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Multidecadal Atlantic climate variability and its impact on marine pelagic communities☆

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ABSTRACT

A large scale analysis of sea surface temperature (SST) and climate variability over the North Atlantic and its interactions with plankton over the North East Atlantic was carried out to better understand what drives both temperature and species abundance. The spatio-temporal pattern of SST was found to correspond to known climate indices, namely the Atlantic Multidecadal Oscillation (AMO), the East Atlantic Pattern (EAP) and the North Atlantic Oscillation (NAO). The spatial influence of these indices is heterogeneous. Although the AMO is present across all regions, it is most strongly represented in the SST signal in the subpolar gyre region. The NAO instead is strongly weighted in the North Sea and the pattern of its influence is oscillatory in space with a wavelength of approximately 6000 km. Natural oscillations might obscure the influence of climate change effects, making it difficult to determine how much of the variation is attributable to longer term trends. In order to separate the influences of different climate signals the SST signals were decomposed in to spatial and temporal components using principal component analysis (PCA). A similar analysis is carried out on various indicator species of plankton: *Calanus finmarchicus*, Phytoplankton Colour Index and total copepod abundance, as well as phytoplankton and zooplankton communities. By comparing the two outputs it is apparent that the dominant driver is the recent warming trend, which has a negative influence on *C. finmarchicus* and total copepods, but has a positive one on phytoplankton colour. However natural oscillations also influence the abundance of plankton, in particular the AMO is a driver of diatom abundance. Fourier principal component analysis, an approach which is novel in terms of the ecological data, was used to analyse the behaviour of various communities averaged over space. The zooplankton community is found to be primarily influenced by climate warming trends. The analysis provides compelling evidence for the hypothesis that cold water species are gradually being replaced by more temperate species in the North Atlantic. This may have detrimental effects for the entire marine ecosystem, by affecting on organisms such as fish larva for example. The second group, a phytoplankton subset consisting primarily of diatom species, is primarily influenced by the AMO rather than the average temperature trend. This result highlights the importance of natural oscillations to certain functional groups, in particular those subgroups which are less directly metabolically affected by changes in temperature.

1. Introduction

In this study the effect of both natural climatic oscillations and recent northern hemisphere warming trend on sea surface temperature (SST) was investigated. The results of this analysis were then used to determine what drives the dominant behaviour of various indicator species of plankton as well as plankton communities. An understanding of the spatio-temporal structure of plankton abundance and its temporal drivers is of interest to marine policy makers because of the impact the plankton has on the rest of the marine ecosystem and to various industries such as fisheries (Donnelly et al., 2011). There are a number of natural oscillations that might influence the overall climate of the North Atlantic, such as the Atlantic Multidecadal Oscillation (AMO) (Schlesinger & Ramankutty, 1994), the North Atlantic Oscillation (NAO) (Jones et al., 1997) and (Wallace, 2000) and the East Atlantic Pattern (EAP) (Wallace & Gutzler, 1980). However the influence of these oscillations is not spatially homogeneous. Cannaby and Husrevoglu (2009) broke the SST down into its dominant spatial and temporal components using a method called empirical orthogonal function (EOF) analysis or principal component analysis (PCA) (Joliffe, 2004). They found the

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dominant mode of variability to be given by the AMO, followed by the EAP and the NAO, accounting in total for 48% of the variation in the SST over their region of interest. Beaugrand et al. (2009) carried out a similar analysis on SST data without first removing the linear trend and restricting the spatial region to the North East Atlantic from 1958 to 2005. The results showed that the first component explained 46.35% of the variability and resembles the Northern Hemisphere Temperature (NHT) trend. The second component explained 15.17% and resembled the subarctic gyre index, which is a measure of the strength of the circulation in the subarctic gyre (Beaugrand et al., 2009). The third component explains 11.28% of the variability and resembles the NAO. In this study the spatio-temporal structure of the SST across the ocean basin scale was explored both with the median removed and with the linear trend removed in order to explore how this influences the dominant signals. In order to compare with plankton communities the SST data are analysed over the North East Atlantic, as per Beaugrand et al. (2009). This study builds upon previous work by exploring how these climate signals influence both indicator species and the joint behaviour of species assemblages.

The Atlantic Multidecadal Oscillation is believed to play a role in driving SST across the entire North Atlantic but is most strongly weighted in the subpolar gyre. The North Atlantic Oscillation is known to have a dipole in its spatial influence, having a positive influence in the North Sea. The NAO appears to have a negative influence on SST in the subpolar gyre region, where the SST is lower during the positive phase of the NAO. The main driver for most plankton species is believed to be the average warming trend seen over the past few decades (Beaugrand & Reid, 2003; Philippart et al., 2011) but the AMO also has an influence on abundance, especially for those subgroups that are sensitive to wind intensity and water column mixing.

The first section focuses on decomposing the SST into its component trends, in order to understand the spatio-temporal structure of the temperature signal. A comparison is made between linearly detrended signals and signals with the median only removed, in order to highlight how natural oscillations and the warming trend might obscure one another. The fact that long term trends might obscure natural oscillations has been reported by Bonfils and Santer (2011) and Schlesinger and Ramankutty (1994). The SST analysis was carried out over two different time periods. In the first instance large scale features across the entire North Atlantic between 1870 and 2010 were investigated to give an overview over the ocean basin scale. Since the biological data were more sparsely sampled over the open ocean, analysis on this dataset must be restricted to the North East Atlantic, and reliable records only date back as far as 1958 (see Verzulli and Reid (2003) and Batten et al. (2003)). In order to be comparable the SST was also decomposed over the same space and time, meaning there is some change in the ordering of the most important trends. Since the biological data were not detrended the SST data over the restricted region was also not detrended. Although the warming trend might obscure the effects of natural oscillations, it is also an important driver of plankton abundance and so its effect was included in the analysis. The warming trend seen over the past few decades is thought to be a large source of variation in the SST (Cannaby & Husrevoglu, 2009). Other sources of variability are believed to correspond to natural oscillations (Cannaby & Husrevoglu, 2009 and Schlesinger & Ramankutty, 1994).

In the second part of the analysis the influence of these climatic indices on the pelagic ecosystem was investigated. Using data drawn from the Continuous Plankton Recorder (CPR) survey the behaviour of both indicator species and species communities in response to climate drivers was analysed. Planktons are known to be sensitive to changes in climate, to the extent that changes might even sometimes be observed in the biological data before the climate indices themselves (Raitsos et al., 2006 and Letcher, 2009). Furthermore planktons are the primary producers in the oceanic environment, which means the entire marine food chain is reliant on them (Hardy, 1971).

Community structure across a large number of species for the full time series in the North East Atlantic has been studied relatively little using the CPR dataset due to the difficulties associated with modelling multivariate data. Some previous studies of the community structure have classified species assemblages by their spatial distribution. Batten and Walne (2011a) used QQ-plots of the temperature at which a sample of a particular species was collected against the observed sample temperature for all samples to classify 29 species of copepod in the North East Pacific into groups of warm and cold water species. In that study the communities are defined entirely by spatial distribution rather than temporal structure, which may be due to the fact that the time series for the North East Pacific is comparably shorter than for the North East Atlantic. Hunt and Hosie (2005) likewise use the spatial distribution of species to define species groups but these groups are found using cluster analysis. Nishikawa et al. (2010) also use cluster analysis to identify species groups in the southern ocean. By using both cluster analysis and correspondance analysis over species and sampling station they identify two groups from 11 species of euphausiids. Hunt and Hosie (2003) investigate community structure across space in the southern ocean using both cluster and correspondance analyses and by calculating measures of species richness, diversity, evenness and dominance and the relationship between these measures. Some efforts have also been made to describe the structure of species communities by using a network based approach (see e.g. Raymond & Hosie, 2009). Field et al. (1982) explored the species groupings in the River Exe estuary using an inverse analysis of a species by sample matrix. This consisted of finding species groupings using hierarchical clustering methods, where the variables were species and observations were different sampling stations, and using multidimensional scaling. Multidimensional scaling is an ordination technique that uses a dissimilarity matrix. The number of species was reduced by selecting only those that had greater than 4% dominance in at least one station.

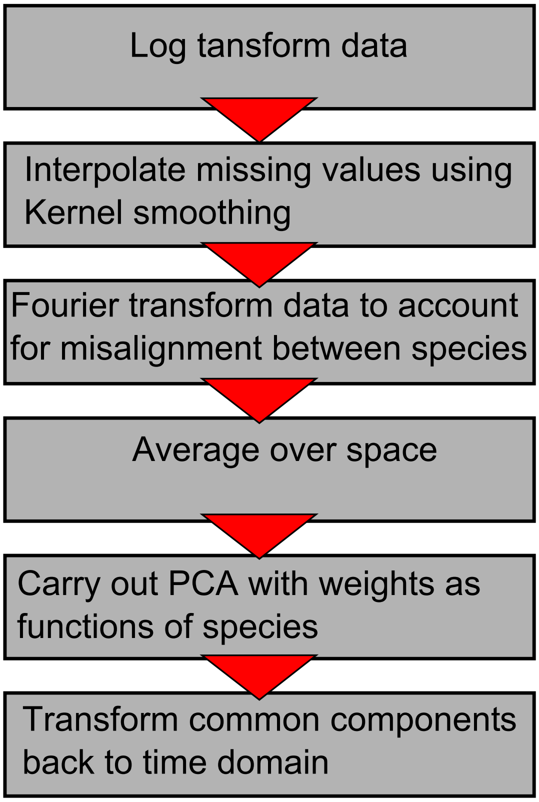
In this study the full time series for the North East Atlantic was used to find species assemblages and their joint functional behaviour. The analysis of the joint behaviour of the communities over time can provide new insights into the behaviour of different functional groups. Within the zooplankton communities it has been hypothesised that there has been a northwards movement of temperate species, whilst cold water species have been in decline in the North Atlantic (Beaugrand et al., 2009; Beaugrand & Reid, 2003 and Helaouët & Beaugrand, 2009). This study draws together the understanding of the spatio-temporal influence of natural oscillations and climate change on SST and the interaction with the ecology of the North East Atlantic, as described by various species of plankton. Bringing together the analysis of both the plankton and the SST demonstrates how both the warming trend and natural oscillations along with their spatio-temporal variability must be considered in order to understand the ecosystem of the North Atlantic.

