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Impacts of climate change on plankton

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EXECUTIVE SUMMARY

Major changes have taken place in both the plant (phyto-) and animal (zoo-) plankton of the seas around the British Isles over the last few decades. They include:

• There have been extensive changes in the planktonic ecosystem in terms of plankton production, biodiversity and species distribution which has had effects other marine life.

• In the North Sea the population of the previously dominant and important zooplankton species, (the cold water species *Calanus finmarchicus*) has declined in biomass by 70% since the 1960s. Species with warmer-water affinities (e.g. *Calanus helgolandicus*) are moving northward to replace the species but are not numerically abundant or as nutritionally (i.e. less lipid rich) important.

• There has been a northward shift in the distribution of many plankton and fish species by more than 10° latitude over the past 50 years. This shift is particularly associated with the shelf edge current running north along the European continental margin.

• The seasonal timing of some plankton production also altered in response to recent climate changes. This has consequences for plankton predator species, including fish, whose life cycles are timed in order to make use of seasonal production of particular prey species.

• The decline of the European cod stocks in the North Sea due to overfishing may have been exacerbated by climate warming and climate-induced changes in plankton production. It is hypothesised that the survival of young cod in the North Sea depends on the abundance, seasonal timing and size composition of their planktonic prey. As the stocks declined they have become more sensitive to the effects of regional climate warming due to shrinkage of the age distribution and geographic extent.

• Future warming is likely to alter the geographical distribution of primary and secondary pelagic production, affecting ecosystem services such as oxygen production, carbon sequestration and biogeochemical cycling.

INTRODUCTION

Macro- and multi-decadal overview of plankton in the North Atlantic

The Continuous Plankton Recorder survey is a long-term sub-surface marine plankton monitoring programme consisting of a network of CPR transects towed monthly across the major geographical regions of the North Atlantic. It has been operating in the North Sea since 1931 with some standard routes existing with a virtually unbroken monthly coverage back to 1946. The CPR instrument is towed at the surface behind "ships of opportunity", sampling plankton onto a moving 270 μ m (micrometre) band of net silk as the vessel and CPR unit traverse the North Atlantic and/or North Sea. Within the CPR instrument, the net silk and its captured plankton are preserved in formalin until they are returned to SAHFOS for routine analysis including the estimation of phytoplankton biomass (Phytoplankton Colour Index),

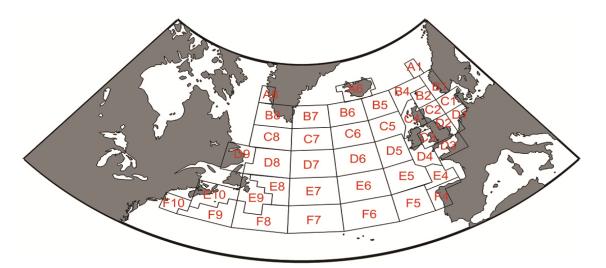


Figure 1a: Regions sampled

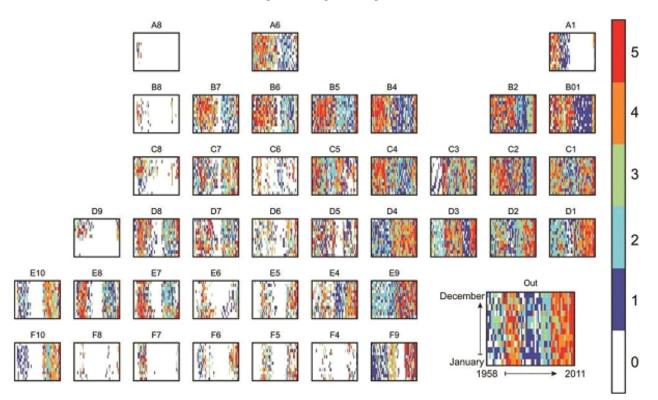


Figure 1b: Sampling effort according to region

and the identification of up to 500 different phytoplankton and zooplankton taxa (Warner and Hays 1994). Direct comparisons between the phytoplankton colour index and other chlorophyll a estimates including SeaWiFS satellite estimates indicate strong positive correlations (Battern *et al.*, 2003; Raitsos *et al.*, 2005). During the processing, the net silk is divided into sections representing 10 nautical miles of towing, and each section is analysed for plankton composition and abundance.

Due to the mesh size of CPR silks, many phytoplankton species are only semi-quantitatively sampled owing to the small size of the organisms. There is thus a bias towards recording larger armoured flagellates and chain-forming diatoms and smaller species abundance estimates from cell counts will probably be underestimated in relation to other water sampling methods. However, the proportion of the population that is retained by the CPR silk reflects the major changes in abundance, distribution and specific composition (i.e. the percentage retention is roughly constant within each species even with very small-celled species) (Edwards *et al.*, 2006). The CPR now has a water sampler housed onboard certain CPRs to provide additional data and sample the whole size-spectrum of plankton using molecular techniques from bacteria and viruses to flagellates and other taxa not normally identified using standard CPR analysis. For the purpose of this assessment, the North Atlantic Basin has been geographically subdivided into different ecoregions. The 40 geographical regions shown in the figures are known as the CPR standard areas. Included in this assessment are some trends in the microzooplankton community and trends in marine pathogens from molecular analysis of the CPR sample archive. The figures 1-7 showing regional trends in standard areas were generated using standard statistical methods for calculating annual means.

