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Impacts of climate change on fish

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EXECUTIVE SUMMARY

The story so far

The shelf seas surrounding the British Isles have warmed four times faster than the global average over the last 30 years. Recent warm conditions are unlike anything in the last 20,000 years, and warming is highly likely due to human activities linked to the global carbon cycle.

Recent warming has caused some cold-water demersal (bottom-dwelling) species to move northwards and into deeper water (e.g. cod, whiting, monkfish), and has caused some warm-water demersal species to become more common or "invade" new areas (e.g. John dory, red mullet).

Pelagic (blue-water) species are showing distributional shifts, with mackerel now extending into Icelandic and Faroe Island waters (with consequences for management), sardines and anchovies invading Irish and North Sea environments, and anchovies establishing breeding populations in the southern North Sea. Teasing apart the relative influences of the North Atlantic Oscillation, the Atlantic Multidecadal Oscillation and Global Warming as drivers for these changes is an important challenge.

When demersal fish communities are assessed at local scales across the region, 36 of the 50 most common species show a response to warming, with 75% of these increasing in abundance, leading to reorganization of local communities. International commercial landings of species identified as warm-adapted (e.g. grey gurnard, red mullet, hake) have increased 250% in the last 30 years while landings of cold-adapted species (e.g. cod, haddock, whiting) have halved.

In warm years, summer spawning fish (e.g. mackerel, horse mackerel) are spawning earlier and further north on the Porcupine Bank. Conversely, spring spawning fish (dab, whiting, lemon sole) are spawning earlier in southern England following cold winters due to females moving further offshore into less preferred but warmer waters.

Body size distributions of fish, both within species and across ecosystems, have been affected by climate change as well as fishing. Warm, lower-oxygen conditions favour smaller individuals, and by 2050 weights of fish could be reduced by 14-24%.

Declines in salmon are strongly correlated with rising temperatures in oceanic foraging areas, with temperature affecting growth, survival and maturation of salmon at sea. Freshwater temperatures have also increased significantly in the last four decades, with implications for survival of juvenile diadromous fish, including both anadromous (river spawning: salmon, trout, shad) and catadromous (sea spawning: eels and flounder) species. For eels, climatic changes in the spawning areas of the Sargasso Sea are likely impacting reproduction and larval survival.

Future predictions: ocean acidification

One-third of all anthropogenic CO_2 has been absorbed by the oceans, mitigating warming but decreasing the pH. Ocean acidification is occurring faster than any time in the last 300 million years, and is expected to continue through the 21st Century leading to a drop of 0.3 to 0.4 pH units.

In addition to compromising calcifying animals, from unicellular algae (e.g. coccolithophores) through to large urchins and bivalve molluscs, ocean acidification is now known to affect fish, with impacts on growth, neurological function, physiology, behaviour and cognitive processing.

More work, combining lab studies, long-term multigenerational studies, studies of natural CO_2 hotspots and of temperate water fish, and mechanistic modelling is needed to predict the full impacts of ocean acidification on fish.

Future predictions: developments in modelling

Ocean temperatures are predicted to rise a further 2 to 4 °C during the 21st Century. Predicting impacts of warming in fish communities is complex; and consortia are now using multiple-modelling approaches (ranging from statistical to mechanism-based) that are forced using an ensemble of climate scenarios to predict the range of likely outcomes for fish around the British Isles.

Models generally predict poleward (northward) movement of species ranges, leading to substantial losses in availability of traditionally harvested species (e.g. horse mackerel, sole, haddock). Models also predict changes to primary production throughout the British Isles, with southern regions (e.g. Celtic Sea, English Channel) becoming up to 10% more productive, while northern regions (e.g. central and northern North Sea) becoming up to 20% less productive, with obvious implications for the fisheries underpinned by these plankton communities.

1. WHAT IS ALREADY HAPPENING?

Climate change context

Since the Industrial Revolution, atmospheric levels of CO_2 have risen from 270 to 390 ppm, and there is great confidence that warming experienced across the globe is being forced by human activities linked to the release of this greenhouse gas into the global carbon cycle (IPCC, 2007a). Around 90% of the excess heat input to the Earth system over the last 50 years has been absorbed by the oceans (Bindoff *et al.*, 2007), causing an increase in average Sea-Surface Temperatures (SST) of 0.7 °C (Smith *et al.*, 2008) to levels considered to be anomalous within the context of the past 20,000 years (Björck, 2011), and emphasising the significance of the oceans in determining the global heat budget. Concurrently, approximately 1/3 of all anthropogenic CO_2 produced (142 billion tonnes) has been absorbed by the oceans, mitigating greenhouse gas-induced warming but causing the average pH of the ocean to drop by 0.1 units (Meehl *et al.*, 2007) and resulting in ocean acidification at a rate faster than any time in the last 300 million years (Honisch *et al.*, 2012). If global emissions continue on the current trajectory, atmospheric CO_2 is predicted to reach 730-1020 ppm by 2100 (Meehl *et al.*, 2007; Raupach *et al.*, 2007), causing further warming during the next century (IPCC, 2007b) including a predicted rise in average global SST of 1.5 to 2.6 °C (Meehl *et al.*, 2007), and leading to a further drop in ocean pH of 0.3 to 0.4 pH units (Royal Society, 2005; Meehl *et al.*, 2007).

