



Large bio-geographical shifts in the north-eastern Atlantic Ocean: From the subpolar gyre, via plankton, to blue whiting and pilot whales

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ABSTRACT

Pronounced changes in fauna, extending from the English Channel in the south to the Barents Sea in the north-east and off Greenland in the north-west, have occurred in the late 1920s, the late 1960s and again in the late 1990s. We attribute these events to exchanges of subarctic and subtropical water masses in the north-eastern North Atlantic Ocean, associated with changes in the strength and extent of the subpolar gyre. These exchanges lead to variations in the influence exerted by the subarctic or Lusitanian biomes on the intermediate faunistic zone in the north-eastern Atlantic. This strong and persistent bottom-up biophysical link is demonstrated using a numerical ocean general circulation model and data on four trophically connected levels in the food chain – phytoplankton, zooplankton, blue whiting, and pilot whales. The plankton data give a unique basin-scale depiction of these changes, and a long pilot whale record from the Faroe Islands offers an exceptional temporal perspective over three centuries. Recent advances in simulating the dynamics of the subpolar gyre suggests a potential for predicting the distribution of the main faunistic zones in the north-eastern Atlantic a few years into the future, which might facilitate a more rational management of the commercially important fisheries in this region.

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1. Introduction

The north-eastern North Atlantic ecosystem is characterised by cold *subarctic* fauna within the subpolar gyre, warm *Lusitanian* fauna from the Bay of Biscay (Fraser, 1958) and, between these, a cold-temperate *boreal* fauna in the mixing area west of the British Isles and south of Iceland (Ekman, 1953). The faunistic boundaries are, however, ill-defined because of very strong annual and inter-annual temperature variability in the boreal region. The cold and warm flanks of the boreal zone are here referred to as *Arctic-boreal* and *Lusitanian-boreal* respectively (Ekman, 1953).

Shifts between Lusitanian and boreal regimes near the Western English Channel (Fig. 1) have previously been described by the so-

called Russell cycle (Russell et al., 1971). This cycle showed an increased influence of Lusitanian waters in the Channel between 1925 and 1935 with a reversal to a more boreal dominated ecosystem between 1965 and 1975 (Southward, 1980). A major northward and westward expansion of the boundary between the subarctic and the boreal zones was also documented during the period 1925–1935, with an influx of several boreal fish species into both Icelandic (Fridriksson, 1949) and Greenlandic (Tåning, 1948) waters. Several of the ecosystem changes observed during the 1920s and 1930s in the northern North Atlantic appear to have repeated themselves in recent years (Drinkwater, 2006). After 1995, many new fish records and the detection of rare southern species were reported in Icelandic (Astthorsson and Pálsson, 2006) and Faroese (Rógvi Mouritsen, personal communication, 2008) waters. Similarly, the marked northward expansion of pipefish into the

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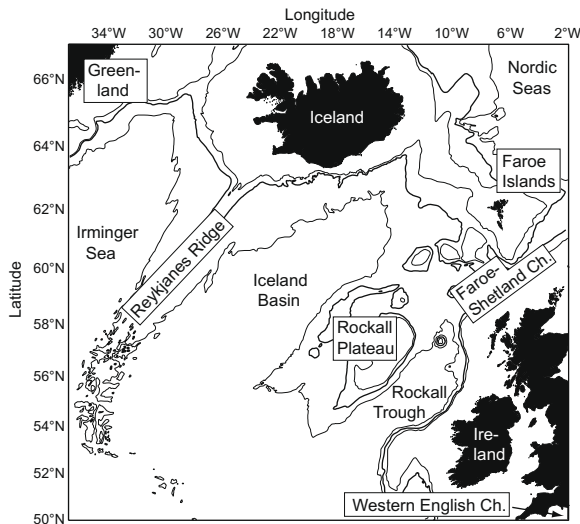


Fig. 1. Map of the north-eastern Atlantic Ocean. The 500 m, 1000 m (thick line) and 2000 m isobaths are shown.

North and Nordic Seas (Kirby et al., 2006) illustrates post-1995 changes in the distribution of warmer water fish species.

The physical oceanography of this region is dominated by the dynamics of the North Atlantic subpolar gyre; a large counter-clockwise rotating body of relatively cold and low-saline subarctic water in the central northern North Atlantic (Fig. 2). During the early 1990s the circulation of the gyre was intense, but declined substantially after 1995 (Häkkinen and Rhines, 2004), leading to a rapid warming and salinification of the north-eastern Atlantic (Hátún et al., 2005b). These changes had a particularly large imprint in the Iceland Basin (Hátún et al., 2005b) (Fig. 2), where the cold and fresh subarctic water masses (Bersch, 2002; Pollard et al., 2004) were replaced by warmer and more saline water masses from the south (Bersch et al., 2007).

It is tempting to suggest that these simultaneous physical and ecological changes are related. Such links have been reported previously, e.g. half century-long time series of the biomass of saithe in Faroese waters (Steingrund and Hátún, 2008) and puffin catches in Iceland (Freydís Vigfúsdóttir, personal communication, 2008) have both been related to the dynamics of the subpolar gyre, although the causal mechanisms have not, as yet, been clarified. Any such link between the marine climate and biota is likely to involve phytoplankton and zooplankton, the basic food resource for all higher marine ecosystems. Phytoplankton abundance in the off-shore waters between Iceland and the Faroe Islands are known to have declined during the period from the late 1950s to 1995 (Reid

et al., 1998). The subpolar front, which outlines the periphery of the subpolar gyre, acts as a boundary for several copepod taxa (Gaard et al., 2008) and large shifts of this front are therefore likely to lead to changes in copepod communities. However, little is known about the long-term variability of the zooplankton community in the waters south of Iceland.

Such changes in the plankton community have consequences for organisms at higher trophic levels, e.g. planktivorous fish, such as the small pelagic gadoid, blue whiting (*Micromesistius pouassou*). This large fish stock spawns west of the British Isles and migrates past the Faroe Islands to its main feeding grounds in the Nordic Seas (Bailey, 1982) and is of considerable importance for both regional fisheries and as a food source for piscivorous fish, squid, seals, and pilot whales. The blue whiting stock biomass tripled in the late 1990s due to a succession of good recruitment years after 1995 (ICES, 2007), but little is known about the underlying causes of these changes.

At even higher trophic levels, piscivorous species such as the long-finned pilot whale (*Globicephala melas*), may also be influenced by changes in food availability. This species occurs year-round in Faroese waters, where it feeds primarily on the squid species *Todarodes sagittatus* and *Gonatus* sp., and blue whiting when squid abundances are low (Desportes and Mouritsen, 1993). Squid, in turn, also prey heavily on blue whiting in the north-eastern Atlantic (Gaard, 1988). The number of pilot whales landed in the Faroe Islands has previously been related to both the biomass of blue whiting in the Norwegian Sea during the

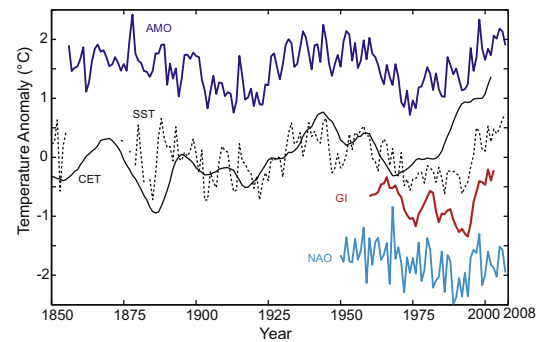


Fig. 3. Climate indices. Annual averages of: the Atlantic Multi-decadal Oscillation (AMO) (Enfield et al., 2001), the SST west of the British Isles (Rayner et al., 2006) (see text), the inverted gyre index (GI) (Hátún et al., 2005b) and the North Atlantic Oscillation (NAO, inverted) (<http://www.cdc.noaa.gov>) are shown. The Central England Temperature (CET) (Parker and Horton, 2005) during the spring months March and April has been plotted over the SST series. The CET is low-pass filtered using an 8-year filter width. The two temperature time series (black) are to scale, the others are not.

