluctuations and variability observed in fish populations are likely to be exacerbated by the predicted effects of climate change, and in some cases may lead to irreversible changes in fish stock resilience and ecosystem dynamics. The capacity for UK fishing fleets to adapt and respond to shifts in fish populations will determine whether new opportunities will be exploited effectively, and therefore determine how UK fishers will fare in the face of climate change. The ability to make accurate predictions about the effects of climate change on marine ecosystems is vital to understanding how ecosystems as a whole are likely to respond, and to identify which species will be the ‘winners or losers’ as a result of warming seas. The literature emphasises the importance of predictive models that capture numerous factors affecting fish responses, as opposed to those that are purely process-based. A flexible, cautious and adaptive approach to fisheries management will be required if fish populations are to withstand the environmental pressures associated with warming seas, especially where fishing intensity is already high.

Chapter 2: Recent impacts of climate change on south-west UK fisheries

Abstract

Health and stability of marine ecosystems is closely linked to the level of local biodiversity. Increased species richness, coupled with a reduction in the abundance of key commercial species, has been reported in some waters surrounding the UK and throughout the North Sea, however, little research has focused on the south-west area of the UK, despite the economic importance of this area for commercial fishing.

This chapter explores how the diversity and richness of the south-west UK fish assemblage has changed over the past three decades, and tests for species-level responses in commercial and non-commercial species.

Marine biodiversity is essential for the successful functioning of marine environments, such that complex and diverse ecosystems with functional redundancy are considered to be more robust against environmental stressors.

The results of this chapter demonstrate that both the richness and diversity of the south-west UK fish assemblage have increased significantly in recent decades. This is likely to be driven by the changes in abundance of some species within the fish assemblage. Many species that are typically associated with warmer waters have increased in abundance during the last three decades, including anchovy, boarfish and John dory, while there has been a decrease in the abundance of many cold-water species such as Atlantic cod, herring and blue whiting, that traditionally underpin UK fisheries. These changes in abundance correlate closely with warming trends in sea temperature, resulting from contemporary climate change. Understanding recent responses in the fish assemblage provides valuable knowledge that can be applied to future projections of climate-driven changes to the fish assemblage.

1. Introduction

The marine realm hosts some of the most diverse ecosystems on the planet, however this diversity is threatened by anthropogenic interferences including exploitation, climate change and pollution (Worm et al. 2006). Climate change in particular has been linked to range shifts in marine organisms (Beare et al. 2004; Bates et al. 2014), physiological and behavioural changes (Genner et al. 2010a), as well as local extinctions and invasions (Cheung et al. 2009), all of which can alter the functioning and diversity of ecosystems. High levels of biodiversity support increased productivity and improved ecosystem function and resilience to exploitation (Worm et al. 2006) compared with impoverished or degraded environments. A number of studies have investigated how the richness and diversity of marine ecosystems and their fish assemblages have changed in the past, and how they may continue to change into the future. Hiddink & ter Hofstede (2008) found an increase in species richness in the North Sea between 1985 and 2006, and attributed this to an increase in sea temperature. Similar observations were made by ter Hofstede et al. (2010) for the North and Celtic seas, driven by increased richness due to a rise in the number of Lusitanian (warm water) species as a result of rising sea temperature.

Predictions of future changes in community composition and diversity vary, but there is a general consensus that species richness will increase at higher latitudes and decrease at low latitudes, due to range expansions and contractions, species invasions and extirpations (Cheung et al. 2009; García Molinos et al. 2015). However, studies have shown that community level responses are not uniform, such that the same species at different geographical locations may respond differently to the same scenario (Genner et al. 2004). These differences may be due to local environmental factors and species interactions, meaning that applying predictions to different fish assemblages may be difficult.

In addition to the impacts of climate change, pressure from commercial fishing has been shown to shape the composition of marine communities (Dulvy et al. 2008; ter Hofstede et al. 2010; Engelhard et al. 2014). The UK fishing industry has experienced significant changes in recent decades, in terms of volume and economic value of landings as well as fleet size and structure (Beare et al. 2004; Marine Management Organisation 2014; Jones et al. 2015). Causes and exacerbating factors of this variability include: over-exploitation of fish stocks resulting in their decline or collapse (Beaugrand et al. 2011), variations in fishing effort due to mitigation measures, such as vessel de-commissioning and restricted access to fishing areas (Marine Management Organisation 2014), technological advances in fishing practices (Engelhard et al. 2014), impacts from climate change (Cheung et al. 2012), as well as the natural variability observed in fish stocks (FAO 2016).

It is important to understand how fish assemblages have changed in the past, as well as identifying the possible driving forces behind these changes, in order to better understand community level responses to stressors such as climate change and exploitation. Given the complex interactions and associations found within marine ecosystems, an assessment of net responses of the entire fish assemblage can give valuable indications about the state of the ecosystem. The importance of considering whole ecosystems in management plans and conservation measures is well documented, for the economic benefits seen in fisheries, as well as the importance for the health of ecosystems and biodiversity. An understanding of past changes in ecosystem dynamics and fish assemblage responses can also be valuable in anticipating how they may respond in the future.

A number of studies have considered changes in fish assemblage composition in marine environments around the world; in particular the North Sea (Dulvy et al. 2008; Simpson et al. 2011; Rutterford et al. 2015), perhaps due in part to the substantial amount of uniform, standardised data available, from sources such as the International Bottom Trawl Survey (IBTS) co-ordinated by the International Council for the Exploration of the Seas (ICES). However, fewer studies have focused on the south-west area of the UK (see Stebbing et al. 2002; Genner et al. 2010b), despite its economic importance for commercial fishing. Therefore, this study aims to assess how the fish assemblage in this area has changed over the last three decades in terms of species richness and diversity (by applying the Shannon-Wiener index of diversity), and at the individual species level. The study will consider the whole fish community, including both commercially valuable species and those that are not currently commercially valuable or viable. In addition, certain species that together make up the majority of the fish population will be analysed to look for changes and trends in their abundance over the same time period. The key research questions this chapter aims to answer are:

1. How has the fish assemblage in the south-west UK changed over the last three decades in terms of species richness and diversity, and what are the possible driving forces behind these changes?
2. How has the abundance of key species within the assemblage changed?

The fish abundance data used in this study are from scientific surveys, and are detailed in *Section 2.1.2*. The geographical area considered by this study is represented by a number of different surveys. As a result, there is an initial need to standardise the data to account for the differences between the surveys, in order to accurately assess the abundance changes observed in certain species. The method is described by Searle et al. (1980) and is detailed further in *Section 2.3.*

2. Methods

2.1 Study area and data sources

A grid-based (Eulerian) approach to data organising and analysis was adopted. The study area covered latitude 47–53°N and longitude 12°W–3°E, and was divided into 75 1°x1° cells (see **Figure 1**). The data used, including their sources, and the processes by which they were manipulated and analysed, are detailed below.

2.1.1 Environmental data

Sea surface temperature (SST) and near bottom temperature (NBT) for the study area were obtained from the Met Office Hadley Centre HadCM3-POLCOMS Shelf Seas model (Tinker et al. 2015). **Figure 2** shows that despite substantial fluctuations in both, the general trend is an increase in average temperature from 1980–2015.

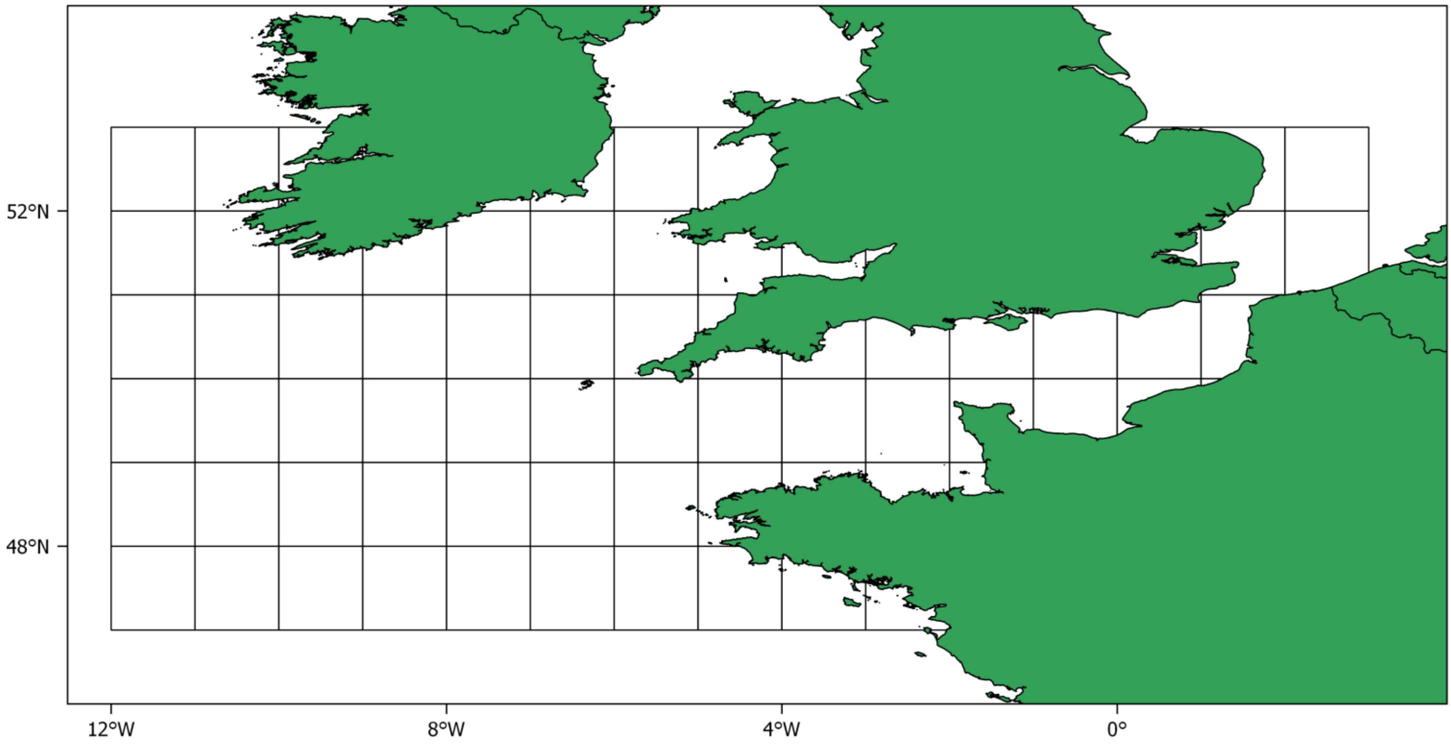

Figure 1: Grid showing the 75 1°x1° cells used in this study, covering the area 47–52°N, 12°W–3°E.

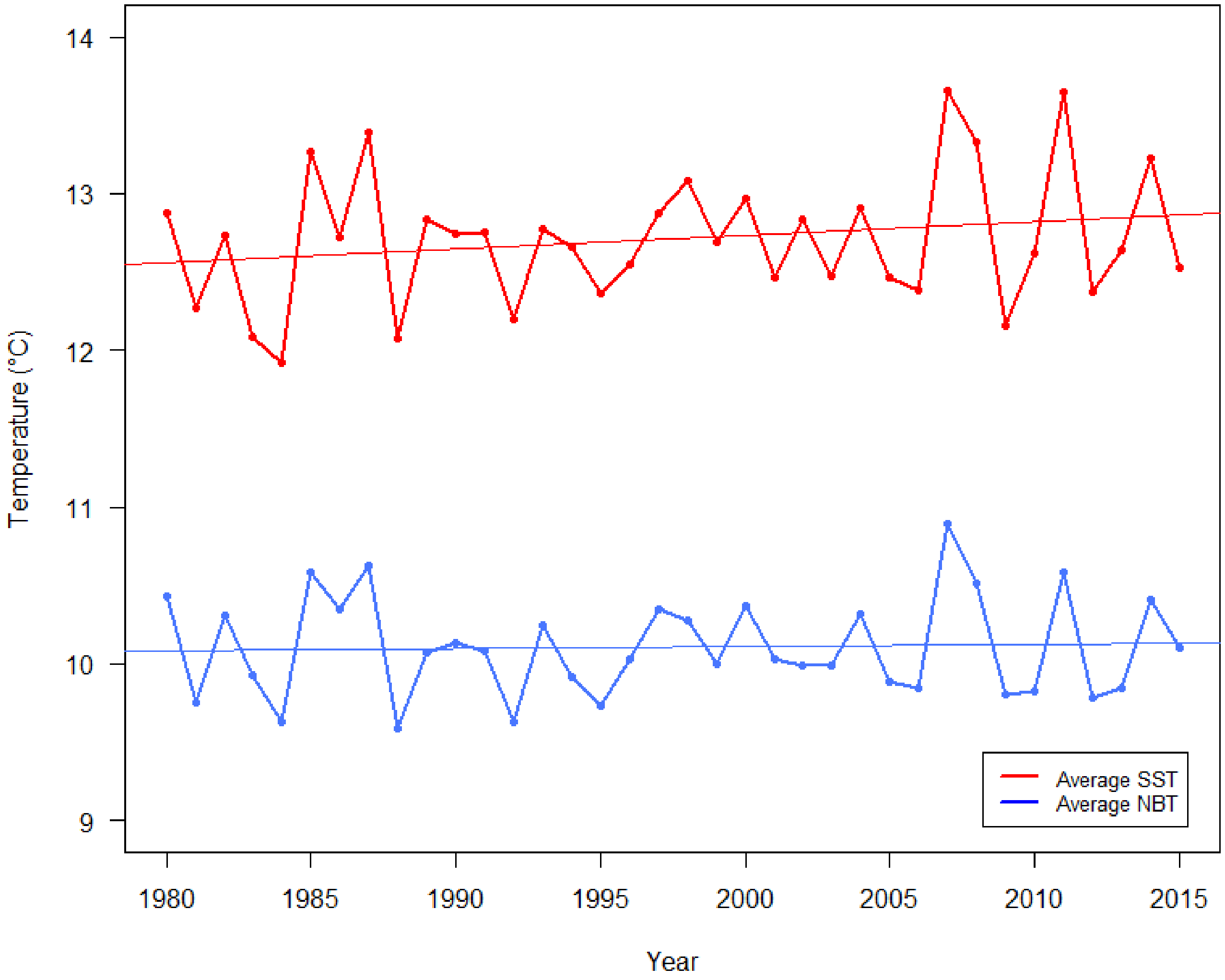

Figure 2: Mean annual sea surface temperature (SST) and near bottom temperature (NBT) trends for 1980–2015 for the geographical area considered by this study. Temperature data were obtained from the Met Office Hadley Centre HadCM3-POLCOMS Shelf Seas model.

2.1.2 Fish abundance

The fish abundance data used in this study were obtained from scientific surveys, which generally provide repeated samples over long time periods, and so are ideal for assessing the state of fish communities (Worm et al. 2009). These data have the advantage over fishery landings data in that they are gathered from a range of sites rather than just those that are optimal for target fishery species. Whilst fishery landings can give valuable information regarding the state of a target species, they do not provide information about the fish assemblage as a whole.

The six scientific surveys are detailed below; these data were obtained from the ICES Datras portal (ICES 2004) or with kind permission from the Centre for the Environment, Fisheries and Aquaculture Science (Cefas).

Cefas Eastern English Channel Beam Trawl Survey (EEC): Conducted by Cefas, this survey began in 1989 and uses a 4m beam trawl. The survey area was extended in 1995 to include the southern North Sea, and additional stations have been added in recent years. Generally conducted in summer months, the primary purpose was to assess abundance of pre-recruit plaice (*Pleuronectes platessa*) and sole (*Solea solea*); therefore survey sites are generally in nursery ground of these species. This study uses data from the period 1990–2014, which amounted to a total of 2,411 hauls.

Cefas Celtic Sea Groundfish Survey (Celtic): This survey covers the Celtic Sea and has experienced a number of gear and spatial changes since 1981 when it began. For consistency, only data from the period 1987–2004 (total of 1,119 hauls) are used in this study, during which time a Portuguese high-headline trawl was used. This survey was usually conducted in the spring.

Cefas South-western Beam Trawl Survey (Western): Conducted by Cefas, this survey covers the western Channel area, uses a 4m beam trawl, and is generally conducted in the first quarter of the year. The survey began in 1984 but experienced a number of vessel changes until 2005, and so for this study the period from 2006–2015 is used for consistency, which includes a total of 792 hauls.

French Southern Atlantic Bottom Trawl Survey (EVHOE): This survey began in 1987, and in 1997 the RV Thalassa was commissioned to replace an older vessel of the same name. To avoid inconsistencies in the data, this study uses data from the period 1997–2013. The survey covers the Celtic Sea and the French portion of the Bay of Biscay, and is conducted in the fourth quarter of the year. A Grande Overture Vertical (GOV) trawl is used, and a total of 1,443 hauls were analysed in this study.

French Channel Groundfish Survey (FR-CGFS): This survey began in 1988, and is conducted in October each year and also uses a GOV trawl. This study uses data from the period 1988–2013, including a total of 2,307 hauls.

Irish Groundfish Survey (IGFS): This survey is conducted in the fourth quarter of each year, and covers the Atlantic shelf regions around Ireland. Data for the period 2003–2008 are used in this study; with a total of 510 hauls.

From each survey, data relating to the study area were extracted, and fish abundances were converted to a catch per unit effort (CPUE) in order to standardise for sampling effort and haul duration. The surveys record fish species by nominal codes which differ between surveys. The coding systems used are World Register of Marine Species AphiaID (WoRMS), Taxonomic Serial Number (TSN), and Cefas specific codes. These codes were all converted to the species common name, identified using the ICES Datras species query tool (ICES 2009) and code information obtained from Cefas. Where more than one common name was associated with a species, the name used by FishBase (FishBase 2012) was used. In some circumstances, codes were duplicated between the different coding systems, such that one code applied to a particular species under WoRMS code, and also a different species under TSN code. In all instances, the alternative species was either: 1) terrestrial, 2) tropical, or 3) too small to be caught using the gear types used by the surveys (i.e. small polychaetes, diatoms), and so an assumption was made about which species the code likely referred to. All non-finfish species, such as crustaceans and cephalopods, were removed. Any data entries that contained the value “-9” as an abundance were also removed; “-9” is an agreed code used by ICES surveys for an instance where there are no data available, for example when a species has been observed in a haul but not counted or not confidently identified. Data from all six surveys were then combined, which comprised 8,582 individual survey hauls, and 247 species of fish (see **Figure 3** for the locations of the hauls from which fish abundance data was used and **Appendix 1** for a full species list).

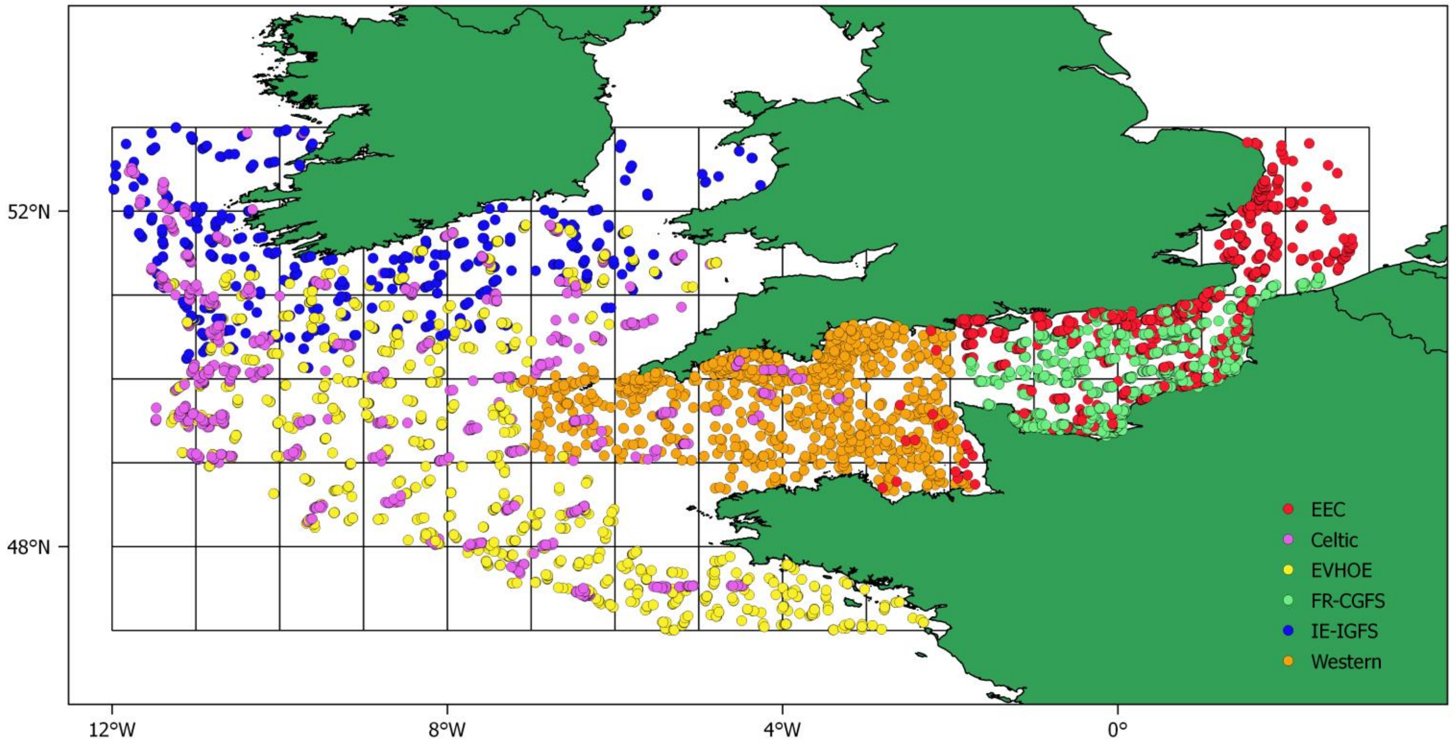

Figure 3: Haul locations from 1987–2015 for the six surveys used in this study; Cefas Eastern English Channel Beam Trawl Survey (EEC), Cefas Celtic Sea Groundfish Survey (Celtic), French Southern Atlantic Bottom Trawl Survey (EVHOE), French Channel Groundfish Survey (FR-CGFS), Irish Groundfish Survey (IE-IGFS), Cefas South-western Beam Trawl Survey (Western).

2.2 Changes in community composition

Changes in the composition and richness of the fish community were investigated using species richness and the Shannon-Wiener index of diversity. Mean species richness (S) was calculated as the average number of species caught per haul, per cell, per year. In order to more comprehensively assess the diversity of the fish assemblage examined in this study, the Shannon-Wiener index was used, allowing diversity to be determined based on the number of species present and their relative abundance; this index is also sensitive to occurrences of rare species (Kwak & Peterson 2007). The Shannon-Wiener index (H) is given by:

$$H = -\sum_{i=1}^{S} p_i \ln(p_i)$$

where S = number of species present in the community, p_i = proportion of S made up by the ith species (calculated from CPUE values). This was calculated per haul, and an average was taken from all the hauls conducted per cell, per year. The trend of both species richness and Shannon-Wiener index was identified for each cell in the study area, and a non-parametric Mann-Kendall test was conducted to determine if the change in species richness and Shannon-Wiener index over time was significant.(significant results were accepted at $p<0.05$).

2.3 Abundance trends of selected species

The 37 most abundant species (or grouped species in some cases) were selected for further analysis; these represented 98% of total CPUE in the dataset (see **Table 1**). Certain groups of species were omitted from this analysis, despite occurring in relatively high abundance (in terms of CPUE) in the dataset; this includes skates, rays and gobies. The basis of this decision is described further in *Chapter 3, Section 2.1.4*, and also *Chapter 3, Section 3*; these species were deemed unsuitable for analysis in *Chapter 3* of this study, and in order for the past and future trends of key species to be comparable, the same species were used throughout the study. In order to assess the trends and changes in abundance of these species, further data standardisation was conducted (in addition to that outlined in *Section 2.1.2*) due to the differences and variations between the six sources of data. Variation between surveys can arise for a number of reasons, including the location and time of year during which the survey is conducted, the vessel and gear type used for sampling, the duration of sampling and expertise of the sampling staff (Trenkel et al. 2004). Further standardisation was conducted as follows: for each species, an average CPUE per decade, per cell, per survey was calculated (cells where a survey was not conducted were left blank, and cells where a survey was conducted but a species was not caught retained a zero). CPUE was then 4^{th} root transformed to reduce skewness and the impact of outliers. A 4^{th} root transformation reduces the impact of outliers even more so than the standard log transformation and can be readily back transformed if required, see O’Hara & Kotze (2010) for further justification of this method.

To obtain a standardised CPUE value for each species from the six surveys, a least-square mean (LS-mean) was calculated, using the '*lsmeans'* package (Lenth 2016) in R (R Core Team 2016). The use of LS-means allows a group mean to be calculated from a linear model (in this case: CPUE (4th)~survey+decade+cell) accounting for covariates and other terms in the model (Searle et al. 1980). LS-means are less sensitive to missing data (compared to a true population mean) because the values are based on the linear model, and can therefore be considered a better estimate of the mean where data sets have missing values. The new LS-mean estimate of abundance was compared to the original survey values, to ensure that there was correlation between them and that the LS-mean values were accurate and appropriate (figures in **Appendix 2A–E**). In some circumstances, the LS-means method produced a negative value of abundance: ~12% of all LS-mean estimates were negative values. This occurred where: 1) all except one survey had not sampled that cell in that decade, or 2) when the abundance of a species was zero for all surveys. In all instances where a negative value was produced, zero was within the 95% confidence interval for that value, and so it was deemed reasonable to change these values back to zero, since it is not biologically possible to have a negative abundance.

These data remained as a 4th root transformed CPUE (unless otherwise stated) for ease of analysis and comparison between species**.** From these standardised estimates of abundance, the change in abundance over time was calculated for each species.

Common name	Scientific name(s)
American plaice	*Hippoglossoides platessoides*
Argentine	*Argentina silus*
	Argentina sphyraena
Atlantic cod	*Gadus morhua*
Atlantic herring	*Clupea harengus*
Atlantic mackerel	*Scomber scombrus*
Blue whiting	*Micromesistius poutassou*
Boarfish	*Capros aper*
Common dab	*Limanda limanda*
Dogfish	*Galeus melastomus*
	Scyliorhinus canicula (Lesser spotted dogfish)
	Scyliorhinus stellaris (Greater spotted dogfish)
	Squalus acanthias (Spiny dogfish)
Dover sole	*Solea solea*
	Solea vulgaris
Dragonet	*Callionymidae spp.*
	Callionymus lyra (Common dragonet)
	Callionymus maculatus (Spotted dragonet)
	Callionymus reticulatus (Reticulated dragonet)
European anchovy	*Engraulis encrasicolus*
European hake	*Merluccius merluccius*
European pilchard	*Sardina pilchardus*
European plaice	*Pleuronectes platessa*
European seabass	*Dicentrarchus labrax*
European sprat	*Sprattus sprattus*
Grenadier	*Coelorinchus caelorhincus* (Hollowsnout grenadier)
	Coryphaenoides rupestris (Roundnose grenadier)
	Hymenocephalus italicus (Glasshead grenadier)
	Macrourus berglax (Roughhead grenadier)
	Malacocephalus laevis (Softhead grenadier)
	Nezumia sclerorhynchus (Bluntsnout grenadier
	Trachyrincus scabrus (Roughsnout grenadier)
Haddock	*Melanogrammus aeglefinus*
Horse mackerel	*Trachurus trachurus*
Grey gurnard	*Eutrigla gurnardus*
John dory	*Zeus faber*
Lemon sole	*Microstomus kitt*
Ling	*Molva dypterygia*
	Molva macrophthalma
	Molva molva
Megrim	*Lepidorhombus boscii*
	Lepidorhombus whiffiagonis
Monkfish	*Lophius piscatorius*
Norway pout	*Trisopterus esmarkii*
Poor cod	*Trisopterus minutus*
Pouting	*Trisopterus luscus*
Red gurnard	*Chelidonichthys cuculus*
Red mullet	*Mullus barbatus*
	Mullus surmuletus
Seabream	*Abramis spp.*
	Boops boops (Bogue)
	Diplodus sargus (White seabream)
	Pagellus spp.
	Pagellus acarne (Axillary seabream)
	Pagellus bogaraveo (Blackspot seabream)
	Pagrus pagrus (Common seabream)
	Sparus aurata (Gilthead seabream)
	Spondyliosoma cantharus (Black seabream)
Silvery pout	*Gadiculus argenteus*
Solenette	*Buglossidium luteum*
Thickback sole	*Microchirus variegatus*
Weever	*Echiichthys vipera* (Lesser weever)
	Trachinus draco (Greater weever)
Whiting	*Merlangius merlangus*

Table 1: Species selected for abundance trend analysis. All species, including those where several species have been grouped, will be referred to by the common name.

3. Results

3.1 Changes in community composition

There was a significant positive correlation over time for both mean species richness (tau=0.429, p=0.001) and Shannon-Wiener index (tau=0.626, p<0.001)(**Figure 4**).

Species richness and Shannon-Wiener index values were tested for correlation against SST and NBT in order to identify concurrent trends in temperature and community changes (**Figure 5**). Positive correlations were found between both diversity indices and temperature variables, although these correlations were quite weak. Species richness and Shannon-Wiener indices appear to have slightly stronger correlation to SST (r values of 0.32 and 0.14 respectively) than NBT (r values of 0.29 (species richness) and 0.12 (Shannon-Wiener index)). In order to explore spatial variation in diversity changes, the rate of change (expressed as the gradient of the line between the mean annual values) for species richness and the Shannon-Wiener diversity index were mapped using Quantum GIS (QGIS 2016) (shown in **Figure 6** and **7** respectively). A one sample Wilcoxon signed rank test on the rate of change across all cells found that for both species richness and the Shannon-Wiener index the rate of change was significant (species richness: $p=2.659E^{-07}$, W=1711, Shannon-Wiener index: $p=8.141E^{-05}$, W=1539). The values of species richness and diversity index are mean values from all the hauls conducted in that cell during a particular year. However, not all cells were sampled in all years, and for certain areas there is a limited number of years during which data were collected. Whilst these cells still demonstrate clear trends, these patterns are less robust than cells for which there are many years of data. **Appendix 3A** and **3B** show the same maps as **Figures 6** and **7** with cells highlighted for which there was less than 6 years of data.

