MCCIP ARC Science Review 2010-11
Plankton

MARTIN EDWARDS[1], MIKE HEATH[2] AND ABIGAIL MCQUATTERS-GOLLOP[1]

[1]Sir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth, PL1 2PB.

[2]Department of Mathematics and Statistics, University of Strathclyde, 26, Richmond Street, Glasgow, G1 1XH.

Please cite this document as:

Edwards, M., M. Heath & A. McQuatters-Gollop (2010) Plankton *in* MCCIP Annual Report Card 2010-11, MCCIP Science Review, 10pp. www.mccip.org.uk/arc

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:

The important decadal climate indicator for the North Atlantic, the North Atlantic Oscillation (NAO), has been generally rising (with occasional negative NAO years) along with Northern Hemisphere Temperatures over the past 30 years and the surface waters of the European Continental shelf have been warming. This has caused extensive changes in the planktonic ecosystem in terms of plankton production, biodiversity, and species distribution which have had effects on fisheries production and other marine life (e.g. seabirds) (Reid & Edwards, 2001; Edwards *et al.*, 2001, 2002; Beaugrand *et al.*, 2003, 2004; Richardson & Schoeman, 2004; Southward *et al.*, 2004; Alheit *et al.*, 2005; Heath, 2005) .

In the North Sea the population of the previously dominant and important zooplankton species, (the cold water copepod *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 as abundant (Beaugrand *et al.*, 2004; Edwards *et al.*, 2007).

There has been a northward shift in the distribution of many plankton and fish species by more than 10^{o} latitude over the past fifty years. This shift is particularly associated with the shelf edge current running north along the European continental margin (Beaugrand *et al.*, 2002; Brander *et al.*, 2003; Genner *et al.*, 2004).

The seasonal timing of plankton production has also been 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 (Edwards & Richardson, 2004).

The decline of the European cod stocks 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 (Brander, 2005).

The effects of an abrupt ecosystem shift in the late 1990s were most pronounced in regions of the north-eastern Atlantic near the 9-10°C sea surface temperature isotherm, a critical thermal boundary between 'warm' and 'cold' water ecosystems. As waters warm this ecosystem boundary has moved northwards.

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. These changes may place additional stress on already-depleted fish stocks as well as have consequences for mammal and seabird populations.

FULL REVIEW

1. What is already happening?

Plankton are at the base of the food chain and are the source of food for all other marine organisms. The carrying capacity of ecosystems in terms of the size of fish resources and recruitment to individual stocks is highly dependent on variations in the abundance, timing and composition of the plankton. These organisms also play a crucial role in climate change through the export from the atmosphere of the important greenhouse gas CO_2 to the deep ocean by carbon sequestration in what is known as the 'biological pump'. Without this process concentrations of CO_2 would be much higher in the atmosphere and the climate of the world would be much warmer.

In Northern European Seas and waters surrounding the British Isles changes in both plant (phyto-) and animal (zoo-) plankton species and communities have been associated with Northern Hemisphere Temperature (NHT) trends and variations in the North Atlantic Oscillation (NAO) index (Edwards *et al.*, 2001; Beaugrand & Reid, 2003). These responses have included changes in species distributions and abundance (Beaugrand *et al.* 2002), the occurrence of sub-tropical species in temperate waters, changes in overall phytoplankton biomass and seasonal length (Edwards *et al.*, 2001), changes in the North Sea ecosystem (Reid & Edwards, 2001; Edwards *et al.*, 2002; Beaugrand 2004), community shifts, phenological changes (timing of life-history events) and changes in species interactions (Edwards & Richardson, 2004). These major changes in the plankton, primarily caused by regional climate warming, have had important impacts on other higher trophic levels (e.g. fish, seabirds). 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). Ocean acidification may become a problem in the future (50-100 yrs).

The observed changes have been significantly linked to regional hydro-climatic variability (SST, salinity, oceanic inflow, wind strength and direction, nutrients and water column stability) that is associated with regional climate warming, the North Atlantic Oscillation and in particular Northern Hemisphere Temperature. It is the significant statistical association with the latter index of hemispheric warming that suggests that the changes are a regional response to global warming. The observations summarised in the executive summary primarily come from the Continuous Plankton Recorder (CPR) survey which spans over 75 years, but are confirmed by other single point time series such as that collected at Helgoland and through intercomparison with satellite measurements.