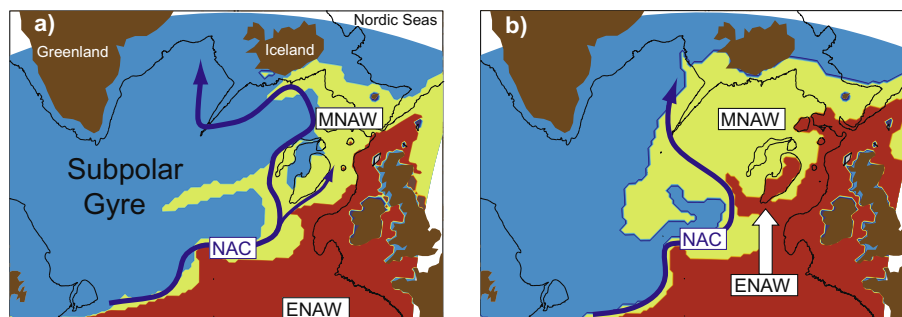


Fig. 2. Water masses. Simulated upper layer (Hátún et al., 2005b) temperatures in the northern North Atlantic Ocean. Annual averages for a cold period (a, 1993) and a warm period (b, 1998) are presented to highlight the large shift taking place. Red and blue colours represent temperatures above 9 °C and below 7 °C, respectively. The green colour represents intermediate temperatures, which in the region south of Iceland illustrates the distribution of Modified North Atlantic Water (MNAW). The currents associated with the eastern rim of the subpolar gyre – the North Atlantic Current (NAC) and its continuation – are indicated by dark blue solid arrows. The white open arrow west of Ireland represents northward advection of relatively warm and saline water of subtropical origin (Eastern North Atlantic Water, ENAW). The 1000 m isobath is shown.

period 1980–1992 (Hoydal and Lastein, 1993) and to the variability of sea surface temperatures (Zachariassen, 1993), but the causal explanations for these possible links remain vague.

The North Atlantic subpolar gyre (Fig. 2), as characterised by the gyre index (Häkkinen and Rhines, 2004; Hátún et al., 2005b) (Fig. 3), is the ‘red thread’ in this work, linking together disparate observations into a coherent whole. The index is calculated from sea surface heights in the northern North Atlantic Ocean, reflecting both the composition of water masses and the associated currents. Using this framework, we illustrate potential links between the physical climate and the reported ecosystem changes by inspecting four trophic levels that *a priori* are expected to be trophically connected. Output from a numerical general circulation ocean model illustrates the principal spatial and temporal variability of the physical climate in the north-eastern Atlantic from 1960. These patterns are extended back in time using observed sea surface and air temperatures as proxies (Section 2.4). Comparable spatio-temporal variability in both phytoplankton and zooplankton abundances is illustrated using data from the Continuous Plankton Recorder (CPR) survey (Reid et al., 2003) (Section 3.1). Using fishery statistics, similar patterns of variability are also identified in the blue whiting stock, albeit for more limited spatial and temporal scales (Section 3.2). Unique data on pilot whale occurrence around the Faroe Islands are used to illustrate comparable patterns back to the early 18th century (Bloch, 1994) (Section 3.3). Taken together, these data sources, from four different trophic levels, show a strong and persistent ‘bottom-up’ influence of the North Atlantic subpolar gyre throughout the north-eastern Atlantic ecosystem.

1.1. Hydrographic shifts in the Iceland Basin

The volume of cold and low-saline water of the subpolar gyre in the Iceland Basin is highly variable (Fig. 2). Immediately east of these subarctic water masses resides Modified North Atlantic Water (MNAW) (Hansen and Østerhus, 2000) – a mixing product of water from the North Atlantic Current (NAC) and warmer and more saline Eastern North Atlantic Water (ENAW) from the inter-gyre Biscay region (Ellett et al., 1986). Subarctic water is also found to the south of the Rockall Plateau (Wade et al., 1997), but the eastward extension of this limb of the subpolar gyre varies. During some periods, this limb approaches the European continental shelf where it constricts the northward flow of the warmer eastern waters.

The subpolar gyre regulates the water mass structure in the Iceland Basin in two ways. When the gyre weakens, it retracts its cold and fresh subarctic waters out of the Iceland Basin, which are then immediately replaced by the much warmer and more saline MNAW (Fig. 2b). The retracting gyre also opens up the ‘window’ for increasing northward penetration of the warm and saline eastern waters, which causes a warming and salinification of the MNAW itself (Hátún et al., 2005b).

The interface between the subarctic waters and the Atlantic water masses defines the subarctic front and thus the flow path of the NAC (blue solid arrows in Fig. 2). The quantity of subarctic water south of the southern tip of the Rockall Plateau (see Fig. 1) varies from nil to significant (Wade et al., 1997). When subarctic water is present at this location, a large proportion of the NAC flows into the Rockall Trough and along the eastern side of the Rockall Plateau, embedding the plateau in subarctic water masses (Fig. 2a). When, on the other hand, the subarctic boundary is located farther west and the NAC mainly flows along the western side of the Rockall Plateau, both the plateau and the region south of Iceland are flooded with warmer and more saline MNAW (Fig. 2b). Due to the splitting of the NAC around the Rockall Plateau, subtle changes in its flow path can cause large and rapid shifts in the marine climate on and around the Rockall Plateau and in the Iceland Basin. Such changes were responsible for e.g.

the large mid-1990s warming and salinification in this region, as indicated by the gyre index (Fig. 3) (Hátún et al., 2005b).

The subpolar gyre has probably regulated the marine climate in the north-eastern North Atlantic throughout the Holocene (~11,700 years ago to present) (Thornalley et al., 2009), which indicates that this is a fundamental and stable link.

2. Methods

To study the wide-spread bio-physical changes described here, it is necessary to use multi-dimensional (spatio-temporal) datasets. Prior to analysis, all data were standardized into a three-dimensional format: latitude, longitude and time (annual or seasonal). Some of the data are natively three dimensional (e.g. sea surface temperature), while in other datasets the depth dimension has been averaged out where relevant (e.g. the simulated temperature and salinity fields).

2.1. Handling spatio-temporal data

Extracting time series or indices from multi-dimensional data requires some form of geographical decomposition. Where available data was sparse, all data points were averaged for a pre-selected region. The weakness of this approach is that the limited knowledge of the studied variable can lead to an inappropriate selection of the area over which to average, so this approach was only used when absolutely necessary. For more complete spatial and temporal datasets, multivariate statistics (e.g. Principal Component Analysis, PCA) (Preisendorfer, 1988) have been used to decompose the data into *modes* of variability. Each mode consists of a spatial pattern (mapping of eigenvectors) and a time series (principal component), and the major variability in the original data presented here resides in the two leading modes. These leading modes likely represent true natural variability modes residing in the data. The time series associated with these modes are therefore extracted without having to subjectively select an area beforehand, and the spatial patterns identify the geographical impact the relevant physical process.

The aforementioned ‘gyre index’ originates from such an analysis. The physical changes depicted in Fig. 2 are characterised by a so-called ‘gyre mode’ of variability, previously obtained by applying a PCA to the sea surface height (SSH) field in the northern North Atlantic (Häkkinen and Rhines, 2004; Hátún et al., 2005b). The gyre index is the first principal component (time series) from this analysis (Fig. 5a). The gyre mode is associated with especially large SSH changes, and thereby changes in circulation, in the Iceland–Irminger basins (Fig. 6a). Dominance of cold and fresh subarctic water in the Iceland Basin (Fig. 2a) is associated with a high index value (implying a strong gyre circulation) and dominance of warmer and more saline MNAW (Fig. 2b) is associated with a low index (weak gyre). The gyre index is consistently plotted inverted in this paper because a low index is associated with high values of most of the discussed parameters (except for the copepod *Calanus finmarchicus*).

An analogous gyre mode based on the important ecological correlate sea surface temperature (SST) (Beaugrand et al., 2002b), instead of SSH, revealed temporal variability that closely follows the gyre index (reproduced in Fig. 5b), and a spatial pattern that outlined the shape of the subpolar gyre (Fig. 6b), thereby highlighting the strong link between these two variables.

The studied biological parameters are not chosen randomly, but based on an *a priori* expectation of correspondence with the previously demonstrated changes in the marine climate (Beaugrand et al., 2002b; Hátún et al., 2005b). While each individual source does not provide conclusive evidence in support of our hypothesis, taken

Table 1

Correlation coefficients between the gyre index and four ecologically important taxa, averaged over the rectangle shown in Fig. 9a.

Species	Correlation coefficient
<i>Acartia</i> spp.	−0.64
<i>Para-pseusocalanus</i> spp.	−0.69
<i>Pseudocalanus elonginatus</i> adult	−0.67
<i>Oithona</i> spp.	−0.64

together, this material gives a consistent picture of a bottom-up regulation exerted by the subpolar gyre. Due to the disparate datasets (e.g. different requirements for low-pass filtering) we only calculate correlation coefficients when the time series are not plotted (Table 1).