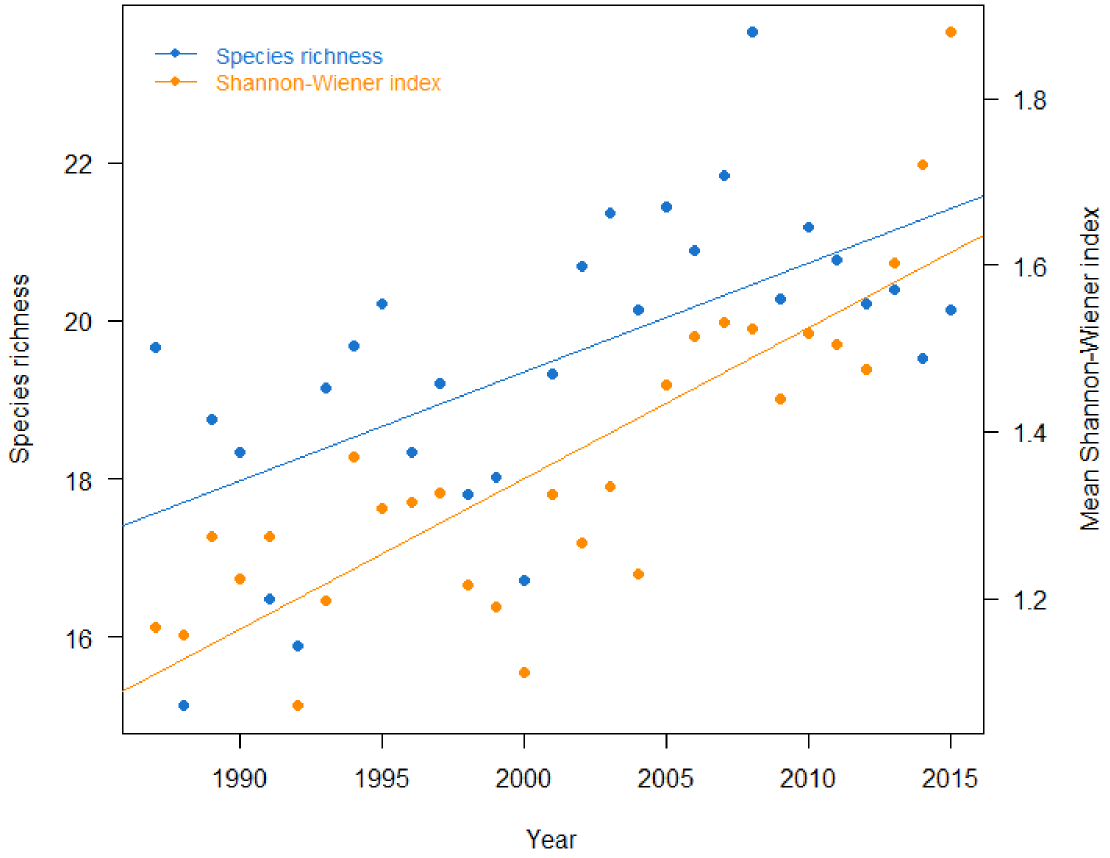

Figure 4: Mean change in species richness (tau=0.429, p=0.001) and Shannon-Wiener diversity index (tau=0.626, p<0.001) across the whole study area, from 1987–2015.

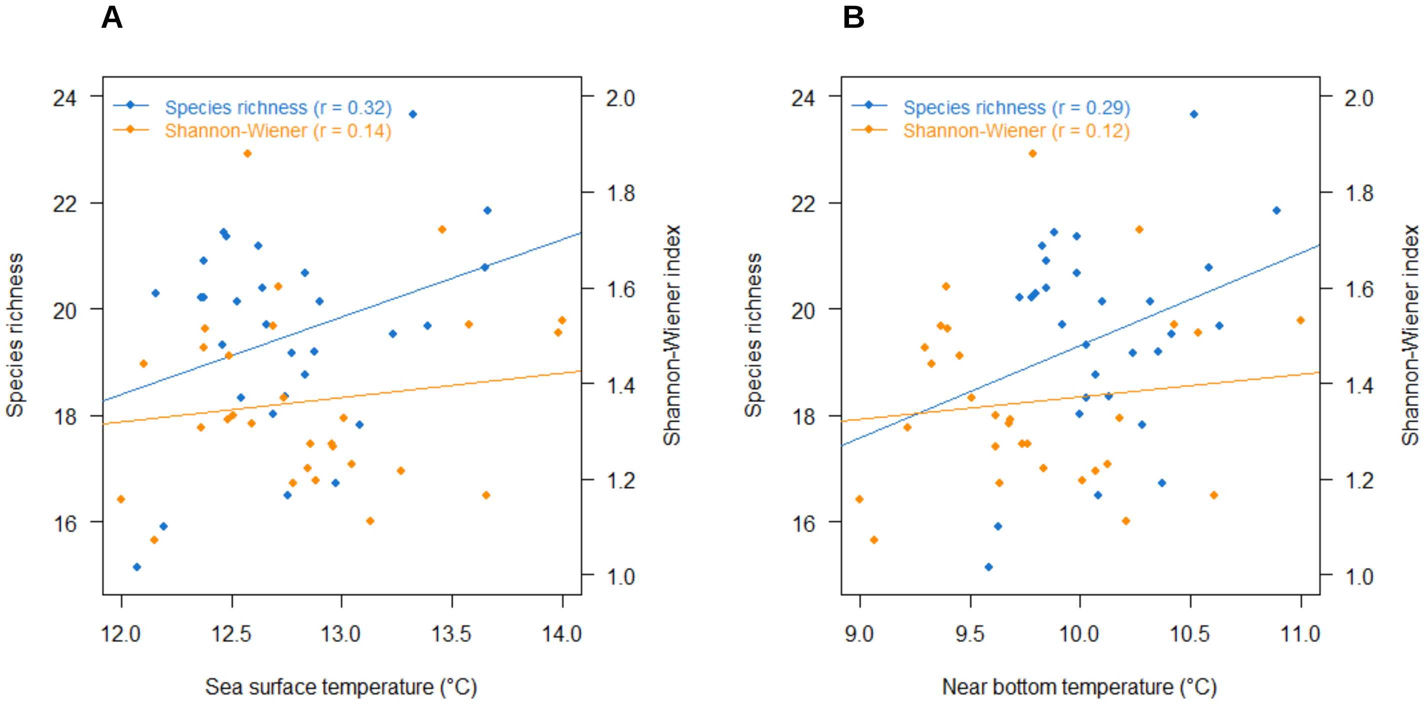

Figure 5: A, Correlation between average sea surface temperature, and average species richness (r=0.32) and Shannon-Wiener index (r=0.14). **B,** Correlation between average near bottom temperature, and average species richness (r=0.29) and Shannon-Wiener index (r=0.12).

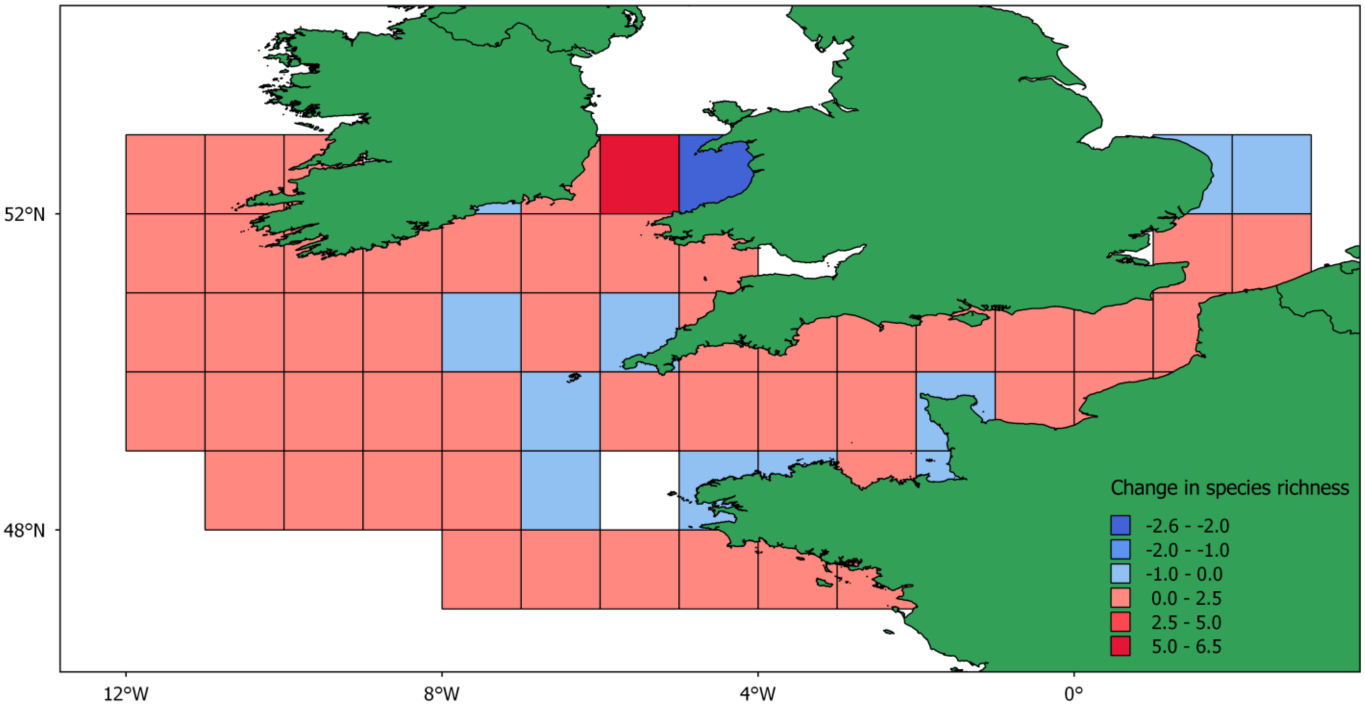

Figure 6: Spatial variation of the rate of change in species richness, from 1987–2015, expressed as the gradient of the line through the annual mean species richness value for each cell. Red indicates an increase in richness, blue indicates a decrease. Blank cells were not sampled during this time.

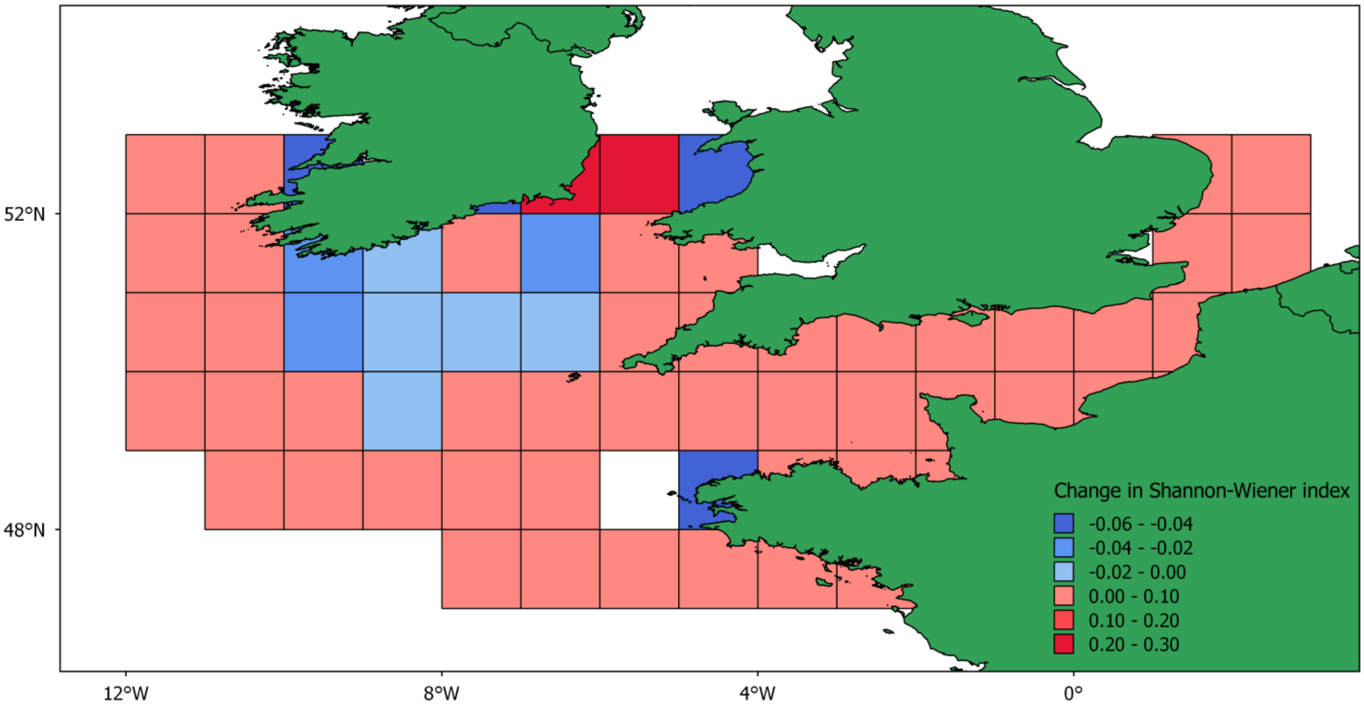

Figure 7: Spatial variation of the rate of change in Shannon-Wiener diversity index, from 1987–2015, expressed as the gradient of the line through the annual mean Shannon-Wiener index value for each cell. Red indicates an increase in richness, blue indicates a decrease. Blank cells were not sampled during this time.

3.2 Abundance trends of selected species

The mean rate of change in abundance was calculated from the LS-mean estimates of abundance for each species, across the study area. These trends are shown in **Figure 8**; red indicates an increase in abundance and blue indicates a decrease in abundance. This figure demonstrates that during the time period investigated, 23 out of 37 species increased in abundance.

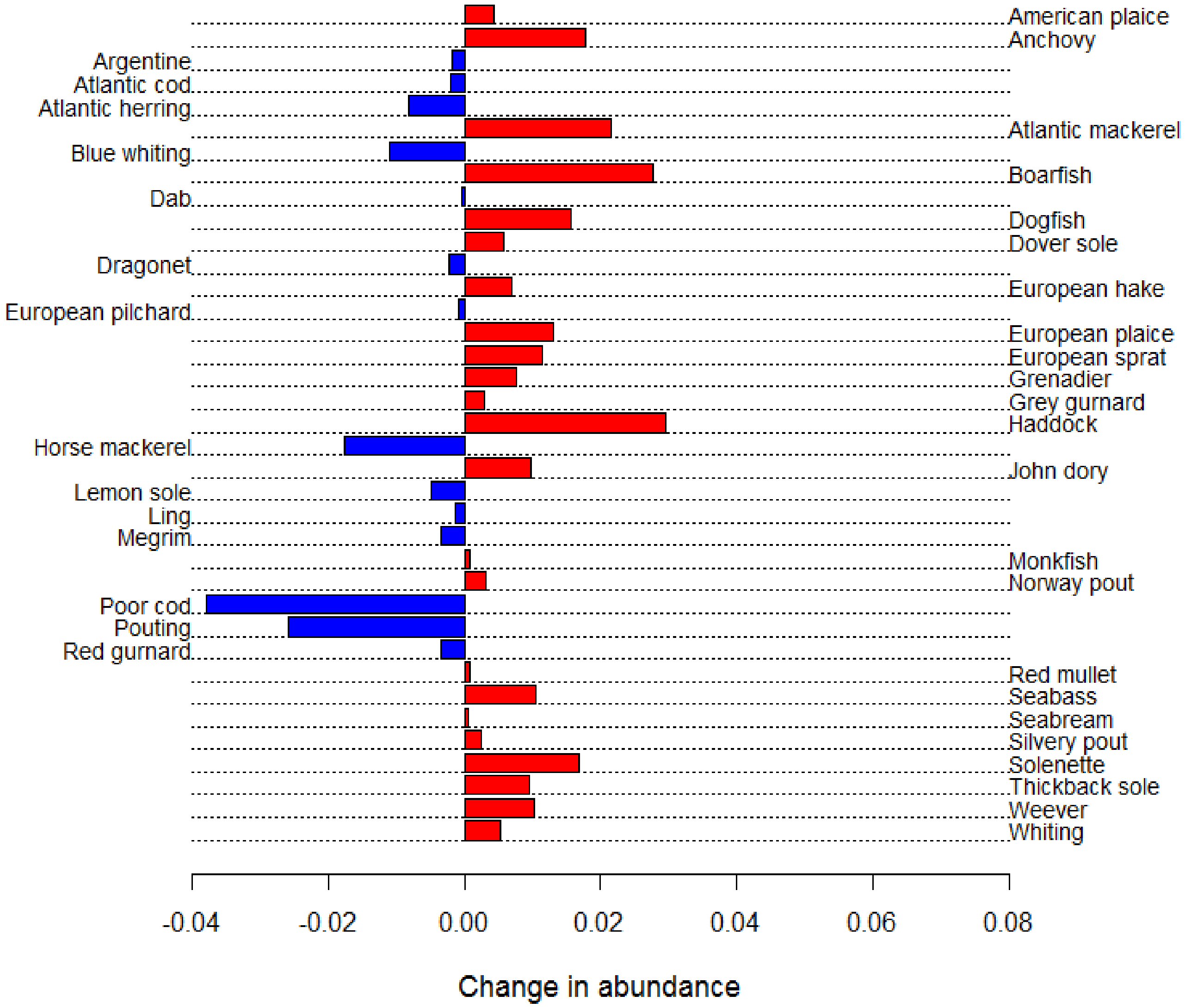

Figure 8: Change in abundance from 1987–2015, expressed as the slope of the line through the decadal mean abundance of each species. Red indicates an increase in abundance and blue indicates a decrease in abundance.

4. Discussion

This study found that over the last three decades, the fish assemblage of the south-west of the UK has increased in both diversity and richness, with some key species showing substantial changes in abundance. Since species richness simply describes the number of species present in an area, it is a fairly crude measure of diversity that can be influenced by a single occurrence of a species. The Shannon-Wiener index addresses this by assessing diversity, based on the number of species and their relative abundance. Both indices increased at a similar rate over the study period (**Figure 4**), suggesting that the increase seen is a genuine increase in the richness and evenness of the fish assemblage, and is not driven by the increased dominance of a select few species. The trend-line of the Shannon-Wiener index is slightly steeper, indicating a greater rate of increase, which could imply that the fish assemblage has become more even, being dominated less by a just a few species.

Average sea temperature has increased in the study area over the last three decades (**Figure 2**), and positive correlations were found between the temperature variables (SST and NBT) and species richness and diversity. The positive correlations observed here are relatively weak, which may be due to a paucity of data early on in the time series used, or due to a relatively moderate warming trend in south-west England compared to nearby regions (e.g. the North Sea). However, it is highly likely that temperature will have an influential role in changing community composition in the future, and given that the effects of climate change are predicted to continue and even intensify, this should be considered an important area for future study.

Similar spatial variation was observed between both indices, in terms of the rate of increase (**Figures 4** and **5**). Whilst the overall trend in both species richness and diversity increases over time, there are some areas that show a decrease over the study period, and these areas differ slightly between the two indices. The reasons for this are unclear, although it could be due, in part, to a deficiency in survey data.

Climate change, including elevated sea temperatures, has been attributed to causing shifts in species distribution by driving species towards the poles (Perry et al. 2005), or into deeper water (Dulvy et al. 2008), resulting in an increase in species richness at higher latitudes and therefore changing community structure (Beare et al. 2004; Genner et al. 2004; Hiddink & ter Hofstede 2008; Simpson et al. 2011; Montero-Serra et al. 2015). The trends observed in many of the 37 species analysed in this study (**Figure 8**) are in accordance with the theory that as average sea temperatures warm, species are moving polewards, either away from areas that have become thermally intolerable, or towards areas that are now thermally suitable. This study shows that many Lusitanian warm water species, for example anchovy (*Engraulis encrasicolus*), John dory (*Zeus faber*) and solenette (*Buglossidium luteum*) have increased in abundance over the last three decades, whereas boreal cold water species such as Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus*), and ling (*Molva molva*) have decreased in abundance. The spatial distribution of Atlantic cod has been well documented (Beaugrand et al. 2003; Hedger et al. 2004; Beaugrand & Kirby 2010), and it is reported that this species has been shifting in distribution for the past 100 years, although more pronounced changes have been observed in the last 2–3 decades (Engelhard et al. 2014).

Increasing average temperature is just one of many environmental consequences of climate change. The relatively shallow, and partially enclosed nature of the English Channel and Irish Sea may make these areas more susceptible to warming, and may exacerbate the effects of climate change. In addition to temperature changes, climate variability will affect salinity, ocean chemistry and circulation. Ocean acidification is considered to be the other major concern resulting from elevated levels of carbon dioxide, and whilst this is not addressed in this study, ocean acidification is known to affect fish communities, both directly and indirectly (Pinnegar et al. 2013; Simpson et al. 2013).

The other main driving force behind the trends observed in species abundance is likely to be the effect of exploitation by the fishing industry. The industry has experienced significant changes over the last few decades, with the establishment of the Common Fisheries Policy (CFP) and enforcement of quotas and restrictions between Member States. However, attempts to reduce fishing effort have been coupled with substantial improvements in fishing practices and technology, which, together with government subsidies, may have masked a decline in profitability (Jones et al. 2015). The number of fishers in the UK dropped by nearly 48% between 1987 and 2014. A number of fish stock collapses have occurred in recent decades, such as the North Sea herring and mackerel (*Scomber scombrus*) stocks in the 1970s (Beare et al. 2004; Marine Management Organisation 2014).The effects of fishing could explain the trends seen in species that is perhaps not so well explained by climate change. Fishing has a direct and drastic influence on the age structure of a fish population, by removing large, mature individuals, thereby reducing the populations' ability to withstand other stressors, such as climate change. Some studies have argued that fishery exploitation may be more important than climate induced warming in defining the abundance and distribution of a species (Dulvy et al. 2008; Engelhard et al. 2014). However, this impact is likely to vary regionally, depending on the levels of exploitation (ter Hofstede et al. 2010). A number of areas within the south-west are closed to certain or all types of fishing, in order to protect, or promote recovery of fish stocks. These include the mackerel box, which occupies a large area of the Western English Channel and Celtic Sea, as well as the Trevose closure, intended to protect Celtic Sea cod, occupying a smaller portion of the same area.

Some of the trends observed in this study are perhaps counter-intuitive, when compared to other literature, fishery landings, or when considering the biology of the species. For example, horse mackerel (*Trachurus trachurus)* has been increasing in abundance in recent years, in terms of scientific survey recordings as well as fishery landings; a fishery for this species has been well established in the North Sea since the 1980's (Beare et al. 2004). However, this study found a substantial decrease in the abundance of horse mackerel over the study period. The reverse is true for haddock (*Melanogrammus aeglefinus*); this study found an increase in abundance over time, however landings of haddock have fallen significantly since the mid-1990s (Marine Management Organisation 2014). Simpson et al. (2011) conducted a similar study on the fish assemblage of the North Sea, and found similar abundance trends for 12 of the 37 species analysed in this study. However, certain species did differ between studies in the trends observed, including haddock, poor cod (*Trisopterus minutus*) and whiting (*Merlangius merlangus*).

These unexpected trends and variability could be due to a number of factors. The spatial distribution of many species can vary annually and seasonally, such that the same areas sampled at different times of year may yield high catches of a particular species, or none at all (Beare et al. 2004). Given that the fishery landings quoted here are total landings for the whole of the UK, they do not give any indication about species distributions in the south-west. Spatial distribution can vary depending on life stage and environmental factors. Many species, such as mackerel, plaice and sole migrate seasonally between optimal feeding, breeding and nursery grounds. The Celtic Sea is typically occupied by juveniles of certain species, notably blue whiting, and mackerel; hence the establishment of the Mackerel Box closure, designed to protect the juveniles of this species and increase recruitment levels. The seasonality, life history and behavioural traits of a species will therefore determine how well that species will be represented by the survey data. Unusual abundance trends could also be influenced by exceptionally strong year classes, as has been observed for haddock (Marine Management Organisation 2014).

The fish abundance data used in this study introduces some bias to the results. Firstly, the gear types used by the surveys may under-represent certain species. A study conducted by Trenkel et al. (2004) assessed differences between survey design, and the effect on estimates of species abundance and community composition. The study found that both sampling method and survey period can have a substantial effect on the results of a survey, and therefore the perception of species abundance and community structure. For certain species, notably hake, mackerel and horse mackerel, survey period was an important factor, however, sampling method contributed more to the variance in abundance estimates. Differences in the identification of species between the surveys used in the study conducted here, as well as differing catchability of species, could affect the abundance and relative proportions of species caught, and therefore may affect the estimates of species richness and diversity. For example, survey gear that sample on or just above the seabed will primarily target benthic and demersal species and may under-represent fast-swimming pelagic species. In addition, the timing of the surveys may also over or under represent certain species. Whilst there is some overlap between most of the surveys, in terms of the geographic area they cover, there are some areas that are only sampled by one survey, and therefore only sampled at one time of year, which again, may affect how well certain species are represented by the dataset. Finally, there was limited data available for some cells in the study area, particularly early on in the time series, which may affect the strength of the trends observed.

5. Conclusions and future work

The rising level of richness and diversity found by this study provides further evidence to the theory that as average temperatures rise due to climate change, many fish species are shifting their ranges, resulting in increased species richness at higher latitudes. This study uses fish abundance data from scientific surveys, rather than fishery landings. However, a comparison between the two would provide an interesting insight into the correlations between them, to see how well survey data is reflected in landings. This would provide support to the fisheries management plans that are developed based on scientific data. It is likely that the changes observed in this study in species abundance and fish assemblage diversity will continue and become more pronounced in the future. This is the focus in the next Chapter that uses this multiple-survey standardised dataset to forecast future changes in the south-west UK fish assemblage.

Chapter 3: Predicted future impacts of climate change on south-west UK fisheries

Abstract

Predictive models have become highly complex and sophisticated in recent years, and are now used widely in studies to predict species distributions in both marine and terrestrial environments. This chapter uses a generalised additive modelling approach to predict how the south-west UK fish assemblage might respond to a potential anticipated climate scenario, during the course of this century.

Fish populations have responded to changing climatic conditions, through range shifts, behavioural changes and in some circumstances, physiological adaptations. This has resulted in compositional and functional changes within marine communities, which in turn have affected the productivity of fishing industries. Given that climate models are forecasting environmental scenarios that, in particular areas, are beyond anything that has previously been experienced, the response of fish communities to climate change is likely to be more pronounced than previously observed responses.

This study demonstrates that, according to the GAM modelling approach used, there are likely to be substantial changes in the composition of the south-west UK fish assemblage by the end of the century. Many species typical of warm water environments, with more southerly ranges and smaller body size, including boarfish, horse mackerel and red mullet are predicted to increase in abundance. This is likely to be coupled with a reduction in the abundance of cold-water, large bodied species, such as Atlantic cod, haddock and monkfish that are currently targeted in UK fisheries. There is also likely to be a decline in the mean trophic level of the fish assemblage; a trend that has been apparent for the last three decades.

Strong scientific evidence will support policies and inform the future management of our seas and fish stocks, and enable the fishing industry to adapt to future changes in commercial fish assemblages. It is hoped that predicting and anticipating the responses of fish communities to climate change, as explored by this study, could enable management plans to consider future changes within fish stocks, rather than be based purely on historic catch data.

1. Introduction

Global climate change is affecting the distribution and range of many species, especially in marine environments. A rise in average sea temperature, ocean acidification, and an increase in sea level are just some of the consequences predicted by climate models that could threaten the functioning of marine ecosystems. A growing number of studies have predicted how climate change is likely to affect fish and marine ecosystems, with varying outcomes, including species range shifts (Jones et al. 2013), local extinctions and invasions (Cheung et al. 2009), and increased fish production at high latitudes coupled with reduced production at mid-low latitudes (Cheung et al. 2010; Blanchard et al. 2012; Barange et al. 2014).

The climatic changes that have been forecasted are also likely to have a significant impact on industries that rely on marine resources, including the fishing industry. Many different predictions have been made about the future of fishing industries, based on different climate scenarios. Cheung et al. (2010) predicted an increase (30–70%) in catch potential for high latitude regions, coupled with a decrease (40%) in catch potential for the tropics by the middle of this century. For the same time period, Jones et al. (2015) forecasted a 10% drop in net present value in the UK as a result of decreased maximum catch potential of key species. Lam et al. (2016) considered climate change impacts in terms of global fisheries revenue, predicting an average reduction of 7.1–10.4% in Maximum Revenue Potential (MRP), under different climate scenarios. The authors state that the anticipated increase in catch potential in high latitude regions will not necessarily translate to an increase in revenue, due to greater quantities of low value fish. An increase in the abundance of small-bodied, rapid turnover species (which are generally lower in economic value), as a result of warming seas, has been reported by a number of studies (Perry et al. 2005; Dulvy et al. 2008; Simpson et al. 2011). These species are typically at lower trophic levels, and their increased prevalence in capture fisheries has been attributed to the practice of “fishing down food webs” (Pauly et al. 1998); a consequence of unsustainable exploitation of large, long-lived species.

The impact of climate change on the fishing industry will likely be observed at local, regional and global scales. As such, and as observed through a consensus within the literature, fishing practices and the policies and management plans that govern them, will need to be dynamic and adaptive to ensure the continuity and success of the fishing industry into the future. In some areas fishing fleets are already adapting to changing conditions; having a better understanding of how the composition of the fish assemblage may change in the future will give fishers a greater capacity to adapt to new opportunities. This may be done through targeting different species, changing fishing practices and gear types as well as targeting new locations (Defra 2013).