Basin scale trends in plankton and natural variability

To summarise the long-term trends in plankton in the North Atlantic Basin we used indices of plankton that included the CPR Phytoplankton Colour Index (PCI) and the sum of the abundance of all counted diatoms (Figure 4) and all counted dinoflagellates (Figure 5) and total copepod numbers and mean copepod size (Figure 6). Using bulk indices like this are less sensitive to environmental change and will quite often mask the subtleties that individual species will give you; however, it is thought that these bulk indices represent the general functional response of plankton to the changing environment. In the North Atlantic, at the ocean basin scale and over multidecadal periods, changes in plankton species and communities have been associated with Northern Hemisphere Temperature (NHT) trends, the Atlantic Multidecadal Oscillation (AMO), the East Atlantic Pattern (EAP) and variations in the North Atlantic Oscillation (NAO) index. These have included changes in species distributions and abundance, the occurrence of sub-tropical species in temperate waters, changes in overall plankton biomass and seasonal length, changes in the ecosystem functioning and productivity of the North Atlantic (Beaugrand et al., 2002; Edwards et al., 2001; Edwards et al., 2002; Reid and Edwards, 2001; Edwards and Richardson, 2004). Contemporary observations over a 10 year period of satellite in-situ blended ocean chlorophyll records indicate that global ocean net primary production has declined over the last decade, particularly in the oligotrophic gyres of the world's oceans (Behenfeld et al., 2006). However, over the whole temperate NE Atlantic there has been an increase in phytoplankton biomass with increasing temperatures but a decrease in phytoplankton biomass in warmer regions to the south (Richardson and Schoeman, 2004), as shown in Figures 2 and 3, respectively. Presumably this is a trade-off between increased phytoplankton metabolic rates caused by temperature in cooler regions but a decrease in nutrient supply in warmer regions. The amount of nutrients available in surface waters directly dictates phytoplankton growth and is the key determinant of the plankton size, community and foodweb structure. In terms of nutrient availability, warming of the surface layers increases water column stability, enhancing stratification and requiring more energy to mix deep, nutrient-rich waters into surface layers. Particularly warm winters will also limit the degree of deep convective mixing and thereby limit nutrient replenishment necessary for the following spring phytoplankton bloom.

It must be noted, however, that climate variability has a spatially heterogeneous impact on plankton in the North Atlantic and not all regional areas are correlated to the same climatic index. For example, trends in the AMO are particularly prevalent in the oceanic regions and in the subpolar gyre of the North Atlantic and the NAO has a higher

impact in the southern North Sea where the atmosphereocean interface is most pronounced. This is also apparent with respect to temperatures across the Northern Hemisphere where the response is also spatially heterogeneous with areas of the North-East Atlantic and shelf areas of the North-West Atlantic warming faster than the North Atlantic average and some areas like the sub-polar gyre actually cooling. Similarly, regime shifts or abrupt ecosystem shifts do not always occur in the same region or at the same time. The major regime shift that occurred in plankton in the late 1980s was particularly prevalent in the North Sea and was not seen in oceanic regions of the North Atlantic. However, a similar regime shift occurred in the plankton colour index 10 years later in the Icelandic Basin and in oceanic regions west of the British Isles. The different timing and differing regional responses to regime shifts have been associated with the movement of the 10°C thermal boundary as it moves northwards in the North Atlantic (Beaugrand et al., 2008).

In examining the long-term trends in the plankton indices, the general pattern is an increase in PCI for most regions in the North Atlantic with differing timings for the main step-wise increase being later in oceanic regions compared to the North Sea. For the dinoflagellates there has been a general increase in abundance in the North West Atlantic and a decline in the North East Atlantic over a multi-decadal period (see Figure 5). In particular, some regions of the North Sea have experienced a sharp decline over the last decade. This decline has been mainly caused by the dramatically reduced abundance of the Ceratium genus in the North Sea. However, Ceratium abundance has recovered in the North Sea over the last two years. For the diatoms there is not really a predominant trend for the North Atlantic Basin as a whole (Figure 4) but some regions show a strong cyclic behaviour over the multidecadal period. The time signal resembles an oscillation of about 50-60 years and a minimum around 1980 reflecting changes in the AMO signal. Trends in copepod abundances have been more stable in offshore regions but have shown a decrease in abundance, particularly in the southern North Sea. In summary, while climate warming is a major driver for the overall biomass of phytoplankton, diatoms are less influenced by temperature and show a strong correlation with the AMO signal and wind intensity in many regions. The increase in diatoms associated with the positive phase of the AMO and the decline in dinoflagellate abundance over the last 10 years in the NE Atlantic can be reflected in the diatom/dinoflagellates ratio favouring diatoms.

Indirectly the progressive freshening of the Labrador Sea region, attributed to climate warming and the increase in freshwater input to the ocean from melting ice, has resulted in the increasing abundance, blooms and shifts in seasonal cycles of dinoflagellates due to the increased stability of the water-column (Johns *et al.*, 2001). Similarly, increases in coccolithophore blooms in the Barents Sea and HABs in the North Sea are associated with negative salinity anomalies and warmer temperatures leading to increased stratification (Edwards *et al.*, 2006; Smyth *et al.*, 2004). It seems likely that an important environmental impact caused by climate change is an increase in the presence of haline stratification

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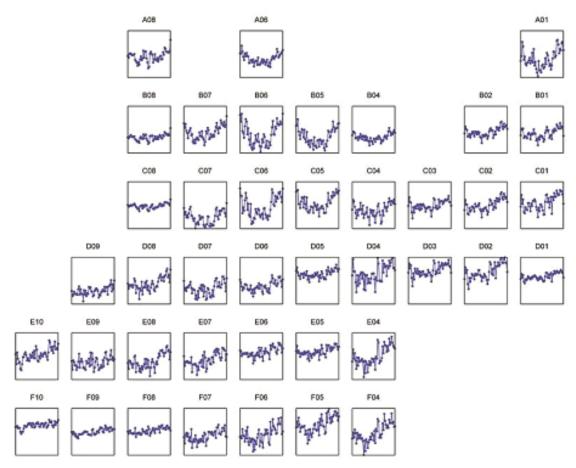