Due to their mid-latitude, northern hemisphere location and semi-enclosed nature, the combined impact of global warming and a recent positive Atlantic Multidecadal Oscillation (AMO – a trend in sea temperature variation in the North Atlantic that fluctuates from positive to negative over a multiple decade timeframe) have caused the seas around the British Isles to warm at a rate four times faster than the global average over the last 30 years (Smith *et al.*, 2008). The rate of warming varies between 0.2 and 0.6 °C per decade over the last 30 years (Rayner *et al.*, 2003; Dulvy *et al.*, 2008) and has resulted in average SST in the North Sea and Celtic-Biscay Shelf regions increasing between 1982 and 2006 by 1.3 °C and 0.7 °C respectively (Sherman *et al.*, 2009). Predictions for further warming through the 21st Century in the region range from 2 to 4 °C (Sheppard, 2004; Heath *et al.*, 2012), with the forecast based on the optimistic Intergovernmental Panel on Climate Change (IPCC) SRES A1B scenario (assuming rapid economic growth, a global population that reaches 9 billion in 2050 and then gradually declines, the quick spread of new and efficient technologies, a convergent world with extensive social and cultural interactions, and a balanced use of fossil fuels with other energy sources) being for a rise of 2.5°C during this century (Meehl *et al.*, 2007; UK Meteorological Office, 2009).

The shelf seas surrounding the British Isles play host to more than 330 species of fish. Due to the economic importance of associated fisheries and the developed nature of member states, invaluable long-term high quality commercial landings and fisheries agency datasets are available, making the region amongst the most richly sampled marine ecosystems in the world. When these data are combined with recent rapid warming, the European continental shelf provides a valuable window into future global effects of warming on fish communities worldwide. In this report we present recent evidence and emerging theories on potential mechanisms of impacts of warming on fish distributions, composition of fish communities, timing and location of spawning events, growth and size distributions in fish communities, and impacts on diadromous species that inhabit both fresh and seawater environments during their life. Looking forward, we present evidence for future impacts of climate change on fish through ocean acidification, and highlight recent work using single or multi-modelling approaches to predict future distributions of fish species and functioning of marine ecosystems, giving recommendations for future research throughout.

The story so far: Changes in fish distributions

The abundances and sizes of fish in commercially-exploited populations in the North Atlantic have been modified substantially by fishing (Jennings and Blanchard, 2004) and altered prey fields (Beaugrand *et al.*, 2003; Beaugrand and Reid, 2003, 2012). Furthermore, as seas warm, fish species are predicted to track preferred thermal conditions (their "climate envelope"), and since biodiversity is generally greater towards the equator (Willig *et al.*, 2003), this predicts for an increase in species richness with warming in mid-latitude regions, including European waters. Such a trend has been shown in the North Sea (Hiddink and ter Hofstede, 2008; Engelhard *et al*., 2011) and Celtic Sea (Briggs *et al*., 2008; ter Hofstede *et al*., 2010) due to a number of small-bodied warm-adapted Lusitanian species (e.g. red mullet (*Mullus surmuletus*), red gurnard (*Chelidonichthys cuculus*) and John dory (*Zeus faber*)) exhibiting range expansions and almost exponential increases in abundance since the mid-1990s (Beare *et al*., 2004a). In the North Sea eight times as many fish species have increased distribution ranges (mainly small-sized Lusitanian species) compared with those whose range decreased (primarily large Boreal species; Hiddink and ter Hofstede, 2008). In the light of North Sea and Celtic Sea patterns, it is perhaps counterintuitive that there has been a temporary decline in species richness in NW Scotland, with the loss of cold-adapted Boreal species outpacing the expected increase in Lusitanian species (ter Hofstede *et al*., 2010), suggesting that caution should be applied to generalised predictions.

When the central distributions of species are considered, there is further compelling evidence for fish species moving polewards and/or into deeper water in response to recent warming in European seas. Several analyses of long-term datasets for the North Sea demonstrate such impacts. Hedger *et al*. (2004) first showed that cod (*Gadus morhua*) had 'deepened' between the 1980s and 1990s. Using English North Sea survey data, 15 of 36 North Sea species analysed by Perry *et al*. (2005) shifted with latitude (13 of 15 species moving polewards, including cod, grey gurnard (*Eutrigla gurnardus*) and monkfish (*Lophius piscatorius*)) and 18 species deepened (including cuckoo ray (*Leucoraja naevus*), dab (*Limanda limanda*) and plaice (*Pleuronectes platessa*)), with 12 species showing both responses over the 25-year period. Further analysis of the same data by Dulvy *et al*. (2008) found overall that the entire demersal fish assemblage had deepened by ~3.6m per decade, with the exceptions of sole (*Solea solea*) and bib (*Trisopterus luscus*) that had moved into shallower waters, perhaps due to an increase in the minimum winter bottom temperatures which may have previously excluded these warm-adapted species from the southern North Sea. When the latitudinal centres of gravity for 19 characterised sub-assemblages were analysed, a more complex picture emerged with abundant, widespread thermal specialists (e.g. grey gurnard and poor cod (*Trisopterus minutus*)) moving northwards due to warming in the southern North Sea, but, in contrast, some small-bodied southern species (e.g. common sole (*Solea solea*)) shifting southwards due to warming. The complex ocean circulation patterns which create invasion routes for warmer-water species into the North Sea through the Channel but also from the north via the continental shelf west of Britain and Ireland, coupled with variable bathymetry (depth profile) and a mosaic of different habitats make predicting latitudinal and depth responses of North Sea species a challenging task.

