

Plankton, jellyfish and climate in the North-East Atlantic

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EXECUTIVE SUMMARY

Extensive changes in plankton ecosystems around the British Isles over the last 60 years, including production, biodiversity and species distributions, have had effects on fisheries production and other marine life. This has been mainly driven by climate variability and ocean warming. These changes include:

- Extensive changes in the planktonic ecosystem in terms of plankton production, biodiversity, species distribution which have effects on fisheries production and other marine life (e.g. seabirds).
- 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 northwards to replace the species, but are not as numerically abundant.
- There has been a shift in the distribution of many plankton and fish species around the planet. For example, during the last 50 years there has been a northerly movement of some warmer water plankton by 10° latitude in the North-east Atlantic and a similar retreat of colder water plankton northwards (a mean poleward movement of between 200–250 km per decade).
- The seasonal timing of some plankton production has 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 due to overfishing may have been exacerbated by climate warming and climate-induced changes in plankton production (Beaugrand *et al.*, 2003). 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

Citation: Edwards, M., Atkinson, A., Bresnan, E., Helaouet, P., McQuatters-Gollop, A., Ostle, C., Pitois, S. and Widdicombe, C. (2020) Plankton, jellyfish and climate in the North-East Atlantic. *MCCIP Science Review 2020*, 322–353.

doi: 10.14465/2020.arc15.plk

Submitted: 07 2019
Published online: 15th January 2020.

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. These changes may place additional stress on already depleted fish stocks, as well as have consequences for mammal and seabird populations. Additionally, melting of Arctic waters may increase the likelihood of trans-Arctic migrations of species between the Pacific and Atlantic oceans.

1. PLANKTON AND CLIMATE CHANGE IMPACTS

Plankton includes both the free-floating photosynthesising life of the oceans, as well as marine microscopic animals. Algal phytoplankton, bacteria and other photosynthesising protists produce *c.* 50% of net global primary production (Field *et al.*, 1998). They export carbon to the deep ocean and as the base of the marine food-web provide food for the animal plankton (zooplankton) which in turn provides food for many other marine lifeforms ranging from microscopic organisms to baleen whales. The carrying capacity of pelagic ecosystems in terms of the size of fish resources and recruitment to individual stocks as well as the abundance of marine wildlife (e.g. seabirds and marine mammals) is highly dependent on variations in the abundance, seasonal timing and composition of this plankton.

In marine environments, the main drivers of change include climate warming, point-source eutrophication, deoxygenation and unsustainable fishing (Edwards, 2016). Furthermore, unique to the marine environment, anthropogenic CO₂ is also associated with Ocean Acidification (OA). OA has the potential to affect the process of calcification and therefore certain planktonic organisms dependent on calcium carbonate for shells and skeletons (e.g. coccolithophores, foraminifera, pelagic molluscs, echinoderms) may be particularly vulnerable to increasing CO₂ emissions (Edwards, 2016). It is also worth noting that while pelagic systems are undergoing large changes caused by climate change, they have also been identified as a form of mitigation of climate change through possible human manipulation of these systems through geoengineering. It has been shown that at small scales the addition of iron to certain oceanic environments (ocean fertilisation) can increase productivity and net export of carbon to the deep ocean. However, this approach is still controversial with largely unknown long-term ramifications for marine ecosystems at the large scale. For example, it could lead to negative effects such as the stimulation of Harmful Algal Blooms (HABs) or hypoxia, but further investigations are needed (Güssow *et al.*, 2010). While there are a myriad of pressures and intertwined

multiple drivers on the marine environment and on plankton ecosystems, some of which are synergistic (for example, the interaction of temperature, ocean acidification and hypoxia) in this report, the focus is on the effects of climate change impacts on planktonic communities.

1.1 Plankton in the policy context

As understanding of the ecological role of plankton in marine systems has developed, plankton have become increasingly used as indicators of environmental status to support marine management under European management mechanisms, which are implemented in UK waters. The UK's Marine Strategy and the EU Marine Strategy Framework Directive (MSFD) (European Commission, 2008) seek to achieve 'Good Environmental Status' (GES) for European Seas. As the base of the marine pelagic ecosystem, indicators of plankton community structure are used to assess the 'pelagic habitat' component of UK and European marine ecosystems under the Directive and Marine Strategy, and are representative of broader pelagic ecosystem status. A suite of plankton indicators recently developed for these policy drivers captures aspects of pelagic diversity (McQuatters-Gollop *et al.*, 2019; OSPAR, 2017e), functioning (OSPAR, 2017c) and productivity (OSPAR, 2017b, d) in the North-East Atlantic and are included in the biodiversity and food-webs state assessments under the MSFD at the OSPAR level and the Marine Strategy at the UK level, while chlorophyll *a* is used as a eutrophication indicator (OSPAR, 2017a). A key challenge under these policy drivers is separating plankton change driven by climate change from change in plankton caused by directly manageable pressures, such as nutrients and fishing (McQuatters-Gollop, 2012). This information is required so that management efforts can be effectively focused.

Complementarily to the MSFD and UK Marine Strategy that focus on regional- and national-scale management of marine waters, nearshore phytoplankton are integral to the EU Water Framework Directive (European Commission, 2000) which aims to achieve GES of European waters within one nautical mile of shore; the UK remains committed to this goal post-Brexit. Plankton indicators under the Water Framework Directive (WFD) are primarily linked to eutrophication pressures (Devlin *et al.*, 2009). The EU Control of Products of Animal Origin Regulation mandates the monitoring of potential toxin-producing phytoplankton species in shellfish production areas as part of a statutory monitoring programme to protect human health from algal toxins (European Commission, 2017).

Each of these legislative examples demonstrates the importance of plankton monitoring programmes for managing marine resources, informing conservation measures, and protecting human health.

1.2 Plankton and climate change impacts: the North Atlantic wide context

Large-scale trends in plankton and climate variability

The Continuous Plankton Recorder (CPR) 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 provides excellent spatial and temporal coverage around the British Isles. It has been operating in the North Sea since 1931 with some standard routes existing with a virtually unbroken monthly coverage back to 1946. Figure 1 and Table 1 show the distribution of CPR samples and the number of CPR samples in the eight UK ecoregional areas in the North-East Atlantic. The CPR covers most ecoregional areas very well with the exception of the Inner Hebrides of Western Scotland (Region 6) where sampling was not good enough to provide multidecadal time-series data and trends. To summarise the long-term trends in plankton at the large-scale, we used a number of indices of plankton from the CPR survey that included the sum of the abundance of all counted diatoms (number of taxa: 125) and all counted dinoflagellates (number of taxa: 79) and total copepod numbers (number of taxa: 196) for these eight ecoregional areas (Figures 2, 3 and 4). Using bulk indices like this is less sensitive to environmental change and will quite often mask the subtleties that individual species will provide; however, it is thought that these bulk indices represent the general functional group response of plankton to the changing environment an approach that has been adopted for the assessment of GES for the MSFD.

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 and natural climate variability such as the Atlantic Multidecadal Oscillation (AMO); the East Atlantic Pattern (EAP) and variations in the North Atlantic Oscillation (NAO) index (Edwards *et al.*, 2013a). 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.*, 2003; Edwards *et al.*, 2001; Edwards *et al.*, 2002; Edwards and Richardson, 2004; Reid and Edwards, 2001).