The UK fishing industry landed 756 thousand tonnes of fish in 2014, with a value of £861 million (Marine Management Organisation 2014). Whilst the contribution made to GDP (Gross domestic product) by fisheries is relatively small, the regional importance of fishing varies greatly (Pinnegar et al. 2013); many coastal communities are highly dependent on the fishing industry for both income and employment. It is therefore not surprising that there is a growing number of studies focusing on climate scenarios, impacts and possible mitigation measures (Blanchard et al. 2012; Jones et al. 2015). The ability to make informed policy decisions will largely depend on the availability of predictive models that can make reliable and accurate estimations about the impacts of climate change.

Recent advances in ecosystem modelling have seen a shift from simplistic models that use only presence or presence-absence data, towards the use of more complex or multi-model approaches (Araújo et al. 2005; Beaugrand et al. 2011; Jones et al. 2012; Cheung et al. 2013; Jones et al. 2013; Rutterford et al. 2015), which can account for a multitude of environmental and human-impact variables. Models that can describe more complex, often non-linear relationships, are arguably better suited to provide robust estimations of a species response to climate change (Araújo et al. 2005), and therefore contribute to a more comprehensive understanding of how marine organisms and even entire ecosystems will fare in a changing climate.

Climate models are now predicting future environmental conditions that have not yet been experienced by the ecosystem for which they are predicted. These conditions, together with the shifts they may cause in species distribution and abundance, will likely result in the emergence of novel ecosystems (Doney et al. 2012), bringing together species that do not currently exist together. This could significantly alter ecosystem dynamics in terms of species interactions, predation and competition for resources, which in turn will present a number of challenges for conservation and management plans (Buisson et al. 2013). It is possible that species currently occupying areas of high environmental variability will fare better in the face of climate change, than those that occupy very environmentally stable habitats (Hollowed et al. 2013). However, anticipating the adaptive capacity of a species is just one of a number of challenges faced in ecosystem modelling.

The modelling approach applied in this study uses generalised additive models (GAMs), and is developed from the method described by Rutterford et al. (2015). A GAM is a generalised linear model (GLM) with the addition of a smoothing function that can be applied to each variable, without having to specify detailed parametric relationships between the variables (Wood 2006). The degree of smoothness can be determined, as can the exponential family of distribution (i.e. Gaussian, Poisson, Gamma) used by the model. The addition of a smoothing function means that GAMs can account for non-linear relationships, as are commonly found between fish abundance data and environmental variables (Hedger et al. 2004). In this study GAMs are used firstly to assess the importance and influence of different environmental variables (detailed in *Section 2)* on a fish species' distribution. Secondly, the models are used to predict mean decadal fish abundances, from 2010 until the end of 2090, according to a specified climate scenario. The climate data used in this study are based on levels of carbon emissions that equate to a "best case scenario". This study aims to assess the fish assemblage as a whole, and as such, the species used in this study account for a large proportion of the fish assemblage of the south-west of the UK, and includes both commercially valuable, and non-commercial species. The central research questions that this chapter aims to answer are:

1. How might the key species of the south-west UK fish assemblage respond to climate change?

2. Is there likely to be a significant change in the characteristics of the fish assemblage between present day and the end of the century, in terms of body size, trophic level or latitudinal preference?

2. Methods

2.1 Study area and data sources

The study area for this Chapter is the same as detailed in *Chapter 2*, see **Figure 1**. Additional environmental data were required for the GAM, in order to assess the influence of different variables on the abundance of the selected fish species, and ultimately make future predictions based on projected future conditions.

2.1.1 Habitat type

The habitat type within each 1°x1° cell was identified using the European Marine Observation Data Network Seabed Habitats project (EMODnet 2015). The map layers used were EUSeaMap 2012–13 official top copies: Habitat maps (simplified classification). The substrate occupying the majority (>50%) of each 1°x1° cell was identified and recorded according to the EUSeaMap key. Where two habitat types occupied equal proportions of a cell, both were recorded (see **Figure 9** for habitat classification used in the GAMs, and **Appendix 4** for the original EUSeaMap habitat data). Habitat data were not available for some cells at the time when this study was conducted but have since been updated (discussed further in *Section 4*).

2.1.2 Fishing effort

Fishing effort data tables and their associated reports were obtained from the Scientific, Technical and Economic Committee for Fisheries (STECF 2014). This dataset compiles fishing effort from all countries operating within the region, which for this study includes: Belgium, Denmark, France, Germany, Ireland, Netherlands, Portugal, Scotland, Spain, Sweden and the UK (England, Wales, Northern Ireland, Isle of Mann, Guernsey and Jersey). Fishing effort in these tables is given by ICES rectangles, which were converted to 1°x1° cells, and averaged across the time period available (2003–2013), to give an average fishing effort per cell, in units of “hours fished” (see **Figure 10**). The data tables also list fishing effort by gear type, and for the purpose of this study, certain gear types were removed because they do not target finfish. These were: pot (21.79% of all fishing effort), dredge (7.95% of all fishing effort), and those entries where no gear type was recorded (0.14% of all fishing effort). For the purpose of this study it was assumed that fishing effort would remain constant during the time period for which model predictions are made, an assumptions that is discussed further in *Section 4*.

2.1.3 Depth, salinity and climate data

Environmental parameters were obtained from the Met Office Hadley Centre HadCM3-POLCOMS Shelf Seas model (Tinker et al. 2015). These parameters include depth, sea surface salinity (SSS), near bottom salinity (NBS), sea surface temperature (SST) and near bottom temperature (NBT) (see Tinker 2016 for data). These outputs are from the unperturbed ensemble of the model (i.e. default parameters), and are based on a scenario of future changes under the Representative Concentration Pathway (RCP) 2.6; this assumes a “best case scenario” in terms of reducing greenhouse gas emissions, through drastic policy intervention and climate mitigation measures, resulting in a mean temperature increase of 1.5–2.0°C by the end of the century (Vuuren et al. 2011). Salinity and depth data were re-gridded[1] to give an average value per 1°x1° cell, per decade (see **Figures 11** and **12** respectively). Temperature data were manipulated to obtain mean annual SST and NBT, as well as mean winter (Jan, Feb, March) and summer (July, Aug, Sep) values for both SST and NBT, on a per cell per decade basis. Past and predicted mean SST and NBT can be seen in **Figure 13**. **Figure 14** shows anticipated spatial variation in SST for the study area, from 2010–2098.

2.1.4 Fish abundance data and standardisation

See *Chapter 2, Section 2.1.2* for fish abundance data sources and manipulation processes, and *Chapter 2, Section 2.3* for the data standardisation process. Certain groups of species were omitted from this analysis, despite occurring in relatively high abundance (in terms of CPUE) in the dataset; this includes

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[1] Conducted by Katherine Maltby (PhD researcher, University of Exeter).

skates, rays and gobies. This decision was due to these species being poorly characterised by all of the models tested for this study (see *Section 2.2* for further discussion on modelling process). In order to address possible inconsistencies in the identification of these species by surveys, all species of ray and skate were grouped together, as were gobies. This may have influenced how well the model captured trends in the data, and could account for the low predictive power and poor fit of the models. Where negative LS-mean values occurred as a result of the standardisation process, these remained as such until post-modelling and predictions had been made by the GAM. During analysis of the GAM predictions, any negative values of abundance were changed to zero, as it is not biologically feasible to have a negative abundance.

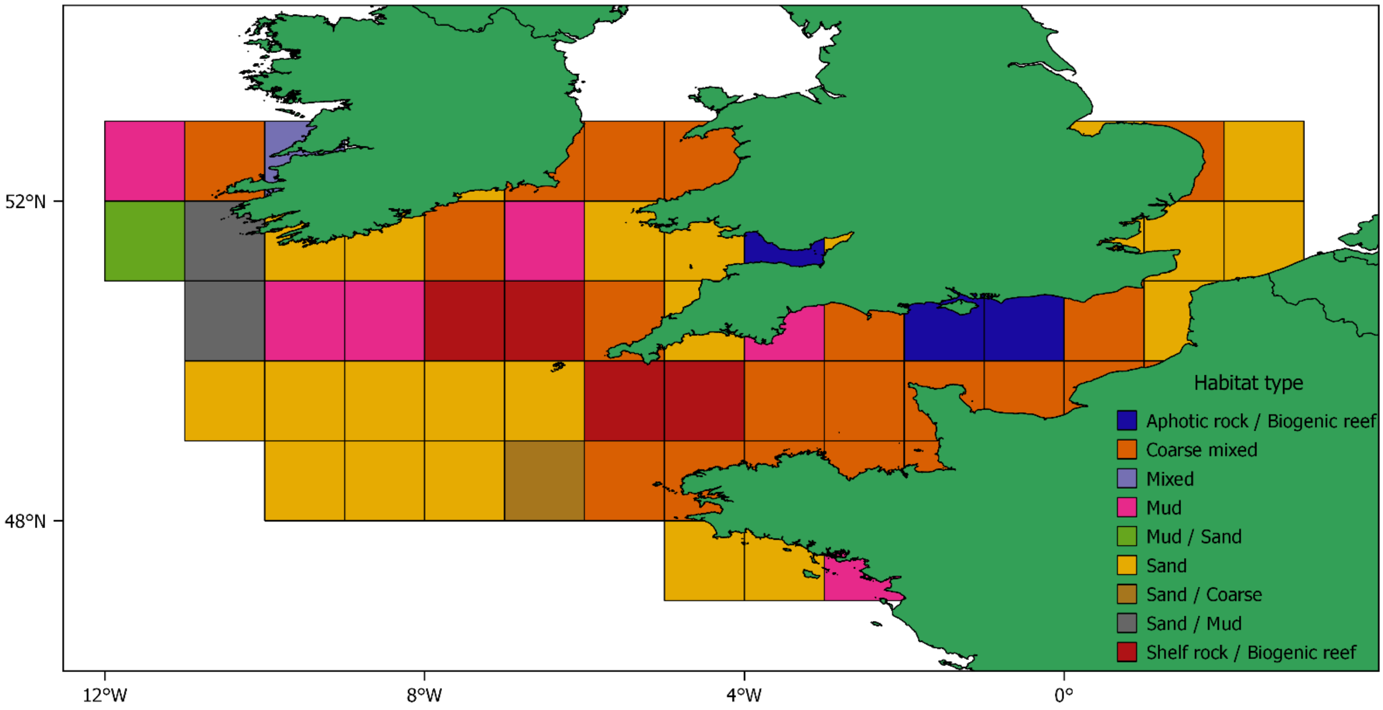


Figure 9: Habitat types used in the GAM, derived from data available through the European Marine Observation Data Network Seabed Habitats project.

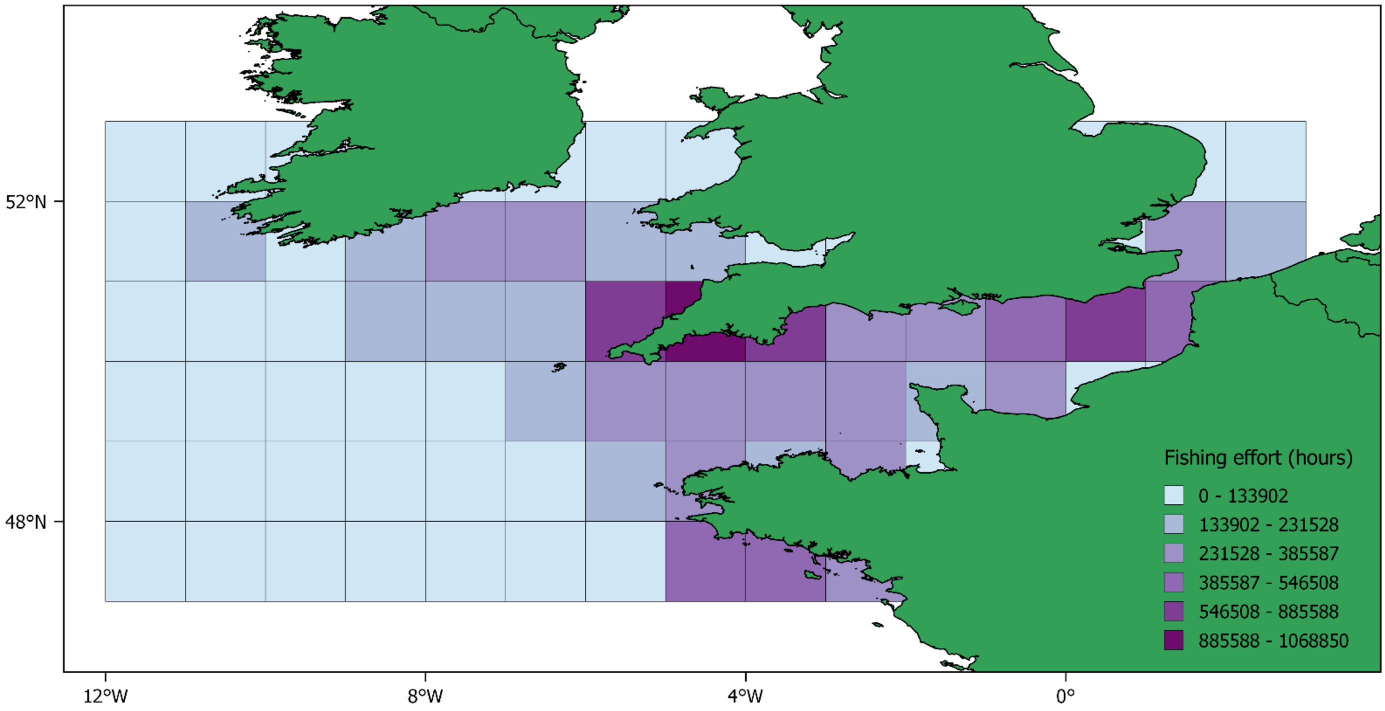


Figure 10: Mean fishing effort per 1°x1° cell in terms of hours fished, from the Scientific, Technical and Economic Committee for Fisheries (STECF).

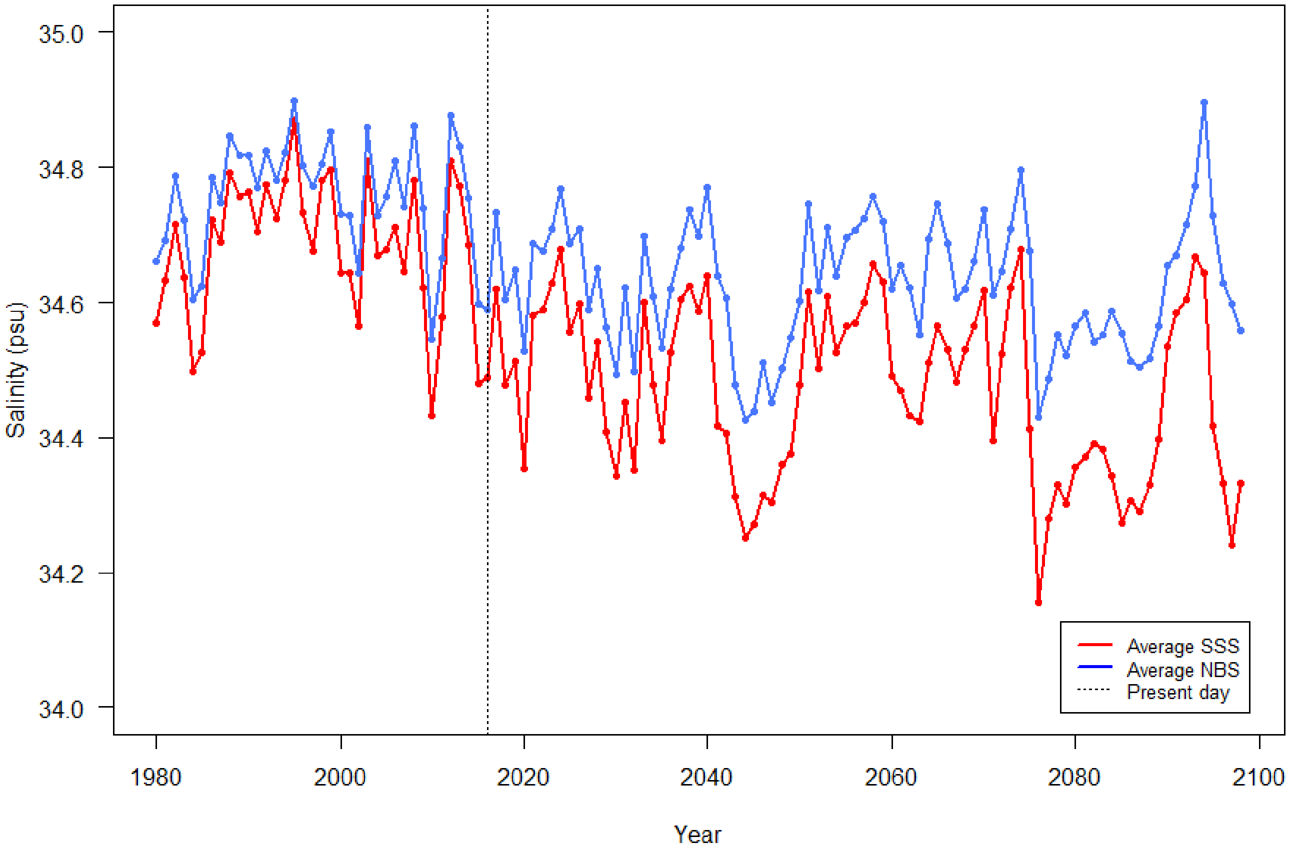


Figure 11: Salinity trends from 1980–2098 for the study area, forecasted by the Met Office Hadley Centre HadCM3-POLCOMS Shelf Seas model.

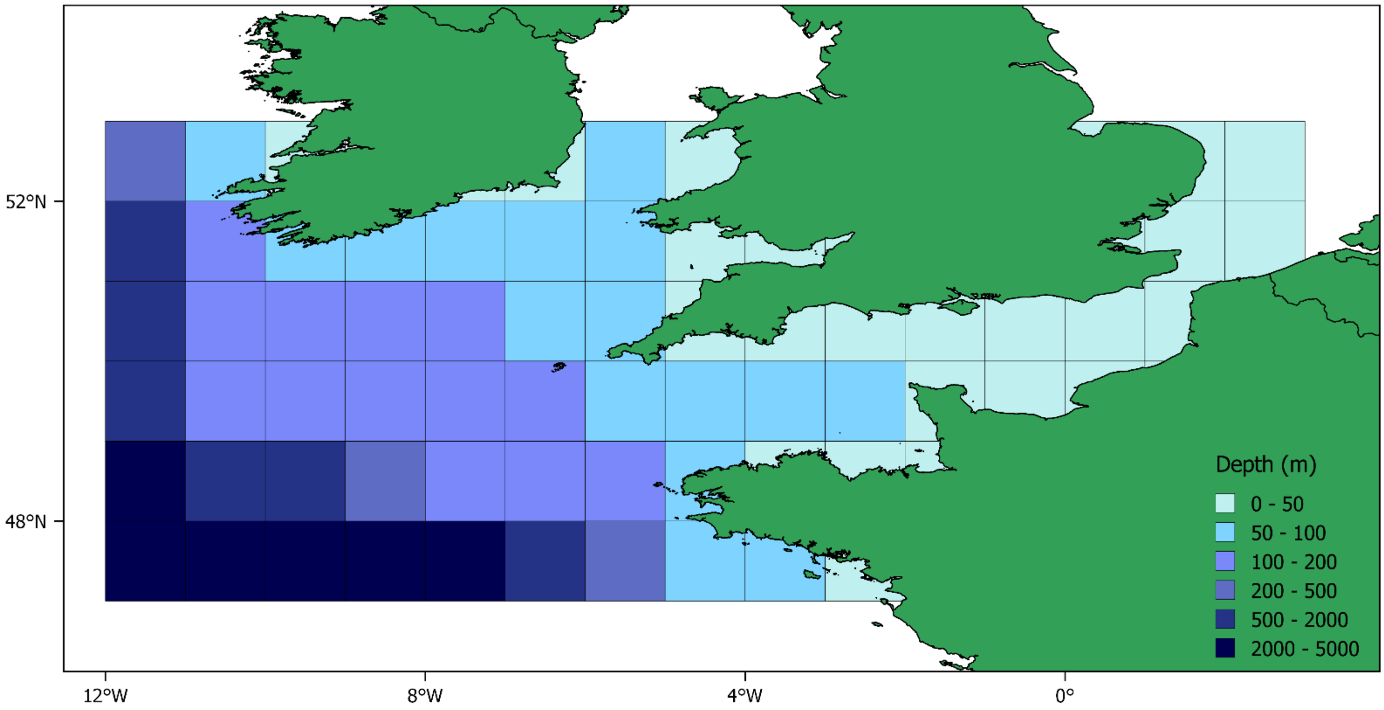


Figure 12: Mean depth per 1°x1° cell, from the Met Office Hadley Centre HadCM3-POLCOMS Shelf Seas model.

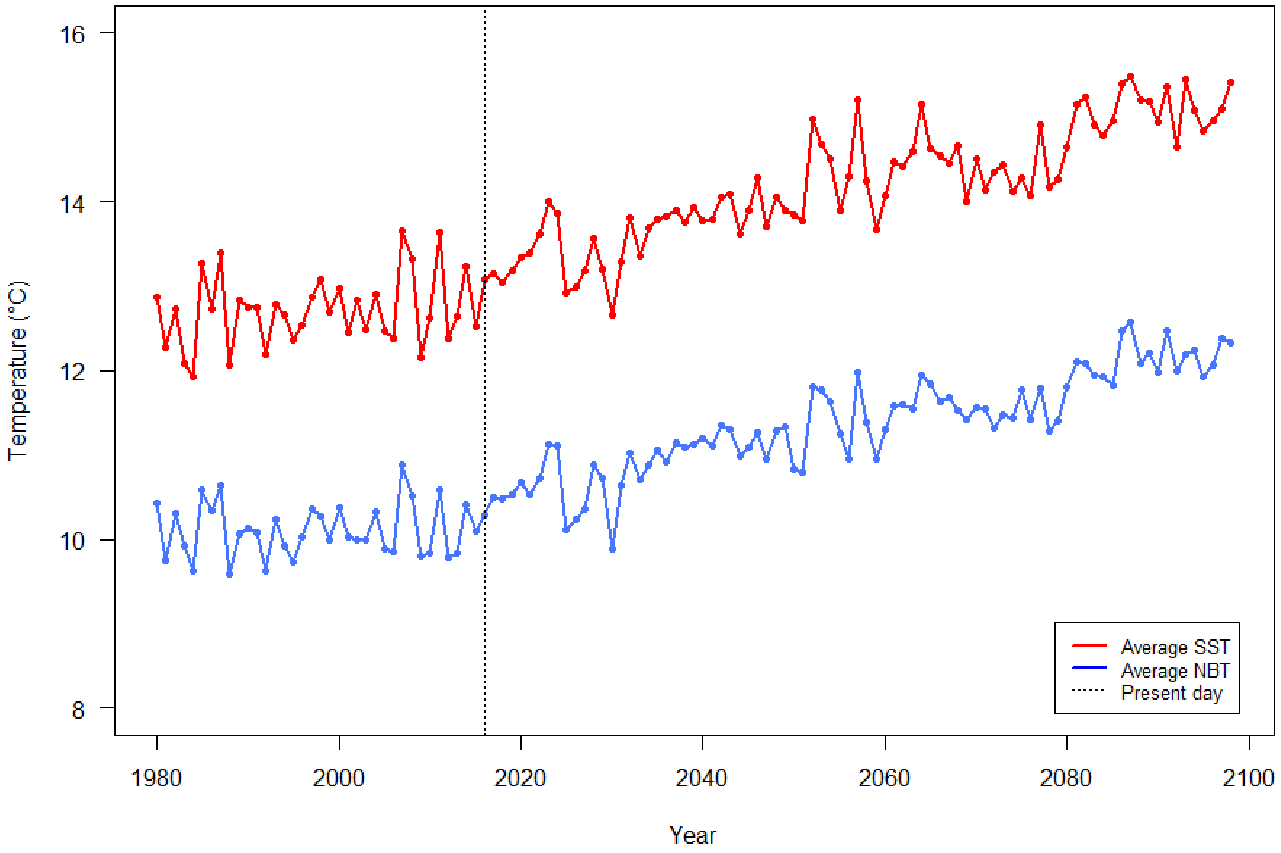


Figure 13: Mean annual temperature trends for the south-west from 1980–2098, for the 75 1°x1° cells used in this study, forecasted by the Met Office Hadley Centre HadCM3-POLCOMS Shelf Seas model.

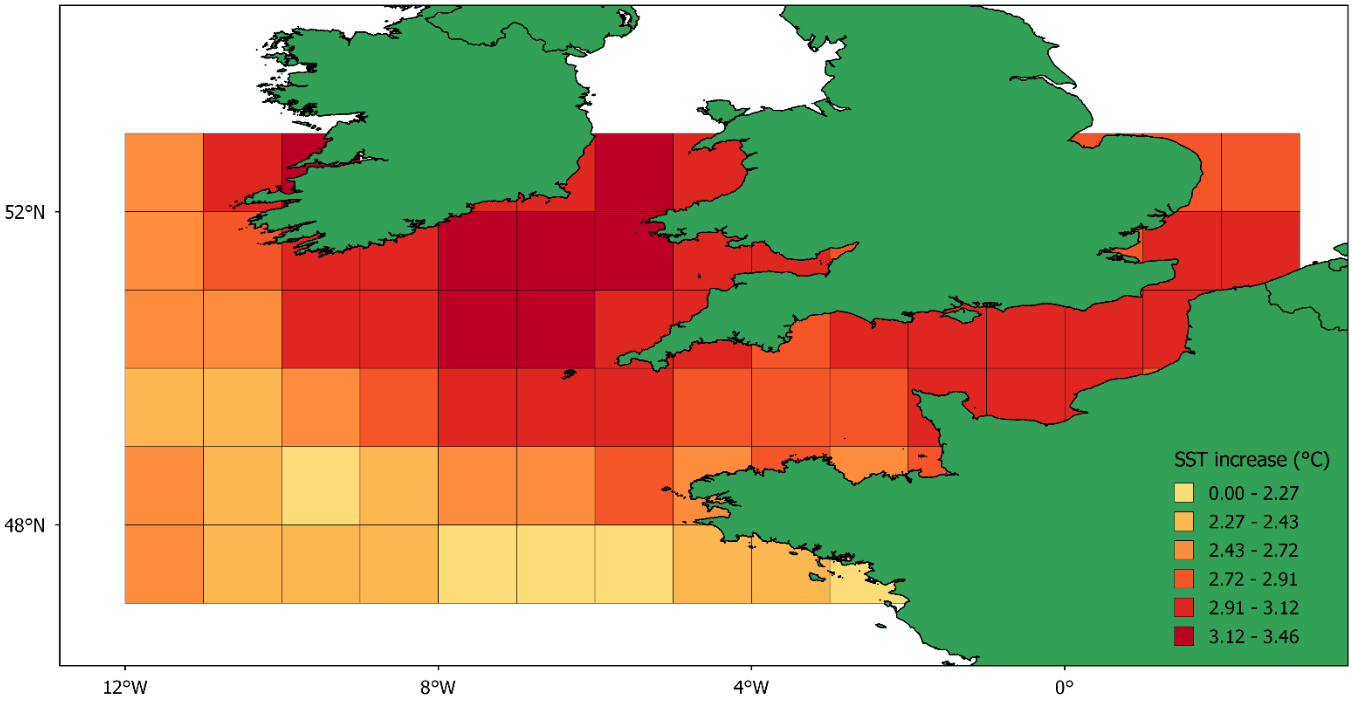


Figure 14: Spatial variation in predicted SST increase for the study area, from 2010–2098, forecasted by the Met Office Hadley Centre HadCM3-POLCOMS Shelf Seas model.

2.2 Modelling

GAMs were developed from the methods described by Rutterford et al. (2015) using the ‘*mgcv*’ package (Wood 2011; 2016) in R (R Core Team 2016). Fish species selected for GAM analysis are outlined in **Table 1** (see *Chapter 2, Section 2.4* for species selection process).

2.2.1 Model development, training and selection

GAMs were developed and trained on data earlier in the time series, in order to test their predictive power before making predictions into the future. Data from the time period 2001–2010 were used for model training, as this period has the most consistent data for all of the surveys. A previous study found no substantial improvement in model fit or function as a result of extending the time series used to train the models (Rutterford et al. 2015). The following variables were included in the full model: depth, habitat, fishing effort, SSS, NBS, annual and seasonal (summer and winter) SST and NBT. Subsequent versions of the model contained all except one of the variables. The influence and predictive power of each variable was assessed, and based on that a decision was made as to whether the variable should be included in the model. The basis for the smoothing function is determined by a value of *k.* For this study a Gaussian distribution was used, and a *k* value of 5 for all variables, to limit the degrees of freedom and avoid over-fitting the data. All variations of the models were tested on all species. The ‘gam.check’ function within the ‘*mgcv*’ package was used to check that the specified distribution was appropriate, and to ensure that the smooth function basis was adequate, and not “over-smoothing” the data. GAMs were also used to predict the data values upon which they had been trained, in order to test the integrity and predictive power of the model (see **Figure 15A** and **15B** for correlations between actual and predicted abundance values for the chosen GAM). The ‘summary.gam’ function was used to generate model statistics, which were assessed to determine the suitability of the model. These include: adjusted r^2, deviance explained by the model and Generalised Cross Validation (GCV). The Akaike Information Criterion (AIC) and hence Akaike weight was also calculated. All of these values, together with the correlation values, were used to determine which model performed best for each species.

In the case of the AIC and GCV values, a lower value is deemed a better fitting model.

The model without the variable for habitat was deemed to be the most suitable model based on the criteria described above (see **Appendix 5** for all model statistics), performing best for 15 out of 37 species. With this model the minimum adjusted r^2 and correlation values across all species were 0.54 and 0.79 respectively.