Occurrence of both Lusitanian and Boreal species in the seas around the British Isles means that many warm-water species have northern limits while some cold-water species have southern limits to their distributions within the region. The Irish Ground Fish Survey shows an increase in abundance of Lusitanian species (including sprat (*Sprattus sprattus*), anchovy (*Engraulis encrasicolus*), sardine (*Sardina pilchardus*) and bluemouth (*Helicolenus dactylopterus*)), to the north and west of Ireland and in the Celtic Sea (Marine Institute, 2009), most likely due to range expansion (Heath *et al*., 2012). In parallel, Boreal species have been declining in the south of Ireland (Lynam *et al*., 2010).

Several theories explain how and why ranges and densities of populations are shifting with warming. It is considered highly unlikely that individual adults of demersal species have moved polewards en masse, particularly if they have specific spawning, nursery and foraging grounds (Heath *et al*., 2012). Indeed species such as cod have broad thermal tolerances (Righton *et al*., 2010) and show little evidence for thermally directed movement even if preferred thermal conditions are available nearby (Neat and Righton, 2007). In contrast, adults of pelagic species are not habitat-attached, and exhibit far more rapid range shifts, although with inter-annual variation according to conditions. For example, boarfish (*Capros aper*) has increased substantially in abundance due to favourable temperatures in the Celtic Sea and the south of Ireland (Pinnegar *et al*., 2002; ICES, 2008), providing a commercially viable fishery for the Irish fleet. Atlantic mackerel (*Scomber scombrus*) tracks productive plankton blooms along the European continental shelf edge each year, and now migrates earlier and is found further north in recent warm years (leading to the current "Mackerel Wars" as the predominantly Irish and Scottish harvested stock extends further into Icelandic and Faroe Island waters, which are not controlled under the Common Fisheries Policy). The recent "invasion" of anchovy and sardine throughout the seas around the British Isles is closely associated with warm conditions (Beare *et al*., 2004a,b), leading to commercial fisheries in SW England. Although it is likely that initially larvae spilled into previously uninhabited areas such as the North Sea, it is now thought that anchovy at least has closed its life cycle in the southern North Sea due to increased winter temperatures since 1987 (Loewe, 2009), with eggs and larvae found off Helgoland in the German Bight (Alheit *et al*., 2007). It is perhaps misleading to think of anchovy and sardine "invading" since in previous warm periods (1860-1890 and 1930-1960) these species have also been present in abundance, and sardines have remained off Cornwall since the 19th Century (Southward, 1974). The relative importance of the North Atlantic Oscillation (NAO - a climatic phenomenon in the North Atlantic driven by latitudinal variations in atmospheric pressure which determines the strength and direction of warm westerly winds and associated currents), the Atlantic Multidecadal Oscillation (AMO, currently positive) and recent anthropogenic CO_2-induced Global Warming need teasing apart to determine whether anchovy and sardine will become a permanent feature in the seas around the British Isles (Alheit *et al*., 2012).

Range expansions are more common in demersal fish as the result of eggs and larvae seeding new habitat. Extreme examples include the 1991 bluemouth population boom in the southern North Sea and the snake pipefish (*Entelurus aequoreus*) boom in the North Sea and west of the UK and Ireland (2003-6), which were both short-lived, suggesting that breeding populations did not become locally established (Heath *et al*., 2012 and references therein). The gradual northward shift in the central tendency of many demersal species (e.g. Perry *et al*., 2005; Dulvy *et al*., 2008) is also likely to begin with higher levels of successful recruitment of larvae and juveniles in the north of the population range relative to the south as temperatures warm. Over decades, this leads to a general northward shift in the population. It is notable that species with northward shifting distributions, as well as being predominantly Lusitanian in origin, generally have faster lifecycles and smaller body sizes than non-shifting species (Perry *et al*., 2005), leading to more small fish in the demersal assemblage (ter Hofstede and Rijnsdorp, 2011), and resulting in a relative propensity of small-bodied Lusitanian species increasing in SW England compared to large-bodied Lusitanian species which may be more susceptible to fishing (Genner *et al*., 2010a).