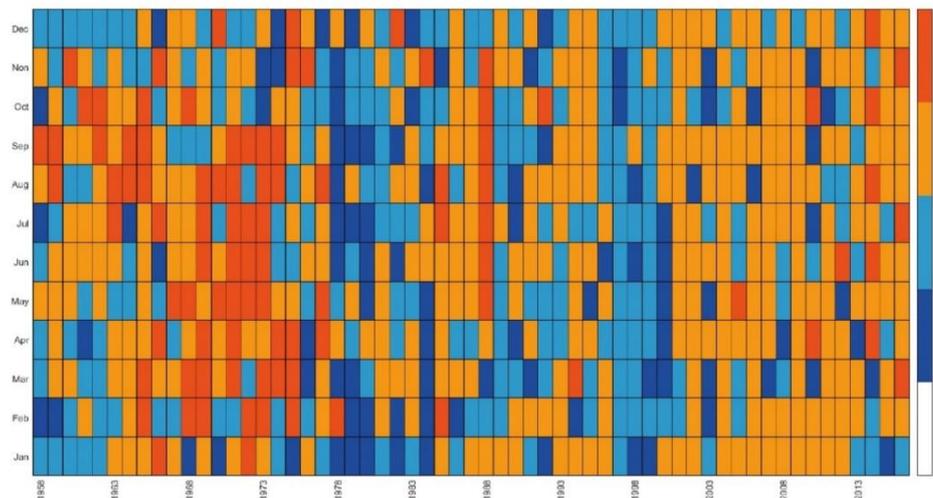
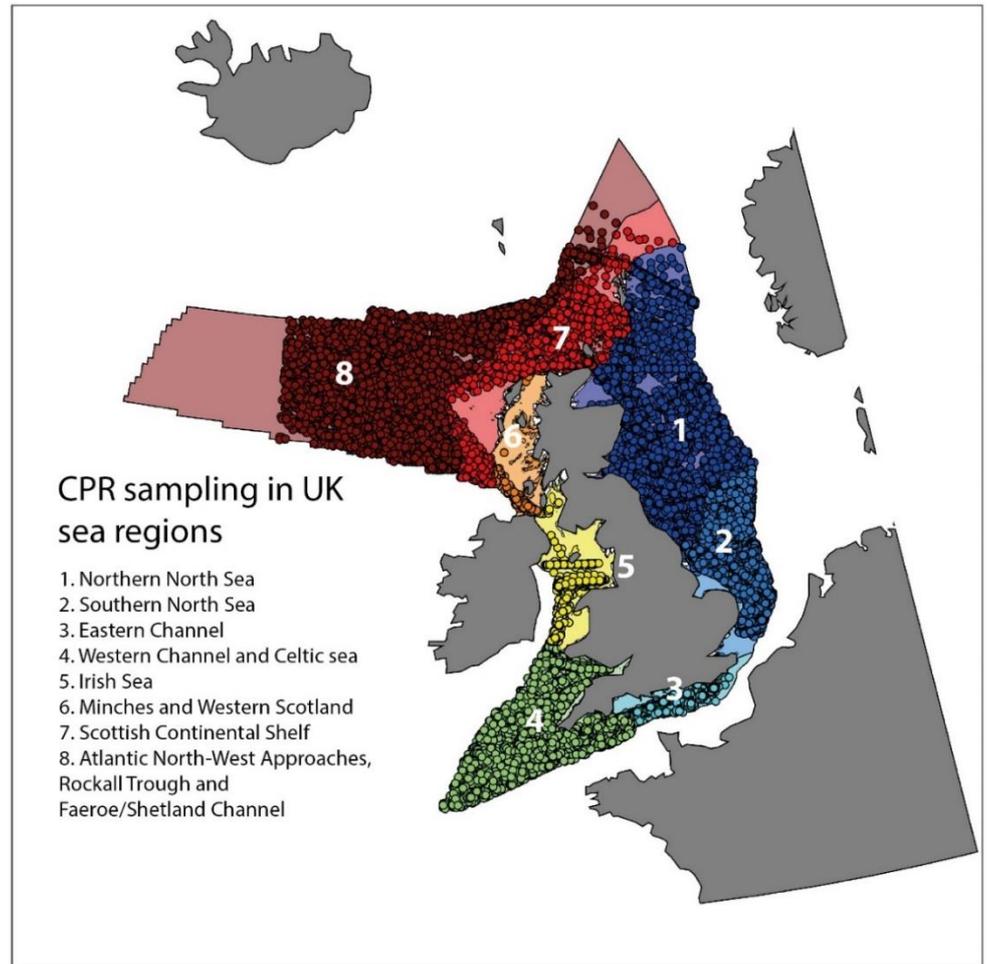


Figure 1: Distribution of CPR samples in UK sea regions (top) and monthly sampling effort from 1958–2016 (bottom; see Table 1). Based on the Charting Progress 2 assessment which sub-divides the UK sea area into eight regions. Total sampling effort based on monthly sampling in UK regional seas, highest percentile in red and lowest percentile in blue.

Table 1: UK regional areas and number of CPR samples per region

| Area number | Area name | Number of samples | Colour on map |
|-------------|---|-------------------|---------------|
| 1 | Northern North Sea | 21 824 | Dark blue |
| 2 | Southern North Sea | 10 152 | Blue |
| 3 | Eastern Channel | 1669 | Light blue |
| 4 | Western Channel and Celtic Sea | 10 568 | Green |
| 5 | Irish Sea | 3498 | Yellow |
| 6 | Minches and Western Scotland | 144 | Orange |
| 7 | Scottish Continental Shelf | 5724 | Light red |
| 8 | Atlantic North West Approaches and Faroe–Shetland Channel and Rockall Trough and Bank | 6180 | Dark red |

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 (Behrenfeld *et al.*, 2006). However, over the whole temperate North-East 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). These changes have been linked to changes in the climate and temperature of the North Atlantic over the last 50 years.

It must be noted, however, that climate variability has a spatially heterogeneous impact on plankton in the North Atlantic and around the British Isles and not all ecoregional areas are correlated to the same climatic index. For example, trends in the AMO are particularly prevalent in the oceanic regions and in the sub-polar gyre of the North Atlantic and the NAO has a bigger impact in the shallower southern North Sea (Harris *et al.*, 2014). This is also apparent with respect to the Northern Hemisphere Temperature 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, abrupt ecosystem shifts do not always occur in the same region or at the same time. The major 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 ecosystem shift occurred in the plankton abundance 10 years later in the Icelandic Basin and in oceanic regions west of the British Isles. The different timing and differing regional responses to ecological shifts have been associated with the

movement of the 10°C thermal boundary as it moves northwards in the North Atlantic as a result of climate warming (Edwards *et al.*, 2013).

In examining the long-term trends in the plankton indices, the general pattern is an increase in phytoplankton biomass for most regions in the North Atlantic and in the ecoregions around the British Isles, with differing timings for the main step-wise increase occurring being later in oceanic regions compared to the North Sea. For the diatoms there is not really a predominant trend for the North Atlantic Basin as a whole (Figure 2) but some regions show a strong cyclic behaviour over the multidecadal period. The time signal resembles an oscillation of about 50 to 60 years featuring a minimum around 1980, reflecting changes in the AMO signal. Particularly large increases in diatom abundance over the last few years are seen in the Irish Sea (area 5). 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 multidecadal period (see Figure 3). 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 dinoflagellate *Tripes* genus (previously *Neoceratium* and *Ceratium* Gomez 2013) in the North Sea. However, *Tripes* abundance has recovered in the North Sea over the last 5 years. Particularly large decreases in dinoflagellate abundances are seen in offshore areas to the west of Scotland (area 8).