Other factors such as eutrophication, fisheries and future acidification may also contribute to plankton variability, but they are believed at present, by general consensus, to be less important than hydro-climatic forcing at large regional scales. However, eutrophication may be a problem at local-scales (Edwards *et al.*, 2006) in certain areas and acidification may be a serious problem in the future if planktonic organisms are unable to adapt fast enough to the changing environment. Little is known of the adaptive capacities or phenotypic plasticity of plankton organisms; however, due to their fast regeneration times they may be able to adapt faster than other higher organisms (e.g. fish). There is some evidence from the southern North Sea that climate change might exacerbate eutrophication effects. In summary, at the ecoregional scale climate change is the dominant driver of long-term plankton trends.

North-East Atlantic Summary

The CPR survey monitors plankton at the pan-oceanic scale and can provide insight into the state of phytoplankton and zooplankton at the regional level. At this regional scale, climate is the main driver of changes in the phyto and zooplankton communities. In the North-East Atlantic, surface isotherms are moving at a rapid rate, with the 10 °C isotherm moving northwards by approximately 22 km yr^{-1}. The 9-10 °C isotherm is a critical thermal boundary for North Atlantic marine ecosystems as it separates the boreal and temperate ecosystems (Beaugrand *et al.,* 2008). In the late 1990s parts of the North-East Atlantic underwent a climate-induced regime shift, the effects of which were most pronounced in regions with sea surface temperatures near the critical thermal boundary (Beaugrand *et al.,* 2008). During the last 50 years there has been northerly movement of warmer-water plankton by 10 degrees latitude in the North-East Atlantic and a similar retreat of colder-water plankton to the north (Beaugrand *et al.*, 2002). While mesozooplankton biomass is decreasing throughout the North-East Atlantic, there has been a northward-progressing shift in the increasing proportion of warm-water *Calanus helgolandicus* relative to that of its cold-water sister species *C. finmarchicus* (Reid *et al.,* 2003). There has also been rapid northward movement of the biodiversity of a key zooplankton group (calanoid copepods) during that time (Beaugrand *et al.*, 2002). According to the CPR's Phytoplankton Colour Index, there has been a considerable increase in phytoplankton biomass over the last two decades in certain areas of the North-East Atlantic and North Sea associated with changes in sea surface temperature (Edwards *et al.,* 2001). Since the regime shift, phenological changes have also been observed in North-East Atlantic phytoplankton. Although the phytoplankton spring bloom has remained relatively stable in time, the marine growing season has been extended, particularly in the summer months and to a lesser extent during winter, due to warming sea temperatures. However, many zooplankton taxa have moved forward in their seasonality, resulting in the seasonal occurrence of food for zooplankton and fish larvae being out of synchrony. This is turn may lead to trophic mismatch and failure of fish recruitment (Edwards and Richardson 2004).

In the North-East Atlantic, climate warming has been found to create hydroclimatic conditions particularly suitable to dinoflagellates (Edwards and Richardson, 2004); this phytoplankton functional group contains the majority of Harmful Algal Bloom (HAB) genera (Smayda, 1997). The bloom frequency of HAB genera around the British Isles appears to be related to climate-regulated changes in dinoflagellate abundance, with an increase during the 1980s regime shift and a decrease in frequency thereafter, a pattern consistent with changes observed throughout much of the North Sea (Edwards *et al.*, 2006). Decadal changes in spatial distribution of some HAB genera in the Northeast Atlantic and North Sea have also been recently linked to climatic influences such as warmer winter SST and changes in the NAO index (Edwards *et al.*, 2006). 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. Although ocean acidification may be a threat to calcareous plankton in the future, presently in the North Atlantic certain calcareous taxa recorded by the CPR are increasing in abundance, a trend associated with climate shifts in Northern Hemisphere temperature. See *MCCIP ARC Science Review 2010-11 Ocean Acidification* (Turley *et al*., 2010).

Listed below are regional specificities in plankton state based on the Charting Progress 2 regions.

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, 2003) that appears to have persisted since then, reducing thermohaline stratification and the definition of frontal regions (Beare *et al.*, 2002).