Figure 2: Mean sea surface temperature per region

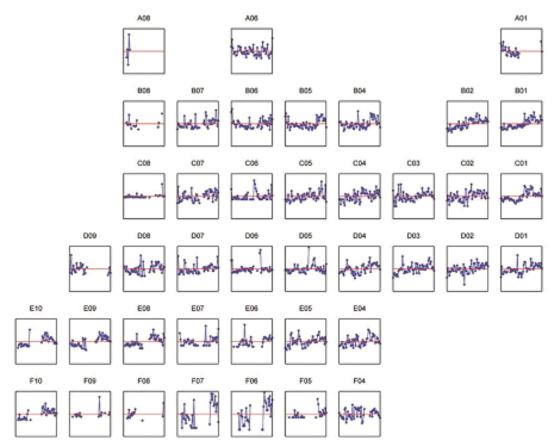


Figure 3: Mean PCIz score per region

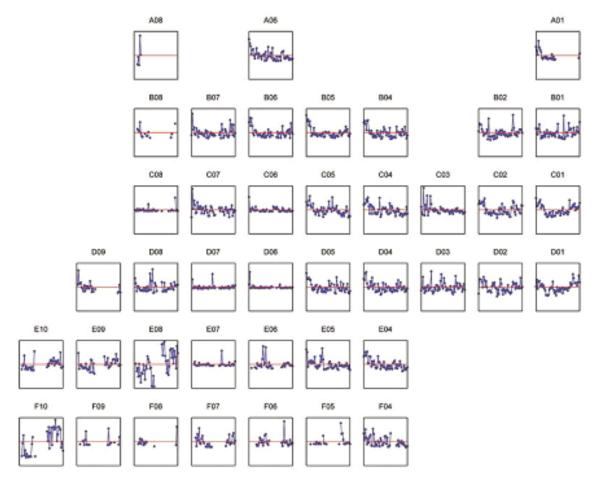


Figure 4: Mean counted diatom z score per region

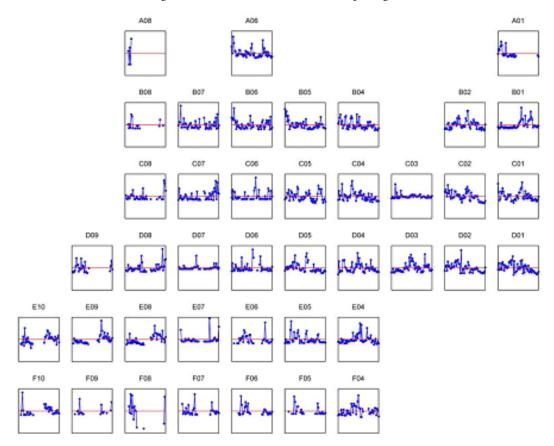


Figure 5: Mean counted dinoflagellatte z score per region

IMPACTS OF CLIMATE CHANGE ON PLANKTON

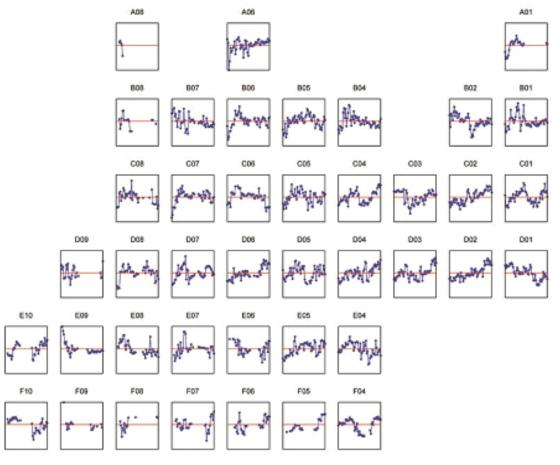


Figure 6: Mean copepod size per region

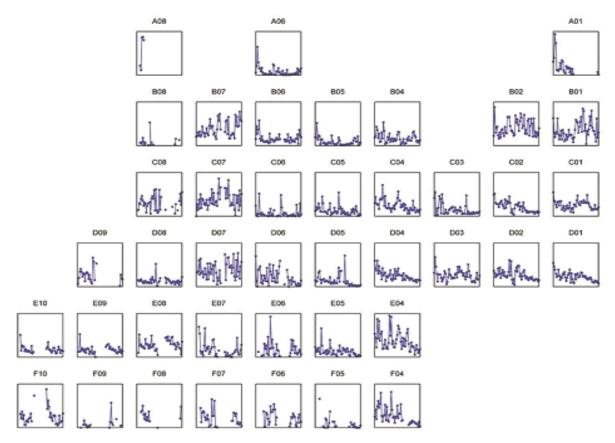


Figure 7: Mean zooplankton abundance per region

in regions susceptible to fresh-water inputs resulting in an increased potential for bloom formation.

Other anthropogenic pressures

Eutrophication: Globally, eutrophication is considered a major threat to the functioning of near-shore ecosystems, as it has been associated with the occurrence and a perceived increase of harmful algal blooms (HABs). HABs in most cases are a completely natural phenomenon having occurred throughout recorded history and disentangling natural bloom events caused by natural hydro-climatic variability, global climate change and eutrophication is difficult. For example, increasing temperature, nutrient input fluctuations in upwelling areas, eutrophication in coastal areas and enhanced surface stratification all have species specific responses. Gowen et al. (2012) performed a thorough review of the relationship between eutrophication and HABs and could not reach a consensus about the role of anthropogenic nutrient enrichment in stimulating the occurrence of HABs. Prediction of the impact of global climate change is therefore fraught with numerous uncertainties. There is some evidence that biogeographical range extensions caused by regional climate change has increased the presence of certain HABs in some regions (Edwards et al., 2006). Regional climate warming and hydrographic variability in the North Sea has also been associated with an increase in certain (HABs) in some areas of the North Sea particularly along the Norwegian Coastal Current (Edwards et al., 2006). The abundance of Prorocentrum spp. and Noctiluca scintillans abundance are strongly correlated with increasing SST (Hinder et al., 2012). The increase in a number of diatom species in the North Sea over the last decade has been associated with increasing wind intensity (Hinder et al., 2012). Phenological studies have also found strong correlations between the movement of dinoflagellates (up to 1 month earlier) in their seasonal cycle and regional climate warming (Edwards and Richardson, 2004). In summary, at the large ecoregional and provincial scale, trends in phytoplankton are associated with hydro-climatic variability. This is not to say, however, that eutrophication is not a problem and may in fact be the primary driver in certain coastal regions and at the more localised scale.

Ocean acidification: Changes in temperature have direct consequences on many physiological processes (e.g. oxygen metabolism, adult mortality, reproduction, respiration, reproductive development) and control virtually all lifeprocesses from the molecular to the cellular and from the regional ecosystem level to biogeographical provinces. Temperature also modulates species interactions (e.g. competition, prey-predator interactions and foodweb structures) both directly and indirectly; ultimately, changes in temperatures caused by climate change can lead to impacts on the biodiversity, size structure, carrying capacity and functioning of the whole pelagic ecosystem. While temperature has direct consequences on many biological and ecological traits it also modifies the marine environment by influencing oceanic circulation and by enhancing the stability of the water column and hence nutrient availability. Under many climate change scenarios, oceanic primary production is predicted to decline due to nutrient limitation.

While temperature, light and nutrients are probably the most important physical variables structuring marine ecosystems, the pelagic realm will also have to contend with, apart from global climate warming, the impact of anthropogenic CO₂ directly influencing the pH of the oceans. Evidence collected and modelled to date indicates that rising CO₂ has led to chemical changes in the ocean which has led to the oceans becoming more acidic. Ocean acidification has the potential to affect the process of calcification and therefore certain planktonic organisms (e.g. coccolithophores, foraminifera, pelagic molluscs) may be particularly vulnerable to future CO₂ emissions. Apart from climate warming, potential chemical changes to the oceans and their effect on the biology of the oceans could further reduce the ocean's ability to absorb additional CO₂ from the atmosphere, which in turn could affect the rate and scale of climate warming.