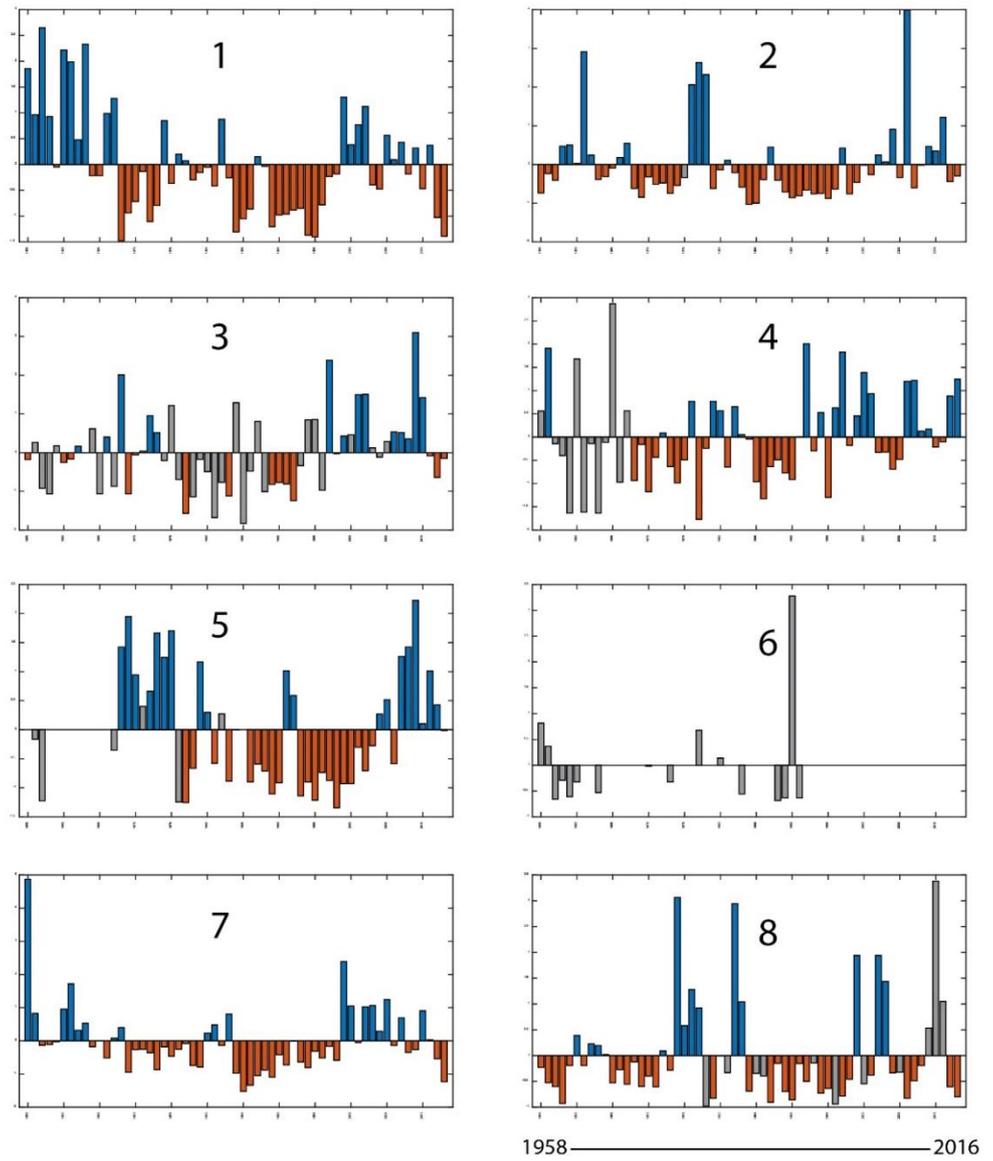


Figure 2: Total diatom abundance (standardised) for the eight ecoregions around the British Isles from 1958–2016. Total diatoms produced using 125 taxa.

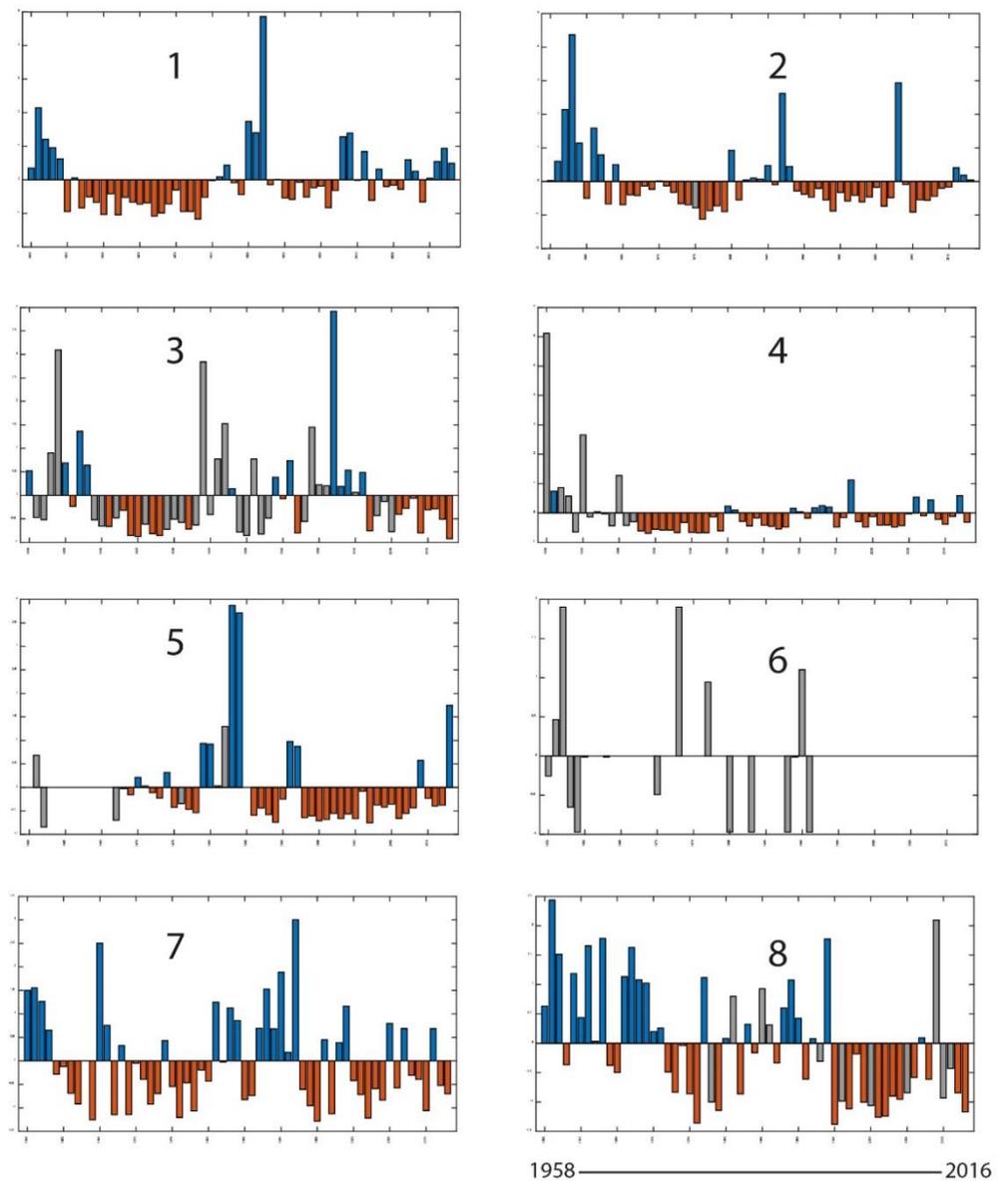


Figure 3: Total dinoflagellate abundance (standardised) for the eight ecoregions around the British Isles from 1958–2016. Total dinoflagellates produced using 79 taxa.