The story so far: Changes in fish communities

Until recently most studies of effects of recent warming on fish species around the British Isles have focused on distributional or vertical range shifts, whether qualitatively (presence-absence) or quantitatively (central tendency and centre of gravity), of species in isolation. The focus on range shifts does not account for constraints on distributional shifts due to dependence of species on essential habitat including favoured substrates, appropriate predator and prey fields, and close proximity to nursery grounds, which may mask species-level responses in spite of dramatic changes to the local densities of fish. In a first analysis of community compositional change using a long time series of scientific trawl survey data (English Channel) and catch data from a power station filter screen (Bristol Channel), Genner *et al.* (2004) demonstrated that temperature shifts had influenced species compositions and abundances and thus whole communities of fish in two locations during the 20th Century.

In a subsequent study, the approach developed by Genner *et al.* (2004) of reducing assemblage data to primary axes of compositional change was expanded to provide a macroecological assessment of local-scale community change across the European continental shelf (Simpson *et al*., 2011a). Using a data-driven Eulerian (grid-based) approach that accommodates for spatial heterogeneity in ecological and environmental conditions, the local associations of species abundance and community diversity were compared with climatic variables in 172 separate 1x1° latitude-longitude cells. Records from 25,612 bottom trawl hauls collected over the period 1980-2008 were used, consisting of >100 million individuals from 177 species sampled in an area covering over 1.2 million km^2. When local-scale abundance trends were compared with temperature records, 36 of the 50 most common demersal species showed a response to warming, with 75% of these increasing in abundance and identified as warm-adapted (e.g. grey gurnard, red mullet and hake (*Merluccius merluccius*)), while 9 cold-adapted species (e.g. cod, haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*)) declined. In spite of surprisingly decadal stability of species presence-absence distributions (condensed to 9 sub-assemblages using unsupervised Bayesian clustering), the combined response (positive or negative) of many species to warming in a given location manifested as a community-level response to warming throughout 82% of the study area, suggesting profound reorganization of communities by warming without prerequisite range or depth shifts. Subsequent analysis of international commercial landings in the north-east Atlantic found a 250% increase in the last 30 years for species identified in this study as warm-adapted, while landings of cold-adapted species halved. The analysis by Simpson *et al.* (2011a) highlights the importance of considering changes in species abundance in established local communities rather than focusing on the arrival or retreat of species (usually at low numbers) near to species range boundaries to assess the full consequences of climate change for commercial fisheries and food security.

Most recently, analysis of the entire fish community (as sampled by the Irish Groundfish Survey; Lynam *et al*., Marine Institute Ireland, in prep) shows generally declining trends in the south (ICES division VIIg) largely attributable to fishing ($p<0.01$), with the decline greatest in the Boreal community ($p = 0.03$). However, in the west and north, Boreal species appear stable while Lusitanian species are increasing ($p<0.01$). This analysis suggests that the effect of marine climate change may already be altering the ecosystem to the west and north of Ireland, where stingray (*Dasyatis pastinaca*), bib, pilchard and anchovy show the greatest increases.

The story so far: Phenology of spawning and migration

There is strong evidence that climate warming has influenced the relative timing (phenology) of annual migrations and spawning events in European waters, with potentially significant effects on population sizes and recruitment. Where spawning is too early or too late to capitalise on available food resources, annual recruitment can be strongly affected. For example, spawning times of cod in the North Sea have changed since the late 1960s, leading to mismatches with the timing of blooms of essential zooplankton prey and, thus, reductions in annual recruitment success (Beaugrand *et al*., 2003). In contrast, the spawning stock of blue whiting increased threefold after 1995 following increases in sea surface temperature, with a clear three-year lag in response (i.e. the time required for new recruits to contribute to the stock biomass; Hátún *et al*., 2009), although blue whiting has since experienced a 20-fold drop in numbers indicating a short-lived population explosion. More effort is needed comparing patterns of larval abundance and recruitment of fish to populations with the climate record (e.g. Lo Yat *et al*., 2011) to determine the knock-on impacts of temperature and climate change on fish populations.

Effects of interannual variations in temperature appear to be location and species specific. For example, in the southern North Sea most species, irrespective of adult migration behaviour or spawning time, appear to spawn earlier in warmer waters (Greve *et al*., 2005). However, in the English Channel earlier spawning following warmer temperatures has only been observed in summer (July to September) spawning species, for example mackerel and horse mackerel (*Trachurus trachurus*; Genner *et al*., 2010b). In contrast, species that spawn in spring spawn later following warmer winters, including lemon sole (*Microstomus kitt*) and pollack (*Pollachius pollachius*) (Genner *et al*., 2010b). This may be related to warmer winters delaying the onset of the annual offshore migration of these species to the overwintering grounds, which in turn delays gonad maturation and spawning. Such delayed migration to offshore waters in warmer years has been identified in flounder (*Platichthys flesus*) from this region (Sims *et al*., 2004).

Recent evidence suggests that the timing and location of spawning for mackerel in the Atlantic is also highly temperature dependent, with warmer temperatures causing an earlier migration in western mackerel stocks, and leading to eggs found further north in warmer years (Johnson and Hughes, in prep). Also seen is a less elongated distribution of eggs in warm years due to increased spawning on the Porcupine Bank rather than spawning spread along the more southerly shelf edge.