2. Methods

The SST data are taken from the Hadley centre dataset (http://www.metoffice.gov.uk/hadobs). The data have been interpolated on to a regular spatial grid of 1 × 1° and are recorded by yearly average. The biological data are taken from raw abundances in the CPR dataset (Beaugrand et al., 2003 and Verzulli & Reid, 2003). The CPR survey is unique in terms of both spatial and temporal coverage. First invented by Sir Alister Hardy in the 1920s, the CPR survey contains monthly abundances for hundreds of species across the North Atlantic since the 1930s (Batten et al., 2003). In this study data from 1958 onwards were used, as this is when the most reliable records for many species begin. Few terrestrial ecological records are as long running as the CPR survey, however in studying the effects of climate long and detailed records are essential. The device is towed by voluntary merchant vessels, which leads to an irregular spatial sampling dependent on shipping routes (Verzulli & Reid, 2003), which must be accounted for. This means the biological data must be mapped on to a regularly spaced grid with a 1 × 1° resolution, in order to be comparable with the SST data.

Before these data could be usefully analysed a certain amount of pre-processing was carried out. The data were log-transformed and then interpolated onto a regular grid before they were analysed. The logarithmic transformation was used to stabilise the variance of the data. As count data are typically expected to resemble a Poisson process skewness of the distribution is expected to be present, resulting from large abundances typically found in plankton datasets. It is likely that the variance of the abundance will be a function of the expected value. The logarithmic transformation removes this relationship such that the transformed data follows a more Gaussian distribution. Results for the biological data are therefore presented on a log-abundance scale thus corresponding to a variance stabilising transformation. Previous studies of the CPR dataset (see for example Verzulli and Reid (2003)) use the same transformation prior to analysis and so this means the results are comparable with other studies. The interpolation method that was used is kernel smoothing (Wand & Jones, 1995) (Scheme 1).

The data must be interpolated in order to be analysed on a regular spatial grid, as the raw abundances are irregularly sampled in spaced due to the sampling being dependent upon shipping routes (see Verzulli & Reid, 2003). Data on a regularly sampled grid can be more easily analysed and interpreted. Abundances at unsampled locations were estimated as a weighted sum of abundances at nearby locations. The weights were taken to be functions of the distance between the location for which the abundance is being estimated and the location at which a sample exists. The kernel function is symmetric about zero and produces a larger weight for locations which are closer. In this case the kernel function is chosen to be Gaussian, which fulfils these criteria. The variance of the Gaussian function also allows the specification of a bandwidth, a parameter which controls how much the data are smoothed. The larger the bandwidth the more the data are smoothed. Some care must be taken in selecting the bandwidth, as too large a bandwidth will smooth out important features of the data, whilst too small a bandwidth will make the resulting estimates too noisy (Wand & Jones, 1995). In order to interpolate the data in this way it must be assumed that the abundances are relatively smooth in space. This is a reasonable assumption because most species will be adapted to certain climates and so there are unlikely to be sudden changes in abundance across space.



Scheme 1. Algorithm for carrying out sparse species PCA.

Both the SST and the biological data are multivariate in nature, consisting of time series recorded across multiple locations. The biological data in addition contains records for a large number of different species. This complex structure makes the data difficult to interpret intuitively. This means statistical techniques for producing summaries of the dominant trends are required. One such method that has been applied to the CPR dataset previously is principal component analysis (Beaugrand et al., 2003). Principal component analysis (PCA) is a technique for finding directions of maximal variance through a dataset (Joliffe, 2004). This is particularly useful in scenarios where there are a large number of variables to be considered, since often most of the structure can be explained using a much smaller number of principal components. The components are orthogonal to one another and are constructed by taking weighted sums of variables, with the weights chosen so as to maximise the amount of variance explained. A matrix of weight vectors can be found by a singular value decomposition of the data covariance matrix. This also returns a diagonal matrix, which contains the explained variances for each component. There are various methods for choosing the number of components to retain, but one of the most commonly used is the threshold on the cumulative explained variance (Joliffe, 2004).

Previous studies of the CPR dataset have investigated the spatio-temporal behaviour of indicator species (Beare et al., 2003 and Beaugrand et al., 2003). Beaugrand et al. (2003), for example, use a method called Spatial PCA on the CPR dataset. Responses of indicator species can be decomposed in both space and time in order to determine the most important climatic drivers and the relative importance of these drivers to the species across space (Walther et al., 2002). In doing so the amount of variability attributable to natural oscillations and to climate change can be better understood (Brown et al., 2011). Typically when investigating long term changes yearly averages are taken, as the seasonal cycles can obscure long term trends. PCA is used to produce weights in space and components as functions of time. The interpretation of the weights is that they give an indication of the spatial distribution of the species and the importance of different climate influences at different locations. Under this framework it is assumed that the abundance of each species is a linear combination of common signal, which is assumed to be the climate signals given by the analysis of the SST data. Cannaby and Husrevoglu (2009) decomposed the SST signal over a specified region in a similar way in order to determine the spatial pattern of different climate indices. In this case the interpretation of the weights determines a particular climate trend influence in determining the SST trend. In this analysis we extended the region eastwards to include the North Sea.

An alternative to using Spatial PCA on the CPR data is species PCA, which is introduced in this study as a new way of analysing community structure in ecological datasets. Here the spatial location rather than the species is fixed. The weights are functions of species and the signals are functions of time. The interpretation of the weights is that they represent functional groups of species, e.g. groups of those species that behave in a similar way. The time courses represent the joint behaviour of these groups. This is used in a similar way to the inverse analysis used by Field et al. (1982), except that rather than sampling stations the observations are different time points. The number of variables is reduced by restricting the number of non-zeros in the weight vector, rather than by selecting them based on their dominance.

In this model some care must be taken to account for the effects of temporal misalignment. Misalignment refers to when variables follow similar time courses but with a time lag. This is a common occurrence in biological datasets, for example in the growth curves of children (Sangali et al., 2008). Some species might respond more rapidly to climate effects than others, for instance changes may take time to propagate through the food chain. This can lead to species having a similar functional behaviour but with some time lag. This can be accounted for by computing principal components in the Fourier domain. PCA does not account for time lags but under a Fourier transformation lags become multiplicative constants, which can be accounted for so long as the principal component in the Fourier domain is concentrated to a small set of adjacent frequencies and the time lag, τ, is relatively small compared to the length of the time series. The resulting components are transformed back into the time domain so as to be interpretable. This approach differs from previous studies of the CPR data because it allows the study of community behaviour, whereas most prior work has focused on one or two individual species (Beare et al., 2003).

The ultimate goal is to determine the relationship between different plankton groups and different climate drivers. Typically a relationship between two time courses can be found using a simple linear regression model. It is assumed that the biological variable is proportional to a given climate driver plus a constant. Supposing the $z_i(t)$ is the ith principal component drawn from the biological data at time t and $c_j(t)$ is the jth component of the SST then $z_i(t)$ can be modelled as a constant, plus a multiple of $c_j(t)$ plus some error term, given by $\epsilon_j(t)$. The coefficient for the ith principal component of the biological data and the jth principal component of the SST data is given by $\beta_{i,j}$.

$$z_i(t) = \beta_{i,j} c_j(t) + \epsilon_j(t) \tag{1}$$

A hypothesis test can be done to determine whether the correlation is significant, with a null hypothesis of $\beta_{i,j} = 0$. Since the value of the data at one time point may not be independent from the value at preceding time points it may be necessary to correct for the effects of autocorrelation, which is the cross-correlation of a signal with itself. One possible approach to this is to adjust the effective degrees of freedom when calculating the p-value from the hypothesis test (Pyper & Peterman, 1998). The proportion of the variation in the biological component explained by the SST component can be calculated from the error terms. This is given by $1-\frac{\sum_k \epsilon_j(t_k)^2}{\sum_k z_i(t_k)^2}$, where t_k is the discrete time points at which the data are recorded, in this case each year. If the explained variance is close to 1 this means that most of the variation in the biological component is explained by the SST component. In this case the two time courses are close to being proportional with some small amount of noise. A value close to 0 indicates that there is very little relationship between the two variables. Another measure of linear dependence is the Pearson's correlation coefficient, which is calculated from the covariance of the two variables divided by the standard deviations of both variables multiplied together. It takes values between -1 and $+1$, with a negative value indicating a negative relationship, under the assumption of a linear relationship, so that one variable increases as the other decreases, and a positive value indicating a positive relationship, with both variables increasing together. The Pearson's correlation coefficient can be seen as a measure of how much two variables vary together. The proportion of the variance explained can also be calculated from the squared value of the Pearson's correlation coefficient, meaning that when the absolute value of the correlation coefficient is close to 1 a large proportion of the variation is explained by the model. Using these measures it is possible to determine the strength and nature of the relationship between the physical and biological variables, which will allow us to interpret the effects of these climate indices on the ecosystem.

3. Results

3.1. Sea surface temperature

In order to understand how warming effects vary in space a geographical summary of the warming trend across recent decades is produced. Fig. 1 shows the change in SST over the past few decades plotted across space. This is found by averaging over the years 1890 till 1969 and subtracting from the average from 2000 to 2009. It is apparent from this that over most of the North Atlantic the SST has increased over the past few decades, which is in line with the average climate warming trend (eNHT). The exception to this is around the subpolar gyre, which has instead cooled. Part of the reason for this might relate to changes in the circulation of the oceans, due to an influx of fresher waters (Montero-Serrano et al., 2011). There are also patches where the ocean seems to be warming slightly faster. These include regions around the coast of Greenland, the coast of parts of North America and the southern North Sea. Reasons for this increased warming might include bathymetry and the proximity to land masses. When the SST, having only the mean removed, is broken down into its component trends, the most dominant component is the warming trend. The first component also contains some oscillatory behaviour with a period similar to the AMO (Thompson et al., 2010). In fact the AMO accounts for just over 30% of the variation in this trend before detrending. This means that it behaves very similarly to the NHT signal.