Trends in copepod abundances (Figure 4: only large copepod species abundance shown) have been more stable in offshore regions, but the small species have shown a large decrease in abundance over the last few years, particularly in the southern North Sea and English Channel (areas 2 and 3). 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 (Edwards *et al.* 2013; Harris *et al.* 2014).

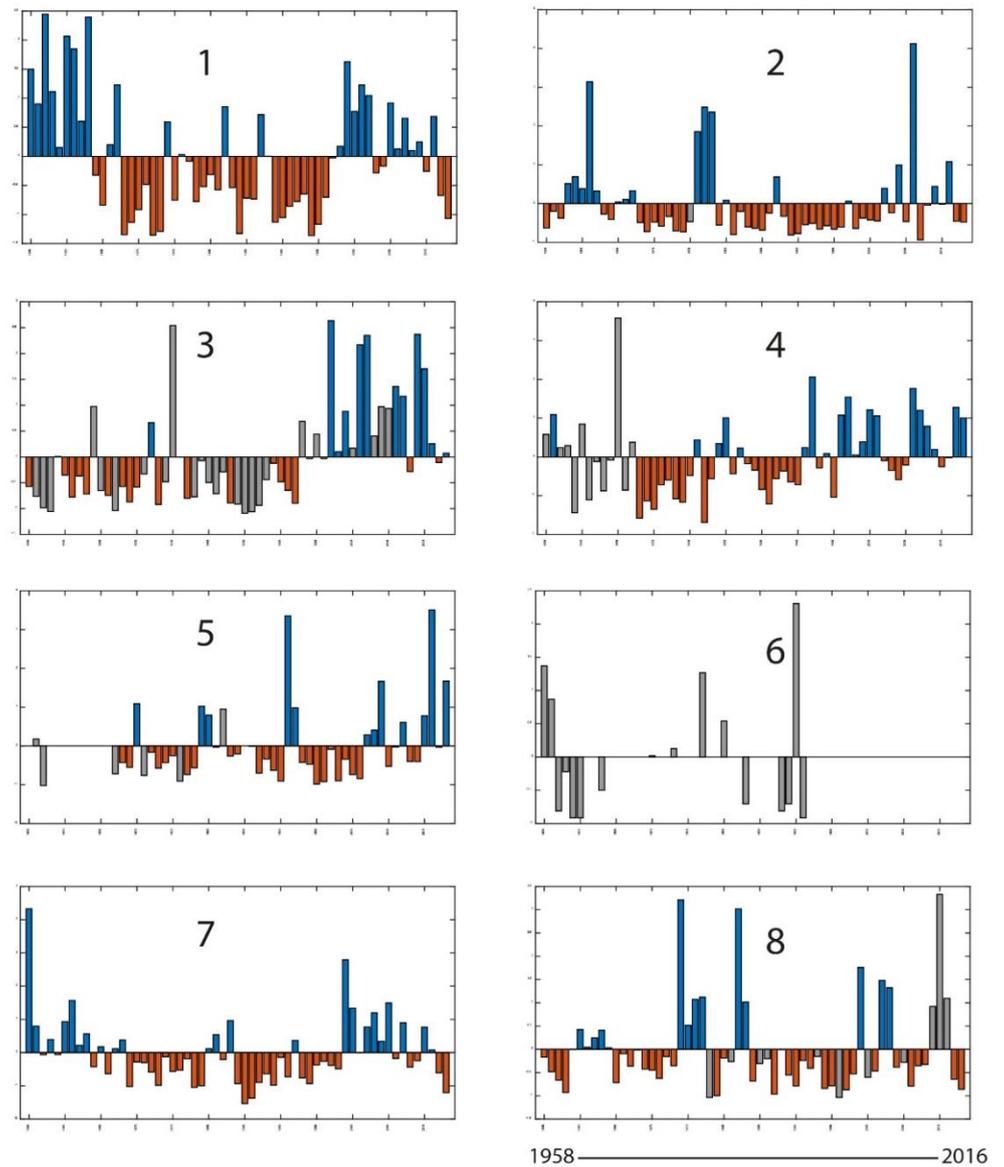


Figure 4: Total large copepod abundance >2mm (standardised) for the eight ecoregions around the British Isles from 1958–2016. Total copepods produced using 196 taxa.

West of the British Isles, 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. Similarly, increases in coccolithophore blooms in the Barents Sea and changes in the distribution of harmful algal bloom species in the North Sea over a multi decadal scale are associated with negative salinity anomalies and warmer temperatures leading to increased stratification (Edwards *et al.*, 2006).

To the north of the British Isles, the Barents Sea and Arctic sea regions have been warming at a faster rate than other regional areas of the North Atlantic (Rahmstorf *et al.*, 2015). Taking the North Atlantic as a whole, of particular note is the emergence of a coldwater anomaly in the North Atlantic south of Greenland (sub-polar gyre region) since 2014 (see Figure 5). This area experienced record cold conditions in 2015 thought to be caused by Atlantic wide circulation changes and specifically by the slowing down of the Atlantic Meridional Overturning Circulation (AMOC) (Rahmstorf *et al.*, 2015; Caesar *et al.*, 2018). The consequences of this anomaly on the climate, Atlantic circulation and plankton of the North Atlantic will be an ongoing and pressing investigation.

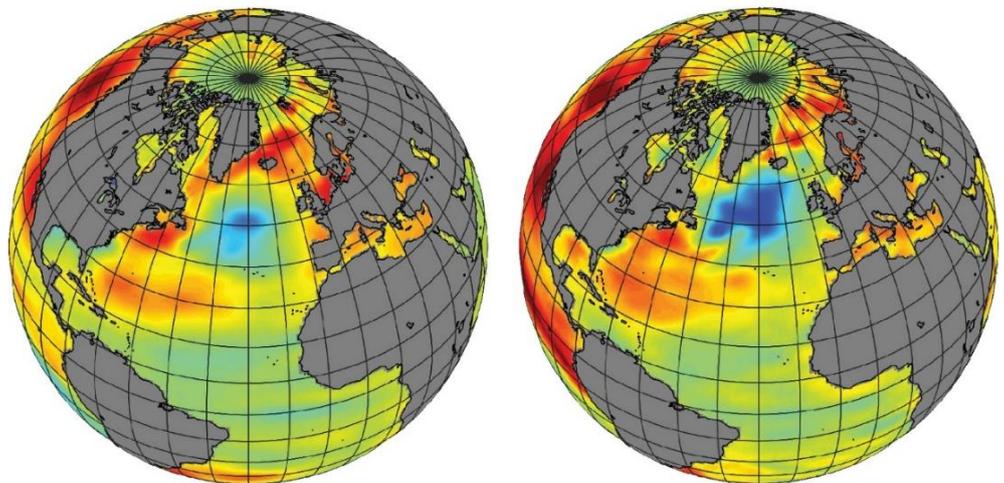


Figure 5: Maps of Sea Surface Temperature (SST) anomalies for 2014 (left) and 2015 (right) for the Northern Hemisphere. Anomalies calculated on the mean of the period 1960–2013 for 2014 and 1960–2014 for 2015. Based on GISS data <http://data.giss.nasa.gov/gistemp/>. See also SAHFOS Global Marine Ecological Status Report for more information (Edwards *et al.*, 2016).

In summary, in the North Atlantic, at the ocean-basin scale and over multidecadal periods, changes in plankton species and communities have been impacted by climate change with strong correlations with the Northern Hemisphere Temperature (NHT), 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 (e.g. AMO and NAO index) and the other due to forced anthropogenic warming (Harris *et al.*, 2014). 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.*, 2003; Edwards *et al.*, 2001; Edwards *et al.*, 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 climate change and the warming of the North Atlantic. 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.*, 2016).