Data from weekly plankton monitoring in the coastal north-western North Sea (off Stonehaven; Heath *et al.*, 1999a; Marine Scotland monitoring website) show large year-to-year differences in the importance of diatoms for the phytoplankton community. In 2006 and 2008 dinoflagellates were anomalously high in abundance whilst diatoms were low, and vice-versa in 2007 when, unusually, *Skeletonema* spp. formed a dense spring bloom off Stonehaven. Dinoflagellates of the genus Ceratium have steadily declined off Stonehaven since 1997, in line with the open northern North Sea. However, in marked contrast to the open northern North Sea, the copepod *Calanus finmarchicus* has increased in abundance by an order of magnitude between the late 1990s and 2008. The species was particularly abundant in 2006, 2007 and 2008, as was *Calanus helgolandicus*. It is unclear why the local trend in *C. finmarchicus* appears to be opposite to that predicted for the effect of climate change, and opposite to that in the wider northern North Sea where *C. helgolandicus* has increased in dominance.

The two *Calanus* species show different seasonal dynamics off Stonehaven: *C. finmarchicus* is carried into the area in the spring as late stage copepodites and produces one, maybe two generations of offspring, none of which survive through the winter locally. *C. helgolandicus* is also carried into the area as late stage copepodites, but in the autumn, and accumulates to large numbers in September which then decline rapidly so that the overwinter numbers are very low.

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 & Celtic Sea (Region 4)

The Western Channel and Celtic Sea region is more temperate than the North Sea, and is characterised by annual mean SST of above 12 °C. The late 1980s regime shift was less pronounced in this region, as the mean SST here was already above the critical thermal boundary of 9-10 °C. The Channel portion of this region is distinguished by high numbers of decapod larvae within the plankton community. Further offshore into the Celtic Sea, this area is characterised by high plankton productivity and large populations of *Calanus helgolandicus*. A number of important long-term plankton monitoring sites are located in this region and were responsible for observing a multi-decadal climate oscillation known as the Russell Cycle.

Irish Sea (Region 5)

The plankton community in the Irish Sea contains warm-temperate 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.

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 plankton time-series monitoring site in Loch Ewe (Marine Scotland monitoring website), and an autonomous monitoring buoy is seasonally deployed in Loch Torridon. 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.

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 cold-temperate boreal species and includes Atlantic and offshore species as well as some shelf species. No long-term time-series are available for inshore areas, however the CPR survey monitors offshore regions. 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 warm-temperate 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 0ºC. 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.,* 1999b). 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. Hydrographic conditions in the Faroe-Shetland Channel have been monitored at least annually since the early 1900s, and monitoring of C. finmarchicus abundance was added to the sampling in the mid-1990s. Since the 1960s, the volume of Arctic water in the Channel has fluctuated by ±10% around a declining trend. Fluctuations have shown a weak inverse relation to the North Atlantic Oscillation Index. However, the concentration of overwintering *C. finmarchicus* in the Arctic water has shown no declining trend since 1990, and in fact was at a peak in winter 2008/09. It is likely that the overwintering copepods in the Channel reflect were produced during the preceding summer at higher latitudes in the Norwegian Sea, and then carried south during the winter.

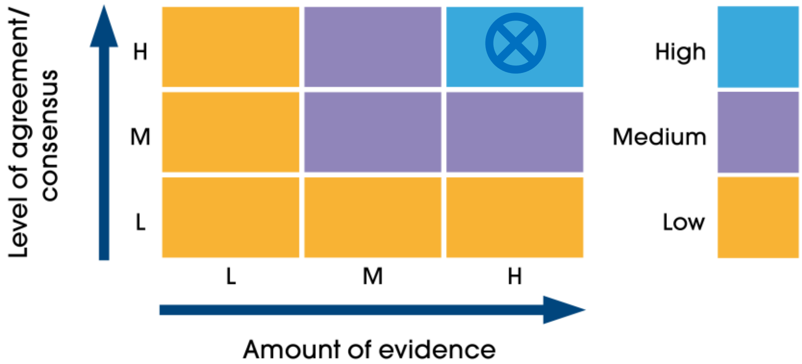
2. What could happen in the future?