It is also useful to decompose the linear detrended data. The linear trend is probably one of the strongest sources of variability across the North Atlantic. When this trend is removed there is a change in the importance of subsequent components and their ordering. Geographical patterns of various climate signals become more clearly defined. Since the first component on the non-detrended data resembles the NHT and the NHT and the AMO are not orthogonal, it may not be possible to find the spatial pattern of the AMO without first detrending the data. Fig. 2 shows the breakdown of the SST once the linear trend has been removed. The linear trend is first subtracted at each location then spatial principal component analysis is used to separate the trends. After linear detrending the first component accounts for 34.63% of the variance, with the second and third accounting for 13.68% and 10.54% respectively.

The first component is present across all regions but its influence is centred upon the subpolar gyre. The weights are positive but much smaller about the rest of the North Atlantic. The first component shows a strong oscillatory behaviour, with a period of close to 60 years. This means that both in its spatial distribution and its temporal structure it resembles the AMO. This agrees with the findings of

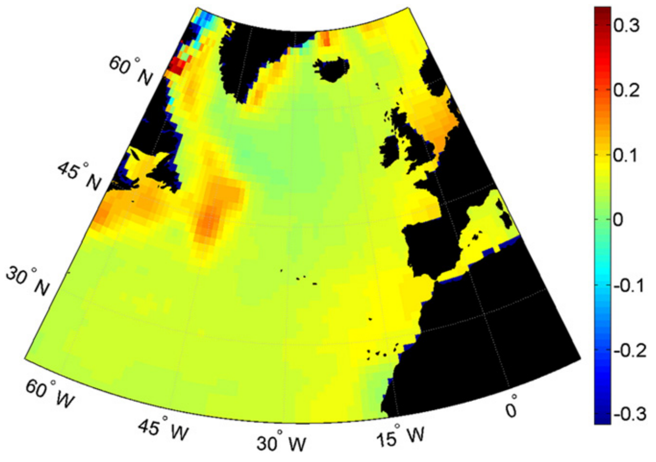


Fig. 1. Plot of the change in degrees Celsius in sea surface temperature measured as the sea surface temperature averaged over the years 1890 till 1969 and subtracted from the average from 2000 to 2009.

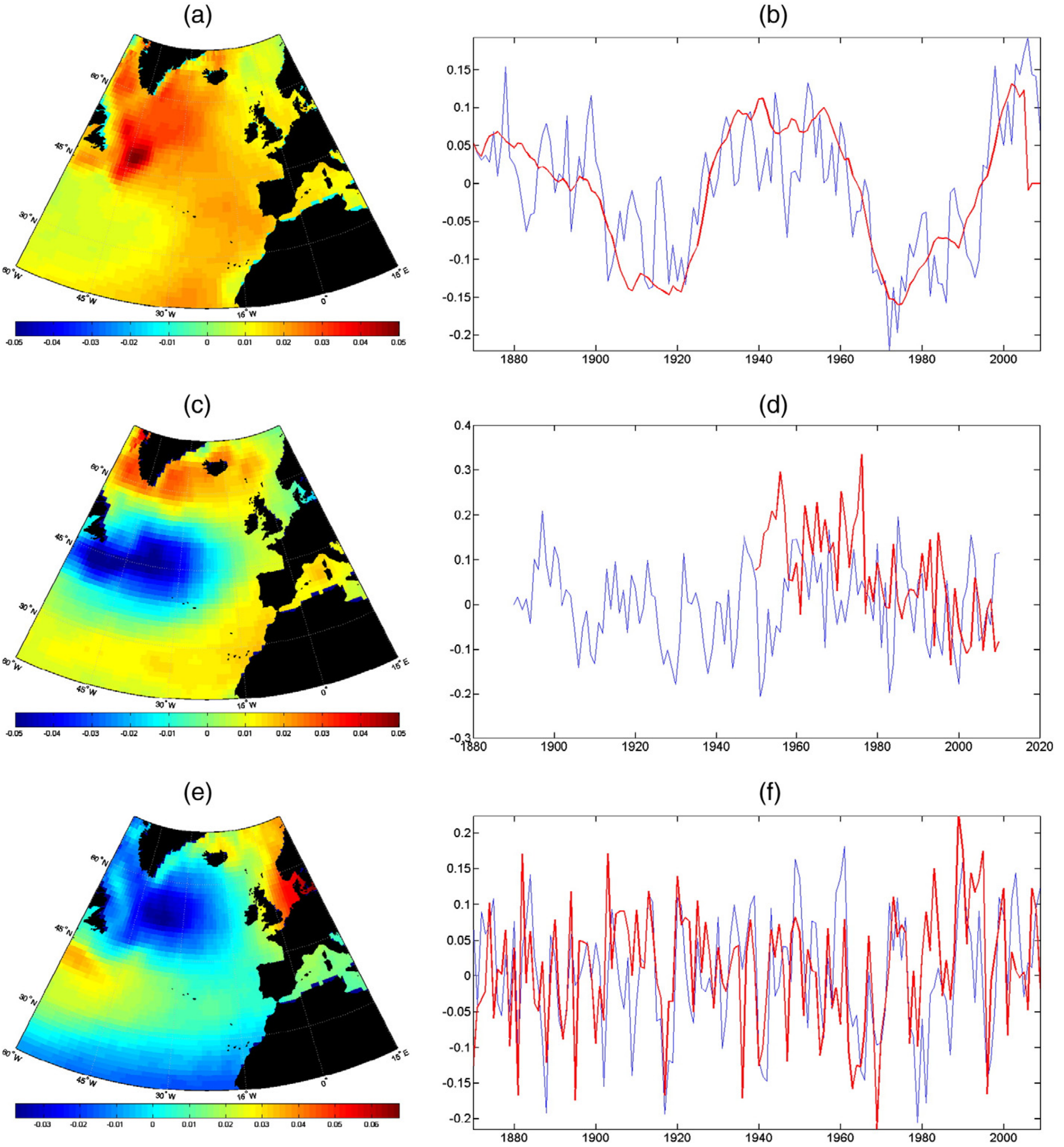


Fig. 2. Loading vectors plotted in space and principal components for the linearly detrended sea surface temperature, which is given as a time course at each location in degrees Celsius. (a) Loadings in space for the first principal component. (b) The first principal component for detrended sea surface temperature across the North Atlantic. The principal component is plotted in blue, with the Atlantic Multidecadal Oscillation overlayed in red. The AMO accounts for 51.89% of the variation in the first PC with a p-value of close to 0 and a Pearson's correlation coefficient of 0.7204. (c) Loadings in space for the second principal component. (d) The second principal component (blue) and the EAP signal from 1950 (red). (e) Loadings in space for the third principal component. (f) The third principal component. The principal component is plotted in blue, with the North Atlantic Oscillation overlayed in red. The NAO accounts for 24.38% of the variation in the first PC with a p-value of 0.0000 and a Pearson's correlation coefficient of 0.4938.

Schlesinger and Ramankutty (1994), which show an oscillatory trend to be the dominant mode of variability in detrended SST across the North Atlantic. The correlation between the first principal component and the AMO is very strong, with the AMO accounting for over half the variation and a Pearson's correlation coefficient of over 0.7. The effective degrees of freedom are given by $n - 2 = 139$, where n is the number of time points. This would suggest that a Pearson's correlation coefficient of 0.7 is highly statistically significant. This indicates that the AMO is an important driver in detrended SST, particularly in the subpolar gyre, which agrees with previous findings (Schlesinger & Ramankutty, 1994 and Cannaby & Husrevoglu, 2009).

The second largest source of variability is not correlated with any known climate indices, meaning it may be some as yet unknown climate oscillation or it may be an aggregation of different oscillations. Unlike the first component the second principal component is negatively weighted across some regions of space and positively weighted across others. This indicates that some regions are responding in an opposite way to others to this trend. It shows a sinusoidal behaviour in space, with negative weights around the subpolar gyre and extending across into part of the region off the coast of North America and positive weights elsewhere. The wavelength of this spatial oscillation can be approximated as twice the distance from the maximum point to the minimum, which in this case is about 40° in latitude, which is approximately 4450 km. This spatial pattern resembles the pattern of the EAP in that it has a north–south dipole in space. Cannaby and Husrevoglu (2009) identify the time course of the second principal component with the EAP, however in this analysis the correlation is fairly weak, with a Pearson's correlation coefficient of only −0.1179. The difference between the time course in this analysis might be due to the inclusion of the North Sea and Mediterranean, which Cannaby and Husrevoglu (2009) omit. In the frequency domain the second principal component has an oscillation with a period of about 18 years. Some climate indices are known to contain similar period oscillations for example as a result of lunar oscillations, which was reported by Yndestad (2006) to have an influence on the NAO. Whether this is the driving force behind the oscillation or it is the result of some unknown factor is unclear and may warrant further investigation. The second component has a weak positive correlation with the NAO signal, which explains about 6% of the variation.