Northward shifts and seasonal (phenology) indicators

A useful indicator of the warming trend in the North Sea (a northward shift indicator) is the percent ratio of the cold-temperate *Calanus finmarchicus* and the warm-temperate *Calanus helgolandicus* copepod species (Figure 6) (Edwards *et al.*, 2016). Although these species are very similar, they occupy distinct thermal niches. The thermal boundary for the arctic-boreal distributed copepod *C. finmarchicus* in the North-East Atlantic lies between ~10–11°C isotherm and is a useful indicator of major biogeographical provinces. *C. 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 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 (Edwards *et al.*, 2016). Over a decadal period *C. helgolandicus* has moved northwards from its particular stronghold in the Celtic Sea to replace *C. finmarchicus* in most of the ecoregional areas of the British Isles (see Figure 6). This is a clear sign of warming waters around the British Isles.

Examination of CPR data up until 2016 revealed the percentage ratio between *C. helgolandicus* and *C. finmarchicus* in 2009 to 2011 was for the first time in twenty years dominated by *C. finmarchicus* in spring (Figure 7). This was a reflection of the particularly cold winter experienced in Northern Europe caused by a very low winter NAO index during that period. Uncharacteristically, during this period the NAO has been in a very low negative phase contributing to the very cold winters experienced in Northern Europe during 2009/2010 and 2010/2011 reflected in below average SST in the North-east Atlantic. Similarly, this has had an effect on the timing of seasonal cycles in the North Sea for many species. The last couple of years have seen a later seasonal peak 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.*, 2016). Between the 1960s and the post 1990s, total *Calanus* biomass in the northern North Sea 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 including fish larvae (Edwards *et al.*, 2016).

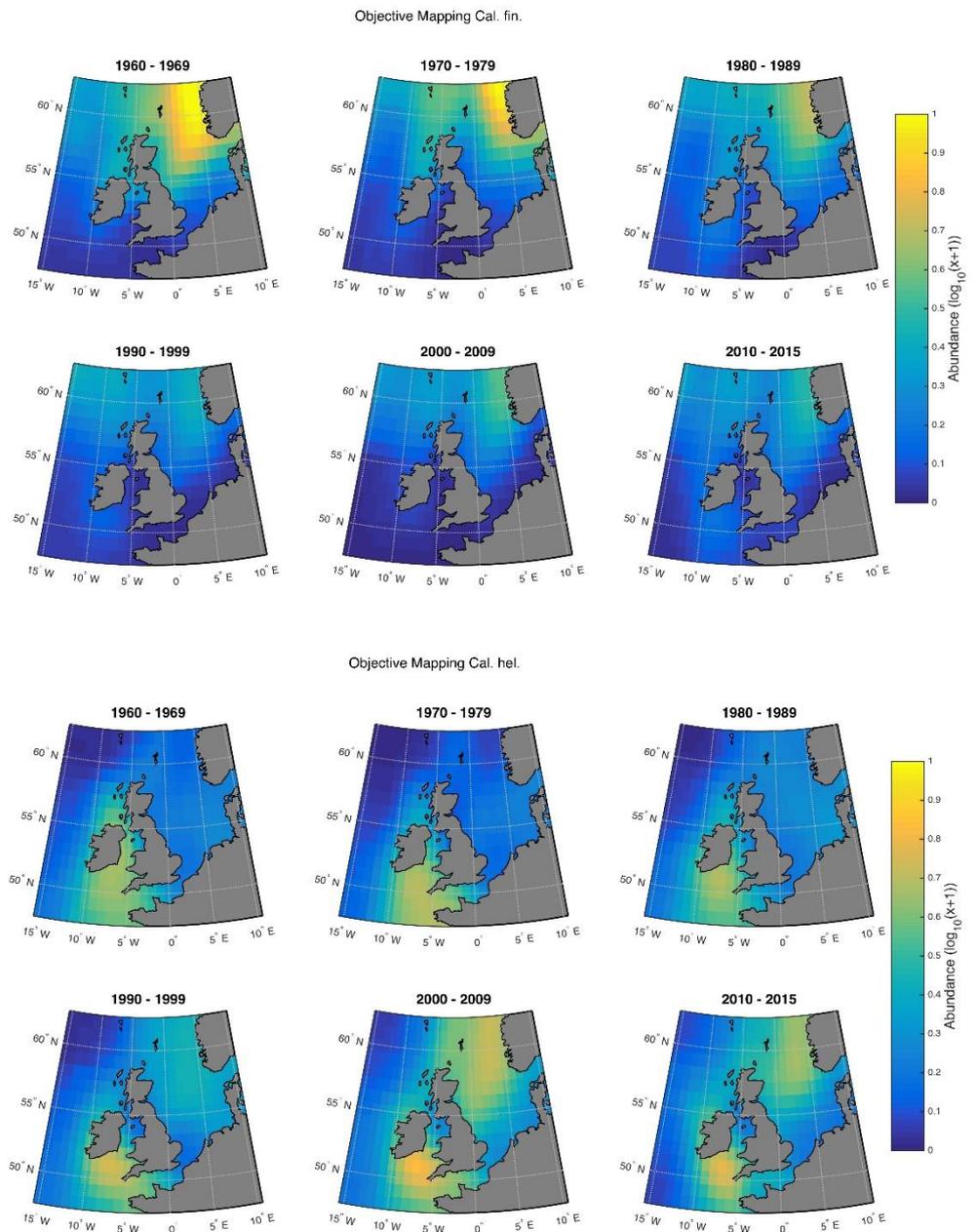


Figure 6: Decadal abundance maps for the cold-water copepod *Calanus finmarchicus* (top) and the temperate copepod *Calanus helgolandicus* (bottom) from 1960–2015. (Data from the CPR survey.)

In summary, since we are only just beginning to understand the complexity of ‘bottom-up’ controls on ecosystem structure, our appreciation of their full ramifications will continue to improve with continued monitoring of the plankton as the global climate changes. How these ‘bottom-up’ controls of ecosystem productivity interact with ‘top-down’ effects, such as fishing, will

be a necessary component of ecosystem management models. Other components of the plankton community are also changing. Gelatinous plankton are difficult to sample routinely but data are also showing changes. For example, long-term monthly changes in the frequency of jellyfish nematocysts (stinging cells) in CPR samples show an increase in frequency of gelatinous zooplankton in the North Sea and North-east Atlantic (Attrill *et al.*, 2007). In many other marine regions worldwide, a proliferation of jellyfish are seen as an indicator of ecosystem degradation. Since some jellyfish feed on fish eggs, fish larvae, and zooplankton, they can exert both top-down and bottom-up control of fish recruitment.