Regional climate warming and hydro-climatic variability has had, and is continuing to have, a major effect 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 (50-100 yrs) 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 (Feely *et al.*, 2004). Potentially, chemical changes to the oceans and its effect on the biology of the oceans could reduce their 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 some very recent evidence from the CPR survey that warming temperatures decrease the size of the plankton community (for both phytoplankton and zooplankton). 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.

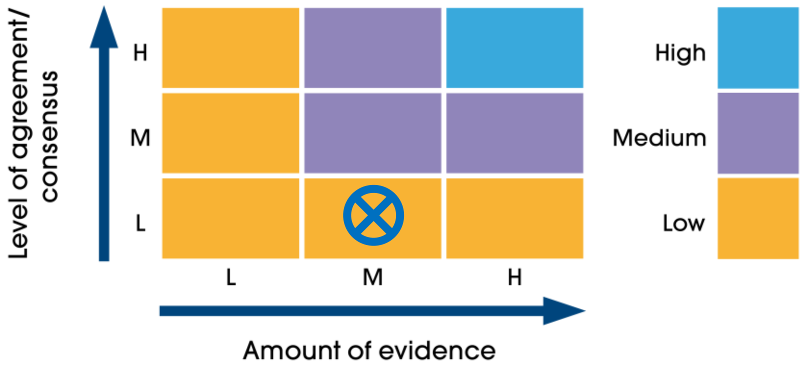
3. Confidence in the science

What is already happening: ***High***



There is a medium to high level of confidence in what is happening to the plankton now based on information from the Continuous Plankton Recorder survey and corroborated through smaller-scale surveys and satellite observations. For example, changes in the biogeography and phenology of plankton are highly significantly correlated with Northern Hemisphere Temperature changes.

What could happen: ***Low***



We are less (medium to low) confident of future scenarios, however, we have a good understanding of how plankton are influenced by changes in key hydrological variables represented in the scenarios such as water-column stability changes and increasing sea surface temperature. SAHFOS are currently using new habitat niche modeling techniques to predict these changes with more confidence.

4. Knowledge gaps

The top priority knowledge gaps that need to be addressed in the short term to provide better advice to be given to policy makers are:

- Understanding and predicting rapid and abrupt ecosystem shifts.
- Mechanistic links between climate warming, plankton and fisheries (and other higher trophic levels such as seabirds) to form a predictive capacity.
- Understanding the rate of genetic adaptation to climate change impacts.
- Identifying species or communities particularly vulnerable to climate change impacts.
- Understanding the processes involved in the biological pump and quantifying its global spatial and temporal variability.
- Determining the mechanisms behind observed temperature increases off the continental margins of Europe including advective processes and their effect on Northern European Seas.
- Filling major gaps in the coverage of physical, chemical and biological measurements in pelagic ecosystems in the global oceans in particular the Arctic Oceans and Nordic Seas.

5. 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 causal mechanisms are not yet clear (Beaugrand *et al.*, 2003; Beaugrand & Reid, 2003). A climate link has also been established between plankton, sandeels and seabirds (Frederiksen *et al.*, 2006).

6. References

Alheit J, Mollmann C, Dutz J, Kornilovs G, Loewe P, Mohrholz V, Wasmund N (2005) Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. *ICES J Mar Sci*, **62**,1205-1215

Beare DJ, Batten S, Edwards M and Reid DG 2002 Prevalence of boreal Atlantic, temperate Atlantic and neritic zooplankton in the North Sea between 1958 and 1998 in relation to temperature, salinity, stratification intensity and Atlantic inflow. *Journal of Sea Research*, **48**, 29-49

Beaugrand G, Edwards M, Brander K, Luczak C and Ibanez F (2008) Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecology Letters*, **11**(11), 1157-1168

Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog Oceanogr,* **60**, 245-262

Beaugrand G (2003) Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. *Fisheries Oceanography*, **12**, 270-283

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. *Nature,* **426**, 661-664

Beaugrand G, Reid PC (2003) Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology*, **9**, 801-817

Beaugrand G, Reid PC, Ibanez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic Marine Copepod Biodiversity and Climate. *Science,* **296**, 1692-1694

Brander K (2005) Cod recruitment is strongly affected by climate when stock biomass is low. *ICES J Mar Sci*, **62**, 339-343