The NAO also appears be an important influence on the SST, although this is positive in some regions and negative in others. It has the most positive weights in the North Sea, which is the location of one of its centres (Barnston & Livezey, 1986). This spatial pattern is seen in the third principal component, which has a dipole in space. The weights are negative in the subpolar gyre, there is a region with positive weights in the southwest and the signal is very strongly positively weighted in the North Sea. The period of the oscillation in space is about 90° in longitude at a height of about 52° latitude, which is about 6170 km accounting for the curvature of the Earth. This spatial pattern is similar to the pattern of the NAO in space (Wallace, 2000). The signal exhibits a short term oscillation and when regressed against the NAO signal has a positive correlation. The Pearson's correlation coefficient is close to 0.5, which is reasonably strong given the degrees of freedom. The correlation with the NAO is stronger post-1965 than it is prior, with an explained variance of 21.8% and a Pearson's correlation coefficient of 0.4670 beforehand and an explained variance of 32.54% and a Pearson's correlation coefficient of 0.5705 afterwards. This can be seen from the plot (Fig. 2(f)), as the two signals ‘behave together’ more frequently in the latter part. In interpreting the change in correlation it is important to note that the sea surface temperature might be considered as non-stationary, that is the mean or the variance of the signal might change over time. This means that the correlation with different climate indices might also change with time. This means that the correlation coefficient should be interpreted as an average over time, although the relationship itself with the climate index may in fact be evolving. In the frequency domain the third principal component not only has oscillations with a period of 8–10 years like the NAO but also has an oscillation with a period of 14 years, which is not present in the NAO signal. The NAO signal has a residual oscillation with period similar to the AMO but because of the orthogonality of the principal components this is not present in the third component, which means the third component only contains those frequencies in the NAO that are orthogonal to the AMO.

Summarising how much of the variation in SST can be understood across different regions using these known climate indices it is possible to see that the AMO is an important effect in certain regions, whilst the understanding of other regions is greatly improved by accounting for the effect of the NAO. There are some coastal regions with complex local climate that are poorly explained by these indices alone. Fig. 3 shows how much of the variation at each location is not explained by the principal components as responses to climate signals. The first component of detrended SST is modelled as a linear function of the AMO. The estimate of the first component from the AMO is given by a linear regression equation. At each location the loading on the principal component at that location multiplied by the estimate of that principal component given by the AMO is calculated, which gives an estimate of how much of the variability is explained by the AMO. The Euclidean distance between the estimate of the variability explained by the AMO and the SST time course at the given location gives an estimate of the total variability over time in the sea surface temperature that is not due to the AMO. This is then renormalized by the Euclidean norm of the time course at that location in order to be comparable over locations. A dark red pixel shows that a large proportion of the variance is not explained by the AMO, whilst a blue pixel shows that most of the SST is driven

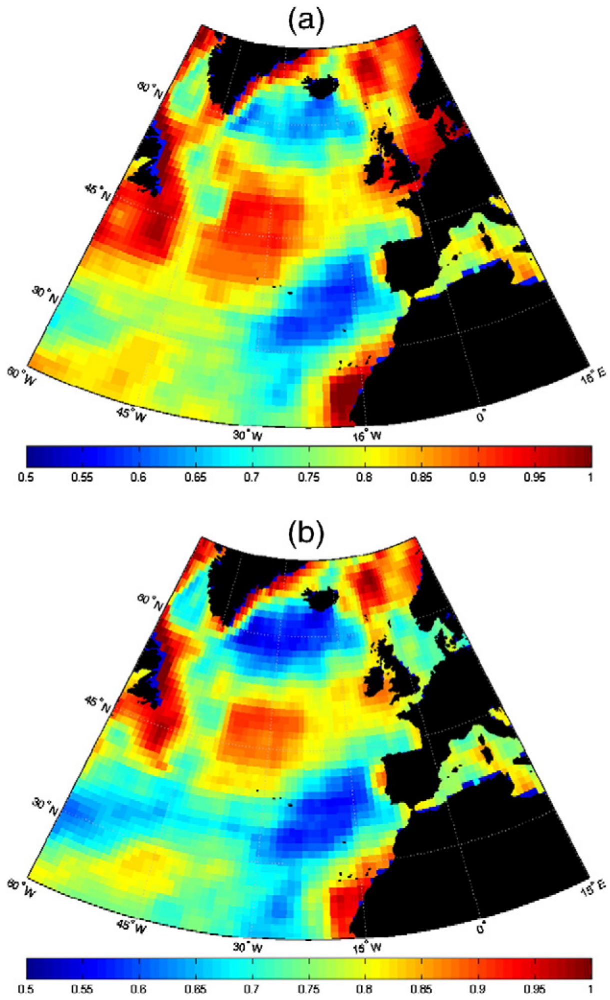


Fig. 3. Plots of the amount of variation in sea surface temperature left unexplained by the principal components modelled as responses to climate indices culminatively. (a) Plot of the amount of variation unexplained at each location explained by the first detrended principal component modelled as a response to the AMO. (b) Plot of the amount of variation unexplained at each location explained by the first three detrended principal components modelled as a response to the AMO and the NAO.

by the AMO. This shows that the AMO explains the least amount of variance in coastal regions, near the Labrador Sea and the North Sea. In these regions there must be additional factors which influence the SST. Since the third component can be modelled as a response to the NAO, this effect can also be incorporated into the estimates of the variance explained. In a similar way the amount of variation explained cumulatively by the AMO and the NAO can be calculated. The biggest difference is that the North Sea is now much better explained, given how important the NAO is to this region. Regions which are well explained become larger. One region where the observed SST remains poorly explained by these two climate signals is the region near the coast of North America. Coastal regions also seem less well explained, in particular around the coast of Greenland.

When comparing with the biological data the SST must be restricted to the same spatial and temporal regions, however this will result in a different set of components because of the spatial variation in the importance of different signals. The time period was restricted to 1958 to 2009 and the same spatial grid is used as is used for the interpolated plankton dataset. There are some changes in the components when the data are restricted to this region only, see Fig. 4. Without detrending the first component resembles the general warming trend and is most strongly weighted in the southern North Sea. With a lag of 9 years the first component of the SST over the CPR space–time region correlates with the NHT with a Pearson's correlation coefficient of 0.5477 and explaining 29.99% of the variation. The second resembles the AMO, having strong weights in the north of the region. With a time lag of 9 years the Pearson's correlation coefficient between principal component 2 of the SST and the AMO signal is 0.6054 and 36.65% of the variation is explained. The NAO signal contains an oscillation of similar period to the AMO with a time lag and the second component might also represent this. Since the lags are the same for both the NHT against the first component over this region and the AMO and the second component, it appears that the data in the north east of the North Atlantic responds later than the average signal over the northern hemisphere. The third component is positively weighted in the North Sea, particularly the south, and the temporal signal is similar to the NAO. The NAO without any time lag accounts for 27.72% of the variation in the third principal component and the Pearson's correlation coefficient is 0.5265. The absence of a time lag is because the North Sea is the region in which the NAO signal has the strongest influence, which can be seen clearly from the analysis of the entire North Atlantic (see Fig. 2). These results are comparable with the results of Beaugrand et al. (2009), whose analysis of the SST in the North East Atlantic finds similar spatial and temporal patterns.

3.2. Biological data

The components that make up the SST are influential in driving the behaviour of plankton species. The relationship between the SST components and the plankton is often stronger for the first two components than the later ones. This is not surprising because it is likely that those effects that have a large influence on the temperature will also have a strong influence on the plankton. The most important driver of plankton variability appears to be NHT climate warming trend but other oscillations were also influential. Fig. 5 shows the relationship between the major trends within each of the plankton groups and the major trends in the non-detrended (only the median has been subtracted) sea surface data over the same region.

Calanus finmarchicus is a cold water copepod, which has been adversely affected by warming waters. The first temperature principal component, which represents the NHT warming trend, appears to have a strong negative correlation with the first spatial principal component on *C. finmarchicus* (see Fig. 6(a)). The time course of the first principal component for *C. finmarchicus* shows a stepwise decrease around 1990 and is positively weighted for most of the North East Atlantic. This shows that *C. finmarchicus* is undergoing a rapid decline over the entirety of the region. Since it is a cold water species as the North Atlantic warms the habitat becomes less well suited to *C. finmarchicus*. The first component accounts for 37.14% of the variance, which means that the NHT climate warming trend is the most dominant driver for this species. The first component also has a weaker correlation with the second SST component, which is the time lagged AMO.

The second principal component for *C. finmarchicus* correlates most strongly with the second SST trend and has a weaker correlation with the other trends. The time course has a peak around 1990 and the spatial pattern shows positive weights in the northwest and negative in the northeast. The second component accounts for 21.01% of the variance and may account for the response to natural variation. The third component not only has some correlation with the third SST component, which appears to be driven by the NAO, but also only accounts for 8.62% of the variation. The fourth component correlates with the third SST component and accounts for less than 5% of the total variation. This suggests that the NAO also drives some of the behaviour of *C. finmarchicus*, although is less important than the influence of the warming trend (see Helaouët et al., 2011). When Spatial PCA is carried out on the data for *C. finmarchicus* with linear trend removed the first principal component resembles the AMO in that it is an oscillation with a period of approximately 60 years. The Pearson's correlation coefficient between the first principal component of the detrended data and the AMO is approximately −0.5. This is to be expected as once the dominant signal, which is the trend of decline across most regions, is removed the second most dominant trend, which is the AMO, becomes the most important. The second component also resembles the AMO and the third has a moderate (Pearson's correlation of approximately 0.25) positive correlation with the NAO.

Total phytoplankton abundance also seems to be primarily driven by climate warming and has a positive relationship with the NHT warming trend (see Fig. 5), although the AMO also appears to have an influence. This is possibly because the AMO is also linked to diatom abundance. The first principal component for the Phytoplankton Colour Index has almost the inverse behaviour to the first component for *C. finmarchicus* (see Fig. 6(b)). Just after 1990 it undergoes a dramatic stepwise increase, which is positively weighted across the entirety of the North East Atlantic (Edwards et al., 2001). This implies that the abundance of phytoplankton is positively influenced by the increasing Northern Hemisphere Temperature. Since the colour index provides an estimate of phytoplankton biomass only this does not indicate whether the composition of the phytoplankton is changing. It may be that this increase is due to certain species responding positive to the increasing temperature or the increase in atmospheric carbon dioxide (Torstensson et al., 2012 and Biswas et al., 2011). This first component accounts for 47.54% of the variation in the colour index data. The second colour index component accounts for 10.51% of the variation and is most strongly correlated with the second SST trend. The time course has a strong negative peak just before 1990. The spatial pattern shows strong positive weights around the northwest of the region, which is an area of interest for the phytoplankton, and some positive weights in the southwest, around 10° west. This suggests that the AMO is a much weaker driver for the phytoplankton than the climate warming trend. The third colour index component, which accounts for 8.24% of the variance, has a weaker correlation with the second temperature component. The fourth component has a negative correlation with the third SST component, which is a response to the NAO. After detrending the data first component of the Phytoplankton Colour Index resembles the AMO with a Pearson's correlation coefficient of approximately 0.64, which suggests that the AMO does influence phytoplankton abundance.