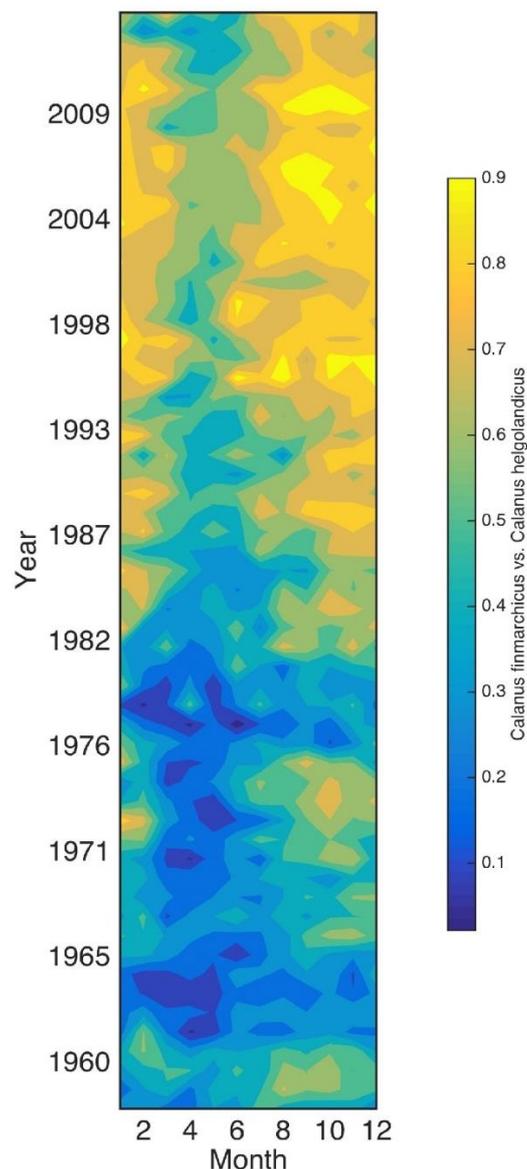


Figure 7: Long-term monthly plots (1960–2016) plots of the percent ratio between Calanus finmarchicus (cold-water/ blue colour) and Calanus helgolandicus (warm-water/ yellow colour) copepods in the North Sea. An increase in the warmer C. helgolandicus can be seen over the last 60 years particularly after the 1980s.

Trends in jellyfish and other gelatinous plankton around the British Isles

Predatory gelatinous zooplankton (Cnidaria and Ctenophora) populations play an important role in our coastal and shelf waters. Limited and sporadic monitoring of these species has hampered understanding of their responses to climate change and the group warrants further research. Many species of gelatinous zooplankton are able to rise rapidly in abundance and form extensive aggregations, commonly known as ‘blooms’, 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 is potentially an indicator of ecosystem instability (Lynam *et al.*, 2011). Jellyfish also form the principle 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.* 2011; Lynam *et al.* 2005, 2011). However, efforts have been undertaken, since 2012, to expand monitoring of gelatinous plankton, in particular the large cnidaria or ‘true jellyfish’. To this effect, a cost-effective standard protocol was designed and tested, that can be applied to any trawl-based fishery survey (Aubert *et al.*, 2018). A harmonised co-ordinated gelatinous data collection programme will help to fill some of the knowledge gaps identified above. Furthermore, visual surface counts from ships of opportunity and long-term information from the CPR can be particularly useful (Attrill *et al.*, 2007; Bastian *et al.*, 2011), in particular when integrated with other data sources to evaluate diversity and abundances (Licandro *et al.*, 2015).

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 across the North-East Atlantic Ocean and shelf seas (Richardson *et al.*, 2009). In oceanic waters, depth >200 m, gelatinous zooplankton abundance between 1946 and 2005 was linked significantly and positively to temperature and total copepod abundance. Notably, jellyfish in the North-East 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 (Attrill *et al.*, 2007; Richardson *et al.*, 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 with climate change since this jellyfish is common in the Mediterranean Sea and considered a warmer-water 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. Nevertheless, *P. noctiluca* occurs in high abundance in the

Mediterranean 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.*, 2011a).

The most common medusae in UK and Irish waters are the scyphozoans *Aurelia aurita* and *Cyanea* spp. and data from plankton nets has shown that these taxa have 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. 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 limited data 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 non-native ctenophore *Mnemiopsis leidyi* was first reported in the North Sea and Baltic Sea in 2005 (Faasse and Bayha, 2006; Antajan *et al.*, 2014). There has been cause for concern regarding the spread of this species given the previous invasions of the Black and Caspian Seas (Shiganova *et al.*, 2001). In parallel with the rise of this predator, fish eggs and larvae from already depleted overfished stocks collapsed in this region (Daskalov and Mamedov, 2007).

Plankton and climate change impacts: ecoregional summaries

Northern North Sea (Region 1)

The northern North Sea was, until recently, a cold-boreal province. However, after the late 1980s regime shift, the northern North Sea is now considered a 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 (species numbers) 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 NAO index, while post 1990 biodiversity patterns appear to have been more influenced by local SST. 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 the Marine Scotland Scottish Coastal Observatory (SCOs) monitoring site at Stonehaven in the coastal north-western North Sea, show large interannual variation in the abundance of plankton. Due to the length of this time-series it is difficult to attribute climate change directly to these observed changes. However, some of these more-localised changes do show similarities with the offshore data collected by the CPR survey. A low diatom abundance was observed from 2001–2004 particularly during the spring bloom period (Bresnan *et al.*, 2009, 2015a). Diatom cell densities subsequently increased for a period since 2005 with *Skeletonema* becoming more abundant during some years. A decrease in the abundance of the summer thecate dinoflagellate *Triplos* has been observed since 2000, but has latterly begun to recover (Bresnan *et al.*, 2016). This is in line with patterns observed in the open northern North Sea by the CPR. A study examining the diversity of the ecologically important diatom *Pseudo-nitzschia* in the North Sea has highlighted diversity differences in the community at a species level between the monitoring site at Stonehaven and that in Helgoland in the southern North Sea (Bresnan *et al.*, 2016).

A strong seasonal signal typical of northern latitudes has been observed in the zooplankton community at Stonehaven (Fanjul *et al.*, 2017, 2018) with timing of the spring diatom bloom having a strong influence in shaping the seasonal signal (Fanjul *et al.*, 2017). The two *Calanus* copepod species, *Calanus finmarchicus* and *Calanus helgolandicus*, show different seasonal dynamics: *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 present at very low levels during the winter and there is a small spring increase in abundance during April–May. These copepodite stages then decline rapidly so that the overwintering numbers are very low (Bresnan *et al.*, 2016).

Considerable interannual variability has been observed in the abundance of both *C. finmarchicus* and *C. helgolandicus* at the Stonehaven monitoring site. Numbers of *C. finmarchicus* have been generally low, but the annual average increased since monitoring began in 1997 until 2013. 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. This is similar to patterns observed in the CPR time-series.

Calanoid copepods are an important food source for the ecologically important sandeel (*Ammodytes marinus*). The synchrony between egg production of *C. helgolandicus* and sandeel hatching has been observed to be an important factor in early larval development which influences year-class strength in this region (Regnier *et al.* 2017). Sandeel abundance in turn influences kittiwakes breeding success however analysis of a 12-year time-series study from this region shows there are some years where this relationship does not hold (Eerkes-Medrano *et al.*, 2017).

Southern North Sea (Region 2)

The plankton community of the southern North Sea primarily consists of 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 ecological shift. Although some localised coastal areas in this region may be affected by eutrophication, this is primarily a problem in inshore coastal waters. 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) (Edwards *et al.*, 2016). 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 (Edwards and Richardson 2004). There has been a general decline in small copepods in this region over the last few years.

Eastern Channel (Region 3)

The Eastern English Channel is characterised by strong tidal currents and shallow bathymetry, leading to well-mixed water columns. There is also substantial freshwater influence, particularly from rivers emanating from the French coast. These influences contribute to the relatively high proportion of benthic larvae in the plankton. Delavenne *et al.* (2013) produced a pelagic habitat typology for the Eastern Channel, producing seven water masses for each of the four seasons of the year. These classifications, based on physical variables, phytoplankton, zooplankton and pelagic fish, reflected the relative stability of the French waters and the central part of the Eastern English Channel, relative to the waters of the Dover strait and the English coastal waters. While regular inshore sampling to monitor phytoplankton and nutrients exists along the Eastern Channel coasts (e.g. Hernández-Fariñas *et al.*, 2014), few fixed point, long time-series data are available from which to determine the responses of plankton to multidecadal environmental change. One such suitable time-series is the inshore time series at Gravelines, located near the Western Port of Dunkirk. Sampling with a standard methodology shows sub-decadal cyclicity but no clear trends in plankton abundance possibly due to the short length of the time-series study.