Presently in the North Atlantic certain calcareous taxa are actually increasing in terms of abundance, a trend associated with climate shifts in the Northern Hemisphere temperature. However, there is some observed evidence from the Southern Ocean that modern shell weights of foraminifera have decreased compared with much older sediment core records with acidification being implicated. It is not yet known how much of an effect acidification will have on the biology of the oceans in the 21st century, whether rapid climate warming will override the acidification problem, and whether or not species can buffer the effects of acidification through adaptation. The CPR survey is providing a critical baseline (both in space and time) and is currently monitoring these vulnerable organisms in case in the future these organisms begin to show negative effects due to acidification.

Plankton biodiversity and invasive species

At the ocean basin scale biodiversity of phytoplankton are related to temperature and an increase in warming over the last few decades has been followed by an increase in diversity particularly for dinoflagellates and marine copepods (Beaugrand et al., 2010). Plankton as a whole show a relationship between temperature and diversity which is linked to the phytoplankton community having a higher diversity but an overall smaller size-fraction and a more complex foodweb structure (i.e. microbial-based versus diatom-based production) in warmer more stratified environments. Climate warming will therefore increase planktonic diversity throughout the cooler regions of the world's oceans as temperature isotherms shift poleward. Apart from thermal boundaries moving progressively poleward and in some cases expanding, the rapid climate change observed in the Arctic may have even larger consequences for the establishment of invasive species and the biodiversity of the North Atlantic. The thickness and areal coverage of summer ice in the Arctic have been melting at an increasingly rapid rate over the last two decades, to reach the lowest ever recorded extent in September 2007. In the spring following the unusually large ice free period in 1998 large numbers of a Pacific diatom Neodenticula seminae were found in samples taken by the CPR survey in the Labrador Sea in the North Atlantic. N. seminae is an abundant member of the phytoplankton in the subpolar North Pacific and has a well defined palaeo-history based on deep sea cores. According to the palaeo evidence and modern surface sampling in the North Atlantic since 1948 this was the first record of this species in the North Atlantic for at least 800,000 years. The reappearance of *N. seminae* in the North Atlantic, and its subsequent spread southwards and eastwards to other areas in the North Atlantic, after such a long gap, could be an indicator of the scale and speed of changes that are taking place in the Arctic and North Atlantic oceans as a consequence of climate warming (Reid *et al.*, 2007). The diatom species may itself could be the first evidence of a trans-Arctic migration in modern times and be a harbinger of a potential inundation of new organisms into the North Atlantic. The consequences of such a change to the function, climatic feedbacks and biodiversity of Arctic systems are at present unknown.

New copepod species found in the southern North Sea

A new invasive copepod species has been found in the North Sea. The copepod species *Pseudodiaptomus marinus* naturally occurs in east Asiatic waters but has been subsequently spreading more widely in the Indo Pacific region over the last decade. The first record of the species in European waters comes from its discovery in the Adriatic Sea in 2007 (Olazabal and Tirelli, 2011). In October 2011, the species was recorded on CPR routes operating in the southern North Sea (Jha *et al.* In prep). The present records extend the known distribution of *P. marinus* across the southern Bight from the Netherlands to the British coast and to the German Bight. It is highly probable the species presence is due to human activity linked to ballast water release or aquaculture.

Trends in marine pathogens and other taxa

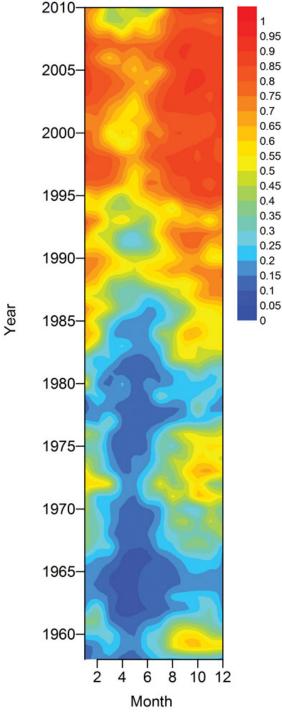
As sea surface temperatures increase, predictions favour an increase in number and range of pathogenic microorganisms. Such changes are difficult to determine over short time periods that cannot separate short-term variations from climate change trends. In a unique long-term time study, Vezzulli et al. (2011) investigated the spread of the pathogenic bacteria, Vibrio, the causative agent of cholera in the North Sea over 54 years, between 1961-2005, and revealed that Vibrio bacteria is increasing in this region. DNA from CPR samples covering 1400 square miles of the Humber area and 16000 square miles of the Rhine area in the North Sea were relative in proportion of Vibrio bacteria in relation to total bacteria, called the Vibrio abundance index (VAI). The VAI was found to steadily increase over four decades which was linked to temperature and copepod abundance but not PCI. The Rhine area was significantly correlated with VAI, which has higher summer SST over 18°C, where Vibrio thrives best (Vezzulli et al. 2004), and was especially marked in the late 1980s when step-wise increase in SST was reported in the Southern North Sea. No significant increase was found in the Humber, which never exceeds 18°C. Vibrio attached to chitin surfaces, so the relationship with Copepods, may reveal the mechanism by which this pathogen spreads.

Tintinnids are ciliated protozoa which are often grouped under microzooplankton. They are an important group of marine micrograzers of nanophytoplankton, transporting nutrients to higher trophic levels and remove between 1027% of phytoplankton production from coastal waters. They show a pelagic distribution which is highest between 20°-30° north or south with virtually no species present in latitudes around 68°N. Overall, their abundance appears to be mainly restricted to coastal and shelf waters where they show a trend in abundance with chlorophyll a. Up until 2000, there was an increase in tintinnids in UK shelf waters and was followed by a marked increase in abundance in 2003. Their appearance was always observed between May and September and no change in the phenology has been detected over the last 50 years (Hinder et al., 2011). However, the abundance of total tintinnids does not reflect individual genus or species patterns. Indeed, several genera, such as Tintinnopsis, have been found to expand their seasonal occurrence from spring and summer into winter in UK coastal waters (Hinder et al., 2011).