Natural oscillations have less of an impact on the total abundance of copepods than they do on individual species like *C. finmarchicus*. The first principal component for total copepod abundance has a negative correlation with the first temperature component (see Fig. 6(c)), which represents the general warming trend over the North East

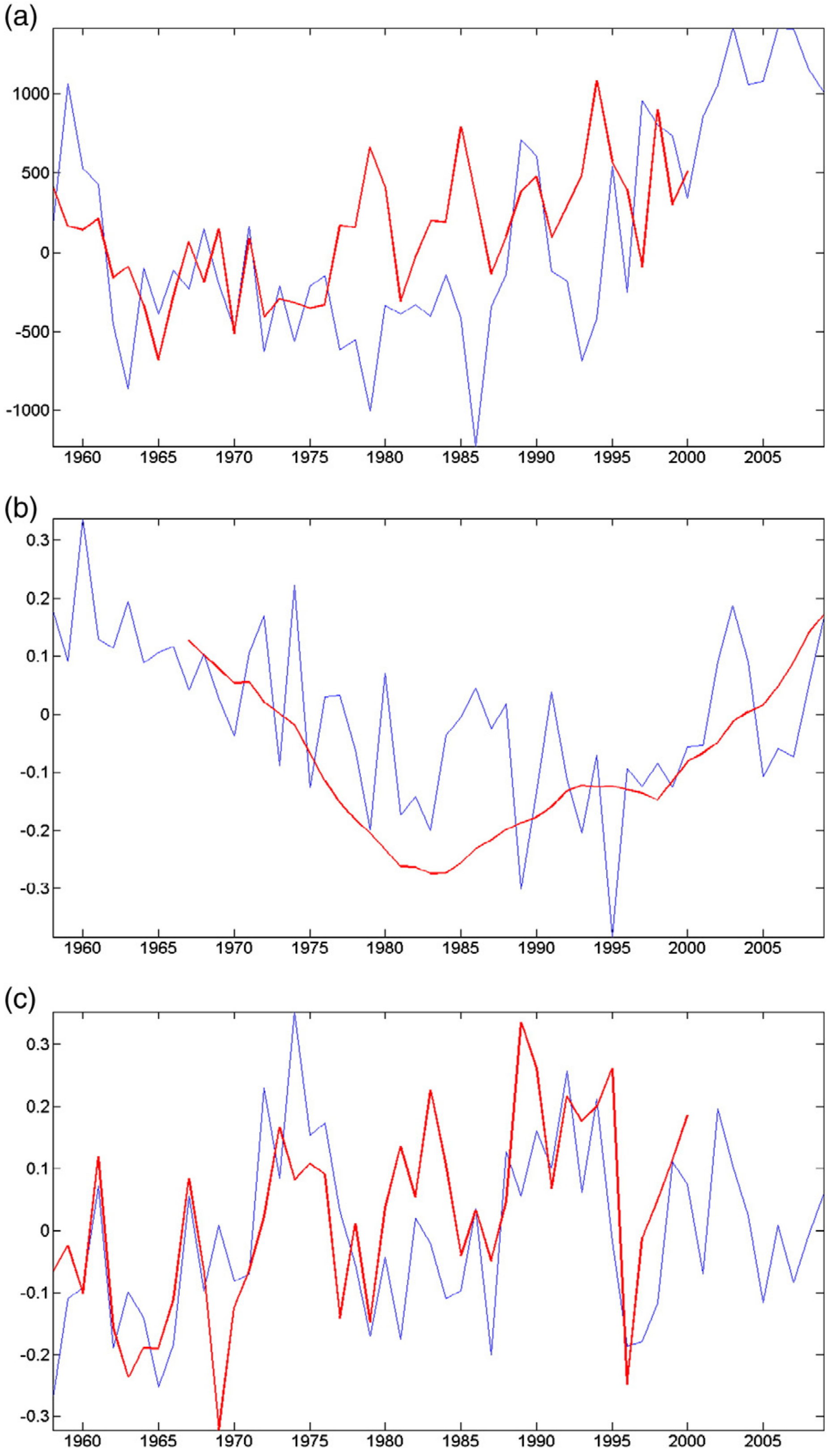


Fig. 4. Plots of the first three principal components on the sea surface temperature over the CPR region. (a) Plot of the first principal component on the sea surface temperature with only the median removed (blue) and the NHT signal lagged by 9 years (red). (b) Plot of the second principal component on the sea surface temperature with only the median removed (blue) and the AMO signal lagged by 9 years (red). (c) Plot of the third principal component on the sea surface temperature with only the median removed (blue) and the NAO signal with no time lag (red).

Atlantic. The temporal trend for total copepod abundance shows a steep decline between 1990 and 2000, with positive weights across the entire spatial region. This trend accounts for 33.49% of the total variation. This implies that although the total copepod abundance is an aggregation of both warm and cold water species on average the abundance is decreasing across the North Atlantic, which may be due to there being more

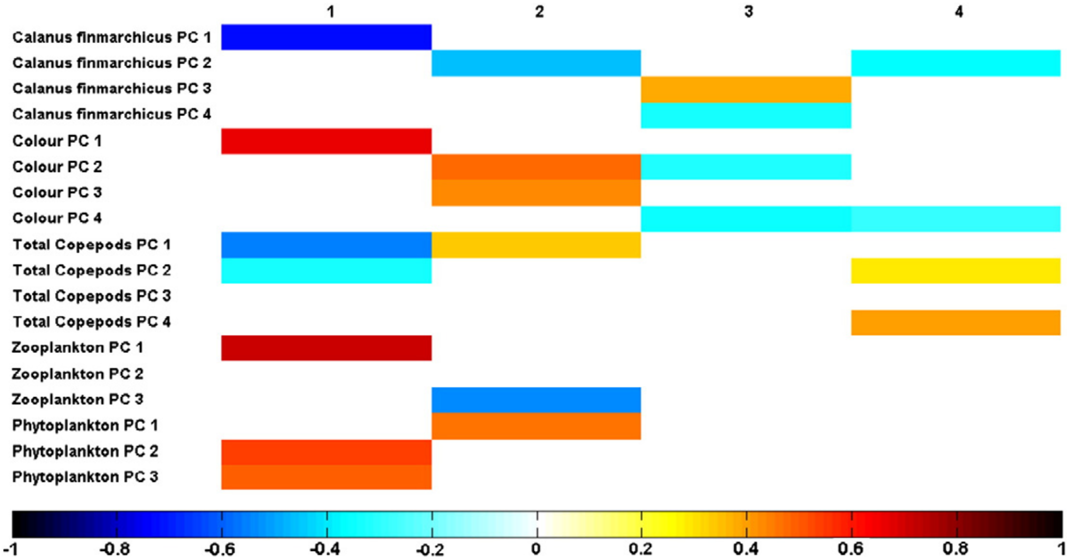


Fig. 5. Pearson's correlation coefficient between each principal component for the biological data and each principal component for the sea surface temperature with only the median removed and restricted to the same region in time and space as the biological data. A dark blue square indicates a strong negative correlation and dark red a strong positive one. A white square in the table indicates that the correlation is not significant, with a p-value of greater than 0.05. There has been no correction for multiple testing, which means approximately 5% of correlations may be spurious. Autocorrelation has been accounted for, see Pyer.

cold water species than warm water species currently and the replacement of warm water species not occurring as rapidly as the decline of cold water ones. The second component of the total copepod abundance, which accounts for 14.72% of the variation, has a fairly weak correlation with the fourth principal component on the SST. The time signal appears to be an oscillation, with a maximum in the early 1970s and a minimum in the early 1990s. Spatially it has positive weights in the south and negative in the northwest. The third component has weak correlations with the SST components and accounts for 8.86% of the variation, whilst the fourth has some correlation with the fourth SST component and accounts for 6.87% of the variation. After repeating the analysis on the detrended data the first principal component does not appear to resemble any of the indices considered in this study but the second component has a strong correlation with the AMO (Pearson's correlation coefficient approximately −0.73).

The trend of decline is not universal to all copepod species and in fact some species are increasing in abundance. The Atlantic Multidecadal Oscillation also appears to have an influence on zooplankton community behaviour but is far less important than the average warming trend. The zooplankton data are mostly comprised of copepod species, although there are a number of other zooplankton species included. The first trend correlates positively with the first SST component, the average warming trend, and begins to increase just after 1990 (see Fig. 6(d)). This trend is similar to the first principal component on total copepod abundance (see Fig. 6(c)) because they both represent the average behaviour of copepod species in some way. This trend accounts for a large portion (50.87%) of the total variation in the abundance across all species averaged in space. Amongst those species whose loadings have a positive real part are Chaetognatha traverse, echinoderm larvae and *Calanus helgolandicus*. These species are increasing along with rising SST. *C. finmarchicus* has instead a weight with a negative real part, indicating its abundance is on average over the whole North Atlantic declining in time, which agrees with the individual species analysis. Other species groups with weights with negative real parts include *Para*/*Pseudocalanus* spp., *Acartia* spp. and *Oithona* spp. *Para*/*Pseudocalanus* and *Acartia* are both groups of small species of copepod, which are more abundant in the northern North Sea than in the southern North Sea. *Oithona* is also a group of copepod species. Since the first component accounts for a large proportion of the variation it is clear that the climate warming trend is an important driver for zooplankton species and could lead to a dramatic change in the composition of the zooplankton community.