Climate change may also modulate the spread and establishment of resident population of harmful invasive species. For example, Antajan *et al.* (2014) reported the establishment of the comb jellyfish *Mnemiopsis leidyi* along ports along the French Channel coast that dated from 2005. This species has yet to become established along the northern side of the English Channel and the anthropogenic and climate change and influences on the spread of this predator is an active area of research (Jaspers *et al.*, 2018).

Western Channel and Celtic Sea (Region 4)

These waters are more substantially influenced by oceanic waters than the eastern Channel and are typically seasonally stratified, although regions of relatively low surface temperatures in summer indicate areas of enhanced tidal mixing, for example south of Ireland, north of Brittany and west of Cornwall. Nutrient concentrations are depleted substantially during the growth season and indeed recent cruises to the Celtic sea have shown that iron concentrations can approach limiting levels in the Celtic Sea (Birchill *et al.*, 2017).

Long-term, full-depth observations of plankton exist at a series of monitoring sites collectively known as the ‘Western Channel Observatory’ (<https://www.westernchannelobservatory.org.uk/>) south of Plymouth and since the Edwards *et al.* (2013) MCCIP report these have exhibited a continued increase in surface- and near-seabed-water temperature, punctuated by the relatively cold period around 2010. This general warming mirrors the long timescale (over ~30 year) warming trend observed across the North Atlantic (O’Brien *et al.*, 2017). Several long-term datasets from Plymouth stations L5 and E1 have been used to consider long-term climate

related changes in zooplankton and fish larvae populations. McManus *et al.* (2016) examined a multidecadal cycle in multiple components of the pelagic food web known as ‘the Russell Cycle’ (Cushing and Dickson, 1976) in relation to the Atlantic Multidecadal Oscillation (AMO) and the North Atlantic Oscillation (NAO). Likewise, Blackett *et al.* (2014) examined long-term data for two relatively warm water siphonophore species and found that establishment of resident populations dated from the late 1960s. These studies provide further evidence for the climatic warming of water temperature as a key factor in the biogeographical scale redistribution of species.

In addition to biogeographical adjustments to climatic warming, phenological adjustments (changes in seasonal timing) can be envisaged as a mechanism by which species can adjust to changing temperatures *in situ* (Beaugrand *et al.* 2014). However, trophic levels may respond to different timing cues, for example spring phytoplankton blooms may be triggered by changes in photoperiod and underwater light (Ji *et al.*, 2010, Wiltshire *et al.*, 2008), whereas their zooplankton grazers may respond more closely to temperature (Mackas *et al.* 2012). This has led to concerns that a warming climate may lead to differential timing shifts between trophic levels and a desynchronisation of the food web (Richardson, 2008). The weekly resolution data at Plymouth L4 was used to examine this in a stratifying coastal shelf site where weekly resolution sampling was possible (Atkinson *et al.*, 2015). Only a minority of species showed strong shifts in phenology and even for these, mismatches with food increases did not clearly penalise the grazer. Two factors appeared to provide resilience to this mismatching. First, food concentrations were relatively high throughout the year, enabling species with diverse diets to be partially immune from timing shifts. Second, mortality strongly shaped the phenology of species (Cornwell *et al.* 2017), obscuring the phenology shifts observed.

Zooplankton populations can be modified both directly through temperature and indirectly through climatic effects on their phytoplankton food sources. At the Plymouth L4 site the phytoplankton community displays large inter-annual variability and strong seasonal patterns (Widdicombe *et al.*, 2010). Twenty three years (1993–2015) of data show diatoms have increased during the autumn and declined significantly during the winter while annual averages do not show significant change. Conversely, coccolithophores have also increased significantly during the autumn, but not at other times or between years. *Phaeocystis* was routinely found, albeit in low numbers, during the autumn until 2002 when it disappeared until reappearance in 2013. These changes suggest a recent revival of the autumn bloom in the western English Channel. Dinoflagellate numbers have not changed significantly and are highly variable between seasons and years. Despite this, a slight increase in the overall proportion of diatoms relative to dinoflagellates is in line with findings based on CPR data across the North-East Atlantic and North Sea (Hinder *et al.* 2012). However, an almost 10-fold change in the mean biomass of both diatoms and dinoflagellates that can occur between successive years

at L4 (Atkinson *et al.* 2015) means that evidence of a long-term change is not conclusive, especially when based on annual averages as subtle changes can occur seasonally. For example, the dinoflagellate *Triplos* has been increasing at Station L4, which is in contrast with observations from the Stonehaven time-series in the north western North Sea where *Triplos* populations are recently recovering after a 10-year decline since 2000.

Unusual species have been recorded in the western English Channel in recent years. A raphid diatom *Plagiolemma distortum* (Nézan *et al.*, 2018), was first observed off the southern coast of Brittany in December 2014 and later in the Celtic Sea and at Station L4 during winter and spring (Kraberg *et al.*, 2018). Subsequent investigations found further records dating back to 1992 in the southern North Sea and eastern English Channel. To date, *P. distortum* has not been recorded in the northern North Sea suggesting this taxa is thus far restricted in its distribution. *Asteromphalus sarcophagus* and *A. flabellatus* were also found during winter months at Station L4 and the effects of climate warming and increased turbulence through winter storms could influence phytoplankton diversity in the future.

Preliminary analysis of 30-year zooplankton trends at Station L4 suggests a decline in several major small copepod species and increases in benthic larvae. This is in line with the wider scale trends in declining small copepods (Edwards *et al.*, 2013). The benthic larvae increase to partially replace copepods at L4 parallels the general pattern found in the North Sea by Kirby *et al.* (2008). Gelatinous and semi-gelatinous predators have increased slightly at L4 over the last three decades, such that the mean carbon content (carbon mass as a percentage of wet mass) in recent years is around 5%, as compared to about 7% three decades ago (McConville, 2017). Again, this is in line with the notion of multidecadal cycles for larger jellyfish species based on data from fisheries surveys in the Irish and North Seas (Lynam, 2011).

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 shown signs of eutrophication such as: (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 (Gowen *et al.*, 2000).

The main zooplankton grazers comprise small zooplankton species (*Pseudocalanus*, *Temora* and *Acarita*) with *Oithona* peaking in the summer months. Species of *Calanus* recorded are believed to be as a result of oceanic intrusions (Scherer *et al.*, 2016). Increases in the number of jellyfish were observed from 1994–2009 (Lynam *et al.*, 2011).

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 SCObs monitoring station in Millport has been included in this report. The phytoplankton community was monitored at this site between 2005 and 2013. While the phytoplankton community in this area showed regional differences in the timing and composition of the spring diatom bloom compared with other monitoring sites, the time-series study is too short to identify climate-related signals (Bresnan *et al.*, 2016). In contrast to sites in region 6, the autumn diatom bloom is largely absent from this site. The development and positioning of frontal systems have been seen to influence the spatial distribution of some phytoplankton species in this regional sea (Paterson *et al.*, 2017).

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 Harmful Algal Bloom (HAB) monitoring in coastal areas, this region as a whole is poorly monitored (also see Figure 1 for CPR sampling). Investigation of the phytoplankton community in Loch Creran has shown changes in the microplankton community including a decrease in the abundance of diatoms during the spring bloom period. This is believed to be due to changes in rainfall patterns and intensity in area since the 1980s (Whyte *et al.*, 2017). Marine Scotland has been operating a SCObs monitoring site since 2003 in Loch Ewe. 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 during 2005, and a similar pattern of decrease and subsequent recovery of the thecate dinoflagellate *Triplos* has also been observed (Bresnan *et al.*, 2015b, 2016). In general, due to the length of this time-series in this region, it is difficult to attribute climate change directly to these observed changes.