Summary of plankton indicators of climate change

Natural variability versus anthropogenic warming: In the North Atlantic, at the ocean basin scale and over multidecadal periods, changes in plankton species and communities have been associated with Northern Hemisphere Temperature (NHT) trends, the Atlantic Multidecadal Oscillation (AMO), the East Atlantic Pattern (EAP) and variations in the North Atlantic Oscillation (NAO) index. It is estimated that 50% of the change is down to natural climate variability and the other due to forced anthropogenic warming. These have included changes in species distributions and abundance, the occurrence of sub-tropical species in temperate waters, changes in overall plankton biomass and seasonal length, changes in the ecosystem functioning and productivity of the North Atlantic (Beaugrand et al., 2002; Edwards et al., 2001, 2002; Reid and Edwards, 2001; Edwards and Richardson, 2004). Over the last five decades there has been a progressive increase in the presence of warm-water/sub-tropical species into the more temperate areas of the North-East Atlantic and a decline of colder-water species. The mass biogeographical movements are related to changes in sea-surface temperature. A particularly interesting feature over the last five years is the decline in subarctic species to the south-east of Iceland and their movement to the north and west (Edwards et al. status report).

Biogeographical and phenology indicators: A useful indicator of the warming trend in the North Sea (a northward shift indicator) is the percent ratio of the coldtemperate Calanus finmarchicus and the warm-temperate Calanus helgolandicus copepod species (Figure 8). Although these species are very similar they do occupy distinct thermal niches. The thermal boundary for the arctic-boreal distributed copepod Calanus finmarchicus in the North-East Atlantic lies between ~10-11°C isotherm and is a useful indicator of major biogeographical provinces. Calanus helgolandicus usually has a northern distributional boundary of 14°C and has a population optimum lying between 10-20°C; these two species can therefore overlap in their distributions. When these two species co-occur there is a tendency for high abundances of C. finmarchicus earlier in the year and C. helgolandicus later in the year. There is clear evidence of thermal niche differentiation between these two



Calanus helgolandicus / Calanus finmarchicus ratic 0.95

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during 2009/2010 and 2010/2011 reflected in below average SST in the NE Atlantic. Similarly, this has had an effect on the timing of phenology in the North Sea for many species. The last couple of years have seen a later seasonality of plankton compared to the long-term trend which was a trend towards earlier seasonal cycles. While Northern Europe was experiencing cold weather areas in Greenland, the Canadian Arctic and the Labrador Sea hit record temperatures in 2010 resulting in extended melt periods (Edwards et. al. status report). Between the 1960s and the post 1990s, total Calanus biomass has declined by 70% due to regional warming. This huge reduction in biomass has had important consequences for other marine wildlife in the North Sea.

Trends in jellyfish and other gelatinous plankton

Predatory gelatinous zooplankton (Cnidaria and Ctenophora) populations play an important role in our coastal and shelf waters. These species are subject to limited monitoring but the group warrants further research. Many species of gelatinous zooplankton are able to rise rapidly in abundance and form extensive aggregations when suitable environmental conditions arise (e.g. a thermal niche or a high availability of prey, possibly due to overfishing of planktivores) and as such the group are potentially indicators of ecosystem instability (Lynam et al., 2011). Jellyfish also form the principal prey of exotic species such as sunfish (Mola mola) and leatherback turtles (Dermochelys coriacea) that migrate to UK and Irish waters to feed (Houghton et al. 2006).

Sporadic sampling has occurred on scientific surveys that support fisheries assessments and this is typically the best available information (Bastian et al., 2012; Lynam et al., 2005, 2011). However, visual surface counts from ships of opportunity and long-term information from the CPR can be particularly useful (Bastian et al., 2011). The frequency at which gelatinous tissues and nematocysts (stinging cells) are caught in the CPR sampler has been used to map the pattern of gelatinous zooplankton abundance (Figure 7) across the north-east Atlantic Ocean and shelf seas (Gibbons and Richardson, 2009). In oceanic waters, depth >200 m, gelatinous zooplankton abundance between 1946 and 2005 was linked significantly and positively to SST and total copepod abundance. Notably, jellyfish in the Northeast Atlantic show cyclic changes in population sizes (c. 20 year cycle in oceanic waters and 30 year cycle in shelf seas). However, since 1997 they have been increasing in frequency in CPR samples simultaneously in shelf and oceanic waters. (Gibbons and Richardson, 2009; Licandro et al., 2010).

The oceanic scyphozoan, Pelagia noctiluca, was carried into Irish coastal waters during 2007 and resulted in the mortality of over 150,000 farmed salmon in Antrim, Northern Ireland. Concern was prompted that this species is increasing following climate change since this jellyfish is common in the Mediterranean Sea and considered a warmwater species (Licandro et al., 2010). However, historical reports and anecdotal sightings revealed that it has occurred previously in Irish and UK waters and such events are part of an intermittent cycle (Doyle et al., 2008). Nevertheless, P. noctiluca occurs in high abundance in the Mediterranean

Figure 8: The seasonal variation of Calanus helgolandicus to Calanus finmarchicus over time

species as well as successional partitioning in the North Sea, probably related to cooler temperatures earlier in the year and warmer temperatures later in the year.

The percentage ratio between C. helgolandicus and C. finmarchicus in 2009 to 2011 was for the first time in 20 years dominated by C. finmarchicus in spring (Figure 8). This was a reflection of the particularly cold winter experienced in Northern Europe caused by a very low winter NAO index. During the last couple of years the NAO has been uncharacteristically in a very low negative phase contributing to the very cold winters experienced in Northern Europe following warm, dry periods and occurrences of this species in northern waters might be expected to become more frequent following climate change (Licandro *et al.*, 2010). Data from the Irish bottom trawl surveys in 2009 indicated that *P. noctiluca* was present on the Malin Shelf, to the north of Ireland, particularly in subsurface temperatures >13.2 °C (Bastian *et al.*, 2012).

The most common medusae in UK and Irish waters are the scyphozoans Aurelia aurita and Cyanea spp. and data from plankton nets have shown that this community increased in abundance in the Irish Sea between 1994 and 2009 (Lynam et al., 2011). Statistical analyses of these data indicated that catch rates of jellyfish were high following warm and dry periods. Notably, the frequency of cnidarian occurrence from CPR samples in the Irish Sea correlated significantly and positively with the catch rates from the plankton nets (Lynam et al. 2011). In this area, CPR data reach back to 1970 and not only does the cnidarian index indicate higher frequencies of occurrence in the period 1992-2010 relative to 1970-1981, but the data also suggest a period of frequent and extensive outbreaks between 1982 and 1991. Given that the period 1982-1991 was not dominated by warm-dry years it is interesting to note that these outbreaks occurred during structural change in the phytoplankton and copepod community and that this followed a period of overexploitation of planktivorous herring (Lynam et al., 2011).