The second component accounts for 18.34% of the variation but has no clear climate driver from the SST components. The time signal is an oscillation with a peak around 1970 and a minimum in the mid-1990s. The taxa *Centropages typicus*, *Podon* spp., *Evadne* spp., Chaetognatha abundance and echinoderm larvae have strong negative weights on the second component. *C. typicus* is a calanoid copepod and prefers habitats near ocean shelves. Although both *Podon* and *Evadne* can be found in open oceans they are most common in coastal regions. Chaetognatha and echinoderm larvae are found in many regions. One possibility therefore is that the second component could relate to some coastal effect not determined by SST.

The third component on the zooplankton community accounts for 11.37% of the total variation and is correlated with the second SST component, which is driven by the AMO. *C. typicus*, *Evadne* and Chaetognatha eye count all have weights with positive real parts. Echinoderm larvae and *C. finmarchicus* conversely have weights with negative real parts. In the Spatial PCA for *C. finmarchicus* it was shown that the second component on the SST was negatively associated with the second species component, suggesting an inverse relationship between the AMO and *C. finmarchicus*. The zooplankton taxa copepod nauplii has a very strong negative weight on the third component. After detrending the first component of the copepod data is an oscillation with period similar to the AMO, suggesting that the influence of the AMO on the copepods might be obscured by the more dominant long term trend.

Although climate warming is a major driver for phytoplankton in general, when restricting the study to diatom communities this influence becomes far less important. Instead the most important influence seems to be the AMO. The first component of the phytoplankton communities accounts for 43.19% of the total variation across the different species averages and is positively correlated with the second SST principal component. The time signal resembles an oscillation with a period of about 50–60 years and a minimum around 1980. Almost all of the species in the phytoplankton group are diatoms and have positive weights with respect to the first component, including a number of species known to produce harmful toxins, such as types of *Pseudo-nitzschia*. The only negatively weighted species are the two diatoms *Bacillaria paxillifer* and *Gyrosigma* spp. This suggests for the most part that

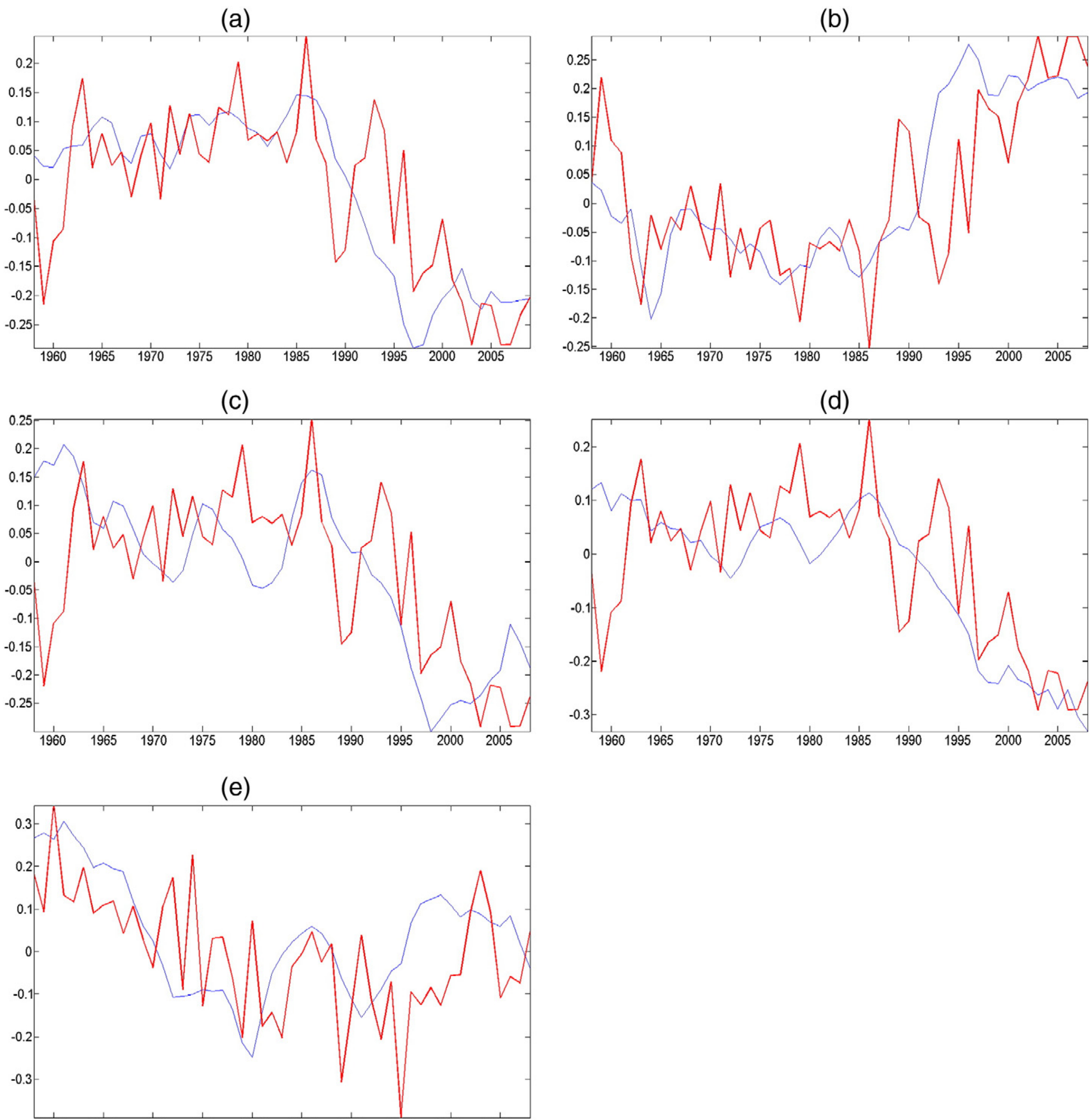


Fig. 6. Plots of the principal components on the plankton species along with the sea surface temperature trends. (a) The first principal component on *C. finmarchicus* (blue) and the first component on sea surface temperature inverted (red). (b) The first component for phytoplankton colour (blue) and the first component for sea surface temperature. (c) The first component on total copepods (blue) and the first component for sea surface temperature (red). (d) The first component on the zooplankton community (blue) with the first component on sea surface temperature (red). (e) The first component on the phytoplankton community (blue) with the second component on sea surface temperature (red).

diatoms are more abundant in the positive phase of the AMO. The second component on the phytoplankton is an increasing trend in time and accounts for 20.8% of the variation. About two thirds of the species have weights with positive real parts, amongst those are diatom species *Paralia sulcata* and *Gyrosigma* spp. Species with negative weights include: *Thalassiothrix longissima*, *Fragilaria* spp. and *Navicula* spp., which are also all diatoms. The second component has a positive correlation with the second SST component. The third component explains 7.19% of the total variation and also has a positive correlation with the first temperature component. The time signal shows a small increase over time, along with an oscillation period around 15 years. The principal components of the diatom species change relatively little after detrending, which supports the theory that the long term warming trend is not a major driver of the diatom community.

In general the climate warming trend accounts for a large portion of the variability in plankton behaviour, between 30% and 40% for most species and over 50% for the zooplankton. The exception to this is the diatoms, for which it accounts for only 20%. This is not surprising because the average warming trend is also the most important influence on temperature variability. This implies that although the influence of climate change is very important to the ecology of the North Sea, the influence of natural oscillations also must not be ignored, as they might account for between 50 and 80% of variability. In particular for the diatom communities where the AMO not only drives over 40% of the variability but also for other species where the AMO and in some cases the NAO are important influences on abundance. Fig. 7 shows the spatial patterns of the variation which is not explained by the principal components modelled as responses to the temperature components across each of the indicator species. A dark red pixel indicates that the modelled component explains relatively little of the variation, whilst a blue pixel indicates that the region is well explained by the component. For *C. finmarchicus* the first component is primarily a response to the first temperature component, the average warming trend. The plankton abundance is best explained by this trend in the northern North Sea and less well explained in the open ocean. Adding in the effect of the second component, which is most strongly correlated with the time-lagged AMO trend improves the description of the variation, particularly in the north of the region. For the Phytoplankton Colour Index the first component is strongly correlated with the average warming trend and this describes much of the variation along coastal regions. Adding the effect of the AMO, which is correlated with the second component, improves the description somewhat. For total copepod abundance much of the variation is described by the first trend, which correlates with the average warming trend, in the southwest. This shows that as with the influence of climate indices on SST, the effect of these indices on plankton populations has a spatial heterogeneity.