The story so far: Growth and body size trends

There is extremely strong evidence that average sizes of individuals within populations of many commercially harvested species have declined over the last century. This has been widely attributed to the direct effects of fisheries, which are intrinsically size selective and typically remove the largest individuals from populations of large-bodied and long-lived species (Law, 2000; Conover and Munch, 2002; Genner *et al*., 2010a). However, the decline in size is also likely to be a consequence of the indirect evolutionary effects of removal of large growing individuals. This leads to smaller-growing and early maturing individuals having greater average survivorship and reproductive output, and thus contributing disproportionately to future population cohorts (Law, 2000). Although such fisheries effects have been suggested to be the main drivers of changes in body size distributions, recent research has suggested that body size distributions have also been affected by climate change.

In particular, research has demonstrated that climatic warming has led to smaller average body sizes both within populations (Portner and Knust, 2007; Rogers *et al*., 2011) and across species in aquatic ecosystems (Daufresne *et al*., 2009). This can be explained by models of fundamental size-dependent thermoregulatory and metabolic responses. Essentially, long-term energy requirements of larger individuals are greater in warmer environments (Gardner *et al*., 2011). However, warmer environments often cannot provide the resources required, and thus smaller individuals of populations should be favoured by selection. Of particular importance is evidence that the lower oxygen levels characteristic of warmer waters limit both growth performance (Portner and Knust, 2007) and the maximum body sizes that a species can reach (Cheung *et al*., 2012). Analyses that take these factors into account indicate that if IPCC high-emission scenarios of climate change are realised, then by 2050 the average body weight of individuals within assemblages will shrink by 14-24% (Cheung *et al*., 2012). A further consideration is physiological cost of overwintering behaviour, which is a key phase in the life history of many species such as sandeels (*Ammodytes marinus*) in the North Sea. Bioenergetic models indicate that rising temperatures will impose additional energetic costs on larger size classes, potentially interfering with overwintering behaviour, driving starvation, and affecting the ability of the population to effectively use seasonal food resources (van Deurs *et al*., 2011).

The story so far: Diadromous species

Many fish species migrate between rivers and sea as part of their life cycle, and climatic variability can impact on them in both environments. Waters around the British Isles contain populations of twaite shad (*Alosa fallax*), sea lamprey (*Petromyzon marinus*), Atlantic salmon (*Salmo salar*) and European eel (*Anguilla anguilla*), all of which may potentially be affected given their distributions are strongly related to temperature variables (Lassalle *et al*., 2009).

Twaite shad, sea lamprey and European eels are southerly-distributed species. Twaite shad appear have greater recruitment success in warm years, leading to predictions of increased population sizes during projected climatic warming (Aprahamian *et al*., 2010). Similarly, in laboratory experiments sea lamprey has increased larval survival at warmer temperatures (Rodríguez-Muñoz *et al*., 2001), so improved recruitment may occur in suitable habitat.

Atlantic salmon is a northerly-distributed species, and populations have been declining since the early 1990s in Scottish rivers, in part due to poor growth of salmon at sea (Peyronnet *et al*., 2007), while over similar timescales Norwegian populations have increased. Overall, the abundance of the Atlantic salmon has declined for each of the three stock complexes assessed by ICES (North America, northern Europe, and southern Europe), particularly multi-sea-winter (MSW) salmon in the southern parts of the species' range (ICES, 2011; Beaugrand and Reid, 2012). Marine survival indices in the North Atlantic have declined and remain low despite major reductions in fishing effort, particularly in marine fisheries (ICES, 2011; Russell *et al*., 2012). It is likely that thermal impacts are greatest on the more southerly populations due to physiological requirements or changes to marine feeding opportunities (Vøllestad *et al*., 2009). This interpretation is supported by evidence that declines in salmon populations are correlated with warmer waters, which have also profoundly restructured zooplankton communities, including euphausiids that form a significant component of the post-smolt salmon diet (Beaugrand and Reid, 2003).

The European eel has a very broad distribution across European waters, but has undergone major declines since the 1980s across Europe. There is strong evidence to suggest that this species undertakes a long-distance breeding migration from European freshwaters to the Sargasso Sea to spawn, and larvae drift back along the Gulf Stream and

North Atlantic current enabling them to colonise freshwater habitats (Aarestrup *et al*., 2009). It is possible that changes to both temperatures in the Sargasso Sea and changes to ocean circulation have affected recruitment. In support of these hypotheses, both sea temperatures in the Sargasso Sea and strength of the North Atlantic Oscillation (NAO) have been significantly correlated with eel catches in northern Europe. It has been hypothesised that during positive phases of the NAO larvae may enter the subpolar gyre and fail to reach recruitment habitat (Durif *et al*., 2011).