2.2.2 Model predictions

The selected GAM was then used to predict decadal abundances for each species per cell, based on predicted annual and seasonal SST and NBT, as well as SSS and NBS forecasted by the Met Office Hadley Centre Shelf Seas model (detailed in *Section 2.3*). The first decade for which predictions were made was 2010 (2011–2020 inclusive), and each subsequent decade up to and including 2090 (forecasted predictions were only available up to and including 2098, so the 2090 period covers 2091–2098). The other variables in the model (depth and fishing effort) remained the same as used for model testing. The predicted abundance values were kept as 4th root transformed CPUE, for ease of interpretation and comparison. The trend of change in abundance as predicted by the GAM was mapped for each species using Quantum GIS (QGIS 2016) in order to assess any spatial variation in abundance trends. Abundance trends of each species per cell were identified and assessed for normality. Since the data were deemed not normally distributed a Wilcoxon signed rank test was conducted using R (R Core Team 2016) for each species, to determine if the overall rate of change (slope) in abundance was significantly different to 0 ($p<0.05$; see **Appendix 6** for test results).

2.2.3 Analysis of model predictions

Values of mean length, central latitude and trophic level were obtained for each species from FishBase (FishBase 2012). There are certain limitations associated with data relating to trophic level; the values may be based on a model output, or analysis of gut content, which gives only a snapshot of the diet consumed and could vary substantially depending on the age and size of the fish (Pinnegar et al. 2002). However, this data can provide valuable indications about community structure within a fish assemblage. Changes in the characteristics of the fish assemblage were assessed by comparing mean length, central latitude and trophic level between species that are predicted to increase in abundance (winners), and those that are predicted to decrease in abundance (losers), using a Mann Whitney U test. In addition, GAM-predicted abundance values were used together with historic data for the south-west fish assemblage (described in *Chapter 2, Section 2.1.2*) to calculate and compare the mean trophic level of the fish assemblage, for each decade from 1980 to 2090. Mean trophic level was calculated for each decade as follows:

$$\frac{\sum_i (a_i t_i)}{\sum a_i}$$

where *a* = abundance and *t* = trophic level.

To give an indication of how the composition of the fish assemblage may change, and how the predicted abundances relate to present day abundances, the values predicted by the GAM for each species were back transformed; from 4th root transformed CPUE to raw CPUE values.

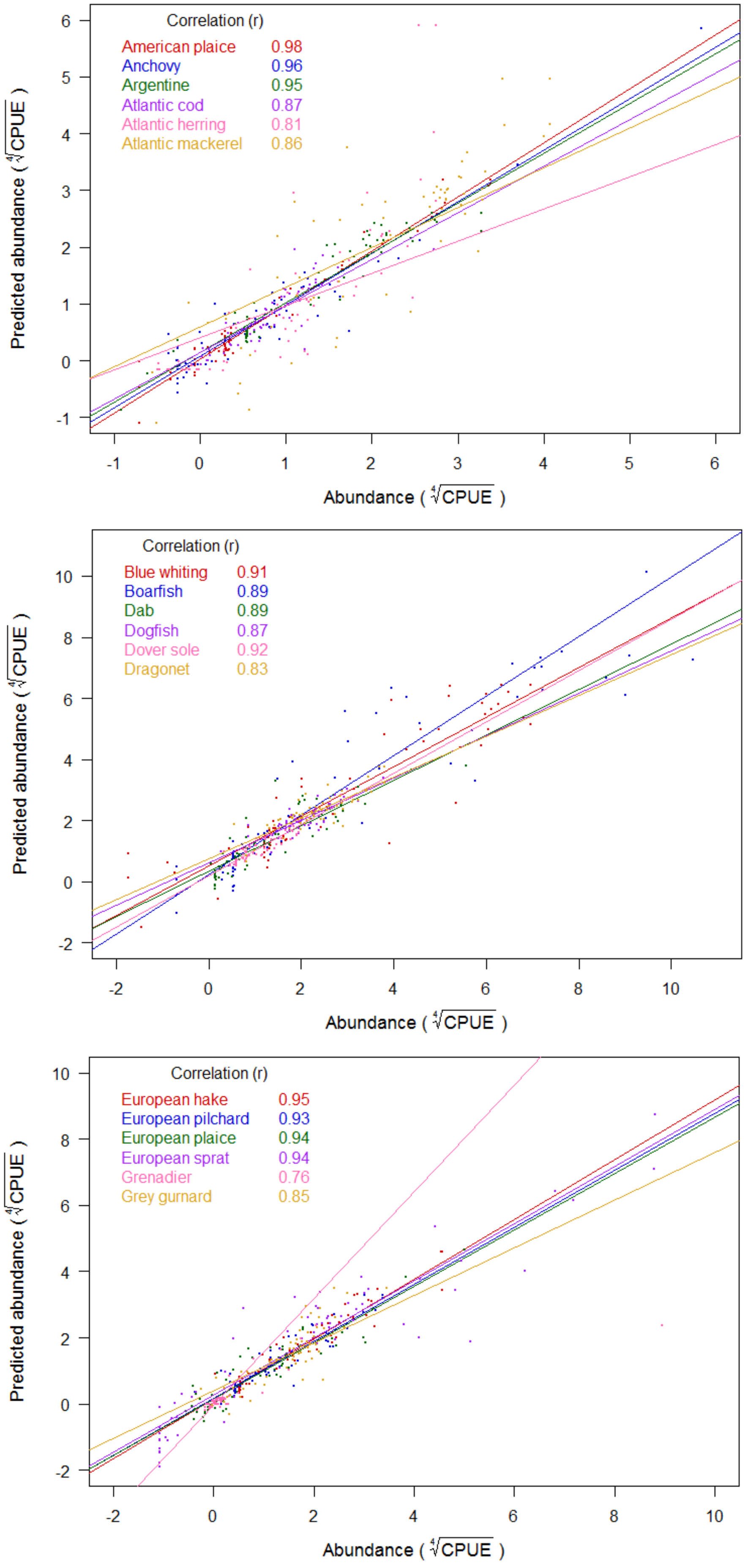


Figure 15A: Correlation (r) between known abundance (least-square mean estimate of abundance) and GAM-predicted abundance, for each species, for the 2000 decade.

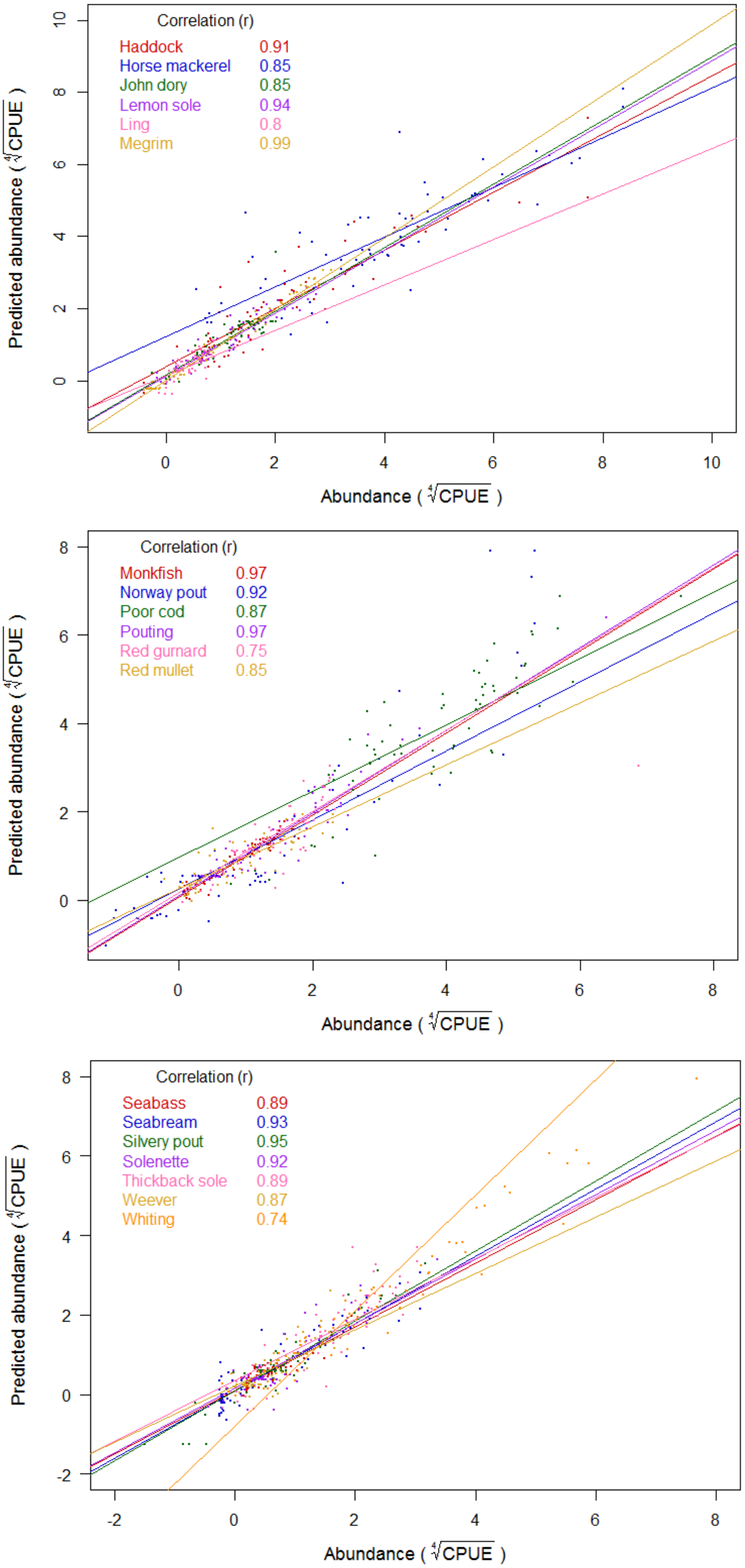


Figure 15B: Correlation (r) between known abundance (least-square mean estimate of abundance) and GAM-predicted abundance, for each species, for the 2000 decade.

3. Results

The selected GAM combined the following variables: depth, fishing effort, SSS, NBS, mean annual SST, mean annual NBT, mean winter SST and NBT and mean summer SST and NBT. From the abundance values predicted by the GAM, an average rate of change was calculated for each species across the study area; expressed as the gradient of the line between the mean decadal abundances (**Figure 16**). 32 of 37 species analysed showed a significant ($p<0.05$) change in abundance over the time period used by the model (non-significant results are represented by grey bars in **Figure 16**). Of those 32, 20 showed an increase in abundance, represented by red bars in **Figure 16**. The results of the one-sample Wilcoxon test can be seen in **Appendix 6**.

Substantial spatial variation in abundance response was predicted for some species; maps for a selection of species is shown in **Figure 17**, the remaining species maps can be seen in **Appendix 7, 8, 9** and **10**. **Table 2** summarises the abundance response observed in all species; these are grouped according to the spatial variation observed; consistent trends (no spatial variation) and majority trends (some spatial variation).

Based on the abundance trends (**Figure 16)**, species predicted to increase in abundance were deemed winners, and those predicted to decrease in abundance were considered losers. The metrics obtained from FishBase were used to determine mean central latitude, length and trophic level for the winners and losers (values in **Appendix 11**), and these were compared using Mann Whitney U tests (**Table 3**). There was a statistically significant difference ($p<0.05$) between the winners and losers mean central latitude ($p=0.0120$, $W=55$), as well as mean body length ($p=0.0131$, $W=56$). The difference between winners and losers mean trophic level was not statistically significant. However, there is likely to be a substantial decline in the mean trophic level of the south-west UK fish assemblage between 1980 and 2098. A non-parametric Mann-Kendall test was performed to assess the trends in trophic level over time. The results ($tau=-0.545$, $p=0.016$) indicate a significant negative correlation between mean trophic level and year (**Figure 18**).

Projected abundances by the GAM models (based on back-transformed CPUE values) suggest that the fish assemblage will become dominated by fewer species by the end of this century (**Figure 19A** and **19B**), and that the abundance of selected species may increase drastically, compared to present day (**Figure 19A**).

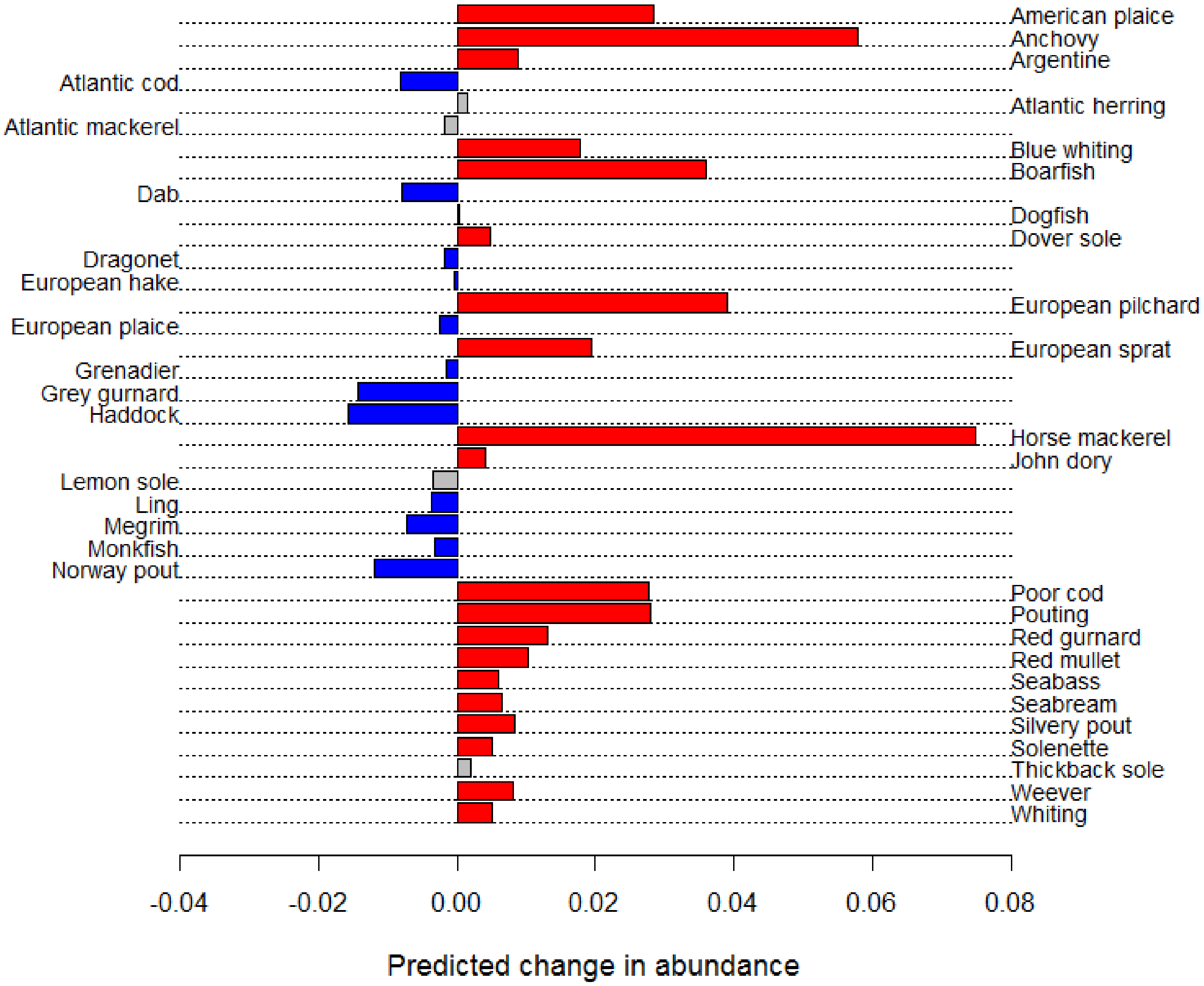


Figure 16: Change in abundance from 2010–2098, as predicted by the GAM, expressed as the slope of the line through the decadal mean abundance of each species. Red indicates an increase in abundance, blue indicates a decrease in abundance, and grey indicates the predicted change is not statistically significant (p>0.05).

Consistent increase	**Majority increase**	**Majority decrease**	**Consistent decrease**
Anchovy (*Engraulis encrasicolus*) Dover sole (*Solea solea*) European pilchard (*Sardina pilchardus*) Horse mackerel (*Trachurus trachurus*) Pouting (*Trisopterus luscus*) Red gurnard (*Chelidonichthys cuculus*) Red mullet (*Mullus barbatus* and *M. surmuletus*) Seabass (*Dicentrarchus labrax*) Weever (*Echiichthys vipera* and *Trachinus draco*	American plaice (*Hippoglossoides platessoides*) Argentine (*Argentina sp.*) Atlantic herring* (*Clupea harengus*) Blue whiting (*Micromesistius poutassou*) Boarfish (*Capros aper*) Dogfish* (see **Table 1**) European sprat (*Sprattus sprattus*) John dory (*Zeus faber*) Poor cod (*Trisopterus minutus*) Seabream (see **Table 1**) Silvery pout (*Gadiculus argenteus*) Solenette (*Buglossidium luteum*) Thickback sole* (*Microchirus variegatus*) Whiting (*Merlangius merlangus*).	Atlantic mackerel* (*Scomber scombrus*) Dragonet (*Callionymus sp.*) European hake (*Merluccius merluccius*) European plaice (*Pleuronectes platessa*) Grenadier (see **Table 1**) Lemon sole* (*Microstomus kitt*). Ling (*Molva sp.*) Megrim (*Lepidorhombus sp.*)	Atlantic cod (*Gadus morhua*) Dab (*Limanda limanda*) Grey gurnard (*Eutrigla gurnardus*) Haddock (*Melanogrammus aeglefinus*) Norway pout (*Trisopterus esmarkii*). Monkfish (*Lophius piscatorius*)

Table 2: Summary of abundance responses, as predicted by the GAM. Grouped according to spatial variation observed; consistent trends (no spatial variation) and majority trends (some spatial variation). * indicates species for which the results were not statistically significant ($p>0.05$).

	Central latitude (°N)	Length (cm)	Trophic level
Winners mean value	39	22.83	3.59
Losers mean value	50.04	47.05	3.84
p- value	0.0120 (W=55)	0.0131 (W=56)	0.2128 (W=87.5)

Table 3: Mean values of central latitude, length and trophic level for species predicted to increase in abundance; winners, and those predicted to decrease in abundance; losers. Mann-Whitney U tests were conducted, p values indicate that differences between the two groups for central latitude and length are statistically significant ($p<0.05$).

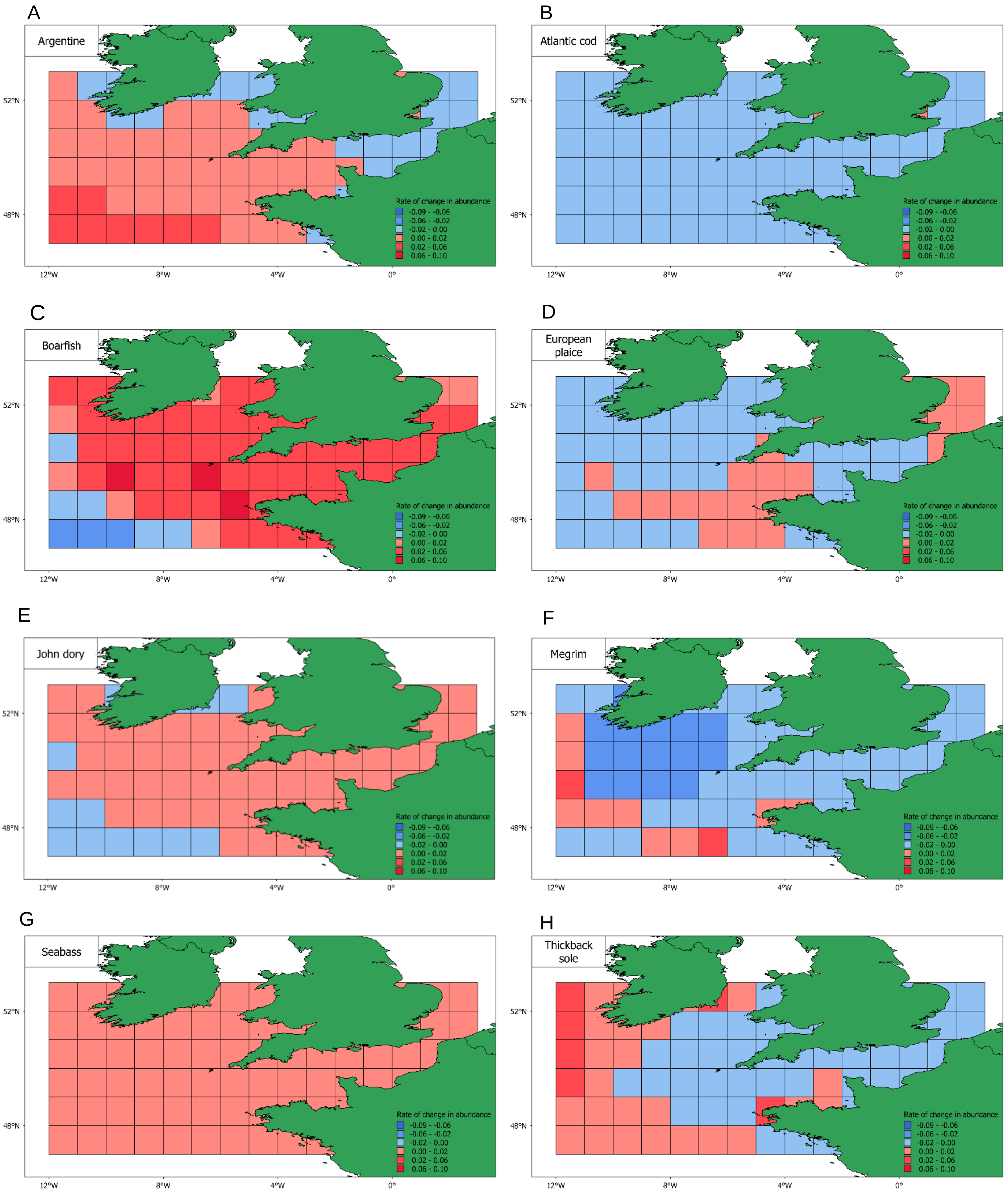


Figure 17: Spatial variation in the rate of change in abundance (expressed as the gradient of the line through the mean decadal abundance values), as predicted by the GAM, for 2010–2098. **A,** Argentine (*Argentina sp*.). **B**, Atlantic cod (*Gadus morhua*). **C**, Boarfish (*Capros aper*). **D**, European plaice (*Pleuronectes platessa*). **E**, John dory (*Zeus faber*). **F**, Megrim (*Lepidorhombus whiffiagonis* and *L. boscii*). **G**, Seabass (*Dicentrarchus labrax*). **H**, Thickback sole (*Microchirus variegatus*).

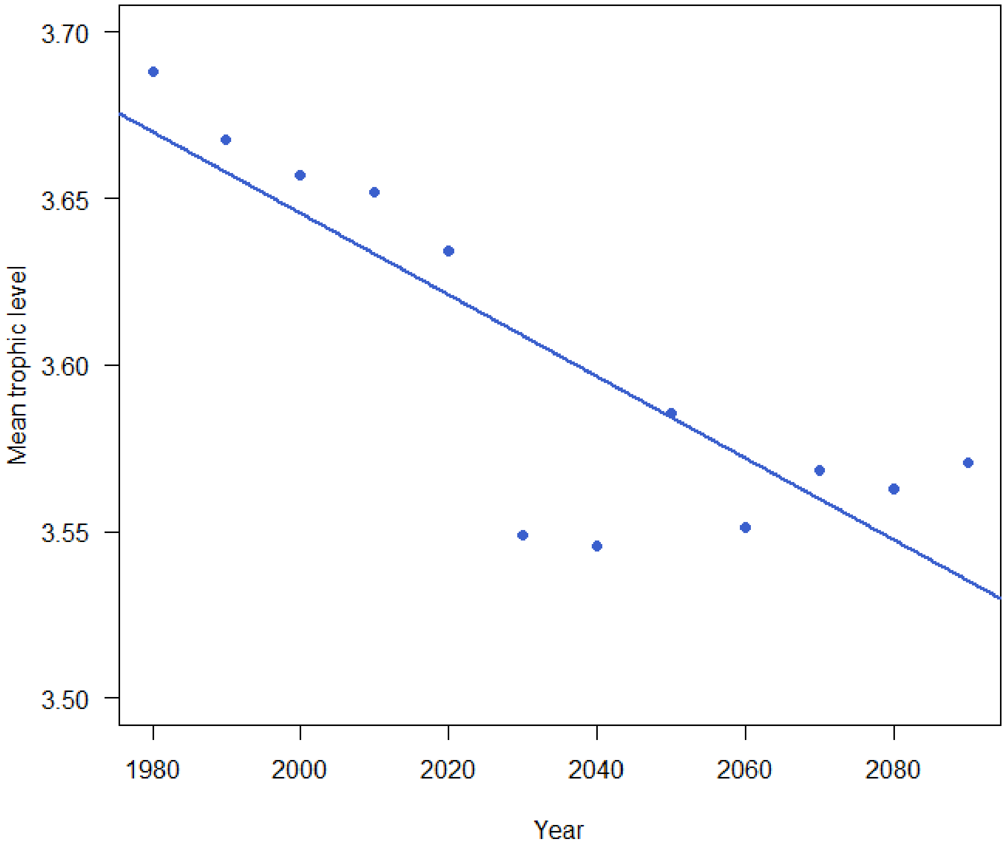


Figure 18: Mean trophic level of the south-west UK fish assemblage, based on historic abundance data from 1980–2000, and GAM predicted abundance data from 2010–2090, Mann-Kendall tau=-0.545, p=0.016.

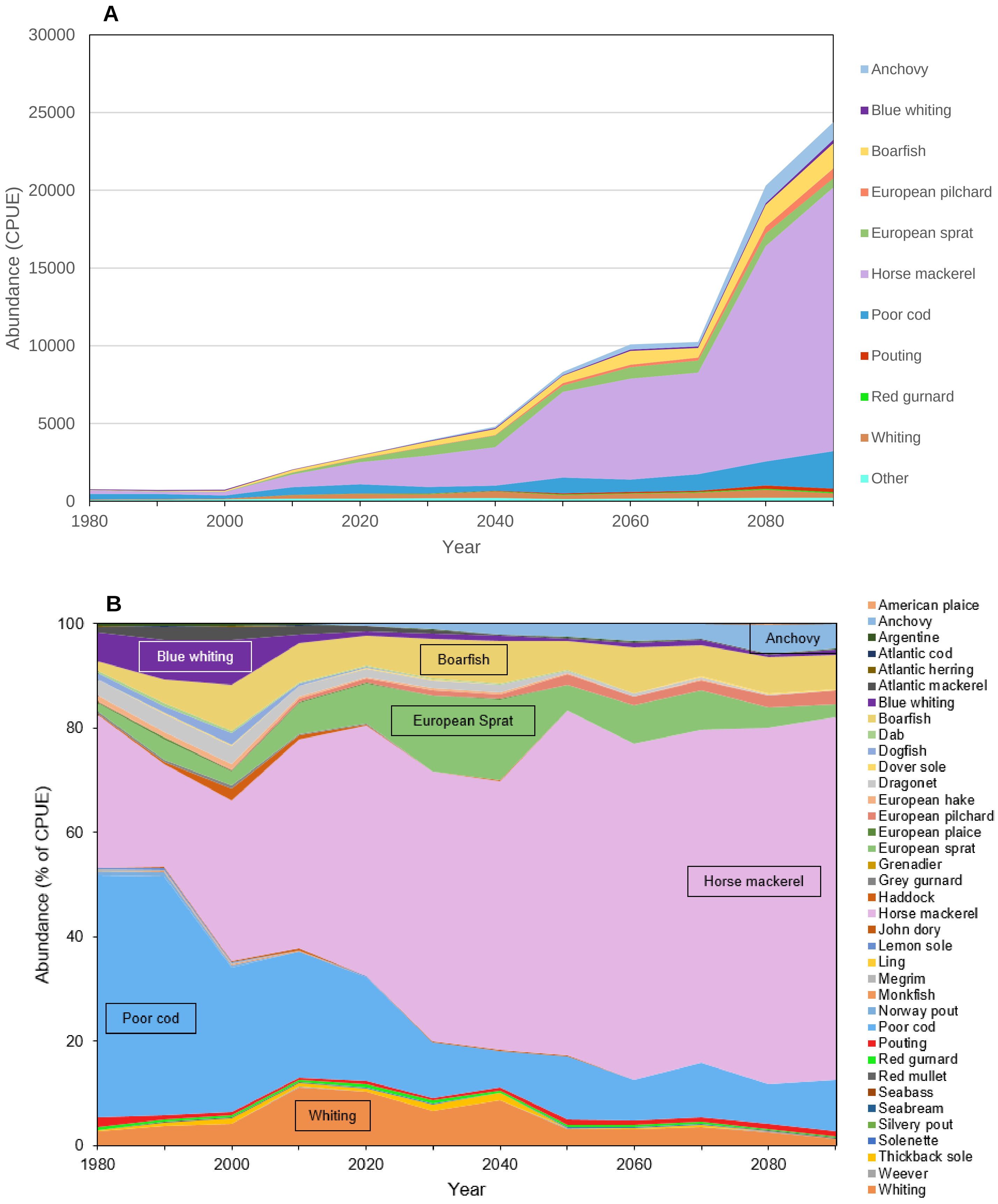


Figure 19: Cumulative abundance (CPUE) of species as predicted by the GAM, back transformed from 4th root transformed CPUE to show the anticipated change in abundance from 1980–2098. **A**, Abundance trends of selected species. **B**, Abundance trends for all species and their relative proportion of the total CPUE.

4. Discussion

The results of this study show that, based on the predictions of the GAM used, there is likely to be a substantial change in the composition of the fish assemblage occupying the waters surrounding the south-west of the UK. Over 80% of the species analysed showed a significant change in abundance by the end of the century. Species that are typically associated with warmer climates (Lusitanian species) such as anchovy, boarfish and John dory were all predicted to increase in abundance, whereas those species associated with colder waters such as Atlantic cod, haddock and monkfish were all predicted to decrease in abundance. This suggests that species distributions may shift towards higher latitudes as average temperatures increase; a pattern already documented in some areas (Perry et al. 2005). The spatial variation observed in the predicted abundances of some species also suggests that where deeper habitats are available, these species will migrate when the temperature at their current location becomes too warm, as has been shown by Dulvy et al. (2008) and Rutterford et al. (2015).