2.2. Climate indices

The gyre index is associated with the Atlantic Multi-decadal Oscillation (AMO) and the North Atlantic Oscillation (NAO), but there are important differences. The AMO signal is defined from SST variability in the North Atlantic, with a clear imprint over the subpolar gyre. The AMO index (Enfield et al., 2001) does not show the general downward trend from the early 1960s to 1995, followed by a sharp reversal, as is seen in the gyre index (Fig. 3). The NAO, defined as the difference of sea-level pressure between the Icelandic Low and the Azores high, is associated with the strength of westerly winds across the northern North Atlantic (Hurrell, 1995), and thus with the atmospheric forcing of the subpolar gyre (Eden and Willebrand, 2001). The annual NAO index (<http://www.cdc.noaa.gov>) does show a general increase in the Westerlies from the early 1960s to the mid-1990s, followed by an abrupt weakening in the winter 1995/96. Since the late 1990s, the NAO index has remained around average values, and has not reversed completely back to the state of the 1960s, as the gyre index has done (Fig. 3, note inverted NAO index).

2.3. Ocean general circulation model (OGCM)

An OGCM was used to depict the large oceanographic changes taking place in a way that cannot be matched by observational data. The Nansen Center version (Bentsen et al., 2004; Drange et al., 2005) of the MICOM (Miami Isopycnal Coordinate Ocean Model) (Bleck et al., 1992) was used, forced with daily mean NCEP/NCAR (Kalnay et al., 1996) reanalyses of fresh water, heat, and momentum fluxes for the period 1948–2003. This regional model covers the North Atlantic Ocean and Nordic Seas (30°N–78°N) with a grid spacing of about 20 km in the north-eastern Atlantic. Boundary conditions were obtained from an equivalent global model that has half the horizontal resolution, but identical vertical resolution (25 isopycnic layers and a mixed layer). The model has previously been found to realistically represent the temporal evolution of the circulation and hydrography in the North Atlantic subpolar gyre (Hátún et al., 2005a,b), and has been used to explore the sensitivity of the ocean circulation in the region to the actual ocean initial state and the atmospheric forcing (Lohmann et al., 2008, accepted for publication).

2.4. Long-term SST proxies for the gyre index

So as to avoid artefacts during the ‘spin-up’ phase of the OGCM, it was only possible to extend the gyre index back to 1960 (Hátún et al., in press). Other climatic indices with longer available time series can be used to characterise the gyre dynamics further back in time in place of the gyre index. As noted above, the gyre index

is closely related to SST over the north-eastern Atlantic and this parameter has therefore been used as a proxy. A SST time series was obtained from the Hadley Centre SST dataset (HadSST2) (Rayner et al., 2006), by averaging over a geographical box covering the region (52.5°N–62.5°N, 27.5°W–12.5°W) and all months in the year (Fig. 3), back as far as the end of the 19th century. To infer the state of the gyre even further back in time, a second alternative proxy is required. The Central England Temperature (CET) (Parker and Horton, 2005) during the spring months March and April represents the Hadley Centre SST series fairly well until around 1980 (Fig. 3) when the relationship breaks down, possibly due to anthropogenic warming (IPCC, 2007). Deep surface mixing takes place in the Rockall Trough during this season and the atmosphere is thus in direct contact with the deeper water masses. The CET series extends back to 1659 and is used as a coarse measure when assessing the very long-term (centennial) changes potentially related to the subpolar gyre.

2.5. Plankton

Plankton data were obtained from the Continuous Plankton Recorder (CPR) survey (Batten et al., 2003; Reid et al., 2003). The survey is a monitoring programme that uses the CPR sampling machine towed at ~10 m depth behind ships of opportunity on standard routes. The plankton sampled represent well the first 20 m of the water column and thus provide a summary picture of the epipelagic zone. Each CPR sample corresponds to 10 nautical miles (~18.5 km) sections of the track followed by the ship and a filtered volume of ~3 m³ of seawater (Warner and Hays, 1994).

2.5.1. Phytoplankton Colour data

Phytoplankton Colour is a visual estimate of chlorophyll, determined from the colour (‘greenness’) of the filtering silks of the CPR survey (Raitsos et al., 2005), and is considered to provide a semi-quantitative estimate of plant biomass in the sea (Reid et al., 1998). The Phytoplankton Colour Index (PCI) has been intercalibrated with satellite based SeaWiFS Chl-a data for the period 1997–2002 and was shown to be significantly correlated at the seasonal scale (Raitsos et al., 2005).

2.5.2. Zooplankton data

The numbers of specimens of each zooplankton taxonomic group present on each section of the filtering silks are recorded and identified by the CPR analysts. Data for adult *C. finmarchicus* (copepodite stages C5 and C6), *Acartia* spp., *Para-pseusocalanus* spp., *Pseudocalanus elongates*, and *Oithona* spp. were used in this study. In addition, a time series dataset was derived for the cold-temperate species assemblage using the methods of Beaugrand et al. (2002a). This assemblage includes the species *Aetideus armatus*, *Pleuromamma robusta*, *Acartia* spp., and *Metridia lucens*.

2.5.3. Spatio-temporal CPR data

The CPR data are highly heterogeneous in space and time. Spatial interpolation using the inverse squared distance method (Lam, 1983) was applied to obtain gridded datasets for further analysis (data were omitted from the analyses for years that were sampled for less than 8 months and for pixels with more than 20 missing years). Temporal variability has been extracted from the gridded plankton data in two ways: (1) by applying standardized (spatialized) PCA (Beaugrand, 2003) (for *C. finmarchicus* and Phytoplankton Colour) and (2) by means of spatially averaging over a pre-selected region (the warmer water copepod species), by using the CIMOTS procedure (Copepod Indicator Monitoring Toolbox System – an averaging procedure that takes into account the

heterogeneity of the CPR sampling in space and time and diel vertical migration of zooplankton (Beaugrand and Ibanez, 2004; Beaugrand, 2004a)).

The spatial PCA patterns presented (Fig. 6c and d) are constructed using a less restrictive threshold that requires more than 30 missing years before pixels are removed from the analysis. This approach is taken to get a broader view of the spatial patterns, which also includes the Iceland–North America CPR line. The eastern domains of these spatial patterns are very similar to those obtained from the more restrictive analysis, and from where the principal components presented are derived.

2.6. Blue whiting catch statistics

Under the NEAFC (North-Eastern Atlantic Fisheries Commission, <http://www.neafc.com>) scheme, vessels report their landings. Annual summaries for national fleets are submitted by contracting parties to the Convention and this information is shared via the NEAFC Secretariat's database. The blue whiting catch statistics applied here are obtained from this database. The data are available as monthly values of the total catch gridded onto 0.5° latitude \times 1° longitude rectangles and differentiated by national fleet.

The period when the migrating post-spawning blue whiting are in Faroese waters is decisive for the northward migration pathway (Hansen and Jákupsstovu, 1992). The Faroese pelagic fleet is highly active during this phase and this fleet has, furthermore, not been limited by political regulation in the Iceland–Faroe region during the reported period, 1980–2007. The catches exclusively from this fleet are thus used to assess the temporal variability of the blue whiting migration pattern (Hansen and Jákupsstovu, 1992) and the fish density in the Iceland–Faroe region.

2.7. Pilot whale catches

A time series of long-finned pilot whale catches in the Faroe Islands exists back to 1584 and is unbroken from 1709 (Bloch, 1994). For every catch, the datasets contain information about the date, location, and number of whales taken. The catch efficiency may have varied for various reasons (e.g. changes in demography, fishing activity, and improvements in vessel and communication technology), but this is not expected to seriously affect the reliability of the data (Bloch et al., 1990; Zachariassen, 1993). The schools of pilot whales are caught by being driven into authorised whaling bays. A grouping of the whaling bays into a north-eastern (N-E) group and a south-western (S-W) group has previously been found appropriate when relating the whale catches to environmental variables (Zachariassen, 1993). The N-E and S-W groups represent, in the long-term average, similar numbers of whale catches.