The North Sea has suffered from data paucity in relation to gelatinous zooplankton since the end of the International Pelagic Trawl Survey for young gadoid fish (1971-1986; Hay *et al.* 1990). These historical trawl data indicated great fluctuations in jellyfish abundance linked to variability in the NAO and increases over time in *Cyanea capillata* abundances in the northern and eastern North Sea (Lynam *et al.*, 2005). In contrast to the Irish Sea data, the CPR cnidarian occurrence index does not correlate with scyphozoan abundances in the North Sea (Lynam *et al.*, 2010). However, the CPR data do indicate an overall increase in the occurrence of gelatinous zooplankton in the North Sea since the early 1980s coincident with a change from a cold to a warm hydroclimatic regime (Licandro *et al.*, 2010).

The ctenophore *Mnemiopsis leidyi* was first reported in the North Sea and Baltic Sea in 2006 (Oliveira, 2007). Whether or not the comb jellyfish was present before 2006 is not known. Nevertheless, there has been cause for concern regarding the spread of this species given the previous invasions of the Black and Caspian Seas. In parallet, with the increase of this species, fish eggs and larvae of stocks that were already overfished collapsed (Daskalov and Mamedov, 2007). Recent work suggests that *M. leidyi* is not abundant enough in the Baltic Sea to cause a decline in the cod stock there (Jaspers *et al.*, 2007). The North Sea is highly productive and containing a diverse range of predator species, thus we consider the current impact of this ctenophore unlikely to be a substantial threat to marine fish.

Summary of regional areas and UK waters

Northern North Sea (Region 1)

The northern North Sea was, until recently, a cold-temperate boreal province. However, after the late 1980s regime shift, the northern North Sea is now a warm-temperate province. Plankton in the northern North Sea generally comprise Atlantic and offshore species as these waters are stratified during summer months. Copepods such as Calanus finmarchicus and Metridia lucens are typically found in this region. Larger sized phytoplankton measured at the Dove time series (DTS) station have undergone a significant change in biodiversity roughly centred on 1988-1990. Prior to this, biodiversity had steadily declined since the start of the time series in 1971 before beginning a general increase from 1990 to the present day. Preliminary analyses indicate that the pre-1990 phase of the time series was more strongly influenced by the monthly North Atlantic Oscillation index, while post 1990 biodiversity patterns appear to have been more influenced by local sea surface temperature. This is interpreted as a shift from basin scale driving of biodiversity to an emergence of local climate as the most important environmental factor. The change in biodiversity coincides with an intrusion of warmer, more saline water into the North Sea in the late 1980s (Beaugrand et al., 2002) that appears to have persisted since then, reducing thermohaline stratification and the definition of frontal regions (Beare et al., 2002).

Marine Scotland Science (MSS) operate a series of coastal ecosystem monitoring sites around the Scottish coast:

(http://www.scotland.gov.uk/Topics/marine/science/ MSInteractive/Themes/Coastal).

Data from the Stonehaven monitoring site in the coastal north-western North Sea, show large year-to-year differences in the abundance of diatoms in the phytoplankton community. A low diatom abundance was observed from 2001 – 2004 particularly during the spring bloom period (Bresnan *et al.*, 2009). Diatom cell densities have increased since 2005 with *Skeletonema* becoming more abundant. One exception to this is the spring bloom of 2007, when diatoms were again infrequently observed. A decrease in the abundance of the summer thecate dinoflagellate *Ceratium* has been observed since 2000. This is in line with patterns observed in the open northern North Sea by the CPR.

The two *Calanus* copepod species, *C. finmarchicus* and *C. helgolandicus*, show different seasonal dynamics at the Stonehaven monitoring site: *C. finmarchicus* is carried into the area in the spring as late stage copepodites. These produce one, sometimes two, generations of offspring none of which survive locally through the winter. *C. helgolandicus* is also carried into the area as late stage copepodites which accumulate in large numbers in August/September. These copepodite stages then decline rapidly so that the overwintering numbers are very low.

Considerable interannual variability has been observed in the abundance of both *C. finmarchicus* and *C. heloglandicus* at the Stonehaven monitoring site. Numbers of *C. finmarchicus*

have been generally low, but the annual average has increased since monitoring began in 1997. A sharp spike in springtime abundance was observed in 2008 and 2009. An extension of the *C. helgolandicus* growing season into the earlier summer months has been observed from the beginning of the monitoring period in 1997 until 2008. In 2009, due to a combination of high *C. finmarchicus* and low *C. helgolandicus* abundances, *C. finmarchicus* became more dominant at this site than *C. helgolandicus* for the first time since 1997. In 2010 extremely low numbers of both species were recorded and *C. helgolandicus* was again the dominant of the two species.

Calcifying zooplankton (*Clione limacina, Limacina retroversa*, gastropod, bivalve and echinoderm larvae) regularly make up a large proportion of the summer zooplankton at Stonehaven but there are no obvious trends in their abundance since monitoring began at this site.

Southern North Sea (Region 2)

The plankton community of the southern North Sea primarily consists of neritic and coastal species which are well-suited to the mixed waters of this region. Decapod larvae, along with copepod species such as Centropages hamatus and Calanus helgolandicus, are commonly found in the southern North Sea. Phytoplankton biomass is greater here than in the northern North Sea, and has been increasing since the 1988 regime shift. Although some localised coastal areas in this region may be affected by eutrophication this is primarily a problem in the Continental region. For the most part changes in plankton in the southern North Sea are driven by climatic variability. Over the last few decades, climate warming in the southern North Sea has been noticeably faster than in the northern North Sea (mainly due to being shallower). This is reflected in the biological response of planktonic organisms; for example, phenological cycles observed in the southern North Sea have moved further forward in time than in the northern North Sea.

Eastern Channel (Region 3)

The Eastern Channel is dominated by neritic and coastal species and a large proportion of the zooplankton biomass is made up of meroplanktonic organisms (organisms that have part of their life-cycle as plankton) and small copepods. The Eastern Channel is marked by generally lower primary production than the southern North Sea.