Anchovy, European pilchard and horse mackerel all showed strong, significant increases in abundance across the study area, and are all typically associated with warm water areas. The increase in anchovy has been documented in other literature (Beare et al. 2004; Petitgas et al. 2012; 2013), and fisheries for this species are already established in the UK (Simpson et al. 2013). However, the appearance of anchovy in UK waters is not a new phenomenon. Studies have demonstrated, and fishermen have confirmed, that anchovy has been present for many decades, but has increased significantly in recent years. This may not necessarily be due to an influx of individuals from further south, rather that environmental conditions here (i.e. a rise in average sea temperature) mean that this species can now complete its entire life cycle within UK waters (Simpson et al. 2013), and so the sub-stock that has been present for many decades is now prospering. Boarfish is another species for which there is now a viable market, and a successful fishery is well established in Ireland (Pinnegar et al. 2013); the results of this study predict that boarfish will continue to increase in abundance over the next century. Other species predicted by this study to increase in abundance include Dover sole, poor cod, pouting, red gurnard, red mullet, seabass, greater weever and lesser weever. All of these species, with perhaps the exception of poor cod and pouting, occur as far south as the north west coast of Africa (FishBase 2012), and so if average temperature is the primary driver behind their distribution, it is unsurprising that the rise in average SST forecasted for the south-west UK will result in an increase in the abundance of these species. This study however, does not consider species that are not currently present in south-west UK waters that may move into this region as environmental conditions become more favourable. Recent years have seen the emergence of many “new” species, some of which are now found in substantial numbers in UK waters, so it is reasonable to assume that this pattern will continue, as sea temperatures continue to rise.

In contrast, many cold-water species, for which there have long been well established fisheries in the UK, are predicted to decrease in abundance. These include Atlantic cod, dab, haddock, ling, monkfish and megrim, as well as other less commercially exploited species such as Norway pout and grenadier. These predicted abundance trends will likely result in compositional changes of the south-west fish assemblage (**Figure 19A** and **19B**).

The general trends of change in abundance, as shown in **Figure 16**, give a broad overview of how species may respond to climate change and the other environmental factors considered by the GAM. However, there is substantial spatial variation seen in the predictions for certain species. Argentine and hake both show a clear boundary between areas of increased and areas of decreased abundance, and to a lesser extent this is also seen for lemon sole, Atlantic herring and thickback sole. This boundary occurs along the continental shelf in the Celtic Sea, and so the abundance trends seen are likely explained by the biology and ecology of the individual species. Argentine is typically a deep, warmer water species, and so although the shallower areas of the English Channel are predicted to warm, they may be an unsuitable environment for this species, due to the depth constraints. The predicted abundance of hake shows a similar pattern; despite having a broad distribution and often considered a Lusitanian species, hake is also typically a deep water species, and so is unlikely to thrive in the shallow areas of the Channel. The same distinct boundaries are seen for American plaice, boarfish, blue whiting, European sprat and John dory except that the abundance trends are reversed, indicating that these species are likely to benefit from the warmer conditions found in these shallower areas. Shallower and semi-enclosed areas such as the English Channel and Irish Sea are likely to experience greater rates of warming, and so could provide more suitable environmental conditions, allowing these species to prosper (**Figure 12**).

The predicted decline in the abundance of grey gurnard is contradictory to the trends seen in the abundance of this species in recent years. Simpson et al. (2011) demonstrated that the abundance of grey gurnard in the North Sea has increased in response to warming; *Chapter 2* of this thesis found a similar trend for the south-west area of the UK. This increase has been attributed to the presence of prey species, such as juvenile cod (Pinnegar et al. 2016). If the south-west of the UK is towards the more southerly end of this species' distribution, then any further northward shift in distribution, as has already been observed (Perry et al. 2005; Dulvy et al. 2008), could result in reduced abundances within the study area. Whilst predator-prey and other biotic interactions are not accounted for by the GAM used in this study, they may be the underlying reasons for many of the trends seen in past and predicted species distribution shifts.

The results of this study suggest that species likely to benefit from climate change will be those that have a lower central latitudinal range and smaller body size. These results are in accordance with the findings of a number of other studies (Pauly et al. 1998; Perry et al. 2005), and suggest that climate change as well as over-exploitation is contributing to the practice of fishing down food webs. This study found no statistically significant difference between winners and losers mean trophic level. However, there has been a decline in the mean trophic level of the whole fish assemblage, and based on the results of the modelling approach used in this study, this trend is likely to continue (**Figure 18**). Jennings et al. (2002) found a similar decline in the mean trophic level of the North Sea demersal fish assemblage, from 1982–2000, but no such trend for pelagic and demersal species combined. Pinnegar et al. (2002) found similar trends in the Celtic Sea; a decline in mean trophic level from both survey data (from 1982–2000) and fishery landings data (1946–1998), driven by a reduction in the abundance of large piscivorous fish, and an increase in smaller lower trophic level fish. Whilst the overall change in mean trophic level observed in this study suggests a significant negative correlation over time (tau=-0.545, p=0.016), there appear to be two distinct trends, divided by a steep drop in mean trophic level around 2030 (**Figure 18**). This could suggest a regime shift, which would have severe consequences for the fishing industry. Further investigation of this pattern, considering the relative influence of exploitation and climate change, could provide a more thorough insight into the trends observed here.

The economic importance of traditional UK fish species is well documented; in 2014 landings of cod and haddock alone accounted for 41% of all demersal landings in volume, and 36% of the value (Marine Management Organisation 2014). Declines in the abundance of cold water species, in particular cod, have been well documented (Beaugrand & Reid 2003; Engelhard et al. 2014) and are predicted to continue, such that some stocks may disappear completely (Drinkwater 2005). A decrease in the abundance of these species, as predicted by this study, could have significant consequences for the fishing industry; fishers may be forced to travel further in order to catch adequate quantities, thereby incurring extra fuel costs, or may be forced to direct their efforts towards alternative species, requiring a change in gear and tactics. Market prices of fish can give valuable indications regarding the demand for a particular species, relative to its availability. Large, high trophic level species tend to fetch a higher price than small, lower trophic level species. As the abundance of a particular species declines the price generally rises, providing demand remains high. Pinnegar et al. (2006) demonstrated that over the last 30 years, the price of large high trophic level species increased, reflecting the declines in abundance. This was coupled with an expansion of pelagic fisheries which flooded the market with smaller, lower trophic level species (e.g. the price of horse mackerel fell by 92% between 1984–1985). On this basis, the price of large traditional species such as cod and haddock could rise drastically, if the predictions of this study are realised. If supply of these species cannot meet demand, this may lead to a greater quantity of imports. On the other hand, if fishers are able to adapt and exploit new fishing opportunities that become available, this could facilitate a shift in the focus of south-west UK fisheries, towards targeting lower value high volume catches of species such as anchovy and horse mackerel. This in turn may result in an expanding export market for the UK.

In contrast to cod and haddock, seabass is one of the species predicted to increase in abundance by the end of the century. This species has experienced a surge in popularity in recent decades, with both commercial and recreational anglers. Heavy exploitation of seabass has had drastic impacts on the state of the stock, such that minimum landing sizes, maximum quantities, and trawling bans have been introduced (Pawson et al. 2007; European Commission 2015), and a complete ban on fishing seabass has been suggested for 2017 (ICES 2016). Whilst this species is particularly vulnerable to over-fishing, studies have shown strong correlation between recruitment success and average temperature (Pawson 1992). If management plans can allow the stock to recover, and sustainable levels of fishing activity can be maintained, this species could become even more important to UK fishers if the increase in abundance predicted by this study is realised.

The need for a flexible and responsive approach to fisheries management is evident from the status of European hake. The successful management of this species has seen a drastic increase in abundance in recent years in the North Sea. Baudron & Fernandes (2015) describe how the high abundance of hake, coupled with low quota for this species and the possible introduction of a discard ban, could mean hake become a “choke” species, resulting in the premature closure of the mixed demersal fishery in the North Sea.

The climate data used in this study are based on RCP 2.6, a “best case scenario” for carbon emissions. This pathway requires a 70% reduction in greenhouse gas emissions between 2010 –2100, to be achieved through drastic changes in energy usage, as well as carbon capture and storage measures which would result in negative carbon emissions from the middle of the century (Vuuren et al. 2011). As such, the results of this study are likely to be a highly conservative and provide cautious estimate of species responses to climate change. The reality could be far more pronounced, with substantial range shifts and abundance changes, more exaggerated than what has been suggested by this study. Further work could apply the models used here to the broader climate data ensemble of future projections, or compare the results of this study with predictions based on RCP 4.5, 6.0 and 8.5.

Figure 15A and **15B** show correlations for each species, between abundance and GAM predicted abundance, and hence test how well each species is characterised by the model. In general most species are characterised well by the model, however, inconsistencies in the dataset and the patchy distribution of certain species may restrict model performance. This is apparent in the correlation for each species, between standardised abundance and actual abundance from each survey (**Appendix 2**). Where a particular survey recorded high abundances of a certain species, another survey may have recorded none, and so the standardised abundance value may not correlate well with either, but would still be considered a more appropriate value than a standard mean. The inconsistencies between different surveys may be due to the methods and sampling gear employed by each of the surveys. Trenkel et al. (2004) assessed the differences between Cefas and the French Groundfish surveys, in terms of survey design, and their effect on estimates of species abundance and community composition. The study found that both sampling method and survey period can have a substantial effect on the results of a survey, and therefore the perception of species abundance and community structure. This may account for some of the discrepancy observed in this study, between abundances of species in different surveys, and therefore determine how well that species is characterised by the model used.

One of the benefits of the modelling process used in this study is the ability to account for non-linear relationships, such that the abundance of a warm-water species will not increase indefinitely with rising temperature, as would be the assumption with a linear response. Advances in ecosystem modelling means that there are a range of well-developed and complex techniques available for assessing species responses to environmental change. Species Distribution Models (SDM) are widely used, and whilst these models are all based on ecological niche theory and therefore incorporate similar variables, the actual algorithms used and therefore the output from the models can vary. A study conducted by Jones et al. (2012) compared the performance of three SDM's; Maxent, AquaMaps and Sea Around Us Project. Whilst all produced plausible distributions and habitat estimates for species, there was variation between models, in terms of test statistics and consistency. A number of studies advise that a multi-model ensemble should be used, where the range of projections produced by all models can be compared and considered (Araújo & New 2007;

Jones et al. 2012). All modelling approaches are based on certain assumptions, and their outputs are restricted by the availability and quality of the data upon which the models are trained. In addition, where models assume a species preferred environmental conditions based upon its current distribution, this does not account for biotic interactions, availability of prey, or restricted dispersal capacity (Pinnegar et al. 2016). GAMs have been found to produce more accurate projections than other modelling techniques (such as GLMs) (Araújo et al. 2005), as well as allowing for complex relationships between predictor variables (Hedger et al. 2004), and being able to incorporate many different variables. The process used in this study however, as with any modelling approach, makes a number of assumptions. Firstly, it is assumed that fishing effort remains a constant factor, which, given that fish stocks are prone to natural fluctuations and management plans and quotas are frequently revised, it is unlikely that fishing effort will remain at a constant level over the next century. However, the locations of fishing ports are unlikely to change, and therefore inshore fishers in particular are constrained to operate in certain areas, given their proximity to fishing ports. Habitat, depth and substrate type are also relatively constant factors, and so the location of productive fishing grounds are also unlikely to change significantly, given that fish are bound to certain depths and habitats (in particular benthic and demersal species), for example for food, breeding and nursery grounds. With consideration to these factors, it was deemed reasonable to assume a constant fishing effort for the purpose of the model. An extension of this study could be to use a metric of fishing effort in the GAM rather than a constant value, whereby fishing effort responds to biomass, to mimic the effect management plans.

Interestingly, the modelling process found that habitat type did not have a major influence on predicting species abundance, and including it as a predictor variable did not improve model fit or predictive ability. Biologically, this seems counter-intuitive, particularly for benthic and demersal species. The importance of habitat to an individual may also depend on the life stage of that individual, which was beyond the scope of this study. Given that many fish migrate seasonally between feeding, breeding and nursery grounds, the habitat requirements of larval stages may differ significantly to that of the mature individual. As such, future work that could assess different life stages of the species considered here may find that habitat as a variable has a greater influence on abundance.

Additionally, habitat types within the study area are very patchy (see **Appendix 4** for the original EMODnet Seabed Habitats data, from which the habitat data used in the GAM was derived); it could be that the 1°x1° cell classification used for the GAM was too coarse-scale and so does not capture the variation between habitat types. Since this study was conducted, the EMODnet habitat classification system has been updated, with habitat now classified for cells where previously there was none. Re-running the models used in this study with the new and updated habitat data may be beneficial, but was beyond the scope and time-scale of this study.

As previously discussed, the fish abundance data used here could also introduce some bias to the study, through the selectivity of the gear types used for sampling, and the time of year during which the sampling is conducted. Most cells within the study area are covered by more than one survey, but there are some areas only sampled by one of the six surveys, and therefore may only be sampled at one time of year. This may not capture the seasonal variation observed in the abundance of some species. In addition, most of the gear types used by the surveys are demersal trawls, which may under-represent pelagic species such as mackerel and blue whiting.

Conclusions and future work

The abundance shifts and compositional changes described by this study should be considered relatively conservative predictions, given that the modelling approach used is based on the “best case scenario” for carbon emissions. This could imply that the actual abundance responses of fish to climate change could be far more pronounced than described here. Future work that considered the whole range of possible climate scenarios would provide a broader range of potential responses, and perhaps identify key species or groups of species most at risk from climate change.

Chapter 4: Discussion

Human activities have increasingly influenced the marine environment during the past few centuries. In recent decades, unsustainable levels of exploitation and the human-induced exacerbation of climate change have resulted in substantial changes to the composition and function of marine ecosystems and communities. As such, changes in fisheries production have been observed and predicted for areas all over the world. This thesis considers the south-west area of the UK; an area of high economic importance to the fishing industry, characterised by small inshore vessels that typically target high-value, lower-volume catches.

Chapter 2 of this thesis demonstrates that the marine fish assemblage around the south-west has changed significantly in terms of species richness and diversity over the last three decades. Trends in both species richness and diversity were positively correlated to rising SST. This chapter also shows that many species typically associated with warm water environments, such as anchovy and boarfish, have increased in abundance over the last three decades, whilst cold water species that are characteristic of UK fisheries, including cod and haddock, have decreased in abundance over the same time period.

Chapter 3 of this thesis considers how the fish assemblage of the south-west may respond to climate change over the course of this century, using predictive models that incorporate a range of environmental factors, and forced according to a specified climate scenario. The climate predictions used in this study are based on the “best case scenario” for carbon emissions (RCP 2.6). A total of 37 species were analysed, and of these, 86% were predicted to demonstrate a significant abundance response; 54% increased in abundance and 32% decreased in abundance. Of the species that were predicted to increase, the majority were warm-water species, many of which had already been increasing in abundance during recent decades (as demonstrated in *Chapter 2* of this study and also reported in previous studies; Beare et al. 2004; Simpson et al. 2011). Additionally, many of the cold water species found in *Chapter 2* to have decreased in abundance over recent decades were projected to continue to do so, such that some of these species including, Norway pout may be absent from as much as 90% of the study area by the end of the century.

The analysis of central latitude, body length and trophic level found significant differences between mean body length and mean trophic level of the winners and losers. This adds further evidence to the theory that climate change will see a shift from large bodied, cold-water adapted species that are generally long-lived and at higher trophic levels, towards a fish assemblage that is more heavily dominated by small-bodied, rapid turnover species. Whilst the difference in trophic level between winners and losers was not statistically significant, there is likely to be a substantial decline in mean trophic level by the end of the century. The dramatic drop in mean trophic level around 2030 that was forecasted by this study could imply a regime shift, which would have severe consequences for the fishing industry. This could be driven by the changing relative proportions of the fish assemblage predicted by this study. **Figure 19B** shows an increase in the proportion of lower trophic level species such as anchovy and sprat around 2030, coupled with a decrease in the proportion of higher trophic level species such as poor cod and haddock. Further investigation of this pattern, considering the effect of exploitation in addition to climate change, could provide a more thorough insight into the trends observed here.

Whilst the data used in this study were standardised to remove, as far as possible, any sources of bias there are still some limitations; primarily a paucity of data early on in the time series. However, these long term scientific survey data sets are becoming invaluable for climate change focussed research. As with many studies currently conducted in this field, the predicted changes in abundance described in *Chapter 3* are constrained by the model that generated them, and the data upon which the model were trained. GAMs have a number of benefits over other ecological models; they are trained on actual abundance data rather than simple presence-absence data, they allow a number of environmental variables to be considered, and do not assume linearity between variables abundance. However, a key factor affecting a species’ ability to respond to climate change through distribution shifts, which was beyond the scope of this study, is the interactions it will have with other species. Predator-prey interactions and competition for food and resources can have a profound effect on the success of a species, as it aims to adapt to a changing climate. In recent years, more studies have focused on interspecific interactions, and now aim to incorporate these into modelling approaches (Blanchard et al. 2012;

Fernandes et al. 2013). Fernandes et al. (2013) found that that when species interactions were considered, the predicted latitudinal shift was reduced by around 20% on average. Incorporating these sorts of interactions into the modelling approach used in this study could offer a more robust method of predictive modelling.

The modelling approach used in *Chapter 3* of this thesis is based on the RCP 2.6 climate scenario; a highly conservative and optimistic scenario. Whilst there are uncertainties within all modelling approaches and climate predictions (Frölicher et al. 2016), the current likelihood of maintaining carbon emissions near to RCP 2.6 is unlikely. Future studies should assess relative impacts of more severe predicted warming trends on south-west fisheries.

The abundance data used in this study result from a sampling method that primarily targets adult life stages, however the effect of temperature on different life stages is likely to be highly variable; for some species temperature may have a highly significant effect on larval stages, but less so on adult stages (Rijnsdorp et al. 2009). Applying the modelling approach used in this study to larval stages may also find a greater influence of habitat as a variable for determining a species response to climate change; as explained in *Chapter 3*, habitat was deemed not to be a good predictor of a species response.

The trends in abundance and fish assemblage composition predicted by this study could have profound consequences for the fishing industry. The majority of vessels operating out of south-west ports are under 10m in length, and generally not equipped for offshore sea conditions, or able to spend many days at sea. It is expected that these vessels may have a reduced capacity to adapt and respond to changing fishing opportunities, when compared to larger, offshore vessels (Defra 2013), and as such, are perhaps more vulnerable to substantial changes in opportunities. The changing composition of the fish assemblage could see a shift in the south-west fishing industry to become increasingly an export market. Adapting to new fishing opportunities will require not only a change in fishing tactics and target species, but an adaptable attitude from consumers, and a willingness to purchase different species to those traditionally associated with UK fisheries. These adaptations will be dependent on appropriate sharing of information regarding best fishing practices and techniques, as well as scientific data relating to emerging and traditional species. It was beyond the scope of this study to consider crustacean and shellfish responses to climate change, but cuttlefish, crabs, scallops and whelks make up a large proportion of the volume and value landed in the south-west (Marine Management Organisation 2014). These species are perhaps at greater risk from the “other climate problem”; ocean acidification, which was not considered by this study but is likely to have significant consequences at the individual and community level.

A flexible and adaptive response to fisheries management will be required, if UK fisheries are to remain sustainable and successful in the future. The same is true for conservation measures such as protected areas; successful conservation schemes will likely improve the health and function of ecosystems, which in turn will have positive impacts on exploited fish populations. The complexity of marine systems means that deciphering the effects of climate change from fishing exploitation, pollution, infrastructure and other human activities, as well natural variability is a great challenge. As human interactions with the oceans are ever-growing, and often increasingly harmful, attempts to mitigate the effects of climate change are essential to ensure the health and resilience of the oceans.

Appendices

Appendix 1: Table of all finfish species from the six surveys used, their common names, scientific names, and associated codes. Some survey entries were only identified to genus or family name.

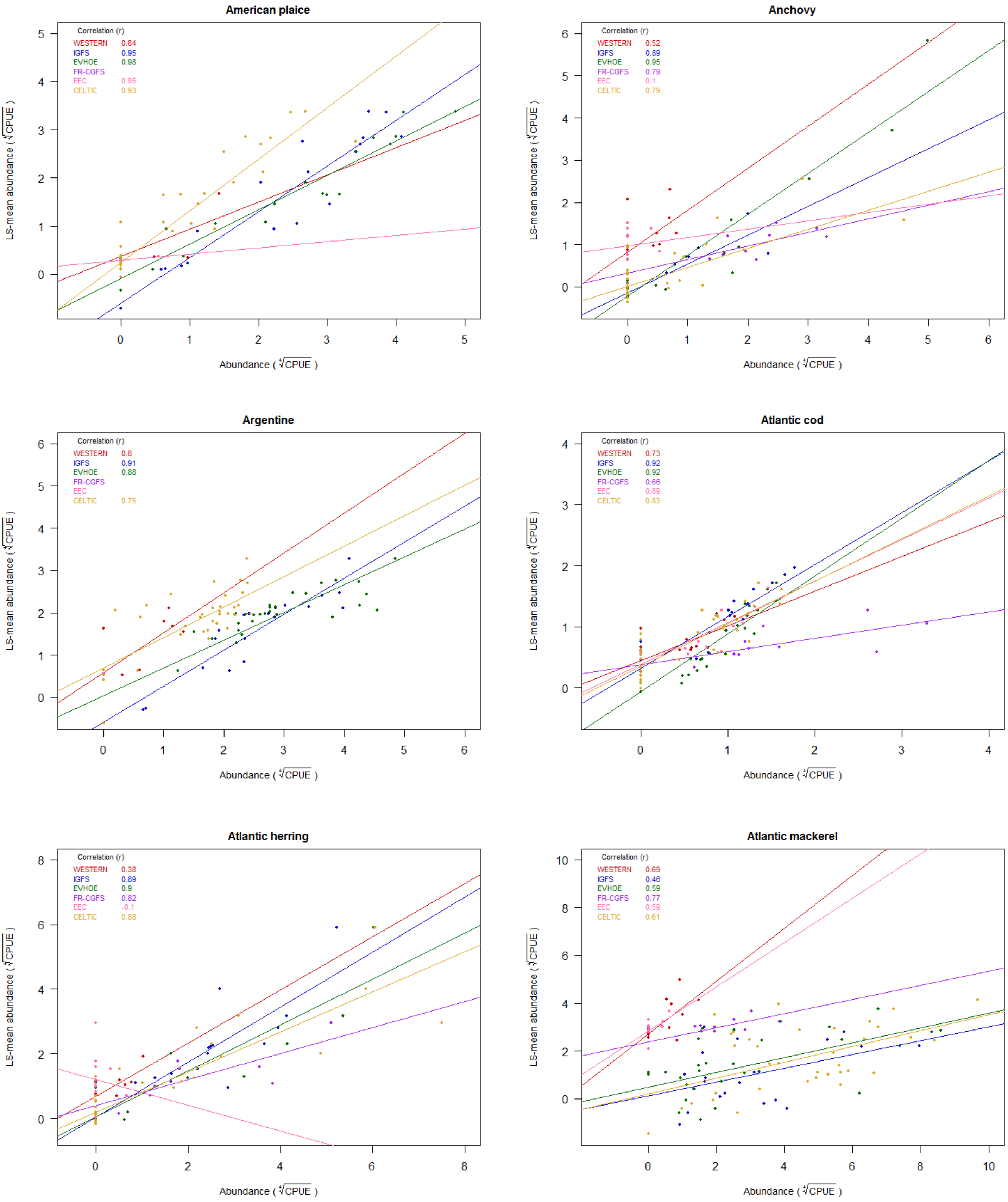
Common name	Scientific name/s	Cefas	WoRMS	TSN
Alfonsino	*Beryx decadactylus*	BER	126394	166155
Allis shad	*Alosa alosa*	AAS	126413	161708
American plaice	*Hippoglossoides platessoides*	PLA	127137	172877
Arctic sculpin	*Myoxocephalus scorpioides*		127202	167317
Argentine	*Argentina sphyraena*	LSS	126716	162071
	Argentinidae spp.	ARG	125508	162057
Atlantic cod	*Gadus morhua*	COD	126436	164712
Atlantic hagfish	*Myxine glutinosa*	HGF	101170	159772
Atlantic herring	*Clupea harengus*	HER	126417	161722
Atlantic mackerel	*Scomber scombrus*	MAC	127023	172414
Atlantic pomfret	*Brama brama*	POA	126783	170290
Atlantic salmon	*Salmo salar*	SAL	127186	161996
Atlantic saury	*Scomberesox saurus*		126392	165612
Atlantic torpedo	*Torpedo nobiliana*	ECR	157868	160834
Atlantic wreckfish	*Polyprion americanus*		126998	167914
Avocet snipe eel	*Avocettina infans*		126304	161619
Axillary seabream	*Pagellus acarne*	SBA	127057	169213
Baillon's wrasse	*Symphodus bailloni*	BLW	273566	614244
Ballan wrasse	*Labrus bergylta*	BNW	126965	170737
Bennett's flyingfish	*Cheilopogon pinnatibarbatus*		126383	616685
Big-eyed rockling	*Gaidropsarus spp.*	ROL	125743	164764
	Gaidropsarus macrophthalmus	AGM	126456	623025
Black cardinal fish	*Epigonus telescopus*	EGT	126858	168298
Black goby	*Gobius niger*		126892	171850
Black scabbardfish	*Aphanopus carbo*	BSF	127085	172389
Black scorpionfish	*Scorpaena porcus*	SPP	127247	166840
Black seabream	*Spondyliosoma cantharus*	BKS	127066	169229
Black wing flyingfish	*Hirundichthys rondeletii*		126386	616693
Black-bellied angler	*Lophius budegassa*	WAF	126554	164502
Black-belly rosefish	*Helicolenus dactylopterus*	RBM	127251	166787
Black-mouth dogfish	*Galeus melastomus*	DBM	105812	160034
Blackspot seabream	*Pagellus bogaraveo*	SBR	127059	169212
Blonde ray	*Raja brachyura*	BLR	367297	160880
Blue ling	*Molva dypterygia*	BLI	126459	164761
Blue whiting	*Micromesistius poutassou*	WHB	126439	164774
Bluntnose six-gill shark	*Hexanchus griseus*	SGS	105833	159819
Bluntsnout grenadier	*Nezumia sclerorhynchus*		126475	165398
Boarfish	*Capros aper*	BOF	127419	166320
Bogue	*Boops boops*	BOG	127047	169218
Brill	*Scophthalmus rhombus*	BLL	127150	172749
Broadnose pipefish	*Syngnathus typhle*	DPF	127393	166467
Brown trout	*Salmo trutta*		127187	161997
Butterfly blenny	*Blennius ocellaris*	BBY	126761	171126
Cadenat's rockfish	*Scorpaena loppei*		127244	166836
Chub mackerel	*Scomber japonicus*	SPM	127022	172412
Clingfish	*Gobiesocidae spp.*	CFX	125477	164457
	Lepadogaster spp.		125781	164475

Common Atlantic grenadier	*Nezumia aequalis*	SRL	126473	165394
Common dab	*Limanda limanda*	DAB	127139	172881
Common dentex	*Dentex dentex*		127467	169224
Common dragonet	*Callionymidae*	DTX	125522	171691
	Callionymus lyra	CDT	126792	171698
Common eagle ray	*Myliobatis aquila*		105860	160983
Common goby	*Pomatoschistus microps*	GMG	126927	171982
Common ling	*Molva molva*	LIN	126461	164760
Common mora	*Mora moro*		126497	164687
Common pandora	*Pagellus erythrinus*	PAC	127060	169215
Common seabream	*Pagrus pagrus*		127063	169207
Common skate	*Dipturus (Raja) batis*	SKT	105869	564126
Common smooth hound	*Mustelus mustelus*	SMH	105822	160242
Common stingray	*Dasyatis pastinaca*	SGR	105851	160959
Common torpedo	*Torpedo torpedo*	ELR	271691	160836
Corbin's sand eel	*Hyperoplus immaculatus*	ISE	126755	171683
Corkwing wrasse	*Symphodus melops*	CWG	273571	614239
Cornish blackfish	*Schedophilus medusophagus*		126833	642554
Crystal goby	*Crystallogobius linearis*	CLG	126878	171971
Cuckoo ray	*Leucoraja naevus*	CUR	105876	564143
Cuckoo wrasse	*Labrus mixtus*	CUW	151501	170739
Dalatias shark	*Dalatias sp.*	DCH	105774	160649
Deepwater ray	*Rajella bathyphila*		105892	564125
Deepwater sole	*Bathysolea profundicola*		127152	173028
Dover sole	*Solea solea*	SOL	127160	173002
	Solea vulgaris		154712	173001
Ekströms topknot	*Zeugopterus (Phrynorhombus) regius*	EKT	236488	616605
European anchovy	*Engraulis encrasicolus*	ANE	126426	161831
European conger eel	*Conger conger*	COE	126285	161341
European eel	*Anguilla anguilla*	ELE	126281	161128
European flounder	*Platichthys flesus*	FLE	127141	172894
European hake	*Merluccius merluccius*	HKE	126484	164795
European pilchard	*Sardina pilchardus*	PIL	126421	161813
European plaice	*Pleuronectes platessa*	PLE	127143	172902
European seabass	*Dicentrarchus labrax*	ESB	126975	170317
European smelt	*Osmerus eperlanus*	SME	126736	162039
European sprat	*Sprattus sprattus*	SPR	126425	161789
Five-bearded rockling	*Ciliata mustela*	FVR	126448	623023
Four-bearded rockling	*Enchelyopus cimbrius*	FRR	126450	164748
Four-spot megrim	*Lepidorhombus boscii*	LBI	127145	172834
Freshwater eel	*Anguillidae spp.*	EEL	125425	161125
Fries's goby	*Lesueurigobius friesii*	FSG	126904	172036
Gadidae	*Gadidae spp.*	GAD	125469	174701
Garfish	*Belone belone*	GAR	126375	165594
Gilthead seabream	*Sparus aurata*	SBG	151523	647901
Glasshead grenadier	*Hymenocephalus italicus*		158961	165406
Goby	*Gobiidae spp.*	GPA	125537	171746
	Gobius spp.	GOB	125988	171833
	Pomatoschistus spp.	POM	125999	171977
Golden grey mullet	*Liza aurata*	MGN	126978	170377
Golden redfish	*Sebastes norvegicus*	REG	151324	166781
Goldsinny wrasse	*Ctenolabrus rupestris*	GDY	126964	170733
Goosefish	*Lophiidae spp.*	ANF	125493	164497
Great sand eel	*Hyperoplus lanceolatus*	GSE	126756	171682
Great torpedo ray	*Torpedo (Tetronarce) nobiliana*		105929	160834
Greater argentine	*Argentina silus*	GSS	126715	162064
Greater forkbeard	*Phycis blennoides*	GFB	126501	164751