3. Results

3.1. Plankton

Plankton variability in the north-eastern Atlantic appears to be linked to the physical *gyre mode* in the North Atlantic, as seen in a PCA of both the Phytoplankton Colour and the *C. finmarchicus* data from the CPR survey. The *gyre mode* is here used as a common term for both the physical and biological modes. From the PCA of SST, phyto- and zooplankton, the *gyre mode* appears as the second statistical mode, while the first mode is associated with changes near the European shelf seas (Fig. 4), and has a temporal variability that closely mimics the Northern Hemisphere Temperature trend (Beaugrand et al., 2002b). This type of variability (the first mode), which previously has been reported as a SST and phytoplankton increase (Edwards et al., 2002) and a *C. finmarchicus* decline (Planque and Fromentin, 1996) in the North Sea, is not discussed further, as

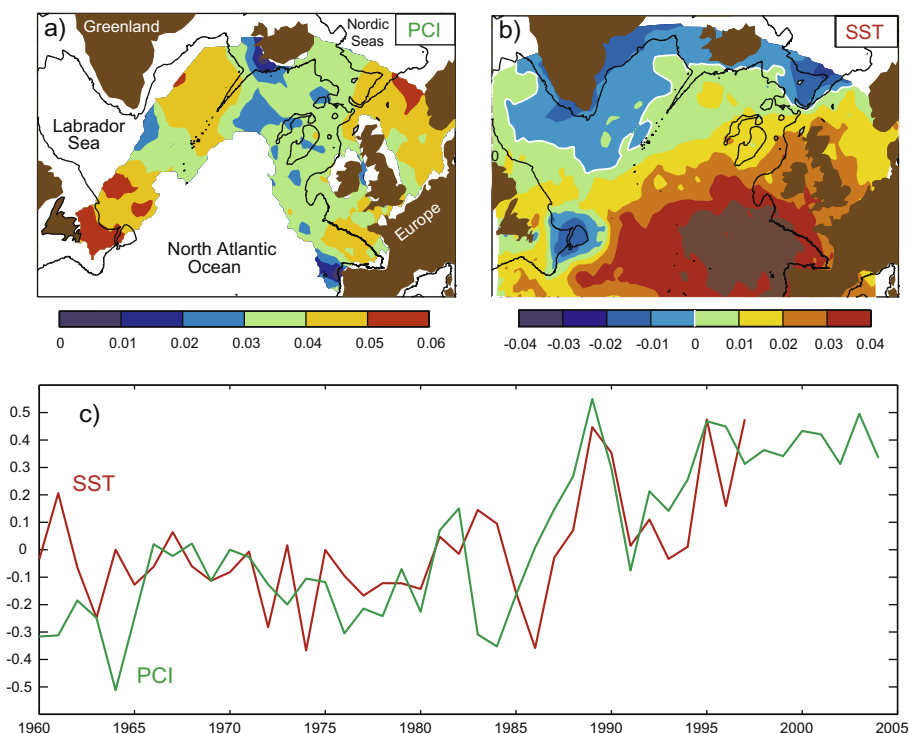


Fig. 4. Variability modes related to Northern Hemisphere Temperature. Spatial patterns of (a) the first Phytoplankton Colour Index mode (PCI), and (b) the first SST mode. (c) The corresponding time series (principal components).

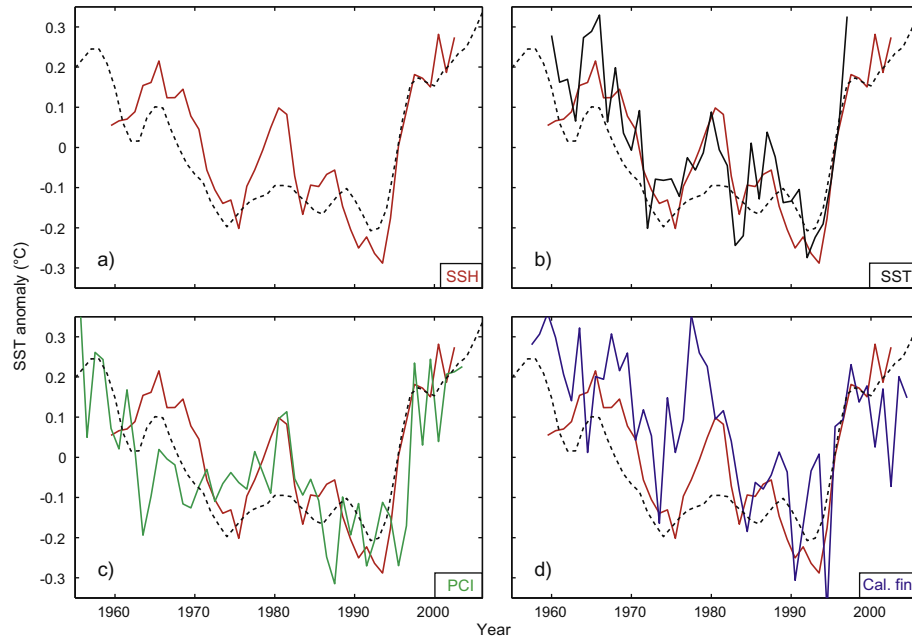


Fig. 5. Time series associated with the gyre mode, whose associated spatial patterns are shown in Fig. 6. (a) The sea surface height (SSH) principal component (inverted gyre index, red), and the north-eastern North Atlantic sea surface temperature (SST) (black dashed, see Section 2.4). These time series are also shown in the other panels, and the units refer to the black-dashed SST series. (b) A previously reported SST principal component (thick black line) based on PCA of observed SST (Beaugrand et al., 2002b). (c) Principal component from PCA of the Phytoplankton Colour Index (PCI) (green) and (d) principal component from PCA of the *Calanus finmarchicus* abundance (blue). Note that the *C. finmarchicus* abundance southwest of Iceland varies opposite to the principal component (the spatial pattern is negative, see Fig. 6d). The results shown in (c) and (d) are new.

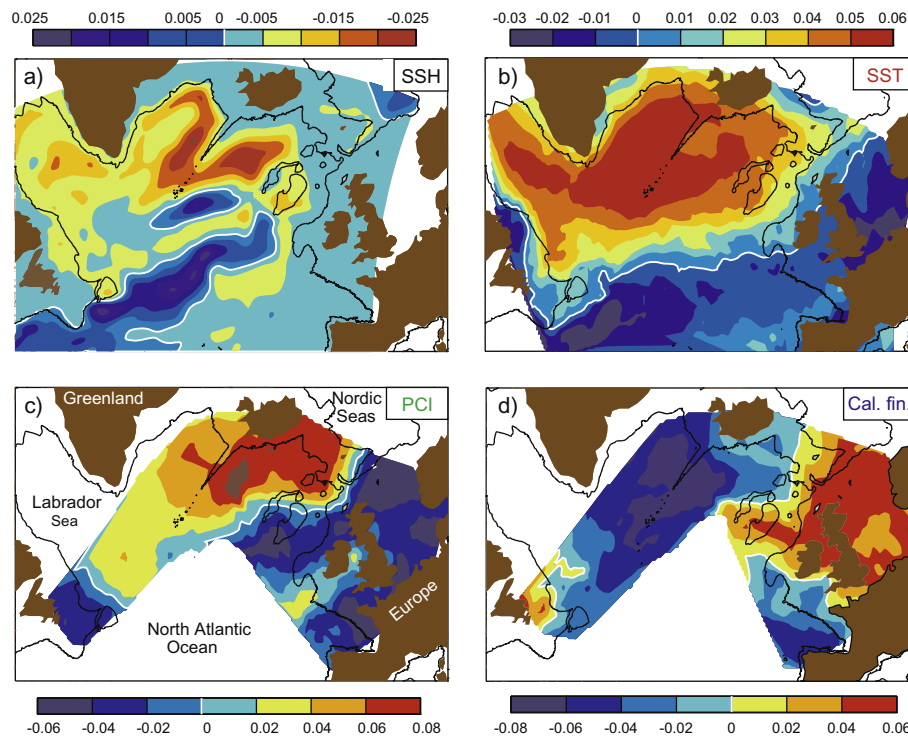


Fig. 6. The spatial patterns associated with the modes, whose time series are provided in Fig. 5. (a) Simulated sea surface height (SSH) (Hátún et al., 2005b), (b) sea surface temperature (SST) (Beaugrand et al., 2002b), (c) Phytoplankton Colour Index (PCI) and (d) *C. finmarchicus*.

it is not directly relevant to the present study of the oceanic subpolar Atlantic.

3.1.1.1. Phytoplankton

Changes in phytoplankton abundance and species composition may directly influence all herbivorous zooplankton and cascade

further up through the food web. The PCA performed on Phytoplankton Colour identified a gyre mode with an associated time series that resembles the gyre index (Fig. 5c). The associated spatial pattern (Fig. 6c) shows that this type of variability is strongest south of Iceland, but extends over a large part of the subpolar gyre, and matches the physical (SSH and SST) spatial patterns. Further-