Western Channel and Celtic Sea (Region 4)

The Western Channel and Celtic Sea region is more temperate than the North Sea and comprises continental shelf waters that are directly influenced by the Atlantic. This region is typically characterised by annual mean SST of above 12 °C; well-mixed, nutrient replete and light-limited winter conditions; distinct plankton blooms in spring; weak thermal stratification and nutrient depletion during summer; and secondary blooms during late summer and/or autumn. However, a distinct frontal region between the French and UK coasts results in a hydrography that is generally seasonally stratified in the north and well-mixed, through strong tidal forcing, in the south (Groom *et al.*, 2008).

Long-term monitoring in the western English Channel (www. westernchannelobservatory.org.uk) has shown a warming of the sea by ca. 0.6°C per decade over the past 20 years and the most prominent temperature increases followed a period of reduced wind speeds and enhanced surface irradiation (Smyth *et al.*, 2010). Weekly plankton samples (since 1992) at station L4 show that the seasonal cycle of the phytoplankton community is characterised by spring diatom, summer coccolithophore and autumn dinoflagellate blooms, with considerable inter-annual variability in magnitude and floristic composition (Widdicombe *et al.*, 2010). Despite the huge variability year-on-year the data suggest that diatoms, and to a lesser extent dinoflagellates, are decreasing while coccolithophores are becoming more common.

Over the 23 year zooplankton sampling period at the L4 monitoring site, trends in total zooplankton reflect those of the dominant component, the copepods. These show typically an irregular pattern often of 2-5 year periods of successive negative and positive anomalies. The last couple of years of data seem to reflect a period of positive abundance anomalies for many of the major zooplankton taxa, including copepods, chaetognaths, siphonophores, medusae, appendicularians as well as most of the meroplankton.

Furthermore, the timing of the seasonal plankton increase (phenology) varies typically by over 3 months over the L4 time series. Interestingly, this large degree of variability is seen for both the timing of the spring bloom and for the appearance of holo- and merozooplankton taxa. Changes in relative timing of these trophic levels may impact upon zooplankton, meroplankton (including decapod larvae), and carbon export to the benthos, with potential effects of harmful algae on commercial fisheries and human health. More detailed investigations of relationships between phyto- and zooplankton phenological patterns are underway to understand predator–prey relationships and their impact on abundance variability (Mackas *et al.*, 2012).

Irish Sea (Region 5)

The plankton community in the Irish Sea contains warmtemperate Atlantic and offshore species and its composition is influenced by the region's hydrological regime (mixed in the winter and stratified during summer). Like the North-East Atlantic as a whole, Irish Sea plankton are primarily regulated by the sea's hydroclimatic regime. However, some coastal regions of the Irish Sea, such as Liverpool Bay, have elevated phytoplankton biomass levels that have been attributed to nutrient enrichment (Gowen et al., 2000). Although nutrient concentrations in some localised areas are elevated, for the most part the Irish Sea has not experienced: a) trends in the frequency of Phaeocystis spp. blooms and occurrence of toxin producing algae; b) changes in the dominant life form of pelagic primary producers; and c) oxygen depletion in nearshore and open waters of the Irish Sea (except the seasonally isolated western Irish Sea bottom water); this suggests that widespread anthropogenic eutrophication has not impacted the Irish Sea at a regional scale.

A comprehensive report of the ecosystem of the Clyde sea area in Region 5 has also been produced (McIntyre *et al.*,

2012). Data from the MSS coastal ecosystem monitoring station in Millport has been included in this report. The phytoplankton community has been monitored at this site since 2005 and no changes that could be attributed to climate change have been observed.

Minches and western Scotland (Region 6)

The Minches and western Scotland region consists of transitional waters which, like the Irish Sea, are mixed during winter and stratified during summer. In addition the region receives freshwater runoff from the Highlands of Scotland via the many fjords along the mainland coast and islands. In general, the plankton community in this region consists of cold-temperate boreal species. Apart from regular HAB monitoring in coastal areas, this region as a whole is poorly monitored. However, there is a well-supported coastal ecosystem monitoring site operated by MSS since 2003 in Loch Ewe (http://www.scotland.gov.uk/Topics/ marine/science/MSInteractive/Themes/Coastal). Some of the phytoplankton community changes observed on the east coast have also been observed at Loch Ewe. For example, Skeletonema has also become more abundant at this site since 2005, and a similar pattern of decrease in the thecate dinoflagellate Ceratium has been observed.

Changes in the *Calanus* community at Loch Ewe over the last decade have mirrored those seen at Stonehaven. The annual average abundance of *C. finmarchicus* increased up until 2009 with a very low abundance observed in 2010. Over the last decade, 2009 was the only year when *C. finmarchicus* dominated the spring *Calanus* community. A low abundance of *C. helgolandicus* was also observed at this site during 2010.

No trends in the abundance of calcifying zooplankton were observed.

Some of the fjords of the Scottish mainland contain distinctive plankton communities which are markedly different from the open coastal waters, and may represent geological relicts. For example Loch Etive supports a persistent population of *Calanus finmarchicus*, despite the fact that the species has declined in the open coastal waters in line with the wider shelf. Such isolated relict populations are clearly vulnerable to climate change (Bailey *et al.*, 2011).

Scottish Continental Shelf (Region 7)

Like the Minches and western Scotland region the Scottish Continental Shelf consists of transitional waters which are mixed during winter and stratified during summer. In general, the plankton community in this region consists of coldtemperate boreal species and includes Atlantic and offshore species as well as some shelf species. MSS have operated a coastal ecosystem monitoring site at Scapa Bay in the Orkney Isles and Scalloway in the Shetland Isles since 2001. The phytoplankton community structure at the Orkney site has a similar composition to that observed at Stonehaven (Region 1) and Loch Ewe (Region 6). In comparison, some differences can be observed in the composition of the phytoplankton community at Scalloway. The thecate dinoflagellate *Ceratium* is infrequently observed during the summer months. Instead, the dinoflagellate community is dominated by genera such as *Gonyaulax* and *Alexandrium*. An increase in the abundance of the diatom *Skeletonema* has been observed at both of these sites since 2005. The abundance of diatoms has also increased during the summer months. At the Orkney site, a decrease in the abundance of the dinoflagellate *Ceratium* has also been recorded. The CPR survey also monitors offshore regions in this area. This region is a particularly productive shelf system, especially around the Orkney and Shetland Islands.