2. WHAT COULD HAPPEN?

Future predictions: ocean acidification

Global Warming, caused by an increase in atmospheric CO_2 due to human activities, is now known to occur in parallel with "The Other CO_2 Problem" or "Global Warming's Evil Twin": ocean acidification (Doney *et al*., 2009). The recent rate of change in ocean pH may be unprecedented in the last 300 million years (Honisch *et al*., 2012), and the associated decrease of carbonate ion concentration in seawater presents profound challenges to calcifying organisms including unicellular algae (phytoplankton), reef-building corals, molluscs (e.g. mussels) and echinoderms (e.g. urchins) that depend on carbonate for construction of their external skeletons. More recently the associated ecosystem consequences for top predators such as fish, birds and marine mammals are also being recognised (Branch *et al*., 2012; Munday *et al*., 2012). Predicting ecosystem-level impacts based on future atmospheric CO_2 and ocean pH projections is clearly challenging, and forecasts range from complete ecosystem degradation (Kroeker *et al*., 2010; Turley *et al*., 2010) to limited impact with minimal consequences (Hendriks *et al*., 2010). However, a growing body of experimental work now demonstrates the range of potential impacts (reviews in: Fabry *et al*., 2008; Doney *et al*., 2009; Hendriks *et al*., 2010; Hofmann *et al*., 2010; Kroeker *et al*., 2010; Branch *et al*., 2012; Munday *et al*., 2012).

The last five years has seen substantial research effort to explore the potential direct impacts of ocean acidification on marine fish, albeit on fish species from beyond the seas surrounding the British Isles. High levels of CO_2 (993 and 2558 ppm, resulting in seawater pH of 7.7 and 7.3 respectively) can affect skeletal growth in fish when compared with present day conditions (380 ppm, pH 8.1), particularly in the dense otolith earbones used by fish for balance and hearing (Checkley *et al*., 2009), however, elevated CO_2 (1050 and 1721 ppm, pH 7.8 and 7.6) does not necessarily affect early development in coral reef fish (Munday *et al*., 2011), and may even promote early growth (Munday *et al*., 2009a). While there is currently no consensus on impacts of ocean acidification on growth, a potential reduction in biomass transfer efficiency caused by elevated CO_2 conditions could have implications for fisheries, so the influence on internal energy budgets should be a focus of future work (Le Quesne and Pinnegar, 2012).

Perhaps more worrying is the mounting evidence that fish in high CO_2 environments are affected at the physiological and behavioural level, with likely consequences for individual survival and population resilience. Fish reared in elevated CO_2 conditions (1000 ppm, pH 7.8) have increased basal metabolic costs and reduced aerobic scope (Munday *et al*., 2009b), similar to the effects of a 3°C temperature rise (of course fish will ultimately experience both in unison). Fish reared in elevated CO_2 conditions (1000 ppm, pH 7.8) also lose important olfactory responses: failing to respond to the scents of suitable habitat (Munday *et al*., 2009c) and conspecifics and predators (Dixson *et al*., 2010). The ability of fish to respond to the auditory cues of predators is similarly compromised at levels of CO_2 predicted for later this century (600 to 1000 ppm, pH 8.0 to 7.8; Simpson *et al*., 2011b), and elevated boldness of CO_2-affected fish (700 ppm, pH 7.9) when exposed to predators leads to higher mortality (Munday *et al*., 2010), particularly for the smallest and most vulnerable new recruits in a seabed community (Ferrari *et al*., 2011). Recent evidence suggests that fish are fundamentally compromised by elevated CO_2 conditions, such that higher cognitive function is compromised (880 ppm, pH 7.9; Domenici *et al*., 2012) and neurological transmission is impaired (945 ppm, pH 7.8; Nilsson *et al*., 2012).

While much progress has been made in exploring impacts of ocean acidification on fish, clearly some important challenges remain. To date the majority of evidence comes from studies on coral reef fish, but since ocean acidification is a global phenomenon concerted effort is needed to explore impacts of ocean acidification on European temperate water fishes. Current studies have generally focused on observing the performance of animals adapted to present day conditions when exposed to future predicted environments. Determining the scope for adaptation of individuals within populations to ocean acidification, and the trans-generational implications of elevated CO_2-conditions is an important next step in predicting ultimate impacts (Miller *et al*., 2012). Indeed, as with any environmental change, there are likely to be winners and losers amongst fish species, with species resilience favouring ecological generalists that are less vulnerable to loss of key habitat or prey fields, and future scope for adaptation favouring highly fecund species with short generation times allowing more rapid evolutionary responses to changing environments. Scope for adaptation can be studied through much-needed multiple-generation longitudinal studies focusing on key model species, but also by exploiting natural CO_2 hotspots (e.g. cold-water volcanic CO_2 vents; Hall-Spencer *et al*., 2008) to determine potential for responses over decades to centuries (Chown and Gaston, 2008; Hofmann and Todgham, 2010). The combination of empirical lab-based experimentation on physiological, life-history and behavioural attributes with modelling approaches (Blackford, 2010; Kaplan *et al*., 2010) is crucial for allowing current knowledge to be translated into population and ecosystem-level predictions, which are ultimately the levels of ecological and societal concern. Finally, models are needed that integrate both direct (e.g. physiology and survival) and indirect (e.g. trophic interactions) processes to predict the full likely impacts of ocean acidification on fish and fisheries (Le Quesne and Pinnegar, 2012).