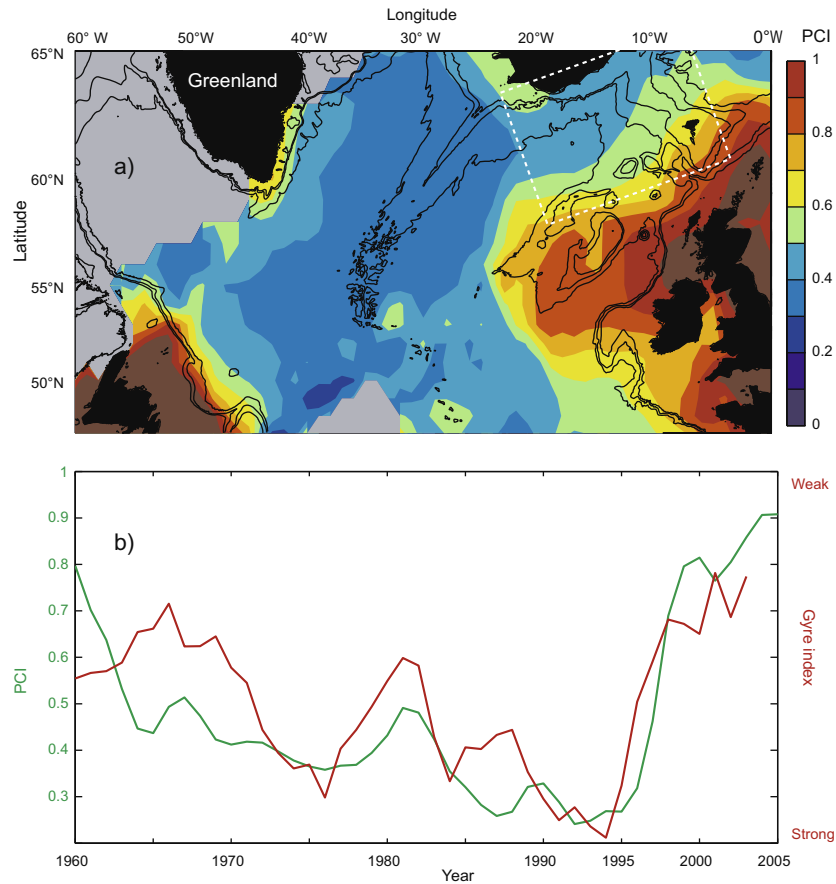


Fig. 7. (a) Total long-term average of the Phytoplankton Colour Index (PCI) over the period 1958–2005. Annual means are calculated for each pixel only if information for more than 8 months is available. Pixels are considered if they have 5 or more years during the period 1958–2005. (b) The inverted gyre index is shown in red and the PCI, spatially averaged over the dashed white rectangle in (a), is shown in green.

more, it shows an out-of-phase phytoplankton variability in the Iceland–Faroe area as compared to the European shelf seas (red vs. blue colours), with a division line roughly following the Faroe–Shetland Channel.

The previously reported steady decline in phytoplankton abundance south of Iceland, interrupted only by a peak in the early 1980s (Reid et al., 1998), abruptly reversed in 1995 (Fig. 5c). The phytoplankton abundance shifted back to the 1960s levels within only 3 years, and in the long-term perspective, the mid-1990s phytoplankton shift and increase was a remarkable event. The principal component time series is closely associated with the phytoplankton abundance averaged over the Iceland–Faroes region only (Figs. 5c and 7). This shows that the statistical Phytoplankton Colour mode captures the true variability in the Iceland–Faroe region. The two ways of extracting temporal variability from the spatio-temporal phytoplankton dataset thus support each other and strengthen our result.

3.1.2. *Calanus finmarchicus* – a subarctic zooplankton species

The copepod *C. finmarchicus* occurs throughout the North Atlantic where it is a major component of the zooplankton, and particularly of the copepod biomass, as well as forming an important trophic link between primary producers and many planktivorous fish. A gyre mode is evident in the *C. finmarchicus* data, and the associated time series is similar to the gyre index (Fig. 5d). The spatial pattern of *C. finmarchicus* displays a co-varying region, southwest of Iceland that is out of phase with the variability in the North Sea (Fig. 6d). This spatial pattern has negative values (blue) in the subpolar area as opposed to positive values (red) in the other datasets (Fig. 6a–c), signifying that the *C. finmarchicus* abundance

decreases when temperatures and phytoplankton abundance increase and vice versa.

The abundance of *C. finmarchicus* in the waters south of Iceland generally increased from the early 1960s to 1995, only interrupted by a strong decline around 1980 (Fig. 5d). After 1995, there was a marked reduction. The time series of the principal component closely represents the variability of *C. finmarchicus* in the waters southwest of Iceland, based on simple averaging alone; a relationship that is strongest near the eastern limit of the main *C. finmarchicus* distribution (near the Reykjanes Ridge) (Planque and Batten, 2000) (Fig. 8). The high frequency of occurrence of *C. finmarchicus* in the CPR samples makes it possible to utilize it as an indicator species (Beaugrand et al., 2002b), and a biological tracer, of subarctic water.

3.1.3. Warm-water zooplankton species

The reduced Arctic–boreal influence after 1995 (weakening of the gyre) opens the way for an increase in the influence of subtropical water and its associated zooplankton fauna. To examine whether the copepod community in the north-eastern Atlantic shifts towards species with warmer water affinities, we have used the so-called *cold-temperate species assemblage* (a misleading name in the present context) of calanoid copepods that are associated with the relatively warm Atlantic water masses east of the subpolar front (Beaugrand et al., 2002a). The abundance of this assemblage of indicator species, extracted from a region between Ireland and Iceland (30°W–10°W, 54°N–63°N) (Fig. 9a) co-varies with the subpolar gyre dynamics, showing very high values in the early 1960s, an intermediate peak around 1980 and very low values in the early 1990s followed by a subsequent increase (Fig. 9b).

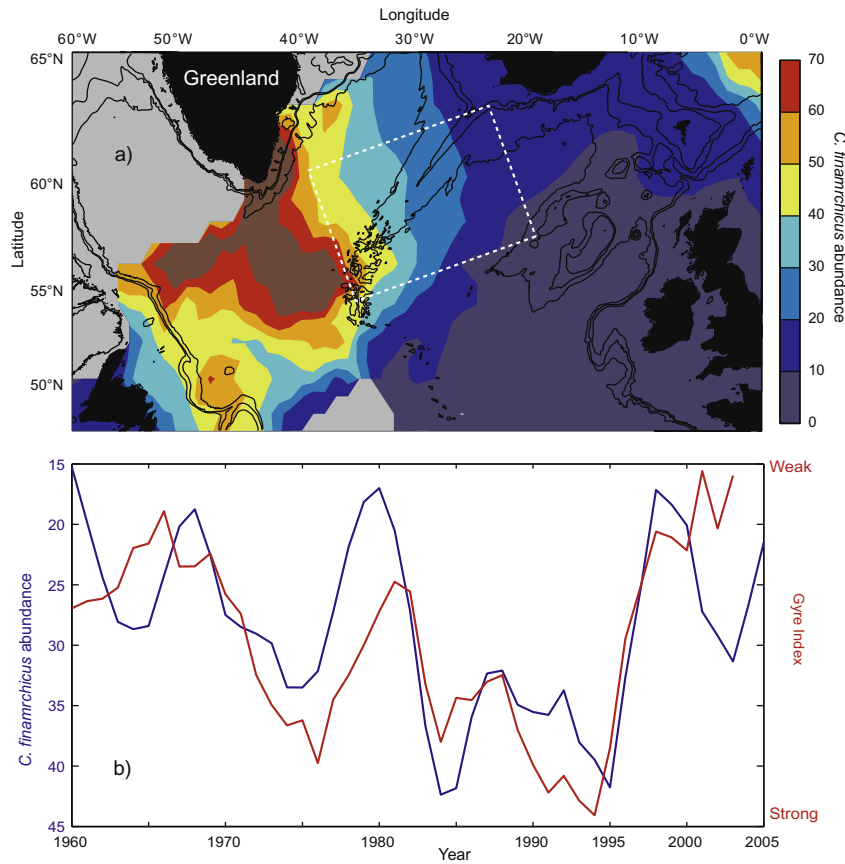


Fig. 8. (a) Total average of *Calanus finmarchicus* abundance over the period 1958–2005. Data filtering as in Fig. 7. (b) The gyre index is shown in red and the abundance of *C. finmarchicus*, spatially averaged over the white dashed rectangle in (a), is shown in blue.

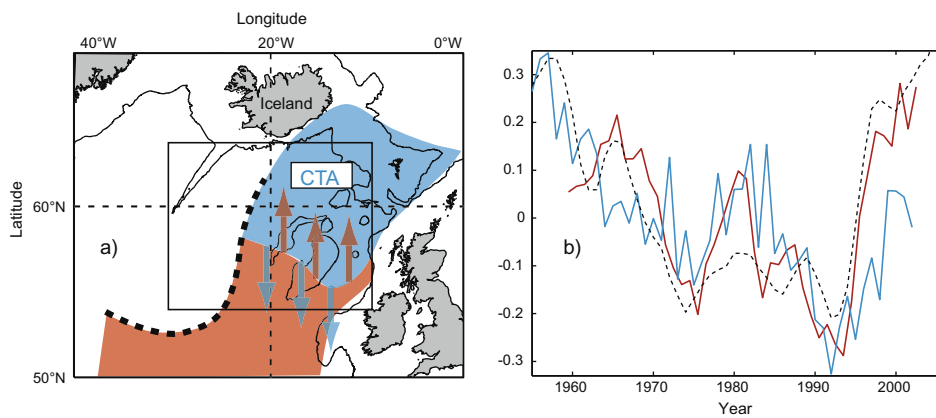


Fig. 9. Calanoid copepods. (a) Typical distributions of cold-temperate (CTA, light blue) and warm-temperate (red) assemblages of calanoid copepods redrawn from (Beaugrand et al., 2002a). The thick black-dashed line in (a) illustrates a realistic position of the subpolar front and the arrows illustrate the seasonal meridional progress. (b) Time series of CTA (light blue) obtained by averaging over the region within the black rectangle in (a). The inverted gyre index and the SST series are shown with the red and the black-dashed curve, respectively.