Atlantic Northwest approaches, Rockall Bank and Trough and Faroe-Shetland Channel (Region 8)

The Rockall Bank and Trough area is oceanic in nature and the plankton consist of both warm-temperate oceanic species as well as cold-boreal species. As this region in on the cusp of the warm-temperate and cold-boreal marine provinces, biogeographical shifts have occurred more rapidly here than in any other region due to advective processes. This region is highly biodiverse because of the higher proportion of warmtemperate species and occasional sub-tropical incursions. The Rockall Bank and Trough region is also characterised by high primary productivity and high zooplankton biomass. It is thought that mesoscale eddies within this region play an important role in maintaining high productivity. The offshore oceanic region is characterised by high productivity, particularly along the continental shelf edge. The shelf edge current and North Atlantic current extend into this region bringing more southerly distributed species to the area.

The Faroe-Shetland area is more complex. The upper 500m of the water column has its origins in the Rockall Trough and poleward flowing North Atlantic Current, and this is reflected in the plankton community. However, below 600m depth in the Faroe-Shetland Channel and Faroe-Bank Channel, there is a counter-flow of cold, less saline water from the deep Norwegian Sea into the Atlantic. This water has its origins in the Arctic and temperatures decline to below 0°C. Here, the plankton community is entirely different. Zooplankton are scarce at these depths during the summer and few diel migrating species enter these waters. But, in the winter abundance of zooplankton is high, comprising mainly overwintering stages of the ecologically important copepod Calanus finmarchicus, and the Arctic copepod Calanus hyperboreus (Heath et al., 1999). Few fish or euphausids enter these cold deep waters, so the overwintering copepods are effectively in a refuge from predation. The overwintering C. finmarchicus in the Faroe-Shetland Channel are thought to be an important seeding area for productive summer populations in the northern North Sea, since a proportion are carried onto the NW Scottish shelf when they migrate back to the surface waters in the spring. For this reason, the abundance of C. finmarchicus in the Faroe-Shetland Channel has monitored annually in December since the mid-1990s. Inter-annual variation in abundance is correlated with the volume of Arctic water in the Channel, which in turn is related to some extent to the North Atlantic Oscillation Index

1. WHAT IS ALREADY HAPPENING?

In the North Atlantic, at the ocean basin scale and over multidecadal periods, changes in plankton species and communities have been associated with Northern Hemisphere Temperature (NHT) trends, the Atlantic Multidecadal Oscillation (AMO), the East Atlantic Pattern (EAP) and variations in the North Atlantic Oscillation (NAO) index. These have included changes in species distributions and abundance, the occurrence of sub-tropical species in temperate waters, changes in overall plankton biomass and seasonal length and changes in the ecosystem functioning and productivity of the North Atlantic. More recently these changes have also has included trans Arctic migration of species from the Pacific to the Atlantic, a change in biodiversity at the ocean basin scale and a move towards smaller sized community composition.

2. WHAT COULD HAPPEN?

Regional climate warming and hydro-climatic variability has had, and is continuing to have, a major affect on the plankton in Northern European seas. Future warming is likely to alter the geographical distribution of primary and secondary plankton production (0-5 yrs), affecting ecosystem services such as oxygen production, carbon sequestration and biogeochemical cycling (20-50 yrs). These changes may place additional stress on already-depleted fish stocks as well as have consequences for mammal and seabird populations.

Ocean acidification may become a problem in the future (50-100yrs) and has the potential to affect the process of calcification and therefore certain organisms such as molluscs and components of the plankton may be particularly vulnerable to future CO_2 emissions. Potentially chemical changes to the oceans and its affect on the biology of the oceans could reduce the ocean's ability to absorb additional CO_2 from the atmosphere which in turn could affect the rate and scale of global warming.

The UKCP09 scenario variables that will most affect plankton are SST and stratification, however, in some small-scale coastal regions freshwater run-off may also play an important role. As SST warms the geographical distribution of primary and secondary plankton production is likely to be impacted, affecting ecosystem services such as oxygen production, carbon sequestration through ocean acidification and biogeochemical cycling (20-50 yrs). Changes in phenology and biogeographical changes in plankton community composition leading to whole ecosystem shifts are likely to result.

Increased length of stratification period is expected to affect phytoplankton community composition through physical means as well as through changes in nutrient cycling as flagellates are generally better suited than diatoms for the predicted stratified nutrient-depleted conditions. There is also recent evidence from the CPR survey that warming temperatures decrease the size of the plankton community (for both phytoplankton and zooplankton) this may also eventually lead to a decrease in size of fish species. A smaller sized community will lead to more regeneration of carbon within the surface layers and it is presumed carbon sequestration to the deep ocean will be less efficient. In summary, these changes in the plankton community may place additional stress on already-depleted fish stocks as well as having consequences for mammal and seabird populations.

Recent evidence from the CPR survey also suggest increase in pathogenic organisms such as Vibrio in UK waters.

3. KNOWLEDGE GAPS

a. Mechanistic links between climate warming, plankton and fisheries (and other higher trophic levels such as seabirds) to form a predictive capacity.

b. Understanding and predicting rapid and abrupt ecosystem shifts.

c. Filling major gaps in the coverage of physical, chemical and biological measurements in pelagic ecosystems in the global oceans in particular the Arctic Ocean and Nordic Seas.

d. Understanding the rate of genetic adaptation to climate change impacts.

e. Identifying species or communities particularly vulnerable to climate change impacts.

f. Understanding the processes involved in the biological pump and quantifying its global spatial and temporal variability.

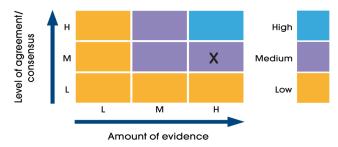
g. Determining the mechanisms behind observed temperature increases off the continental margins of Europe including advective processes and their effect on Northern European Seas.

4. SOCIO-ECONOMIC IMPACTS

Changes in the plankton are thought to have had major impacts on commercial fish stocks around the UK and the general carrying capacity and health of marine ecosystems. For example, the decline in gadoid biomass, especially cod has been linked with plankton, and has also been correlated with the marked reduction in returns of salmon to home waters, although casual mechanisms are not yet clear. A climate link has also been established between plankton, sandeels and seabirds.

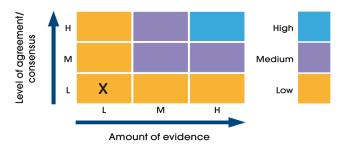
5. CONFIDENCE ASSESSMENT

What is already happening?



What could happen?

Observational evidence is high, however, the ability of models to predict changes in the future are still quite low.



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