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. Marine Scotland has operated a SCObs monitoring

sites 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 dinoflagellate *Tripos* 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. At the Orkney site, a decrease in the abundance and subsequent recovery of the dinoflagellate *Tripos* has also been recorded. Similarly to Region 6, due to the length of this time-series in this region it is difficult to attribute climate change directly to these observed changes. However, the CPR survey also monitors offshore regions in this area which does show changes to the plankton community are related to climate-change impacts. This region is a particularly productive shelf system, especially around the Orkney and Shetland Islands.

Atlantic North-west 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 is 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 (Beaugrand *et al.*, 2009). 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. Plankton studies in this area are scant and mostly as a result of one-off cruises. Differences in the phytoplankton community composition and abundance has been observed on and off the shelf edge (Fehling *et al.*, 2012, Siemering *et al.*, 2016).

The Faroe–Shetland area is more complex. The upper 500 m 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 600 m 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 euphausiids 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 North-West Scottish shelf when they migrate back to the surface waters in the spring. Similarly, to Regions 6 and 7, due to the length of this time-series in this region, it is difficult to attribute climate change directly to these observed changes. However, the CPR survey also monitors offshore regions in this area which does show changes to the plankton community are related to climate change impacts (see ‘Plankton and climate change impacts: the North Atlantic wide context’, above).

Marine Microbes

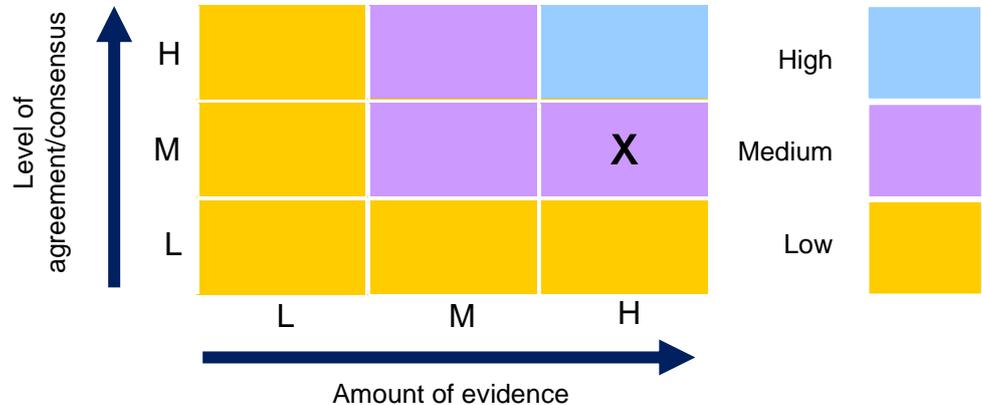
The very small component of the marine plankton community (nano plankton 2–20 µm diameter, picoplankton 0.2–2 µm diameter, marine bacteria and viruses) are poorly monitored. Their very small size and rapid generation times mean that they have the potential to act as early indicators of climate change. Routine monitoring of this component of the plankton community in the UK is scant with the most sustained measurements being made at L4 (Tarran and Bruun, 2015 revealing a distinct seasonality. New technologies are allowing previously unexplored components of the marine ecosystem to be explored on a broader scale, e.g. genetic diversity of marine viruses (Garin-Fernandez *et al.*, 2018), fungi (Stern *et al.*, 2015, Taylor and Cunliffe, 2014) etc. This knowledge gap needs to be filled if the impacts of climate change on the marine environment are to be fully understood.

2. WHAT IS ALREADY HAPPENING?

In summary, in the North Atlantic, at the ocean basin scale and over multidecadal periods, changes in plankton species and communities have been impacted by climate change with strong correlations with the Northern Hemisphere Temperature (NHT), 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 (e.g. AMO and NAO index) and the other due to forced anthropogenic warming (Harris *et al.*, 2014). These have included changes in species distributions and abundance, the occurrence of subtropical 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.*, 2009; Edwards *et al.*, 2010; Edwards *et al.*, 2013; Beaugrand *et al.*, 2019). More recently, these changes have also 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 (Reid *et al.*, 2007; Beaugrand *et al.*, 2010).

What is already happening



3. 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 years), affecting ecosystem services such as oxygen production, carbon sequestration and biogeochemical cycling (20–50 years). These changes may place additional stress on already-depleted fish stocks as well as have consequences for mammal and seabird populations. Currently the distributions of plankton organisms are moving northwards at an average rate of ~23 km per year, although the rates of individual species vary substantially (Beaugrand *et al.*, 2009).

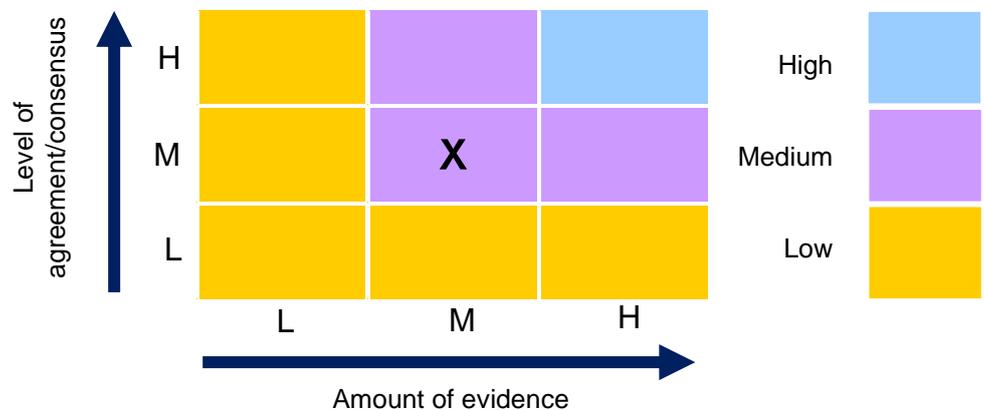
Ocean acidification may become a problem in the future (20–100 years) and has the potential to affect the process of calcification. Therefore, certain taxa such as molluscs and other calcifying organisms of the plankton may be particularly vulnerable to CO₂ emissions. Potential chemical changes to the oceans and their effects on the marine biology could reduce the ocean’s ability to absorb additional CO₂ from the atmosphere, which in turn could affect the rate and scale of global warming.

Warming and potentially acidification will increase the risks to natural carbon stores and carbon sequestration. As temperature increases, the geographical distribution of primary and secondary plankton production is likely to be impacted, effecting ecosystem services such as oxygen production, carbon sequestration and biogeochemical cycling (10–100 years). 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 processes 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 (Beaugrand *et al.*, 2010). 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.

Risks to species and habitats and opportunities for new organisms to become established. Recent evidence from the CPR survey also suggests an increase in pathogenic organisms such as *Vibrio* in UK waters related to warming temperatures (Vezzulli *et al.*, 2011). Continued warming will allow new species colonisations as well as potential new pathogens and Harmful Algal Bloom species.

What could happen in the future?



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

4. KEY CHALLENGES AND EMERGING ISSUES

Priority challenges

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

- Identifying species and habitats particularly vulnerable or resilient to climate change impacts and separating the impacts of climate from other anthropogenic pressures such as nutrients.
- Understanding the risks to species and habitats and the potential opportunities for new species colonisations as well as potential new pathogens and Harmful Algal Bloom species.

Emerging issues

- Understanding the risks caused by warming temperatures and acidification on native marine organisms.
- Understanding the processes involved in the biological pump (plankton draw-down of atmospheric CO₂) and understanding future changes (risks to natural carbon stores and carbon sequestration).
- Understanding the rate of genetic adaptation to climate change impacts.

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