Furthermore, the abundances of ecologically important copepod species such as *Pseudocalanus*, *Acartia*, and *Oithona* in the region south of Iceland mentioned above are all significantly correlated to the gyre index (Table 1). This indicates that when the relatively large copepod *C. finmarchicus* withdraws from the northern north-eastern North Atlantic (e.g. during the mid-1990s event), many smaller copepod species invade the region in its place.

3.2. Blue whiting

The characteristic spatio-temporal variability of the gyre mode is also observed in the planktivorous blue whiting stock.

3.2.1. Mid-1990s changes

The reported annual catch statistics from all national fleets provides the only data that have a sufficient spatial and tempo-

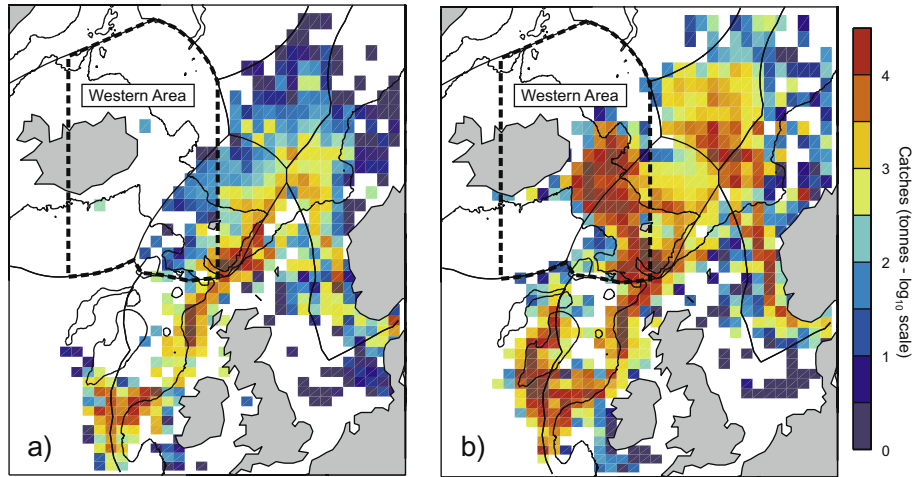


Fig. 10. Catches of blue whiting. The annually averaged catches by all national blue whiting fleets during (a) high-gyre index years (1990–1995) with negligible catches in the Western Area, and (b) low-gyre index years (1998–2003) with large catches in the Western Area. The Western Area is confined in the north and south by the Icelandic and the Faroese Exclusive Economic Zones (EEZs) and in the east by the 6°W meridian (thick dashed lines). The catches are binned into 0.5° latitude by 1° longitude boxes and \log_{10} -transformed. All EEZ boundaries are shown with the thin black curves.

ral coverage to demonstrate changing patterns in the stocks of blue whiting. Catches northwest of the European continental shelf – near the Rockall Plateau, near the Faroe Bank Channel and on the Iceland–Faroes Ridge, are highly variable (Fig. 10). This variability is illustrated by a particularly pronounced shift from the 1990–1995 period, when fisheries activity was largely confined to a strip along the continental shelf (Fig. 10a), to the period 1998–2003, when the catches northwest of the shelf increased substantially (Fig. 10b). Acknowledging the potential uncertainties and biases associated with the fisheries statistics, we assume that these data reflect the distribution of blue whiting. A spatial asymmetry between the European shelf seas and the Iceland–Faroe region, similar to the spatial patterns of the gyre mode (Fig. 6), is clearly apparent in the observed distribution.

3.2.2. Distribution-gyre link

The spatial variability of blue whiting in the Iceland–Faroe region (Hansen and Jákupsstovu, 1992) is illustrated using the catches taken exclusively by the Faroese fleet during the post-spawning migration period. To link this to the climate-plankton variability modes, we selected a *Western Area* in Icelandic and Faroese waters, where the climate-plankton components show largely coherent variability (Figs. 6 and 10). A western index (WI) time series is produced simply by dividing the Faroese catches within the Western Area by the total Faroese catches during the migration months April–June. This gives a relative measure of the catches (%) taken in the Western Area that is used as a proxy for the relative density of fish in this region.

The WI illustrates temporal variability in the east–west spatial shifts and is seen to resemble the gyre index (Fig. 11a). This suggests that the association between large shifts in the marine climate and the spatial distribution of blue whiting are not limited to the late-1990s event, but might be a robust link, at least since the commercial fishery started in the late 1970s. During periods with a strong subpolar gyre and cold conditions, e.g. in 1983 and from 1990 to 1995, the WI drops below 10%, meaning that less than ten percent of all Faroese blue whiting catches during this period were obtained within the Western Area. During periods with a weak gyre, e.g. 1980–82 and 1986–87, the WI exceeds 50%. After 1998, the gyre index has been persistently low and the WI has been greater than 50% every year (Fig. 11a).

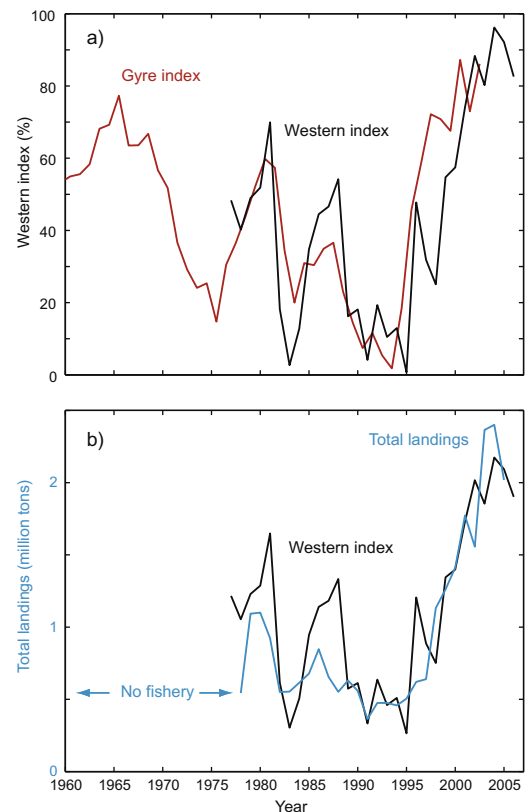


Fig. 11. The western index for blue whiting catches (black) plotted together with (a) the inverted gyre index and (b) the total annually averaged blue whiting landings by all fleets.

3.2.3. Total catch – gyre link

The total catches of blue whiting throughout the year, in all areas and by all national fleets (ICES, 2007) co-vary with the WI (Fig. 11b). Years when the blue whiting density in the Western Area is large are generally years when the total catches are large. This illustrates the economic importance of understanding the distribution dynamics of this species.

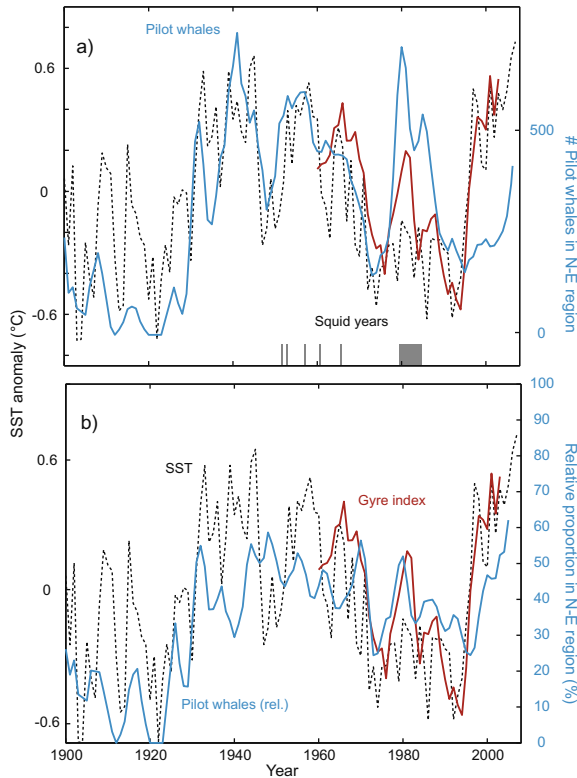


Fig. 12. Pilot whales and the marine climate. (a) The number of whales beached at the north-eastern (N-E) region of the Faroe Islands (low-pass filtered with a 3-year band width) (blue), the inverted gyre index (red) and SST anomalies in the north-eastern Atlantic (black dashed). Years when squid were abundant are marked along the bottom axis. (b) As (a), but with the relative proportion of whales beached in the N-E region of the Faroe Islands (blue).