Fish futures in the face of uncertainty

Warming and increased acidity have been projected to continue in the oceans over the 21st Century. There is high uncertainty in how much change is likely (which depends on emission scenarios, climate models and processes within models: Steinacher *et al.*, 2009; Kjellstrom *et al.*, 2011; Rowlands *et al.*, 2012), however, various global and regional climate model projections under IPCC climate scenarios are now being used to investigate how possible changes might alter fish distributions and abundance, as well as the fisheries they support.

Predicting the consequences of changes in the physical environment and potential food availability for fish and associated fisheries, when many detailed aspects of species' ecological and physiological constraints are still not known, is very challenging (Rijnsdorp *et al.*, 2009; Graham and Harrod, 2009). Different approaches have emerged that tend to focus on particular processes or questions. There are two main approaches that have been used to investigate the consequences of climate change on fish and fisheries which focus on: 1) how species distributions will change in response to environmental habitat changes; and 2) how physical changes will impact on primary producers and food availability for fish and other marine animals, via marine food web processes.

Species distributional models or "ecological niche models" have predicted shifts in the North Atlantic Ocean. Based on thermal preferences from detailed environmental data, a regional climate model and two climate scenarios, Lenoir *et al.* (2011) predicted that species distributional changes could potentially include significant losses of horse mackerel, sole, pollack, haddock, saithe (*Pollachius virens*) and turbot (*Psetta maxima*) but lead to gains in sprats and anchovies. At larger spatial scales, similar species distributional modelling approaches have been carried out in conjunction with global climate models (GCMs). These "bioclimatic envelope" models, which link habitat suitability with population dynamics, have predicted increases in potential fish production in high latitudes and decreases in tropical regions (Cheung *et al.*, 2008, 2009, 2010). Species distributional models are now becoming more detailed in terms of the physiological processes they capture. Process-based models potentially give greater confidence than empirical models when projecting beyond current conditions (Le Quesne and Pinnegar, 2012). By incorporating links between dissolved oxygen, temperature and body growth, Cheung *et al.* (2012) predict that mean assemblage level body weight may decline 14–24% globally from 2000 to 2050 under a high-emission scenario, with up to half of the reductions in size due to physiological responses (with the rest due to changes in distribution and abundance). The authors cite recent changes in the body size of haddock as empirical evidence of such changes (Baudron *et al.*, 2011), and the size-structure and composition of phytoplankton has already been highlighted as an important empirical change in the North Sea (Hinder *et al.*, 2012). Further work is needed to test these predictions alongside alternative hypotheses, as there are multiple drivers of changes in size distributions including the effects of fishing.

Although complex "end-to-end" food web approaches are beginning to consider climate projections (Travers *et al.*, 2009; Fulton *et al.*, 2011; and projects such as MEECE), they are limited in their capacity to resolve global-scale questions due to high data demands, and because regional models tend to differ and do not yet account for invasions of new species from adjacent regions. Addressing the consequences of climate change for re-distributing populations and affecting the composition and productivity of communities, including biotic interactions within (e.g. direct effects such as altered physiology) and among (e.g. indirect effects such as altered prey fields and habitats) species, and predicting across multiple spatial scales, therefore remains a significant challenge (Le Quesne and Pinnegar, 2012).

Using a high-resolution regional coupled physical-biogeochemical model, a recent climate modelling experiment for the Northeast Atlantic shelf suggested that regions less exposed to ocean-shelf exchange (Irish Sea, English Channel and Southern North Sea) could increase in primary production (5-10%) compared with decreases (0-20%) in the Central and Northern North Sea (Holt *et al.*, 2012). These high-resolution regional models are being used to explore climate scenarios in shelf seas around the world by connecting with simplified size-based food web models, which project changes in fish and fisheries. Globally, the model predicts decreases of up to 30-60% in potential fish production across some important areas of tropical and upwelling seas, but increases in high latitude regions of up to 28-89%, strongly mirroring patterns in the predicted change in productivity of large phytoplankton (Blanchard *et al.*, 2012). A mixture of increases/decreases was also predicted within the Northeast Atlantic when aggregated to country EEZ level (Blanchard *et al.*, 2012), altering the sensitivity to fishing impacts. These outputs have been validated with near-past catch data and used to link changes to social and economic consequences associated with fishmeal production and aquaculture growth scenarios (Merino *et al.*, 2012). This simplified modelling approach was designed to take a broad-brush approach across regions, and further work across different spatial/temporal scales, along with more detailed tests of predictions for seas around the British Isles and other regions, is on-going.

Multi-model ensemble approaches are routinely used by physical climate scientists and enable a range of plausible projections to be considered alongside each other (Collins *et al.*, 2012). Comparative studies of different types of species distributional models have already made promising steps towards better understanding model uncertainty (Jones *et al.*, 2012). Moving towards an ensemble approach for fish is crucial to improve our knowledge of uncertainty across physical, chemical, biological and socio-economic components as well as more detailed integration of empirical, experimental, and modelling work. Obvious missing gaps in knowledge still include our understanding of adaptive flexibility of many marine organisms, the differential and additive responses of species to warming and ocean acidification, the consequences of food web modification, and the impacts of multiple human stressors operating in concert. Ultimately, this knowledge is needed to make quantitative predictions of impacts of climate change on fish over ecological and evolutionary timescales.