4. Discussion

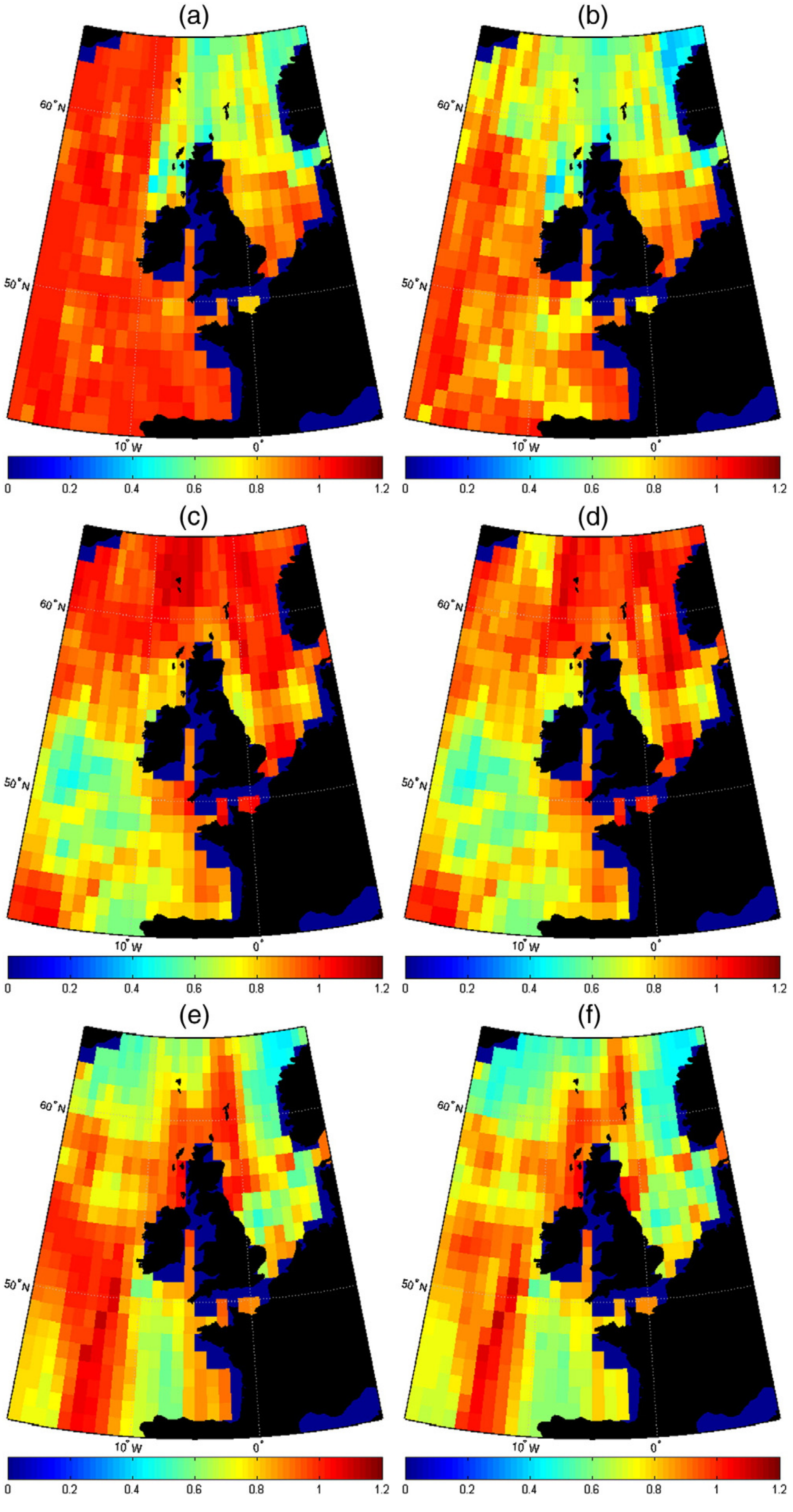
The marine climate and its impact on the ecosystem is an important concern for both environmental managers and members of the fishing industry, as well as society in general (Beaugrand & Kirby, 2010 and Rudd, 2011). What is difficult to determine, is how much of the changes observed can be attributed to natural climate variability, and how much is due to the recent warming trend (Brown et al., 2011). The term ‘climate change’ typically refers to an increase in average global temperature which is thought to be due to rising atmospheric carbon dioxide. Since this increase in carbon dioxide is thought to be a result of increased industrialisation and emissions, the change is believed to be anthropogenic (Schmittner et al., 2011). Over the past few decades an increase has been observed in the average NHT. Although it is impossible to determine whether this is a long term trend or a natural oscillation with a longer cycle than the AMO, it appears to correlate with the increase atmospheric carbon dioxide in the post-industrial era (Schmittner et al., 2011). Cannaby and Husrevoglu (2009) model the long term trend in the SST data post-1870 as a function of carbon dioxide. The issue of climate change is often controversial because of its wide reaching implications. Therefore the question of how much of the recent changes in climate is due to the recent warming trend, and how much is due to natural fluctuations is of vital importance. Natural phenomena that might influence climate include a number of oscillations in atmospheric pressure cells and oceanic currents. Oscillations switch between high and low phases, each lasting for roughly equal duration. These oscillations can often be seen in the temperature signal, where a temporary increase might be seen during a high period and a decrease during the low period.

The spatial influence and the relationship with different species of the various climate indices are non-trivial to describe without the use of statistical techniques. It has been shown for example that the NAO is an important influence in the North Sea but less so in other regions. Even though there is a general trend towards rising temperatures, there are regions of the North Atlantic which have been cooling over the past few decades, as well as other regions which have been warming at a quicker rate. The reasons for this spatial heterogeneity comprise various physical features, such as bathymetry, currents and the positioning of high and low pressure centres.

Before detrending the NHT trend proves to be the factor that explains most of the variance in the SST. The NHT is a measure of atmospheric temperature over the northern half of the globe leading to a single time series. The average temperature in the Northern Hemisphere has risen over the past few decades. A potential cause of this rise in temperature is the observed increase in atmospheric carbon dioxide (Letcher, 2009). Cannaby and Husrevoglu (2009) model the increase in temperature as a function of atmospheric carbon dioxide and subtract this from the SST signal in order to remove the warming effect. The NHT is also subject to an oscillatory effect, which has a period of around 60 years (see Thompson et al., 2010), meaning it is not orthogonal to the AMO. In our study a linear trend is fitted to the SST signal at each location in order to remove the recent warming trend. The NHT also correlates with a time lag to the first principal component on the SST over the CPR region.

After detrending it can be seen that the AMO and the NAO both represent dominant trends in the SST, accounting for the first and third components respectively. It is expected that the AMO will be the dominant mode of the detrended SST as it was first identified by Schlesinger and Ramankutty (1994) as such and a similar oscillation is present in the NHT signal. However by detrending the data the spatial pattern of the influence of the AMO becomes more apparent. The NAO signal is not isolated by using PCA on the SST data with the median only removed because it is obscured by the linear trend but the spatio-temporal pattern of the NAO is isolated when using PCA on the linearly detrended data. Over the CPR region the AMO correlates with a time lagged version of the second component and the NAO with the third. This agrees with the findings of Cannaby and Husrevoglu (2009). Although in the study of Cannaby and Husrevoglu (2009) the EAP signal was also shown to be important in this study the EAP signal has only a very weak correlation with the second component over the region described. These indices influence *local* SST. The plots of the unexplained variance (see Fig. 3) show the spatial heterogeneity of this influence. Coastal regions are least well described using only the AMO and the NAO, meaning other factors must drive the SST in these regions. Around the coast of North America there are a large number of small eddies and the ocean circulation here is complex (Luo et al., 2011), then the behaviour of the SST signal is harder to predict.

The AMO influences temperature changes across the North Atlantic but this influence is stronger where the effects of overturning ocean currents are particularly influential. The AMO has a period of approximately 60–80 years (Knudsen et al., 2011 and Schlesinger & Ramankutty, 1994) and was first identified in linearly detrended SST data. The presence of a 60–100 year oscillation in ice core and tree ring data, likened to the AMO, suggests it is probably a natural oscillation, although evidence for the presence of the AMO during the pre-industrial era is inconclusive (Knudsen et al., 2011). What causes the AMO are currently unknown (Knudsen et al., 2011). It is not thought to be driven by solar cycles and there is some speculation that it is the result of currents, with a decrease in the overturning circulation in the North Atlantic being associated with a cool phase in the AMO (Schlesinger & Ramankutty, 1994). Speculation suggests that the subpolar gyre might move across longitude during the different phases of the AMO (Montero-Serrano et al., 2011). The AMO is associated with changes in rainfall and temperature over the northern hemisphere and can been seen in the NHT time series (Enfield et al., 2001). The AMO may also have an impact on the occurrence of hurricanes in the Atlantic (Knight et al., 2006). Since it is thought to be connected to the circulation of the North Atlantic, the AMO might influence plankton abundance through changes in circulation rather than changes in temperature. The circulation might influence the degree of water column mixing, which in turn might influence the availability of nutrients, or the dispersion of plankton species (see Young


(a)
(b)
(c)
(d)
(e)
(f)
60°N
50°N
10°W
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0
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0.6
0.8
1
1.2

et al., 2012). Cannaby and Husrevoglu (2009) identify the AMO to be the most dominant trend in the detrended SST over a region extending from approximately 50° W to 1° E and 20 to 70° N and our analysis produces similar findings. The temperature difference between the subpolar gyre and the surrounding waters drive convection forces, which governs the behaviour of currents. This may in turn affect the spatial pattern of the AMO and the sea surface height.

One area for further exploration might be to investigate how to separate effects on plankton in a scalar environment, such as temperature, and effects in a vector environment, such as currents. Keister et al. (2011) make some progress in doing this for zooplankton in the Northern California current responding to the Pacific Decadal Oscillation. This is achieved by comparing abundances of copepod species with a transport model for the currents. A multiple regression model is used in order to determine how much of the variability in the copepods can be explained by horizontal water movements. Their results show that a large proportion of the multiyear variability in zooplankton communities in their region of interest is due to horizontal surface advection. Keister et al. (2011), however, do not explicitly address the influence of global temperature changes.

Although Cannaby and Husrevoglu (2009) find it to be the second most important mode of variability in SST, the East Atlantic Pattern (EAP) is perhaps less well understood than the NAO. The EAP behaves similarly to the NAO and consists of a north–south dipole of anomaly centres spanning the North Atlantic from east to west, as well as showing strong multidecadal variability. Barnston and Livezey (1986) define it as having a centre near 55° N and 20 to 35° W with a strong northwest–southeast gradient over western Europe. Owing to the lack of available atmospheric model reanalysis data in the central North Atlantic it is not possible to extend the EAP index back beyond 1948 based on this definition (Cannaby & Husrevoglu, 2009). In this analysis the EAP had only a weak correlation with the temporal signal, although the spatial patterns of the weights did show a north–south dipole which is similar to the spatial pattern of the EAP. The second principal component in this study instead contains an oscillation with an 18 year period, which may warrant further exploration.