Brander K, Blom G, M.F. B, Erzini K, Henderson G, Mackenzie BR, Mendes H, Ribeiro J, Santos AMP, Toresen R (2003) Changes In Fish Distribution In The Eastern North Atlantic: Are We Seeing A Coherent Response To Changing Temperature? *ICES Marine Science Symposia*, **219**, 261-270

Edwards M, Beaugrand G, Reid PC, Rowden AA, Jones MB (2002) Ocean climate anomalies and the ecology of the North Sea. *Marine Ecology-Progress Series*, **239**, 1-10

Edwards M, Johns DG, Leterme SC, Svendsen E, Richardson AJ (2006) Regional climate change and harmful algal blooms in the northeast Atlantic. *Limnol Oceanogr,* **51**, 820-829

Edwards M, Licandro P, Johns DG, John AWG, Stevens DP (2007) Ecological Status Report: results from the CPR survey 2004/2005. SAHFOS Technical Report 4:1-8

Edwards M, Reid P, Planque B (2001) Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960-1995). *ICES J Mar Sci*, **58**, 39-49

Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, **430**, 881-884

Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, Millero FJ (2004) Impact of Anthropogenic CO_2 on the $CaCO_3$ System in the Oceans. *Science* **305**, 362-366

Frederiksen M, Edwards M, Richardson AJ, Halliday NC and Wanless S (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology*, **75**, 1259-1268

Genner MJ, Sims DW, Wearmouth VJ, Southall EJ, Southward AJ, Henderson PA, Hawkins SJ (2004) Regional climatic warming drives long-term community changes of British marine fish. *Proc R Soc Lond, Ser B: Biol Sci*, **271**, 655-661

Gowen RJ, Mills DK, Trimmer M and Nedwell DB (2000) Production and its fate in two coastal regions of the Irish Sea: the influence of anthropogenic nutrients. *Marine Ecology - Progress Series*, **208**, 51-64.

Heath, M.R., Adams, R.D., Brown, F., Dunn, J., Fraser, S., Hay, S.J., Kelly, M.C., MacDonald, E.M., Robertson, M.R., Robinson, S., Wilson, C. (1999a). Plankton monitoring off the east coast of Scotland in 1997 and 1998. *Fisheries Research Services Report* 13/99. http://www.frs-scotland.gov.uk/Uploads/Documents/frsr1399.pdf

Heath, M.R., Beare, D.J., Dunn, J., Fraser, J.G., Hay, S.J. and Turrell, W.R. (1999b). Monitoring the effects of climate change - overwintering abundance of *Calanus finmarchicus* in the Faroe-Shetland Channel. *Fisheries Research Services Report* 14/99. www.frs-scotland.gov.uk/Uploads/Documents/frsr1499.pdf

Heath MR (2005) Changes in the structure and function of the North Sea fish foodweb, 1973-2000, and the impacts of fishing and climate. *ICES J Mar Sci*, **62**, 847-868

Marine Scotland, plankton monitoring data, Stonehaven and Loch Ewe. www.frs-scotland.gov.uk/Delivery/standalone.aspx?contentid=1151

Reid PC, Edwards M (2001) Long-term changes in the pelagos, benthos and fisheries of the North Sea. *Senckenbergiana Maritima*, **31**, 107-115

Reid PC, Edwards M, Beaugrand G, Skogen M and Stevens D (2003) Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. *Fisheries Oceanography*, **12**, 260-269

Richardson AJ, Schoeman DS (2004) Climate Impact on Plankton Ecosystems in the Northeast Atlantic. *Science*, **305**, 1609-1612

Smayda TJ (1997) Harmful algal blooms: Their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnology and Oceanography,* **42**, 1137-1153

Southward AJ, Langmead O, Hardman-Mountford NJ, Aiken J, Boalch GT, Dando PR, Genner MJ, Joint I, Kendall MA, Halliday NC, Harris RP, Leaper R, Mieszkowska N, Pingree RD, Richardson AJ, Sims DW, Smith T, Walne AW, Hawkins SJ (2004) Long-Term Oceanographic and Ecological Research in the Western English Channel. Adv Mar Biol, **47**, 1-105

Turley, C., C. Brownlee, H.S. Findlay, S. Mangi, A. Ridgwell, D.N. Schmidt, and D.C. Schroeder (2010) Ocean Acidification in MCCIP Annual Report Card 2010-11, MCCIP Science Review, 27pp. www.mccip.org.uk/arc