3.3. Pilot whales

The migration and distribution of long-finned pilot whales in this region also appears to be related to the gyre mode. Clear changes in N-E/S-W grouping percentages may indicate changes in the direction from which schools approach the islands, and may thus shed light on the pilot whale migration (Zachariassen, 1993).

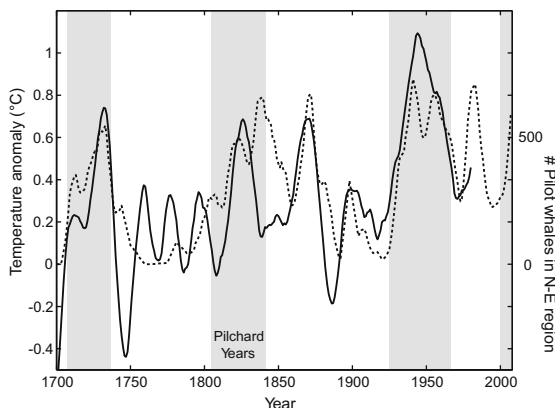


Fig. 13. A three-century perspective. The number of whales beached at the north-eastern (N-E) region of the Faroe Islands (dashed line), and the Central England Temperature (CET) anomaly (solid line). The time series have been low-pass filtered using band widths of 3 and 12 years, respectively. The summer pilchard period in the Western English Channel (Southward, 1974) are illustrated with light grey bars. The CET does not represent the SST west of the British Isles after around 1980 (see Fig. 3), and the post-1980 period is thus omitted.

3.3.1. Twentieth century

Pilot whale catches in the N-E region of the Faroe Islands closely follow the gyre index and SST variability in the Rockall–Iceland area during the period 1900–1990 (Fig. 12a) – a weak gyre and warm conditions are associated with large catches. But the catches around 1980 were higher than expected from the environmental indicators, and the post-1995 decline of the gyre and increase in temperatures did not result in a corresponding increase in pilot whales.

The total Faroese catches (N-E and S-W) have persistently declined since the early 1980s and this decline is strongest in the S-W area (not shown). The proportion of the total catches (%) from the N-E bays follows the main temperature changes during the 20th century, illustrating that the climate signal is clearer in the N-E region than in the S-W region (Fig. 12b). This N-E/S-W distribution index does show a large post-1995 increase. Hence, although the number of whales caught in the N-E bays did not increase much after 1995, these catches represent a larger proportion of the total catches in recent years than at anytime previously during the 20th century.

3.3.2. Three centuries

The pilot whale catches in the N-E region and the Central England Temperature (CET), used as a proxy for the long-term oceanic temperature variability west of the British Isles (Section 2.4) give a temporally unique perspective of the discussed variability. These series co-vary fairly closely from 1709 to the 1980s, except for a period around 1840 (Fig. 13). It therefore appears that large pilot whale catches in the N-E region have coincided with periods of warming in England.

4. Discussion

Bio-geographical terminology is a useful way of describing the integrated ecosystem changes discussed here. A high gyre index – the ‘red thread’ connecting the individual elements – is associated with dominance of subarctic water masses, and the Arctic-boreal fauna they contain, in the region south of Iceland. A low gyre index is, on the other hand, associated with dominance of warmer water masses and their mixed Lusitanian-boreal fauna. The region south of Iceland is thus an intermediate zone where the relative influence of the boundary faunas is highly variable. Stated simplistically, the gyre mode of variability illustrates the large-scale, long-term interplay between the dynamics of the subpolar gyre, the NAC, and the Arctic-boreal and the Lusitanian-boreal faunistic zones, in the north-eastern Atlantic Ocean.

These bottom-up bio-physical relations between the dynamics of the subpolar gyre, phytoplankton, zooplankton, blue whiting, and pilot whales in the north-eastern North Atlantic generally show close correspondence, but reasonable causal mechanisms have still to be identified. Constrained by the limitations of available datasets, it is only possible to provide partial explanations for the observed co-variations. Possible causal mechanisms that are consistent with established knowledge are outlined below for each of the trophic levels.

4.1. Phytoplankton

Subtropical and subpolar water masses meet and mix in the waters west of Ireland (Fig. 2). In terms relating to primary production, this region is a transition zone between the *seasonally mixed subtropical gyre biome* and the *subpolar biome* (Sarmiento et al., 2004). During summer, the seasonally mixed subtropical gyre biome becomes nutrient limited due to strong stratification. Primary production in the subpolar biome is generally not

constrained by nutrients, but it can be light-limited due to deep mixed layers. Somewhere along the transition zone between these biomes, there is a favourable compromise (corresponding to an appropriate mixed-layer depth) between nutrient and light limitation which causes increased mean primary production. In the long-term average (1958–2005), a phytoplankton maximum region is observed around the Rockall Trough/Plateau area (Fig. 7a). As the subpolar gyre weakens, the confluence of the subarctic and subtropical water masses, and thus the transition zone, will shift northwards and westwards. The bipolar phytoplankton variability pattern, with negative values at the Rockall Trough entrance and positive values in the waters south of Iceland (Fig. 6c), is probably associated with such geographical shifts of the transition zone.

The literature on long-term phytoplankton changes in the north-eastern Atlantic is limited. The general decreasing trend from the early 1960s to 1995 has previously been documented using the same type of data (Reid et al., 1998), and was updated to show the post-1995 change in Reid (2005).

4.2. Zooplankton

The effect of the gyre circulation on zooplankton has several possible explanations. The direct effect of advection is clearly important. As discussed in Section 3.1, a weak gyre circulation is characterised by reduced abundances of *C. finmarchicus* (Figs. 5d and 6d), but increased abundances of the cold-temperate species assemblage (Fig. 9b), and of four other ecologically important warm-water copepod species (*Acartia* spp., *Para-pseudocalanus* spp., *Pseudocalanus elonginatus*, and *Oithona* spp., Table 1). A variable transport of subarctic water from the central subpolar gyre to the waters south of Iceland can explain the co-variation between the gyre index and the distribution of *C. finmarchicus*. Advection can also explain the negative relation between the gyre index and both the cold-temperate species assemblage and other copepod species with warmer water affinities, since the source of these species is in the warmer and in part 'Lusitanian' waters that enter and dominate the Iceland Basin when the subpolar gyre weakens and retracts towards the west.

Important over-wintering populations of *C. finmarchicus* are distributed in the large bodies of cold water of the subpolar gyre and central Norwegian Sea (Fig. 8a) (Planque and Batten, 2000). *C. finmarchicus* can over-winter in the Iceland Basin (Heath, 2004), and it is to be expected that changes in its biomass will reflect the highly variable volume of subarctic water in this basin (Fig. 2).

In addition to these direct effects, zooplankton is, of course, dependent on its food supply and primary production. However, trophic linkages cannot explain both the decline of *C. finmarchicus* and the increased abundance of warmer water zooplankton species that coincides with a weakening subpolar gyre and increase in phytoplankton biomass.

A steady decline of *C. finmarchicus* in European shelf seas (Fromentin and Planque, 1996) and an increase of the same species in the Mid-Atlantic Bight (Beaugrand, in press) during the last four decades have previously been connected to an intensifying North Atlantic Oscillation (NAO) or an increasing Northern Hemisphere Temperature. In the central Atlantic Ocean the abundance of *C. finmarchicus* does not follow a steady trend, but as demonstrated here it showed a general increase until the mid-1990s followed by a sudden decline.

4.3. Blue whiting

Changes in the distribution of blue whiting in the Iceland–Faroe region are most likely caused by both a variable total stock size and by shifts in the migration pattern. The subpolar gyre can influence both processes either (i) directly by regulating the currents and/or

hydrographic conditions that influence behaviour and migration routes or (ii) indirectly via trophodynamics. Previous work has demonstrated that the distribution of spawning activity near the Rockall Plateau can be controlled by the hydrographic regime – spawning is more southerly and is limited to the continental shelf during cold Arctic-boreal regimes (strong gyre), while intense spawning takes place both on the shelf and on the Rockall plateau during warmer Lusitanian-boreal regimes (weak gyre) (Hátún et al., in press).

The observed changes in spawning distribution may have given rise to the marked increases in recruitment that led to a tripling in the size of the stock. Possible mechanisms include a larger spawning area, the wider dispersion of eggs and larvae, and increase in growth and therefore also in survival rate due to the higher temperatures (a direct influence). Increased food availability (an indirect influence) in the downstream region may also have contributed to improved survival through increases in phytoplankton abundance (Fig. 6c) and the abundance of the copepods *Pseudocalanus*, *Acartia* and *Oithona* (Table 1), the most important larval prey items for blue whiting (Bailey, 1982).