3. KNOWLEDGE GAPS

a. Environmental change can have direct (e.g. physiology, behaviour, growth, timing of spawning and migration) and indirect (e.g. altered prey fields, changes to thermal stratification of seas) impacts on fish. More work is needed to combine individual-based laboratory experiments and exploration of long-term survey data (commercial and fishery-independent fish data, ichthyoplankton and holoplankton data, environmental data) with statistical and process-based models to develop the holistic understanding needed to make robust predictions for the future.

b. There is growing evidence from lab-based experiments and mechanistic modelling that in some cases today's animals will struggle or perish in tomorrow's environment (temperature and/or ocean acidification). A major unknown is the natural variation and scope for adaptation within individuals, populations and species over the next century (5 to 50 generations). Longitudinal (multiple-generation) studies of European temperate water species are needed to assess the response of fish to changing conditions in a more realistic scenario of steadily (albeit experimentally accelerated) changing conditions (warming and/or falling pH).

c. The 2010 report recommended more effort be put into 'scaling-down' effects of climate change to focus on the seas surrounding the British Isles. This creates a conflict for the academic research community, since localised (often viewed as parochial) studies are more difficult to publish in top journals. Furthermore, the localised scale inherently demands a higher resolution, which adds levels of complexity (e.g. habitat, bathymetry, local oceanography) that can be glossed over more easily on the global scale. More strategic collaboration and targeted funding is needed to bring together British and Irish researchers to combine expertise and resources at the regional scale to explore impacts of climate change on fish within the seas surrounding the British Isles.

These three recommendations are inspired by conversations with many specialists at conferences and meetings and responses to a general call to the community specific to this report, and expand on several of the 15 gaps identified in the 2010 report.

4. SOCIO-ECONOMIC IMPACTS

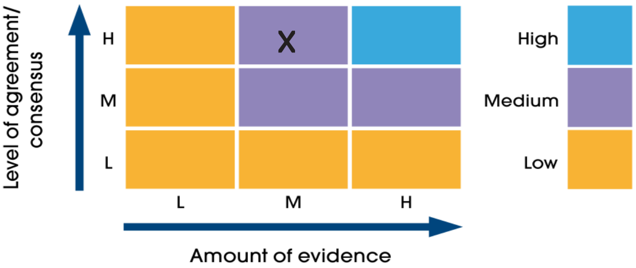
It is clear that many fish species are moving (where possible) due to recent warming. This has clear implications for management, as stocks are moving into regions under different jurisdiction (e.g. mackerel moving into Iceland and Faroe Island waters), and presents difficult challenges for marine spatial planning where marine reserves or local moratoria become ineffective over time for species they are intended to protect. The use of 'mobile MPAs' is now being discussed more openly (e.g. Oceans of Potential conference, Plymouth, Sept 2012).

The QUESTFISH consortium have made substantial progress tying together climate, ecology and socioeconomic factors to understand current impacts of climate change and explore future opportunity and limits to wild and farmed fish producing (see 'Fish futures in the face of uncertainty' section in main report).

Impacts of warming on fish communities will lead to changing fisheries resources and opportunities, with many Lusitanian species faring in well in the seas around the British Isles compared to a few (commercially-important) Boreal species losing out. Fishing fleets will need to adapt their methods and gear to take advantage of these changes, and markets, retailers and consumers will need to adapt if domestic catches are to remain a major component of the British and Irish diet.

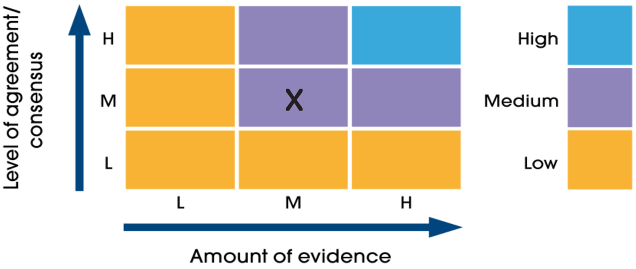
5. CONFIDENCE ASSESSMENT

What is already happening?



There is generally a high level of agreement between different studies, demonstrating range shifts, declines in Boreal and increases in Lusitanian species, community-level change, phenological effects of warming on spawning and migrations, and changes in size structures of species and communities. There is only a medium level of evidence, with more work needed on community change, links between ichthyoplankton and climate data, studies on links between growth and temperature, and exploration of longer times-series, including commercial landings data.

What could happen?



There is substantial effort being made with various modelling approaches to predict future distributions and abundances of fish species, including predicting species that may invade suitable habitat in future conditions. However, there is only medium level consensus between these approaches. There is between low to medium level evidence available for what could happen, with the majority coming from modelling rather than empirical studies. The temperate water research community could learn much from the tropical water research community regarding studies to investigate impacts of future warming and ocean acidification on fish physiology and behaviour.

The level of confidence in each case is similar to the 2010 report.

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