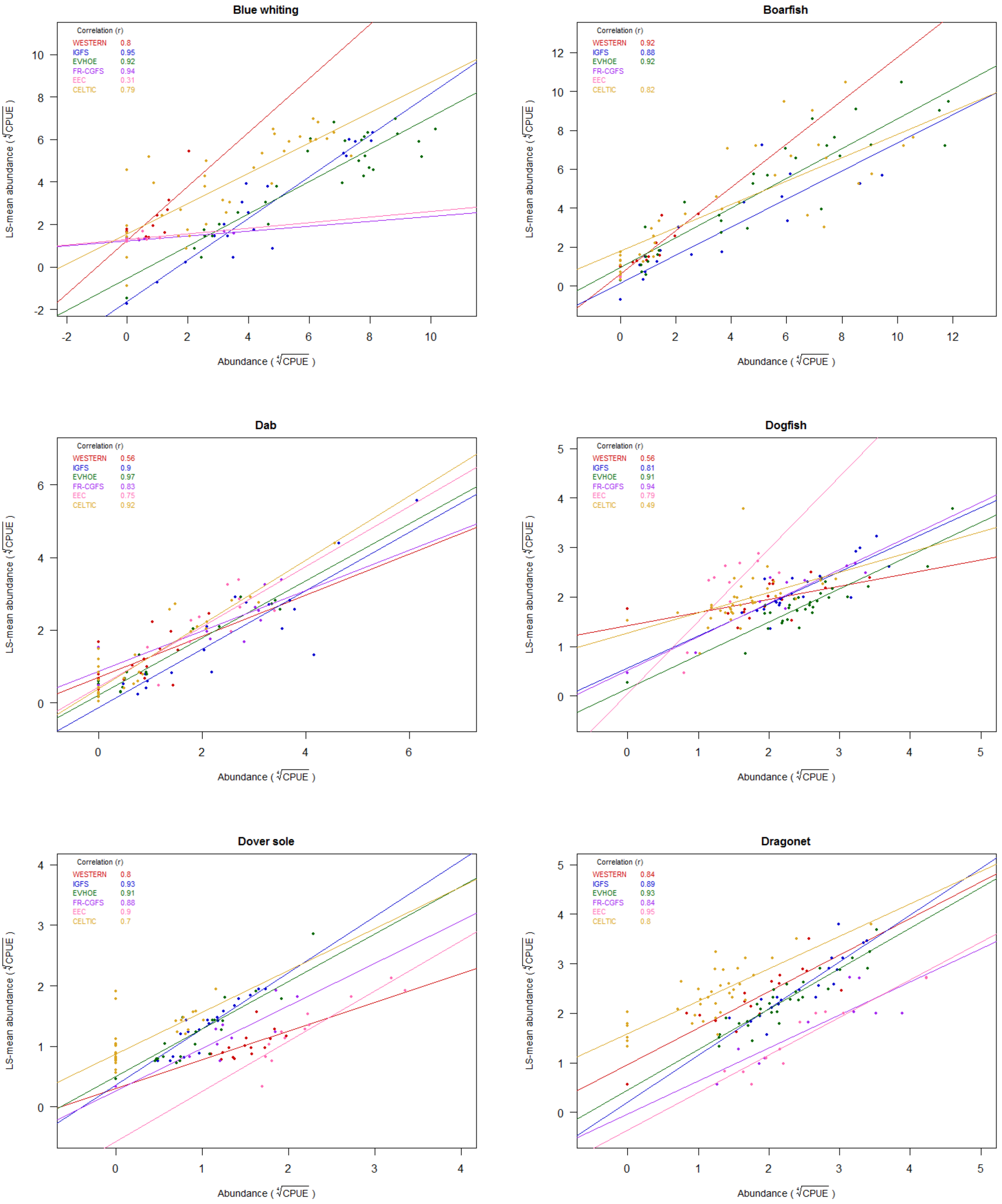
Greater pipefish	*Syngnathus acus*	GPF	127387	166464
Greater spotted dogfish	*Scyliorhinus stellaris*	DGN	105815	160067
Greater weever	*Trachinus draco*	WEG	127082	170992
Grenadier	*Macrouridae spp.*		125471	165332
Grey gurnard	*Eutrigla gurnardus*		150637	167044
	Eutrigla sp.	GUG	150636	150636
Grey triggerfish	*Balistes capriscus*	TRF	154721	173138
Gurnard	*Chelidonichthys spp.*	GUR	126178	167051
	Trigla spp.	GUX	126180	167038
	Trigloporus spp.	GUS	154461	167045
Haddock	*Melanogrammus aeglefinus*	HAD	126437	164744
Hollowsnout grenadier	*Coelorinchus caelorhincus*	HRT	398381	
Hooknose	*Agonus cataphractus*	POG	127190	167454
Horse mackerel	*Trachurus trachurus*	HOM	126822	168588
Imperial scaldfish	*Arnoglossus imperialis*	ISF	127124	172806
Jeffrey's goby	*Buenia jeffreysii*	JYG	126872	636752
Jewel lanternfish	*Lampanyctus crocodilus*	LAC	126612	162649
John dory	*Zeus faber*	JOD	127427	166287
Lancet fish	*Notoscopelus kroyeri*		272728	
Lantern fish	*Diaphus spp.*		125819	162583
	Lampanyctus spp.	LNX	125825	162632
	Myctophidae spp.	MYX	125498	162575
	Myctophum spp.		125829	
Large-eyed rabbitfish	*Hydrolagus mirabilis*	RTF	105826	161017
Lemon sole	*Microstomus kitt*	LEM	127140	172888
Leopard-spotted goby	*Thorogobius ephippiatus*	LSG	126937	172043
Lesser forkbeard	*Raniceps raninus*	LFB	126442	164777
Lesser sand eel	*Ammodytes tobianus*	TSE	126752	171676
Lesser spotted dogfish	*Scyliorhinus canicula*	LSD	105814	160065
Lesser weever	*Echiichthys vipera*		150630	630409
Long- nose skate	*Dipturus (Raja) oxyrinchus*	LNS	105872	564148
Longfin gurnard	*Chelidonichthys obscurus*	GUL	127263	643891
Long-nose velvet dogfish	*Centroscymnus crepidater*		105908	160725
Long-snouted seahorse	*Hippocampus guttulatus*	SHE	154776	645018
Longspine snipefish	*Macroramphosus scolopax*	SNI	127378	551497
Long-spined sea scorpion	*Taurulus bubalis*	SSN	127204	167390
Lozano's goby	*Pomatoschistus lozanoi*		126925	637881
Lumpfish	*Cyclopterus lumpus*	LUM	127214	167612
Marbled electric ray	*Torpedo marmorata*	MER	271684	160838
Mediterranean bigeye rockling	*Gaidropsarus biscayensis*		126452	550591
Mediterranean horse mackerel	*Trachurus mediterraneus*	HMM	126820	168590
Mediterranean scaldfish	*Arnoglossus laterna*	SDF	127126	172805
Mediterranean slimehead	*Hoplostethus mediterraneus*		126404	166140
Megrim	*Lepidorhombus whiffiagonis*	MEG	127146	172835
Monkfish	*Lophius piscatorius*	MON	126555	164501
Montagu's seasnail	*Liparis montagui*	MSS	127220	167581
Moonfish	*Lampris guttatus*	OPA	126522	166326
Mueller's pearlside	*Maurolicus muelleri*	PLS	127312	162187
Mullet	*Mugilidae spp.*	MUL	125546	170333
Nilsson's pipefish	*Syngnathus rostellatus*	NPF	127389	166463
North Atlantic codling	*Lepidion eques*		126493	164690
Northern cutthroat eel	*Synaphobranchus kaupii*	SBK	126328	635794
Northern rockling	*Ciliata septentrionalis*	NNR	126449	164780
Northern wolffish	*Anarhichas denticulatus*	CAJ	126757	550561
Norway bullhead	*Micrenophrys sp.*	NVB	126151	643516
	Micrenophrys lilljeborgii		127201	644150

Norway goby	*Pomatoschistus norvegicus*	NVG	126929	171983
Norway pout	*Trisopterus esmarkii*	NOP	126444	164756
Norway redfish	*Sebastes viviparus*	REV	127255	166779
Norwegian skate	*Dipturus (Raja) nidarosiensis*	RNS	105762	160886
Norwegian topknot	*Phrynorhombus norvegicus*	NKT	127147	172831
Painted goby	*Pomatoschistus pictus*	PTG	126930	171980
Pearlfish	*Echiodon drummondii*	PRL	126663	165116
Pike- perch	*Sander lucioperca*		151308	650172
Pipefish	*Syngnathidae spp.*	PFX	125606	166443
Piper gurnard	*Trigla lyra*	PIP	127266	167041
Pollack	*Pollachius pollachius*	POL	126440	164728
Pollock	*Pollachius virens*	POK	126441	164727
Poor cod	*Trisopterus minutus*	POD	126446	164754
Porbeagle shark	*Lamna nasus*	POR	105841	159911
Porgies	*Sparidae spp.*	SBZ	125564	169180
Pouting	*Trisopterus luscus*	BIB	126445	164755
Rabbit fish	*Chimaera monstrosa*	RBF	105824	161022
Raitt's sand eel	*Ammodytes marinus*	MSE	126751	171677
Red bandfish	*Cepola macrophthalma*	RPF	126835	170281
Red gurnard	*Chelidonichthys cuculus*		127259	692071
Red mullet	*Mullus spp.*	MUX	126034	169416
	Mullus barbatus		126985	169419
Red scorpionfish	*Scorpaena scrofa*	SCS	127248	166839
Rendezvous fish	*Polymetme corythaeola*		127300	162191
Reticulated dragonet	*Callionymus reticulatus*	RDT	126795	171712
River lamprey	*Lampetra fluviatilis*	LAR	101172	159719
Rock goby	*Gobius paganellus*	RKG	126893	171854
Rock gunnel	*Pholis gunnellus*	BTF	126996	171645
Rooster hind	*Epinephelus acanthistius*		273832	167749
Rosy dory	*Cyttopsis rosea*		127425	166280
Roughhead grenadier	*Macrourus berglax*	RHG	126472	165421
Roughsnout grenadier	*Trachyrincus scabrus*		126482	550660
Roundnose grenadier	*Coryphaenoides rupestris*	RNG	158960	165350
Sand goby	*Pomatoschistus minutus*	SDG	126928	171978
Sand lance	*Ammodytes spp.*	SAN	125909	171671
	Ammodytidae spp.	SAX	125516	171670
Sand smelt	*Atherina presbyter*	SMT	272030	166025
Sand sole	*Pegusa lascaris*		127156	173051
Sandy ray	*Leucoraja circularis*	SAR	105873	564128
Sar's wolf eel	*Lycenchelys sarsii*	LCS	127101	631033
Scale-rayed wrasse	*Acantholabrus palloni*	SRW	126957	170742
Sea lamprey	*Petromyzon sp.*	LAM	101169	159721
	Petromyzon marinus	SLY	101174	159722
Sea tadpole	*Careproctus reinhardti*	CSR	127212	167522
Seabream	*Abramis spp.*	FBR	154271	163665
	Pagellus spp.		126079	169211
Seaweed pipefish	*Syngnathus spp.*		126227	166444
Shagreen ray	*Leucoraja fullonica*	SHR	105874	564134
Shore clingfish	*Lepadogaster lepadogaster*	SCF	126518	164478
Shore rockling	*Gaidropsarus mediterraneus*	SRR	126457	164766
Short silver hatchetfish	*Argyropelecus hemigymnus*		127309	162219
Shorthorn sculpin	*Myoxocephalus scorpius*	BRT	127203	167318
Shortnose greeneye	*Chlorophthalmus agassizi*		126336	162430
Short-snouted seahorse	*Hippocampus hippocampus*	SNH	127380	166497
Silver hatchetfish	*Argyropelecus olfersii*	HTF	274967	622706
Silver scabbardfish	*Lepidopus caudatus*	SFS	127088	172391
Silvery pout	*Gadiculus argenteus*	SYP	126435	164772

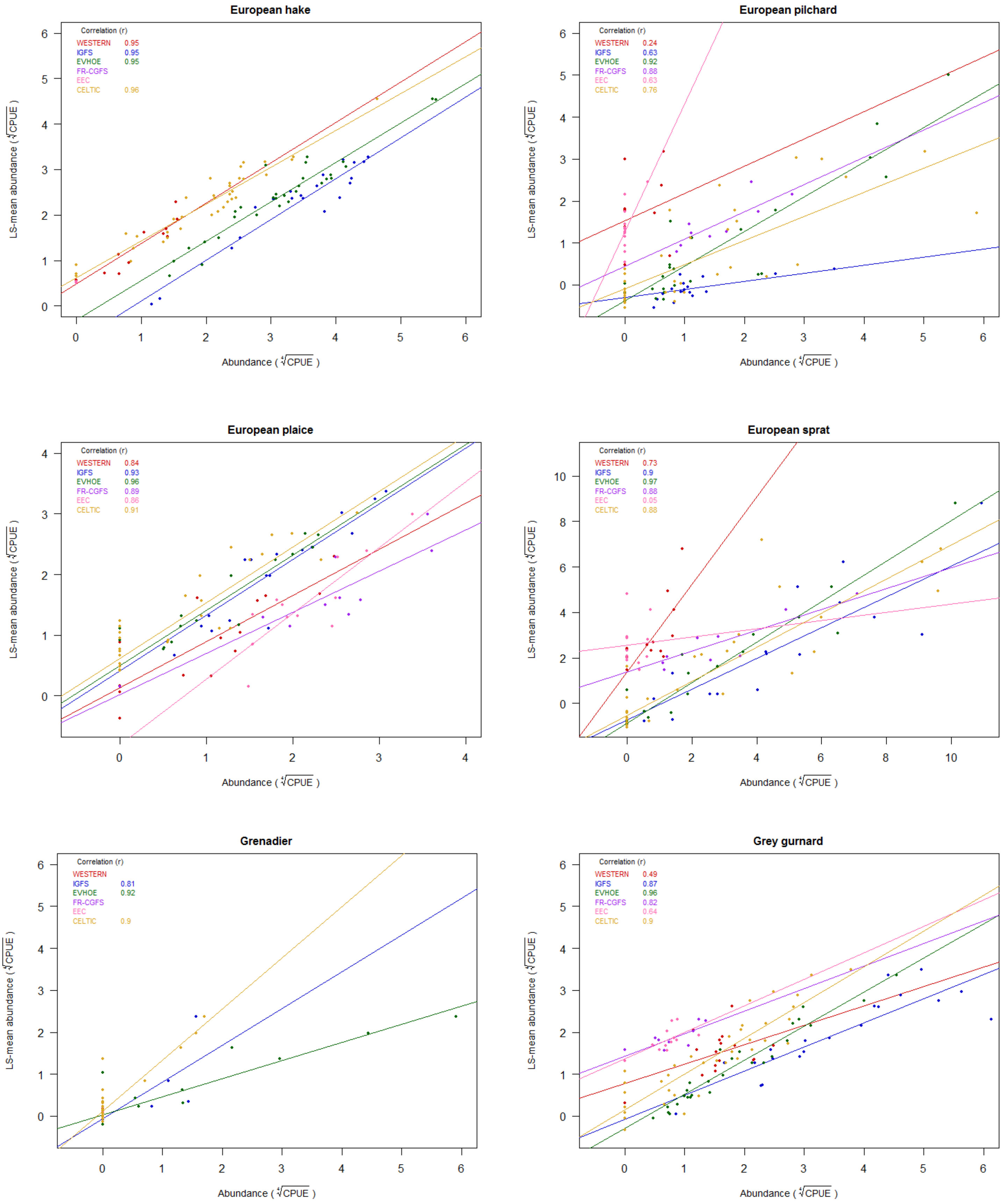
Slender codling	*Halargyreus johnsonii*	HGA	126489	164692
Slickhead	*Alepocephalidae spp.*	SMY	125507	162303
Small-eyed ray	*Raja microocellata*	PTR	105885	160882
Small-headed clingfish	*Apletodon dentatus*	SCL	126510	642604
Small-mouthed wrasse	*Centrolabrus exoletus*	SMW	126961	170730
Smooth sand eel	*Gymnammodytes semisquamatus*	SMS	126754	171680
Snailfish	*Liparis liparis*		127219	167578
	Liparis liparis	SSL	293624	
Snake blenny	*Lumpenus lampretaeformis*	SBY	154675	631023
	Ophidion barbatum	OPB	126675	164846
Snake pipefish	*Entelurus aequoreus*	SKP	127379	644927
Softhead grenadier	*Malacocephalus laevis*	SRT	272392	165389
Solenette	*Buglossidium luteum*	SOT	127153	173021
Spanish ling	*Molva macrophthalma*	SLI	126460	623033
Spiny dogfish	*Squalus acanthias*	DGS	105923	160617
Splendid alfonsino	*Beryx splendens*	LWB	126395	166156
Spotted dragonet	*Callionymus maculatus*	SDT	126793	171699
Spotted lantern fish	*Myctophum punctatum*	SLF	126627	162723
Spotted ray	*Raja montagui*	SDR	105887	160883
Starry ray	*Amblyraja radiata*	SYR	105865	564149
Starry smooth-hound	*Mustelus asterias*	SDS	105821	160240
Steven's goby	*Gobius gasteveni*	GSV	126890	171859
Streaked gurnard	*Trigloporus lastoviza*		154462	167046
Striped red mullet	*Mullus surmuletus*	MUR	126986	169418
Sturgeon	*Acipenseridae spp.*		125424	161064
Sunfish	*Mola mola*		127405	173414
Thickback sole	*Microchirus variegatus*	TBS	274304	173026
Thick-lipped grey mullet	*Chelon labrosus*		126977	170371
Thin-lipped grey mullet	*Liza ramada*	MTN	126980	170376
Thornback ray	*Raja clavata*	THR	105883	160901
Thor's scaldfish	*Arnoglossus thori*	ART	127128	172809
Three-bearded rockling	*Gaidropsarus vulgaris*	TBR	126458	164765
Three-spined stickleback	*Gasterosteus aculeatus*		126505	166365
Tompot blenny	*Parablennius gattorugine*	TBY	126770	636467
Tope shark	*Galeorhinus galeus*	GAG	105820	160181
Topknot	*Zeugopterus punctatus*	TKT	127151	172829
Transparent goby	*Aphia minuta*	TPG	126868	172033
Tub gurnard	*Trigla (Chelidonichthys) lucerna*	TUB	127262	643890
Turbot	*Scophthalmus maximus*	TUR	127149	172748
	Zeugopterus spp.		126125	172828
Twaite shad	*Alosa fallax*	TAS	126415	161716
Two-spotted clingfish	*Diplecogaster bimaculata bimaculata*	TSC	236458	164483
Two-spotted goby	*Gobiusculus flavescens*	TSG	126898	171974
Undulate ray	*Raja undulata*	UNR	105891	160900
Velvet belly lantern shark	*Etmopterus spinax*	VBY	105913	160670
Viviparous eelpout	*Zoarces viviparus*	ELP	127123	165324
Wedge sole	*Dicologlossa cuneata*		127154	173031
White Seabream	*Diplodus sargus*		127053	169194
Whiting	*Merlangius merlangus*	WHG	126438	164758
Witch flounder	*Glyptocephalus cynoglossus*	WIT	127136	172873
Yarrell's blenny	*Chirolophis ascanii*	YBY	127071	171571



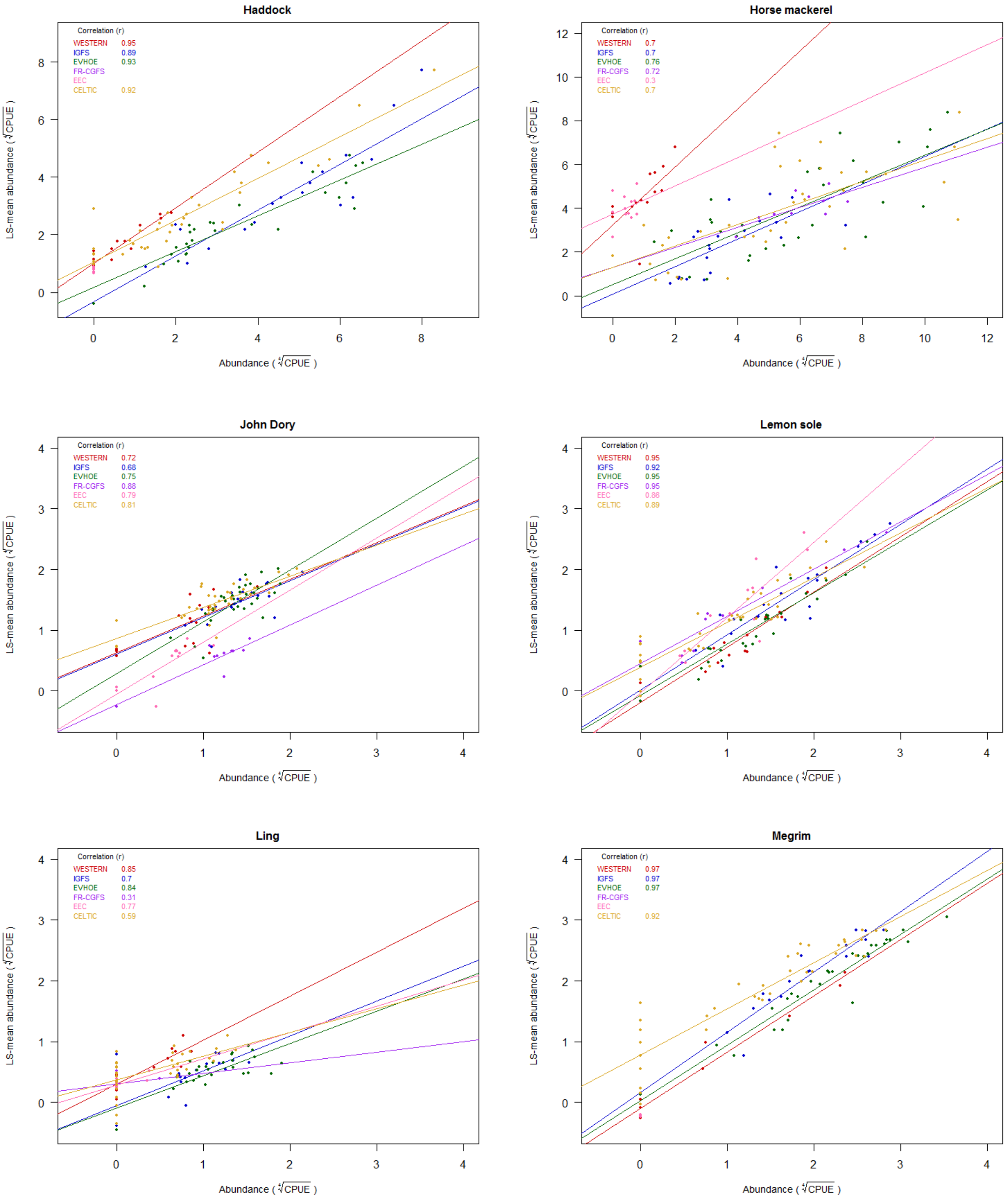
Appendix 2A: Correlation (r) between least-square mean estimate of abundance (4th root transformed CPUE), and average abundance (4th root transformed CPUE) from each survey, for each species between 2000–2010.



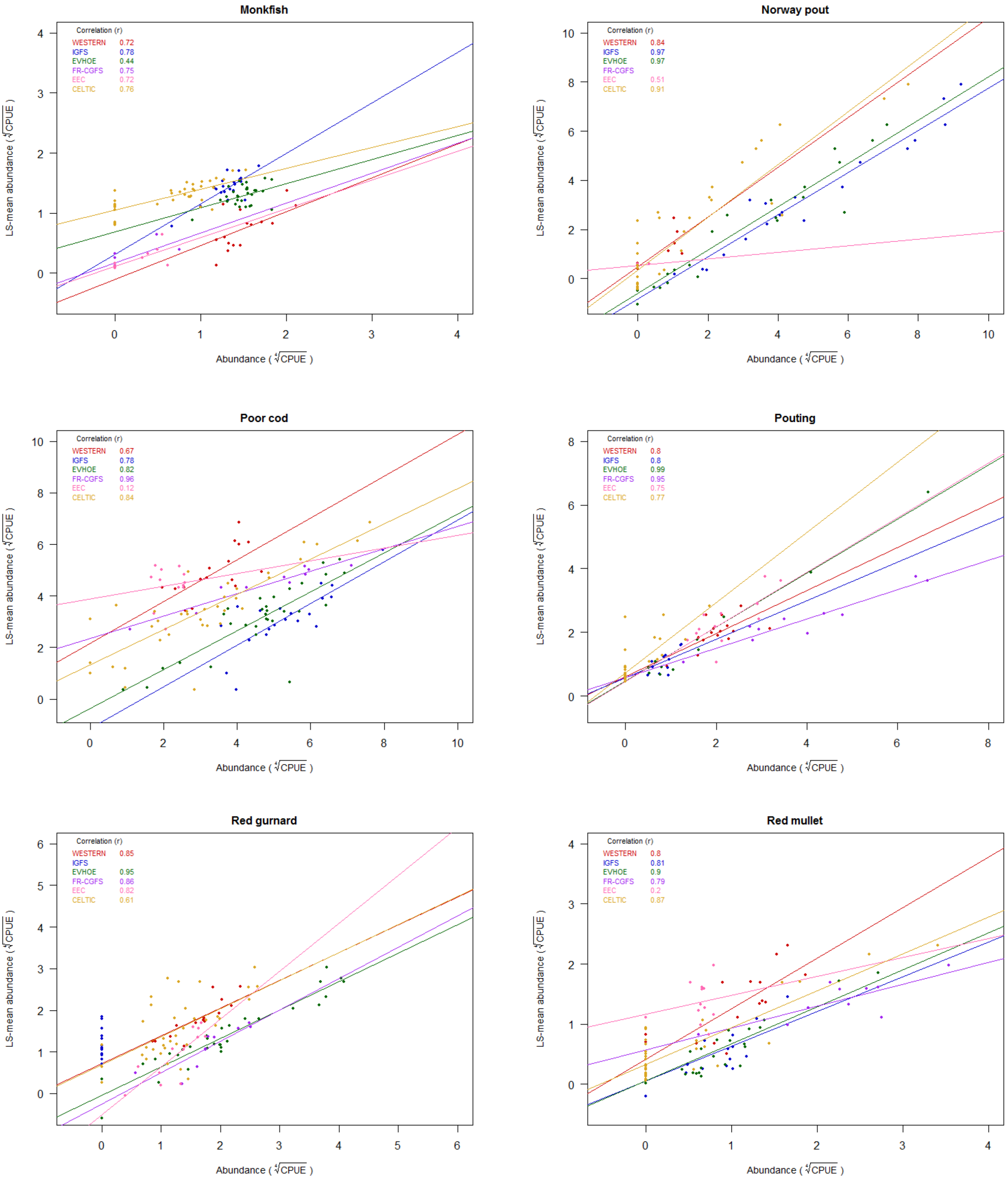
Appendix 2B: Correlation (r) between least-square mean estimate of abundance (4th root transformed CPUE), and average abundance (4th root transformed CPUE) from each survey, for each species between 2000–2010.



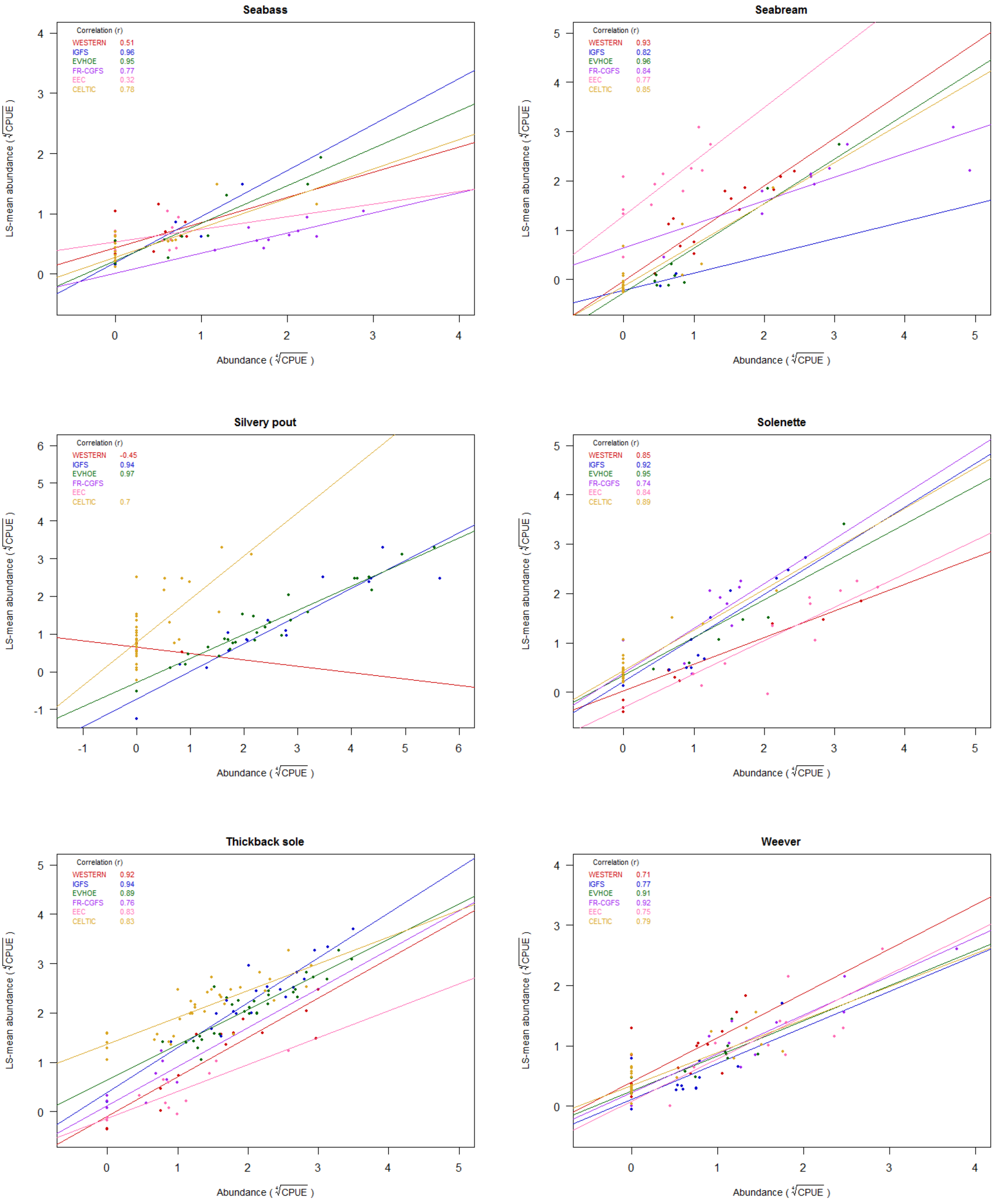
Appendix 2C: Correlation (r) between least-square mean estimate of abundance (4th root transformed CPUE), and average abundance (4th root transformed CPUE) from each survey, for each species between 2000–2010.