Variations in the distribution of spawning activity near the Rockall Plateau can also influence the post-spawning migration. Spent and initially passive fish (Hansen and Jákupsstovu, 1992) starting near the Rockall Plateau will drift along a western route towards the Iceland–Faroe area, whereas those spawning near the European continental shelf will be carried north-eastwards through the Faroe–Shetland Channel by the Continental Shelf Current. The post-spawners do not, however, remain passive until they reach the feeding areas in the north. They gradually start to feed as they move northwards, rebuilding first tissues and then subsequently fat content (Jacobsen et al., 2002). The increased abundance of phytoplankton and more diverse zooplankton community in the Iceland–Faroe region during Lusitanian-boreal regimes probably also provides more food for adult blue whiting, possibly drawing migrating post-spawners westwards. Unfortunately, large zooplankton species favoured by blue whiting as prey, e.g. adult euphausiids, are less well represented in the CPR dataset, and it is therefore not possible to explicitly verify the trophic linkage between plankton abundance and adult blue whiting distribution. While the links between the plankton and the gyre are expected to continue, the potential impact that the large and efficient multinational pelagic fishing fleet can have on the blue whiting stock size could change the historical relationship with the gyre in the future.

4.4. Pilot whales

The long-finned pilot whale is a marine mammal that is well insulated from its environment and travels between areas of widely different conditions (Bloch, 1994; Bloch et al., 2003). It is therefore unlikely that a direct temperature response can explain the link between the gyre index and pilot whale catches in the Faroes (Fig. 12). This whale is also a strong swimmer and therefore unlikely to be affected by changes in ocean currents associated with variations in the gyre.

A more likely explanation is that the gyre affects the main food items of the pilot whale, the squid species *T. sagittatus* and blue whiting (Desportes and Mouritsen, 1993; Gaard, 1988). In years when squid are abundant around the Faroe Islands (*squid years*) (Jákupsstovu, 2002) (see Fig. 12a), they appear to have migrated/drifted through the Iceland–Faroe region and approached the islands from the north. It is thus likely that the pilot whales caught in the N-E region of the Faroe Islands have also followed this prey between Iceland and Faroe Islands, and approached the Faroes from the north. The close co-variability between the N-E whale catches and the gyre dynamics, as represented by the SST

(Figs. 12 and 13), are probably linked via the variable abundance and distribution of squid and/or blue whiting in the Iceland–Faroe region.

A weakening of the subpolar gyre tends to increase the abundance of blue whiting in the Western Area (Figs. 10 and 11a). Predators following this population will be drawn into the Iceland–Faroe region, resulting in an increase in the proportion of catches taken in the N-E bays (Fig. 12b). Weakening of the gyre and corresponding increases in the SST series plotted in Fig. 12a have previously been associated with westward expansions of the blue whiting spawning distribution from the Continental Shelf to include the area around the Rockall Plateau (Hátún et al., in press). Intensive spawning took place near the plateau in the warm late 1950s and in the 1960s (Bainbridge and Cooper, 1973), but this declined in the cooler late 1960s–early 1970s, in synchrony with decreased whale catches. Schmidt (1909) observed a ‘striking absence’ of blue whiting fry west of the Rockall Bank during the period 1904–1908 (cold conditions), which also was a period with very limited whale catches in the N-E region.

The apparent blue whiting – pilot whale link suggests that a large increase in N-E bay whale catches would have been expected after 1995 (Fig. 11a), but this did not happen (Fig. 12a). However, the proportion of the N-E catches relative to the total catches in the Faroe Islands did increase rapidly after 1995 (Fig. 12b), consistent with the mechanism discussed above. The reduced occurrence of whales around the Faroe Islands after 1995 is probably related to low levels of squid. The question of why the abundance of squid has not increased after 1995 simultaneous with the increased Lusitanian-boreal influence and blue whiting (prey) densities, however, remains open.

4.5. Relation to previously reported ecosystem shifts

The present work can be related to previously reported large shifts in the ecosystems in Greenlandic (Tåning, 1948) and Icelandic (Fridriksson, 1949) waters, in the Nordic Seas (Drinkwater, 2006; Toresen and Østvedt, 2001) and in the Western English Channel (Cushing, 1982). The characteristic ecosystem changes in the English Channel, represented by the so-called Russel cycle, are described in a large body of literature (Cushing, 1982; Southward, 1974, 1980). Although the ecosystem changes presented here are rather geographically remote from those in the English Channel, we suggest that the two sets of changes may in fact be manifestations of the same basin-scale processes. The Russel cycle illustrates north–south shifts in the transition zone between boreal and Lusitanian fauna, which is a more southerly and warmer water expression of the faunistic exchanges demonstrated here.

The pronounced Lusitanian regime reported near the Channel beginning during the 1925–35 period and terminating during the 1965–75 period, closely coincides with a weak subpolar gyre and thereby warmer conditions in the north-eastern Atlantic, more phytoplankton and warm-water copepods in the Iceland–Faroe region, a north- and westward shift in the blue whiting stock (Southward, 1980) and more frequent occurrences of pilot whales in this region (Fig. 12). The Russel cycle has also been associated with shifts between herring periods (cold, boreal) and pilchard periods (warm, Lusitanian) in the Western English Channel (Cushing, 1982). The period 1935–65 was a summer pilchard period, but such periods probably took place during the first half of the 17th century, the early years of the 18th century and in the first 30 years of the 19th century as well (Fig. 13) (Southward, 1974). These periods all coincide with years when large catches of pilot whales were taken and there are indications of a weak gyre (Fig. 13). Despite its anecdotal character, this supports our proposed link between the

gyre mode and the Russel cycle and puts the discussed changes in a 300-year long perspective.

Ample evidence has shown a northward shift of warm-water species in the North Sea and adjacent shelf seas during the last four decades (Beaugrand, 2003; Edwards et al., 2002); a development associated with the temperature trend of the Northern Hemisphere (Beaugrand et al., 2002b) (the first mode, Fig. 4). Particularly pronounced was a rapid temperature increase in the late 1980s, also known as the ‘1980s regime shift’ (Beaugrand, 2004b; Reid et al., 2001). It has also been acknowledged that the ecosystems in the subpolar Atlantic have not experienced a similar trend, but the details in the oceanic regions have been more diffuse (Beaugrand et al., 2002b). The gyre mode clearly shows that the increased Arctic-boreal influence south of Iceland opposed the hemispheric warming trend until 1995. This mode also clearly illustrates the very rapid reversal towards a Lusitanian-boreal dominated ecosystem when the subpolar gyre started to decline in 1995. This has led to a regime shift comparable to, and maybe even more extensive than, that in the 1980s.

4.6. Forecasting potential

The apparent link between the state of the ecosystem in the north-eastern North Atlantic and the dynamics of the subpolar gyre opens up the possibility of now-casting and potentially forecasting ecosystem changes in this region. A one-year time-lag between the atmospheric forcing and the gyre response (Eden and Willebrand, 2001), a subsequent year between the gyre dynamics and the marine climate in the Iceland–Faroe region (Hátún et al., 2005b) and possibly an additional year before the plankton is impacted, suggests that 2- to 3-year predictions of ecosystem change may be feasible. Model experiments promise the potential for the longer-term forecasts (5–10 years) of the development of the subpolar gyre (Lohmann et al., 2008, accepted for publication).

5. Conclusions

For the region bounded by the Rockall–Hatton Plateau in south, the Faroe Islands in east, Iceland in north, and the Reykjanes Ridge in west (see Fig. 1), we find:

- Large subarctic-subtropical water-mass exchanges, related to the strength of the subpolar gyre, enforce a bottom-up control of the marine ecosystem, which is characterised by a highly variable influence of the Arctic-boreal and Lusitanian-boreal faunas.
- In this region, when the subpolar gyre is *strong*: (i) phytoplankton abundance is *low*, (ii) *C. finmarchicus* abundance is *high*, (iii) abundance of warm-water zooplankton species is *low*, (iv) the density of blue whiting is *low*, and (v) the occurrence of pilot whales is *low* and *vice versa* when the gyre is weak.
- The pronounced mid-1990 decline of the subpolar gyre from a strong gyre state to a weak state strongly impacted the phyto- and zooplankton communities, the blue whiting stock, and the distribution of pilot whales, in this region.
- The state (Arctic-boreal/Lusitanian-boreal influenced) of the ecosystem in the north-eastern North Atlantic can possibly be forecast 2- to 10-years ahead by utilizing simulations of the subpolar gyre circulation.

Acknowledgements

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