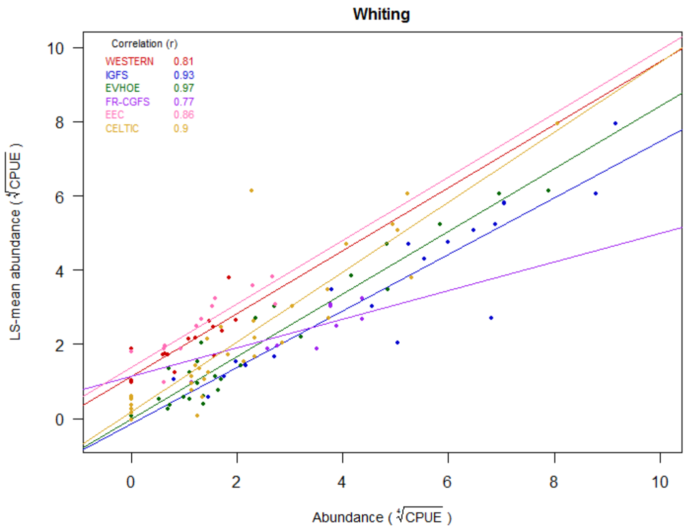
Appendix 2D: Correlation (r) between least-square mean estimate of abundance (4th root transformed CPUE), and average abundance (4th root transformed CPUE) from each survey, for each species between 2000–2010.



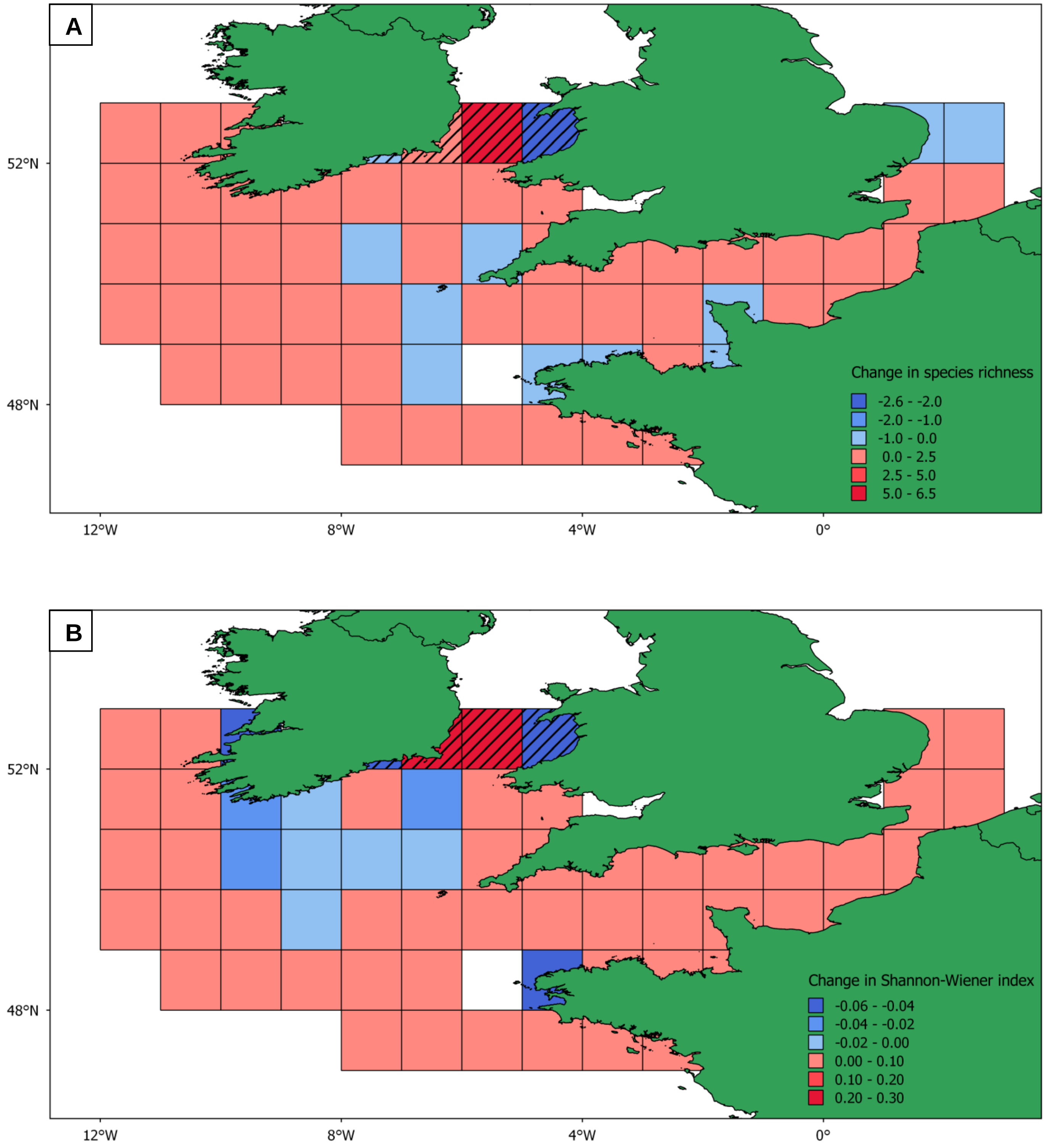
Appendix 2E: Correlation (r) between least-square mean estimate of abundance (4th root transformed CPUE), and average abundance (4th root transformed CPUE) from each survey, for each species between 2000–2010.



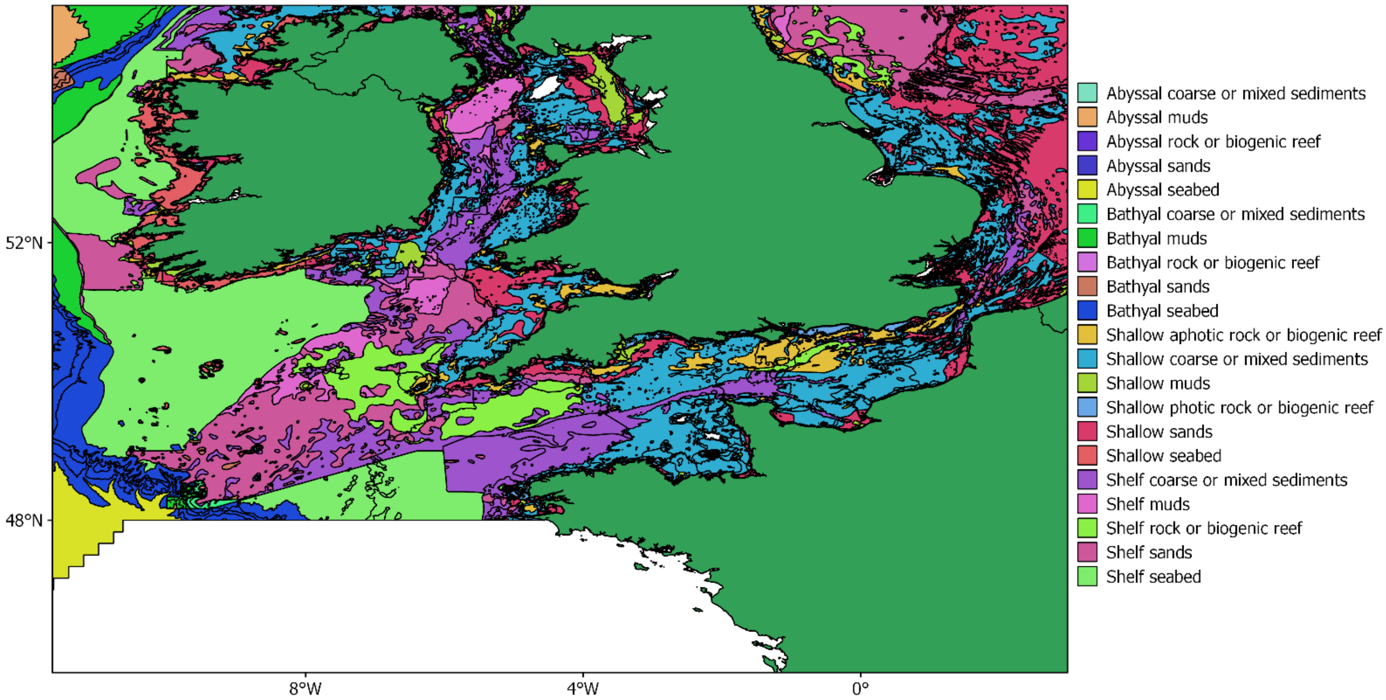
Appendix 2F: Correlation (r) between least-square mean estimate of abundance (4th root transformed CPUE), and average abundance (4th root transformed CPUE) from each survey, for each species between 2000–2010.



Appendix 2G: Correlation (r) between least-square mean estimate of abundance (4th root transformed CPUE), and average abundance (4th root transformed CPUE) from each survey, for each species between 2000–2010.



Appendix 3: Spatial variation of the rate of change in species richness (**A**) and Shannon-Wiener diversity index (**B**), from 1987–2015, expressed as the slope of the line through the annual mean species richness value for each cell. Red indicates an increase in richness, blue indicates a decrease. Blank cells were not sampled during this time and hashed areas indicate cells that were sampled 5 or fewer years during the 1987–2015 period.



Appendix 4: EUSeaMap data layer available through the European Marine Observation Data Network Seabed Habitats project, from which a representative habitat type was derived per 1°x1° cell, to be used in the GAM.

Species	**Variable**	Depth, fishing effort, habitat, salinity, temperatures	Depth, habitat, salinity, temperatures	Depth, fishing effort, habitat, temperatures	Depth, fishing effort, habitat, salinity	Depth, fishing effort, salinity, temperatures	Fishing effort, habitat, salinity, temperatures	Depth, fishing effort, habitat, salinity, just annual temperatures	Depth, fishing effort, habitat, salinity, just seasonal temperatures
American plaice	AIC	67.3147	50.0728	63.4063	157.5612	30.6481	25.5490	108.0307	79.8303
American plaice	Akaike weight	0.0000	0.0000	0.0000	0.0000	0.0725	0.9275	0.0000	0.0000
American plaice	Adjusted r2	0.8765	0.9065	0.8839	0.4457	0.9316	0.9358	0.7529	0.8488
American plaice	Deviance Explained	0.9350	0.9544	0.9373	0.6233	0.9640	0.9734	0.8367	0.9269
American plaice	GCV	0.2385	0.1952	0.2188	0.8298	0.1320	0.1577	0.3804	0.3181
American plaice	Correlation	0.9671	0.9771	0.9683	0.7897	0.9819	0.9867	0.9149	0.9629
Anchovy	AIC	79.8324	66.8417	65.9942	137.8919	84.7169	76.6602	78.5186	91.8717
Anchovy	Akaike weight	0.0006	0.3938	0.6015	0.0000	0.0001	0.0029	0.0011	0.0000
Anchovy	Adjusted r2	0.8643	0.8906	0.8928	0.6218	0.8450	0.8711	0.8663	0.8345
Anchovy	Deviance Explained	0.9193	0.9373	0.9475	0.7076	0.8886	0.9232	0.9178	0.8989
Anchovy	GCV	0.2617	0.2191	0.2509	0.5612	0.2475	0.2484	0.2494	0.3111
Anchovy	Correlation	0.9589	0.9682	0.9734	0.8412	0.9428	0.9610	0.9582	0.9483
Argentine	AIC	61.1927	58.6899	58.8162	110.4900	57.0751	61.1476	92.3115	84.5718
Argentine	Akaike weight	0.0601	0.2101	0.1972	0.0000	0.4711	0.0615	0.0000	0.0000
Argentine	Adjusted r2	0.8665	0.8714	0.8702	0.6878	0.8682	0.8658	0.7710	0.8032
Argentine	Deviance Explained	0.9232	0.9245	0.9208	0.7786	0.9067	0.9196	0.8449	0.8793
Argentine	GCV	0.1994	0.1881	0.1825	0.3780	0.1599	0.1925	0.2903	0.2755
Argentine	Correlation	0.9609	0.9616	0.9597	0.8827	0.9523	0.9590	0.9192	0.9379
Atlantic cod	AIC	37.1103	35.0259	36.4794	82.6257	37.4921	38.8675	53.5330	54.0284
Atlantic cod	Akaike weight	0.1551	0.4397	0.2126	0.0000	0.1281	0.0644	0.0000	0.0000
Atlantic cod	Adjusted r2	0.7016	0.7099	0.7013	0.3293	0.6750	0.6912	0.5928	0.5913
Atlantic cod	Deviance Explained	0.8179	0.8185	0.8086	0.4898	0.7510	0.8065	0.7100	0.7123
Atlantic cod	GCV	0.1287	0.1220	0.1227	0.2320	0.1116	0.1296	0.1505	0.1528
Atlantic cod	Correlation	0.9048	0.9052	0.8996	0.7003	0.8669	0.8985	0.8427	0.8440
Atlantic herring	AIC	149.6210	159.7501	157.5426	185.1737	165.0698	149.7462	154.1944	147.6567
Atlantic herring	Akaike weight	0.2111	0.0013	0.0040	0.0000	0.0001	0.1983	0.0214	0.5637
Atlantic herring	Adjusted r2	0.6669	0.6024	0.6154	0.3589	0.5417	0.6656	0.6316	0.6751
Atlantic herring	Deviance Explained	0.8073	0.7519	0.7578	0.5156	0.6621	0.8038	0.7582	0.8040
Atlantic herring	GCV	0.8257	0.9141	0.8757	1.2170	0.8915	0.8176	0.8050	0.7723
Atlantic herring	Correlation	0.8989	0.8683	0.8708	0.7186	0.8152	0.8975	0.8718	0.8970
Atlantic mackerel	AIC	171.3942	171.4521	193.3610	211.6305	181.9459	193.1165	216.1899	202.8729
Atlantic mackerel	Akaike weight	0.5059	0.4915	0.0000	0.0000	0.0026	0.0000	0.0000	0.0000
Atlantic mackerel	Adjusted r2	0.6835	0.6826	0.5322	0.3490	0.6057	0.5371	0.3054	0.4555
Atlantic mackerel	Deviance Explained	0.8288	0.8242	0.6903	0.5249	0.7283	0.7003	0.5036	0.6413
Atlantic mackerel	GCV	1.2466	1.2204	1.5049	1.9000	1.2186	1.5230	2.0698	1.7606
Atlantic mackerel	Correlation	0.9106	0.9081	0.8313	0.7254	0.8541	0.8374	0.7104	0.8018
Blue whiting	AIC	157.5422	157.3585	142.8428	206.3909	202.6624	155.7481	181.7351	173.2837
Blue whiting	Akaike weight	0.0006	0.0007	0.9971	0.0000	0.0000	0.0016	0.0000	0.0000
Blue whiting	Adjusted r2	0.9006	0.9009	0.9208	0.7674	0.7740	0.9034	0.8524	0.8689
Blue whiting	Deviance Explained	0.9502	0.9495	0.9651	0.8350	0.8280	0.9504	0.9174	0.9183
Blue whiting	GCV	1.0747	1.0538	0.9738	1.7752	1.6078	1.0175	1.4269	1.1375

Blue whiting	Correlation	0.9748	0.9745	0.9824	0.9138	0.9101	0.9749	0.9578	0.9585
Boarfish	AIC	213.1609	210.9340	225.3267	231.6004	217.5399	212.3222	218.7746	220.5603
Boarfish	Akaike weight	0.1734	0.5281	0.0004	0.0000	0.0194	0.2638	0.0105	0.0043
Boarfish	Adjusted r2	0.8523	0.8569	0.8160	0.7927	0.8279	0.8555	0.8367	0.8306
Boarfish	Deviance Explained	0.9041	0.9056	0.8714	0.8487	0.8637	0.9091	0.8904	0.8836
Boarfish	GCV	2.1002	2.0036	2.4321	2.6218	2.0056	2.1211	2.2461	2.2758
Boarfish	Correlation	0.9509	0.9517	0.9335	0.9213	0.9294	0.9535	0.9437	0.9400
Dab	AIC	144.2398	145.6818	144.6722	151.4338	135.1354	141.8774	149.1748	138.8077
Dab	Akaike weight	0.0086	0.0042	0.0070	0.0002	0.8203	0.0282	0.0007	0.1308
Dab	Adjusted r2	0.6947	0.6879	0.6869	0.6338	0.7201	0.7051	0.6586	0.7209
Dab	Deviance Explained	0.8055	0.8023	0.7879	0.7215	0.7896	0.8098	0.7594	0.8239
Dab	GCV	0.7007	0.7201	0.6755	0.7039	0.5445	0.6683	0.7083	0.6466
Dab	Correlation	0.8977	0.8959	0.8877	0.8496	0.8888	0.9001	0.8715	0.9078
Dogfish	AIC	80.8782	81.1712	104.1133	106.2558	73.8337	81.0451	106.7029	81.9692
Dogfish	Akaike weight	0.0269	0.0232	0.0000	0.0000	0.9096	0.0247	0.0000	0.0156
Dogfish	Adjusted r2	0.5700	0.5658	0.3656	0.3097	0.5999	0.5689	0.3246	0.5629
Dogfish	Deviance Explained	0.7422	0.7328	0.5944	0.4913	0.7210	0.7418	0.5372	0.7399
Dogfish	GCV	0.2645	0.2602	0.3658	0.3453	0.2115	0.2653	0.3634	0.2708
Dogfish	Correlation	0.8620	0.8566	0.7741	0.7019	0.8504	0.8616	0.7343	0.8610
Dover sole	AIC	-0.3874	11.6027	16.9888	22.8905	13.3880	-2.2935	15.7561	6.5754
Dover sole	Akaike weight	0.2756	0.0007	0.0000	0.0000	0.0003	0.7148	0.0001	0.0085
Dover sole	Adjusted r2	0.8272	0.7856	0.7725	0.7257	0.7644	0.8319	0.7641	0.8028
Dover sole	Deviance Explained	0.9023	0.8633	0.8818	0.7919	0.8208	0.9026	0.8352	0.8753
Dover sole	GCV	0.0750	0.0824	0.1073	0.0886	0.0759	0.0711	0.0828	0.0765
Dover sole	Correlation	0.9501	0.9294	0.9397	0.8900	0.9061	0.9502	0.9141	0.9358
Dragonet	AIC	90.0251	88.8081	106.7452	117.1096	97.5431	91.7799	111.9091	87.7587
Dragonet	Akaike weight	0.1567	0.2879	0.0000	0.0000	0.0037	0.0652	0.0000	0.4866
Dragonet	Adjusted r2	0.6392	0.6444	0.5152	0.4043	0.5594	0.6247	0.4808	0.6486
Dragonet	Deviance Explained	0.7827	0.7804	0.6762	0.5597	0.6647	0.7620	0.6709	0.7781
Dragonet	GCV	0.3053	0.2934	0.3699	0.4108	0.2950	0.3017	0.4175	0.2836
Dragonet	Correlation	0.8852	0.8839	0.8232	0.7485	0.8155	0.8735	0.8204	0.8826
European hake	AIC	83.5789	81.5285	113.4830	103.9585	82.6937	89.2787	107.8290	68.4779
European hake	Akaike weight	0.0005	0.0015	0.0000	0.0000	0.0008	0.0000	0.0000	0.9972
European hake	Adjusted r2	0.8655	0.8695	0.7821	0.8087	0.8604	0.8514	0.7952	0.8955
European hake	Deviance Explained	0.9221	0.9226	0.8733	0.8758	0.9013	0.9096	0.8644	0.9489
European hake	GCV	0.2843	0.2697	0.4590	0.3608	0.2419	0.2994	0.3786	0.2621
European hake	Correlation	0.9603	0.9606	0.9347	0.9359	0.9494	0.9538	0.9298	0.9742
European pilchard	AIC	100.3310	115.3402	129.8159	158.1312	116.6696	101.9843	119.5856	112.9894
European pilchard	Akaike weight	0.6943	0.0004	0.0000	0.0000	0.0002	0.3038	0.0000	0.0012
European pilchard	Adjusted r2	0.8493	0.8058	0.7540	0.5985	0.7963	0.8452	0.7917	0.8148
European pilchard	Deviance Explained	0.9223	0.8853	0.8520	0.7260	0.8651	0.9186	0.8758	0.8991
European pilchard	GCV	0.4149	0.4668	0.5807	0.8352	0.4367	0.4178	0.4959	0.4827
European pilchard	Correlation	0.9606	0.9411	0.9233	0.8525	0.9305	0.9586	0.9363	0.9485
European plaice	AIC	80.3903	96.6994	97.4251	130.2695	84.9665	79.5362	108.9820	79.8481
European plaice	Akaike weight	0.2534	0.0001	0.0001	0.0000	0.0257	0.3884	0.0000	0.3323
European plaice	Adjusted r2	0.8058	0.7447	0.7418	0.5372	0.7770	0.8075	0.6887	0.8073
European plaice	Deviance Explained	0.8814	0.8367	0.8351	0.6563	0.8341	0.8796	0.8009	0.8818
European plaice	GCV	0.2584	0.3244	0.3287	0.5066	0.2438	0.2503	0.3955	0.2553

European plaice	Correlation	0.9390	0.9151	0.9141	0.8102	0.9136	0.9380	0.8955	0.9394
European sprat	AIC	149.5022	204.7538	218.8024	239.3103	205.4810	141.7540	213.9105	163.1291
European sprat	Akaike weight	0.0203	0.0000	0.0000	0.0000	0.0000	0.9796	0.0000	0.0000
European sprat	Adjusted r2	0.9254	0.8161	0.7740	0.6568	0.8063	0.9343	0.7894	0.9078
European sprat	Deviance Explained	0.9671	0.8863	0.8867	0.7424	0.8631	0.9707	0.8783	0.9553
European sprat	GCV	1.0802	1.9022	2.8839	2.9239	1.7535	0.9424	2.3321	1.2140
European sprat	Correlation	0.9835	0.9416	0.9418	0.8618	0.9292	0.9853	0.9374	0.9774
Grenadier	AIC	-51.2858	-50.2621	-53.5136	28.5692	8.4676	23.1737	-53.2331	-17.8186
Grenadier	Akaike weight	0.1371	0.0822	0.4177	0.0000	0.0000	0.0000	0.3630	0.0000
Grenadier	Adjusted r2	0.9225	0.9207	0.9248	0.6986	0.7915	0.7436	0.9239	0.8671
Grenadier	Deviance Explained	0.9553	0.9526	0.9552	0.7782	0.8640	0.8587	0.9529	0.9241
Grenadier	GCV	0.0324	0.0320	0.0304	0.0987	0.0771	0.1122	0.0296	0.0561
Grenadier	Correlation	0.9774	0.9760	0.9774	0.8822	0.9299	0.9269	0.9762	0.9614
Grey gurnard	AIC	111.4699	121.2460	103.2777	127.6410	114.1857	110.3423	122.8904	118.7214
Grey gurnard	Akaike weight	0.0158	0.0001	0.9517	0.0000	0.0041	0.0278	0.0001	0.0004
Grey gurnard	Adjusted r2	0.6602	0.5945	0.7029	0.5268	0.6081	0.6644	0.5717	0.6054
Grey gurnard	Deviance Explained	0.7855	0.7262	0.8141	0.6385	0.6846	0.7833	0.6886	0.7234
Grey gurnard	GCV	0.4159	0.4640	0.3668	0.4785	0.3760	0.4015	0.4550	0.4348
Grey gurnard	Correlation	0.8864	0.8523	0.9026	0.7992	0.8275	0.8851	0.8299	0.8506
Haddock	AIC	130.5101	128.4592	142.8370	204.9356	166.3543	145.0045	158.0782	134.0899
Haddock	Akaike weight	0.2526	0.7045	0.0005	0.0000	0.0000	0.0002	0.0000	0.0422
Haddock	Adjusted r2	0.8526	0.8570	0.8199	0.4735	0.7142	0.8143	0.7647	0.8420
Haddock	Deviance Explained	0.9163	0.9166	0.8963	0.6113	0.7838	0.8972	0.8489	0.9033
Haddock	GCV	0.6163	0.5833	0.7431	1.6945	0.8979	0.7967	0.8706	0.6134
Haddock	Correlation	0.9574	0.9576	0.9470	0.7822	0.8858	0.9475	0.9218	0.9506
Horse mackerel	AIC	219.5894	218.3065	216.7731	249.0903	205.6293	221.3516	220.1483	224.7812
Horse mackerel	Akaike weight	0.0009	0.0018	0.0038	0.0000	0.9924	0.0004	0.0007	0.0001
Horse mackerel	Adjusted r2	0.5449	0.5495	0.5565	0.2260	0.6056	0.5270	0.5257	0.4970
Horse mackerel	Deviance Explained	0.7018	0.6946	0.6916	0.4150	0.6863	0.6799	0.6593	0.6534
Horse mackerel	GCV	2.3139	2.2142	2.1246	3.4113	1.6519	2.3282	2.1996	2.4318
Horse mackerel	Correlation	0.8381	0.8337	0.8319	0.6453	0.8289	0.8250	0.8127	0.8089
John dory	AIC	7.5548	14.8552	1.6771	56.7472	19.3815	30.1410	51.8355	13.8597
John dory	Akaike weight	0.0501	0.0013	0.9463	0.0000	0.0001	0.0000	0.0000	0.0021
John dory	Adjusted r2	0.8248	0.7989	0.8410	0.5998	0.7694	0.7432	0.6345	0.8040
John dory	Deviance Explained	0.9000	0.8723	0.9113	0.7339	0.8255	0.8381	0.7667	0.8805
John dory	GCV	0.0845	0.0871	0.0784	0.1657	0.0839	0.1121	0.1576	0.0885
John dory	Correlation	0.9489	0.9342	0.9549	0.8574	0.9088	0.9159	0.8764	0.9385
Lemon sole	AIC	59.8996	88.8622	73.6192	125.7437	46.4579	56.5367	70.5296	62.3891
Lemon sole	Akaike weight	0.0012	0.0000	0.0000	0.0000	0.9920	0.0064	0.0000	0.0003
Lemon sole	Adjusted r2	0.7953	0.6671	0.7401	0.3571	0.8293	0.8067	0.7536	0.7847
Lemon sole	Deviance Explained	0.8830	0.7889	0.8365	0.5148	0.8855	0.8928	0.8473	0.8687
Lemon sole	GCV	0.1962	0.2878	0.2264	0.4669	0.1395	0.1910	0.2179	0.1936
Lemon sole	Correlation	0.9399	0.8885	0.9150	0.7180	0.9410	0.9450	0.9212	0.9323
Ling	AIC	-2.6932	-0.9831	-3.6560	23.3410	3.0840	-6.2853	18.7677	15.5153
Ling	Akaike weight	0.1096	0.0466	0.1773	0.0000	0.0061	0.6603	0.0000	0.0000
Ling	Adjusted r2	0.6316	0.6168	0.6300	0.3975	0.5464	0.6540	0.4542	0.5035
Ling	Deviance Explained	0.7647	0.7447	0.7474	0.5356	0.6233	0.7833	0.6006	0.6772
Ling	GCV	0.0654	0.0652	0.0614	0.0886	0.0619	0.0626	0.0846	0.0866

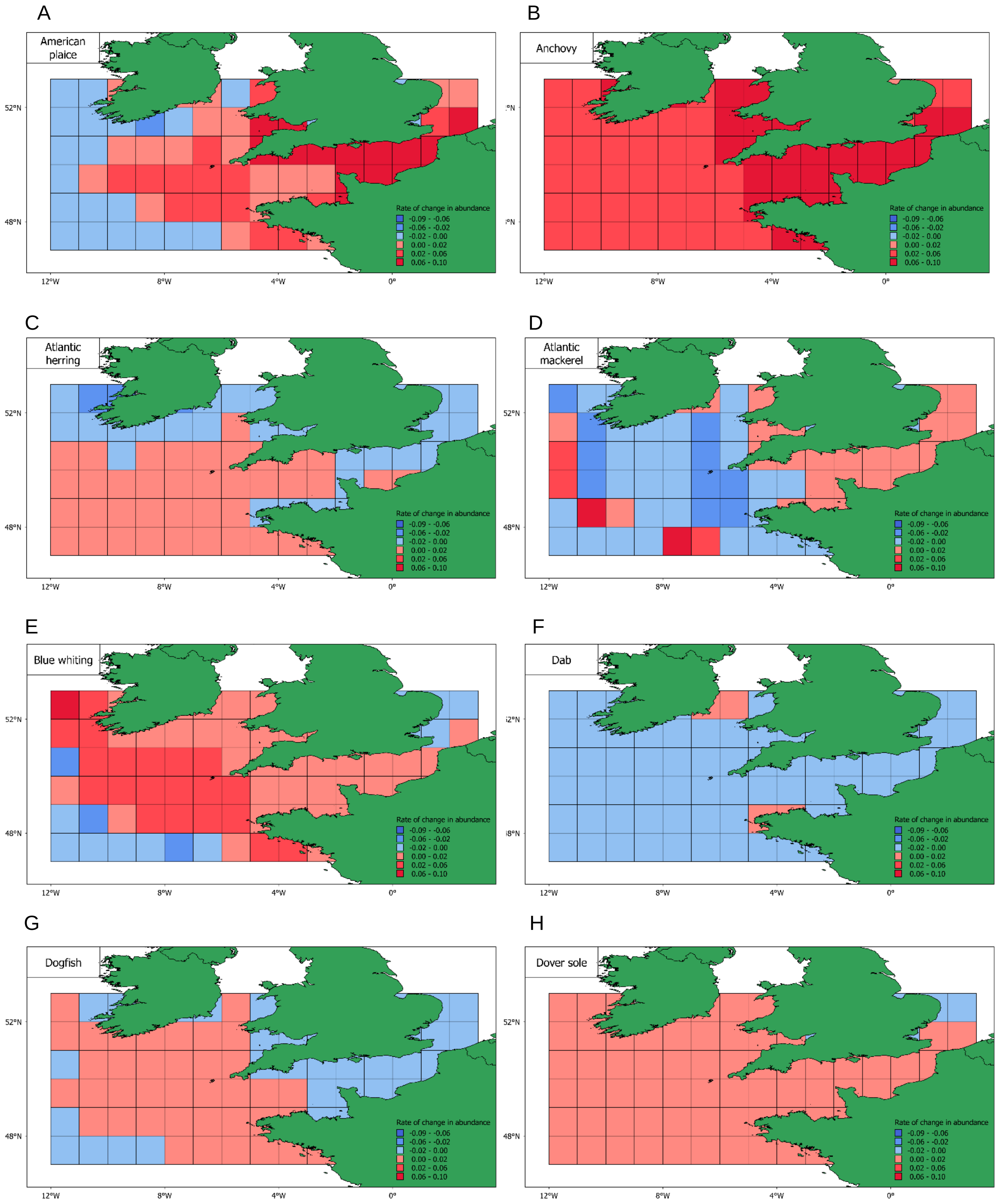
Ling	Correlation	0.8746	0.8630	0.8646	0.7320	0.7895	0.8853	0.7753	0.8234
Megrim	AIC	-7.5239	-8.9496	9.5864	94.3392	-9.8913	9.1172	57.7836	15.3740
Megrim	Akaike weight	0.1586	0.3234	0.0000	0.0000	0.5179	0.0000	0.0000	0.0000
Megrim	Adjusted r2	0.9728	0.9734	0.9642	0.8565	0.9734	0.9644	0.9201	0.9607
Megrim	Deviance Explained	0.9861	0.9860	0.9816	0.9109	0.9838	0.9809	0.9496	0.9804
Megrim	GCV	0.0735	0.0698	0.0963	0.3194	0.0604	0.0918	0.1750	0.1090
Megrim	Correlation	0.9930	0.9930	0.9908	0.9544	0.9919	0.9904	0.9745	0.9902
Monkfish	AIC	-33.5807	-29.0423	-27.7160	48.0537	-36.9909	-35.2069	0.4298	-36.4027
Monkfish	Akaike weight	0.0768	0.0079	0.0041	0.0000	0.4228	0.1733	0.0000	0.3151
Monkfish	Adjusted r2	0.9008	0.8915	0.8892	0.6107	0.8983	0.9030	0.8289	0.9045
Monkfish	Deviance Explained	0.9424	0.9312	0.9299	0.7253	0.9234	0.9420	0.9028	0.9419
Monkfish	GCV	0.0429	0.0430	0.0440	0.1385	0.0339	0.0408	0.0756	0.0394
Monkfish	Correlation	0.9709	0.9650	0.9644	0.8519	0.9609	0.9706	0.9503	0.9706
Norway pout	AIC	148.6280	146.3448	156.7800	216.6031	161.9409	136.8661	165.2560	157.6797
Norway pout	Akaike weight	0.0028	0.0086	0.0000	0.0000	0.0000	0.9885	0.0000	0.0000
Norway pout	Adjusted r2	0.8820	0.8866	0.8639	0.6374	0.8520	0.9029	0.8424	0.8630
Norway pout	Deviance Explained	0.9337	0.9387	0.9177	0.7659	0.9103	0.9506	0.9003	0.9209
Norway pout	GCV	0.8337	0.8330	0.8928	2.2286	0.9690	0.7581	0.9881	0.9426
Norway pout	Correlation	0.9663	0.9690	0.9580	0.8753	0.9542	0.9751	0.9490	0.9598
Poor cod	AIC	163.3034	167.9625	161.6210	194.3177	169.9364	166.9927	184.4204	167.1141
Poor cod	Akaike weight	0.2660	0.0259	0.6169	0.0000	0.0096	0.0420	0.0000	0.0396
Poor cod	Adjusted r2	0.7168	0.6938	0.7245	0.4965	0.6635	0.7008	0.5909	0.7001
Poor cod	Deviance Explained	0.8255	0.8089	0.8307	0.6158	0.7482	0.8198	0.7217	0.8192
Poor cod	GCV	0.9774	1.0431	0.9534	1.4033	0.9568	1.0568	1.2788	1.0575
Poor cod	Correlation	0.9091	0.9002	0.9121	0.7849	0.8656	0.9058	0.8505	0.9055
Pouting	AIC	71.6168	73.3427	129.5191	115.7550	68.3034	69.6847	85.4361	92.7377
Pouting	Akaike weight	0.1076	0.0454	0.0000	0.0000	0.5641	0.2828	0.0001	0.0000
Pouting	Adjusted r2	0.8889	0.8853	0.7159	0.7678	0.8893	0.8919	0.8574	0.8403
Pouting	Deviance Explained	0.9341	0.9304	0.8267	0.8465	0.9213	0.9343	0.9052	0.8955
Pouting	GCV	0.2297	0.2319	0.5714	0.4307	0.1912	0.2183	0.2631	0.2993
Pouting	Correlation	0.9665	0.9646	0.9097	0.9201	0.9599	0.9666	0.9515	0.9464
Red gurnard	AIC	76.3653	76.8246	86.3354	93.9244	84.1377	71.7255	83.5359	72.2662
Red gurnard	Akaike weight	0.0505	0.0402	0.0003	0.0000	0.0010	0.5141	0.0014	0.3924
Red gurnard	Adjusted r2	0.7198	0.7128	0.6724	0.6176	0.6535	0.7420	0.6695	0.7378
Red gurnard	Deviance Explained	0.8254	0.8091	0.8002	0.7374	0.7282	0.8450	0.7600	0.8367
Red gurnard	GCV	0.2384	0.2291	0.2848	0.2953	0.2343	0.2278	0.2414	0.2233
Red gurnard	Correlation	0.9086	0.8996	0.8950	0.8591	0.8535	0.9194	0.8719	0.9149
Red mullet	AIC	77.7528	88.7001	75.4726	88.4812	66.5518	76.4489	74.7994	81.0800
Red mullet	Akaike weight	0.0036	0.0000	0.0111	0.0000	0.9622	0.0068	0.0156	0.0007
Red mullet	Adjusted r2	0.6082	0.5290	0.6173	0.5337	0.6415	0.6133	0.6235	0.5809
Red mullet	Deviance Explained	0.7366	0.6761	0.7325	0.6853	0.7060	0.7337	0.7410	0.7069
Red mullet	GCV	0.2307	0.2712	0.2169	0.2736	0.1731	0.2224	0.2167	0.2373
Red mullet	Correlation	0.8583	0.8223	0.8559	0.8283	0.8403	0.8566	0.8610	0.8409
Seabass	AIC	-14.4961	-16.2951	-20.3797	29.5660	-11.2814	-16.3730	24.3502	-2.3529
Seabass	Akaike weight	0.0397	0.0977	0.7530	0.0000	0.0080	0.1016	0.0000	0.0001
Seabass	Adjusted r2	0.7377	0.7440	0.7617	0.4217	0.6840	0.7445	0.4761	0.6806
Seabass	Deviance Explained	0.8443	0.8441	0.8594	0.5608	0.7358	0.8447	0.6143	0.8090
Seabass	GCV	0.0572	0.0545	0.0523	0.0987	0.0490	0.0545	0.0922	0.0692

Seabass	Correlation	0.9190	0.9189	0.9271	0.7495	0.8578	0.9193	0.7840	0.8999
Seabream	AIC	103.4766	101.8574	126.4322	154.8824	93.2764	101.6394	129.8567	102.4373
Seabream	Akaike weight	0.0058	0.0131	0.0000	0.0000	0.9566	0.0146	0.0000	0.0098
Seabream	Adjusted r2	0.7753	0.7797	0.6701	0.4521	0.7952	0.7804	0.6495	0.7770
Seabream	Deviance Explained	0.8569	0.8561	0.7794	0.5862	0.8423	0.8566	0.7616	0.8529
Seabream	GCV	0.3631	0.3473	0.5078	0.7468	0.2738	0.3462	0.5305	0.3482
Seabream	Correlation	0.9258	0.9253	0.8830	0.7661	0.9178	0.9256	0.8732	0.9236
Silvery pout	AIC	-0.8126	4.9147	42.8150	137.7427	45.6447	26.9840	91.0197	24.4913
Silvery pout	Akaike weight	0.9460	0.0540	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Silvery pout	Adjusted r2	0.9498	0.9456	0.9022	0.5145	0.8975	0.9239	0.7856	0.9273
Silvery pout	Deviance Explained	0.9809	0.9783	0.9482	0.6471	0.9442	0.9652	0.8759	0.9632
Silvery pout	GCV	0.1139	0.1180	0.1599	0.5783	0.1631	0.1442	0.3209	0.1242
Silvery pout	Correlation	0.9904	0.9891	0.9739	0.8050	0.9719	0.9826	0.9363	0.9816
Solenette	AIC	100.0243	104.7059	131.2198	118.0360	84.2967	98.0339	108.2442	101.7667
Solenette	Akaike weight	0.0004	0.0000	0.0000	0.0000	0.9984	0.0010	0.0000	0.0002
Solenette	Adjusted r2	0.6887	0.6615	0.4837	0.5682	0.7495	0.6967	0.6417	0.6754
Solenette	Deviance Explained	0.8067	0.7827	0.6755	0.6969	0.8244	0.8070	0.7700	0.7875
Solenette	GCV	0.3502	0.3681	0.5738	0.4297	0.2495	0.3327	0.3898	0.3461
Solenette	Correlation	0.8987	0.8853	0.8235	0.8352	0.9085	0.8988	0.8779	0.8877
Thickback sole	AIC	131.7327	132.2976	132.7826	149.9281	119.1938	127.3137	143.5509	125.4315
Thickback sole	Akaike weight	0.0018	0.0013	0.0011	0.0000	0.9382	0.0162	0.0000	0.0415
Thickback sole	Adjusted r2	0.6505	0.6451	0.6461	0.5107	0.7005	0.6769	0.5699	0.6851
Thickback sole	Deviance Explained	0.7827	0.7736	0.7847	0.6508	0.7836	0.8063	0.7148	0.8065
Thickback sole	GCV	0.5834	0.5772	0.6035	0.7115	0.4303	0.5592	0.6732	0.5319
Thickback sole	Correlation	0.8850	0.8798	0.8865	0.8072	0.8856	0.8987	0.8458	0.8985
Weever	AIC	72.6478	84.9070	76.4027	77.6278	61.9287	70.7690	70.3579	74.1550
Weever	Akaike weight	0.0045	0.0000	0.0007	0.0004	0.9663	0.0116	0.0143	0.0021
Weever	Adjusted r2	0.5860	0.4827	0.5484	0.5298	0.6281	0.5962	0.5898	0.5690
Weever	Deviance Explained	0.7395	0.6455	0.6893	0.6591	0.7191	0.7404	0.7168	0.7126
Weever	GCV	0.2229	0.2557	0.2223	0.2196	0.1667	0.2128	0.2012	0.2189
Weever	Correlation	0.8602	0.8035	0.8304	0.8125	0.8483	0.8607	0.8470	0.8445
Whiting	AIC	133.6177	133.3212	169.5490	208.3723	114.2894	133.5168	176.8327	145.9367
Whiting	Akaike weight	0.0001	0.0001	0.0000	0.0000	0.9998	0.0001	0.0000	0.0000
Whiting	Adjusted r2	0.8863	0.8863	0.7937	0.5869	0.9147	0.8860	0.7679	0.8608
Whiting	Deviance Explained	0.9339	0.9321	0.8696	0.6857	0.9444	0.9321	0.8533	0.9173
Whiting	GCV	0.6357	0.6180	1.0602	1.7629	0.4248	0.6211	1.1921	0.7610
Whiting	Correlation	0.9665	0.9655	0.9328	0.8284	0.9719	0.9655	0.9242	0.9578

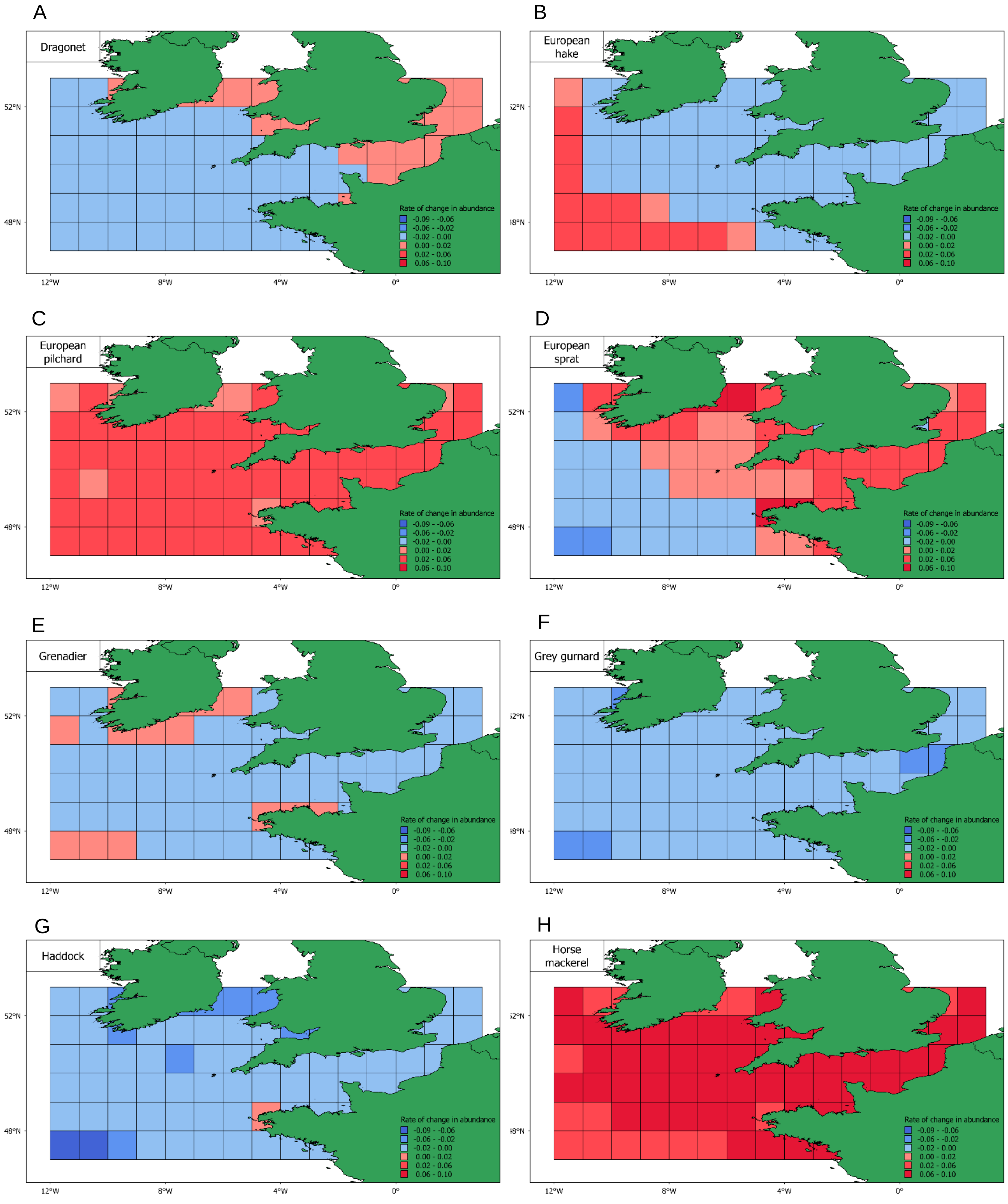
Appendix 5: Table of results of GAM testing. Each model was tested on each species; the highlighted column (model with all variables except ‘habitat’ variable), performed best for most species.

Species	Z	p-value
American plaice	1664	4.20E-09
Anchovy	2775	7.89E-14
Argentine	2132	4.48E-06
Atlantic cod	17	1.66E-12
Atlantic herring	1543	2.91E-01
Atlantic mackerel	912	1.11E-01
Blue whiting	2215	1.74E-09
Boarfish	2690	2.31E-12
Dab	71	1.44E-10
Dogfish	1413	4.41E-01
Dover sole	2555	3.61E-11
Dragonet	972	2.54E-02
European hake	856	6.61E-03
European pilchard	2775	7.89E-14
European plaice	825	2.46E-03
European sprat	1941	5.54E-07
Grenadier	350	1.56E-04
Grey gurnard	0	5.33E-13
Haddock	12	9.01E-13
Horse mackerel	2775	7.89E-14
John dory	2311	6.61E-07
Lemon sole	1093	1.13E-01
Ling	34	4.66E-13
Megrim	310	4.14E-05
Monkfish	60	4.60E-12
Norway pout	0	5.36E-09
Poor cod	2681	3.27E-12
Pouting	2774	8.22E-14
Red gurnard	2773	8.57E-14
Red mullet	2775	7.89E-14
Seabass	2775	7.89E-14
Seabream	1731	1.93E-09
Silvery pout	1981	3.81E-06
Solenette	2410	5.82E-09
Thickback sole	1408	6.00E-01
Weever	2775	7.89E-14
Whiting	1586	4.47E-02

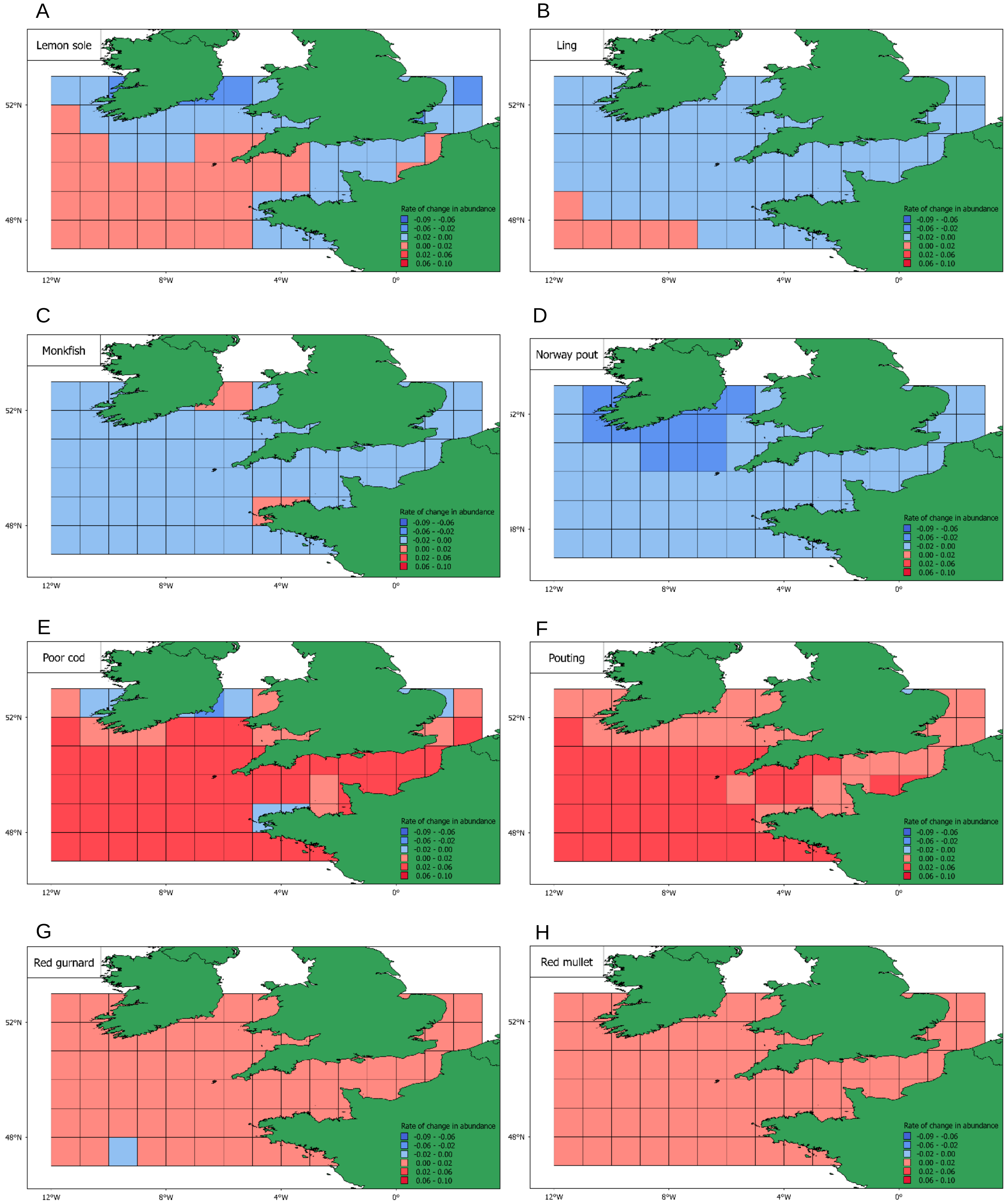
Appendix 6: One-sample Wilcoxon signed rank test results for the rate of change in abundance (as predicted by the GAM), for all species, from 2010–2090. Significant results accepted at $p<0.05$.



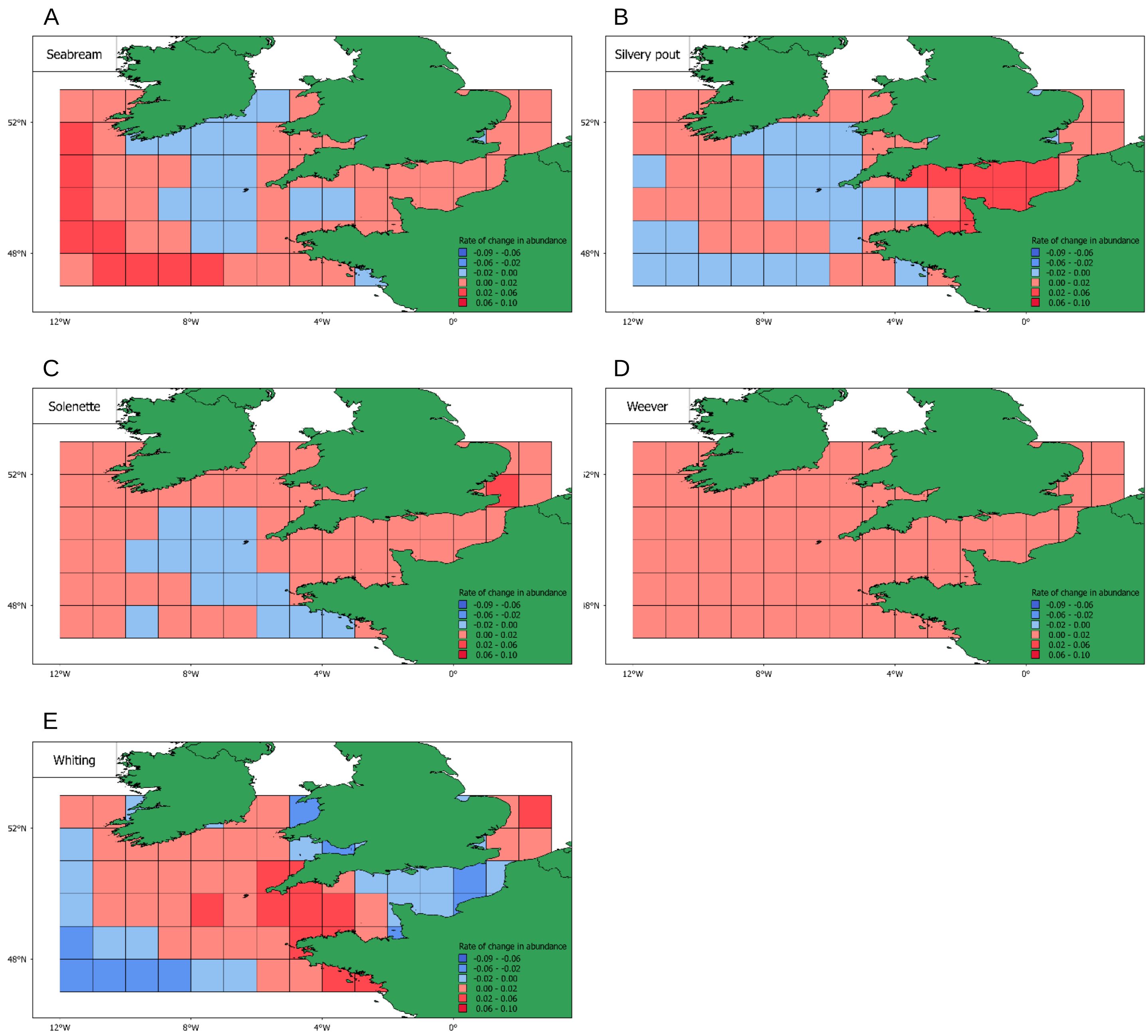
Appendix 7: Spatial variation in the rate of change in abundance as predicted by the GAM, for 2010–2098. **A,** American plaice (*Hippoglossoides platessoides*). **B**, Anchovy (*Engraulis encrasicolus*). **C**, Atlantic herring (*Clupea harengus*). **D** Atlantic mackerel (*Scomber scombrus*). **E**, Blue whiting (*Micromesistius poutassou*). **F**, Dab (*Limanda limanda*). **G**, Dogfish (see **Table 1**). **H**, Dover sole (*Solea solea* and *S. vulgaris*).



Appendix 8: Spatial variation in the rate of change in abundance as predicted by the GAM, for 2010–2098. **A**, Dragonet (see **Table 1**). **B**, European hake (*Merluccius merluccius*). **C**, European pilchard (*Sardina pilchardus*). **D**, European sprat (*Sprattus sprattus*). **E**, Grenadier (see **Table 1**). **F**, Grey gurnard (*Eutrigla gurnardus*). **G**, Haddock (*Melanogrammus aeglefinus*). **H**, Horse mackerel (*Trachurus trachurus*).



Appendix 9: Spatial variation in the rate of change in abundance as predicted by the GAM, for 2010–2098. **A**, Lemon sole (*Microstomus kitt*). **B**, Ling (*Molva sp*.). **C**, Monkfish (*Lophius piscatorius*). **D**, Norway pout (*Trisopterus esmarkii*). **E,** Poor cod (*Trisopterus minutus*). **F**, Pouting (*Trisopterus luscus*). **G**, Red gurnard (*Chelidonichthys cuculus*). **H** Red mullet (*Mullus barbatus* and *M. surmuletus*).



Appendix 10: Spatial variation in the rate of change in abundance as predicted by the GAM, for 2010–2098. **A**, Seabream (see **Table 1**). **B**, Silvery pout (*Gadiculus argenteus*). **C**, Solenette (*Buglossidium luteum*). **D**, Weever (see **Table 1**). **E**, Whiting (*Merlangius merlangus*).

	Species	Central latitude	Common length	Trophic level
Winners	American plaice	59	30	3.8
	Anchovy	12.5	13.5	3.12
	Argentine	47.5	20	3.62
	Blue whiting	52.5	22	4.03
	Boarfish	36	13	3.135
	Dover sole	42	35	3.165
	European pilchard	41	20	3.05
	European sprat	48	12	3.01
	Horse mackerel	24	22	3.64
	John dory	13	40	4.455
	Poor cod	47	20	3.715
	Pouting	43.5	30	3.655
	Red gurnard	20.5	27.6	3.81
	Red mullet	38	20	3.29
	Seabass	41.5	50	3.63
	Seabream	41.5	30	3.34
	Silvery pout	49	10	3.6
	Solenette	30.5	8	3.31
	Weever	39.5	10	4.2
	Whiting	53.5	23.5	4.265
Losers	Atlantic cod	59	100	4.215
	Dab	57.5	25	3.29
	Dragonet	40.5	15	3.27
	European hake	47	45	4.4
	European plaice	54	40	3.245
	Grenadier	22	30	3.465
	Grey gurnard	45	30	3.71
	Haddock	57	35	4.035
	Ling	55	106	4.4
	Megrim	47.5	25	4.34
	Monkfish	52.5	100	4.45
	Norway pout	63.5	19	3.22
Non-significant	Atlantic herring	56.5	30	3.29
	Atlantic mackerel	47.5	30	3.57
	Dogfish	37.5	60	3.72
	Lemon sole	57.5	30	3.215
	Thickback sole	37.5	14	3.28

Appendix 11: Central latitude, common length and trophic level for each species, grouped according to winners (species predicted to increase in abundance) losers (species predicted to decrease in abundance), and those species without statistically significant responses. All data obtained from FishBase (FishBase 2012), except for common length values for dab and lemon sole; obtained from the Marine Life Information Network (MarLIN 2014) and american plaice common length, obtained from the FAO FishFinder (FAO 2010).

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