The NAO has a strong positive influence on the North Sea but the response of SST in the subpolar gyre is inversely related to the NAO (Hurrell, 1995). The North Atlantic Oscillation (NAO) is believed to have a period of about 8–10 years (Jones et al., 1997). This oscillation has been identified in both the SST signal and in ice core records (Hurrell, 1995). The NAO is a measurement of fluctuations in the difference of atmospheric pressure at sea level between the Icelandic low, a permanent low pressure centre, and the Azores high, a permanent high pressure centre located near the Azores in the Atlantic Ocean, which controls the strength and direction of the westerly winds into Europe (Jones et al., 1997 and Wallace, 2000). The NAO is thought to have an influence on the ecology of the North Atlantic, such as abundance of plankton. Fromentin and Planque (1996) claim a link between the NAO and the two copepod species *C. finmarchicus* and *Calanus helgolandicus*. Whilst a high phase is detrimental to *C. finmarchicus*, *C. helgolandicus* seems to benefit from it. Furthermore the NAO is thought to influence the length of the blooming season of phytoplankton and the number of Arcto-Norwegian cod (Ottersen et al., 2001). The influence of the NAO on wind anomalies also affects ocean circulation, meaning it has an impact on ocean currents. In both our and Cannaby and Husrevoglu's (2009) study the NAO was found to be the third most dominant mode in SST across the North Atlantic.

The relationship between climate warming and plankton is one of great importance. A reduction in the downward circulation of organic material caused by changes in planktons' seasonal cycles, production and composition resulting from changes in temperature and ocean acidification may even exacerbate the problem of atmospheric carbon dioxide (Philippart et al., 2011). Beaugrand et al. (2010) explore the relationship between carbon cycles and both biodiversity and composition of species in the North Atlantic. They suggest that the increasing dominance of smaller organisms may have negative effects on the downward biological carbon pump. Fig. 5 shows the relationship between the SST over the CPR region and various plankton groups. The most important driver for the plankton behaviour is the first component, the recent warming trend. Some species have a positive relationship with the recent warming trend, generally those that flourish in warmer climates, whilst others have a negative relationship, such as cold water species like the copepod *C. finmarchicus*. These changes will affect larger organisms that predate upon plankton. Across the different species the recent warming trend seems to account for anywhere between 20% (phytoplankton communities) and over 50% (zooplankton communities). This means more than 50% of the variation in plankton abundance might be the result of natural oscillations or other environmental factors not attributable to climate warming. For many plankton species groups the most important influence is the recent warming trend but the complex behaviour is better understood when the effect of natural oscillations is taken into consideration. It is apparent that the influence of these different trends on abundance varies spatially for the indicator species. The community analysis across the entire time period, which has not been well studied in the North East Atlantic before using the CPR dataset, allows one to identify which climate trends are important in driving the joint behaviour of functional groups and which species respond positively or negatively to these trends. For example one can identify those species whose abundance is increasing in line with the recent NHT warming trend and those species whose abundance is decreasing as the NHT increases.

Amongst the zooplankton communities warm water species are in general increasing with rising temperatures and cold water species are in decline on average across the North East Atlantic. However the pattern of these responses is spatially heterogeneous. Helaouët and Beaugrand (2009) also state that changes in abundance of different species vary across the edges of its ecological niche and in particular that the North Sea lies at the edge of an ecological niche for cold water copepod *C. finmarchicus*, making it vulnerable to rising temperatures in this region. For example other studies have shown the potential for an increase in *C. finmarchicus* at the very northern edge of its distribution (Reygondeau & Beaugrand, 2011), particularly in the Barents Sea, an area which is not included in our study. Although certain species are increasing, total copepod abundance has overall declined in relation to increasing SST. Copepods are small crustaceans, which spend their entire lifecycle in the plankton. Their spatial distribution is influenced by temperature, with some species preferring cooler conditions and others preferring warmer waters (Helaouët et al., 2011). Batten and Walne (2011b) find that during warm years species that tend to prefer more temperate conditions are found further north in the North East Pacific. About 30% of the variation in total copepod abundance across space is driven by rising temperature. What drives the rest of the variation is unclear but factors unrelated to climate variations, changes in nutrients or variation in the behaviour of predator–prey relationships might all

Fig. 7. Plots of the amount of variation in plankton abundance left unexplained by the principal components modelled as responses to climate indices culminatively. (a) Plot of the amount of variation not explained by the first sea surface temperature component in *Calanus finmarchicus* at each location. (b) Plot of the amount of variation not explained by the first two sea surface temperature components in *Calanus finmarchicus* at each location. (c) Plot of the amount of variation not explained by the first sea surface temperature component in total copepod abundance at each location. (d) Plot of the amount of variation not explained by the first and second sea surface temperature components in total copepod abundance at each location. (e) Plot of the amount of variation not explained by the first sea surface temperature component in Phytoplankton Colour Index at each location. (f) Plot of the amount of variation not explained by the first two sea surface temperature components in Phytoplankton Colour Index at each location.

contribute. The total copepod count is an aggregation of the abundance of all different species of copepods. The abundance of copepods is sometimes used as an indicator of the zooplankton in general. Some transient plankton, organisms such as fish larvae which only spend part of their lifecycle in the plankton, predates upon copepods. This means that the abundance of copepods might have a knock on effect upon the stocks of larger organisms. The indicator species *C. finmarchicus* is a cold water copepod, which is often found in the North Sea. *C. finmarchicus* is characterised by its stores of omega-3 fatty acids and protein, which make it an excellent food source for young fish larvae. *C. finmarchicus* is believed to respond to changes in temperature and Helaouët et al. (2011) report that the North Sea lies at the edge of its ecological niche, making it more vulnerable to climate effects in this region. This agrees with our findings.

Almost 50% of the variation in phytoplankton colour seems to be driven by warming effects, with total phytoplankton abundance appearing to be increasing across the whole of the North East Atlantic. This suggests that increasing temperatures have a positive effect on phytoplankton abundance. This may be related to an increase in light intensity or longer seasonal growth periods. Phytoplankton colour is an index which measures the total biomass of phytoplankton. Phytoplankton consist of any species that photosynthesize and are primarily single-celled organisms. They are divided in to two main subgroups: dinoflagellates, which are characterised by their tendril-like flagella and diatoms, which are unicellular and have a rigid cell wall (Hardy, 1971). Phytoplankton are the primary producers in the plankton. The phytoplankton play roles in the Earth's oxygen production and given there is little free-floating multicellular plant-life in the open ocean, the role of the phytoplankton in the food chain is fundamental. One of the main influences on their abundance is zooplankton grazing. Reid et al. (2007) use the CPR dataset to identify changes in patterns of plankton in the North Atlantic. One of their findings is that species of Pacific phytoplankton are beginning to be found in samples taken from the North Atlantic. McQuatters-Gollop et al. (2011) discuss whether phytoplankton are increasing or declining and how the CPR dataset suggests there has been an increase in Phytoplankton Colour Index over recent decades, which agrees with our findings. The increase in total abundance of phytoplankton is also observed in other datasets (McQuatters-Gollop et al., 2011). McQuatters-Gollop et al. (2007) further show that the increase in phytoplankton abundance due to changes in temperature can be separated from changes in abundance due to nutrient supply. Using forward stepwise regression they select physical and biological variables that have a significant relationship with the Phytoplankton Colour Index. Their results suggest that a peak in phytoplankton abundance occurred around 1989, influenced by increased SST and the positive phase of the NAO. This corresponds to the stepwise increase in the first component of the colour index. Since this component is positively weighted across the North East Atlantic it is apparent that the abundance is on average increasing across the whole region. Furthermore they show through the linear regression model that the increase in phytoplankton cannot be explained completely by changes in nutrients, which suggest that temperature is a driver of phytoplankton abundance.

The second SST component has a secondary influence on the total abundance after the recent warming trend on many species. The exception to this is the phytoplankton group, which is predominantly composed of diatoms, for which it is the most important driver (see Fig. 5). The second SST component in this region correlates with a time lagged version of the AMO and may represent changes in response to wind intensities in the plankton. Diatoms are able to survive in most temperature ranges but are sensitive to changes in mixed layer depth (Falkowski & Oliver, 2007) This suggests that diatoms are not affected by temperature, aside perhaps from a secondary effect caused by changes in their predators, so much as hydro-climatic variability. This is due to the fact that their abundance is driven by wind intensity and subsequent water column mixing (Falkowski & Oliver, 2007). Further work is needed in order to better understand the mechanisms by which the AMO influences the behaviour of diatoms and in order to understand how ocean circulation, which is believed to drive the AMO (see Schlesinger & Ramankutty, 1994), influences plankton communities as a whole. The AMO also seems to have some relationship with phytoplankton abundance, which may be due to its influence on diatom communities. For other groups this trend accounts for between 10 and over 20% of the variation.

The third and fourth components of SST are far less important as drivers of plankton abundance, although the third component has some correlation with *C. finmarchicus* abundance. This component behaves like the NAO and this agrees with previous studies that suggest the NAO influences the behaviour of certain copepods (Ottersen et al., 2001), although it accounts for a relatively small proportion of the variation.

Not all species are susceptible to temperature increases and even for those that are the effect of natural oscillations their abundance is also important. The AMO can be seen to also have an influence on the abundance of different species, particularly those such as the diatoms. In addition to these factors there are various other variables which cannot be accounted for as responses to rising temperature or as responses to natural oscillations. The plankton forms a complex ecosystem and so there are many other potential influences on their abundance which might be further explored. The challenge in understanding the behaviour of plankton communities comes from distinguishing between change driven by natural variability and change driven by climate change. Principal component analysis allows trends to be separated from one another by producing orthogonal time courses. Furthermore it is possible to visualise the complex spatio-temporal behaviour and heterogeneity using PCA, when such structure would be difficult to interpret from the data alone. We see that there is a 'regime shift' in zooplankton communities driven by the recent NHT warming trend (see Beaugrand et al., 2008), whilst the NAO is of lesser importance but still has an influence. For both the SST and marine ecology of the North Atlantic, however, the effect of natural oscillations such as the AMO may also play a larger role than previously believed. In conclusion we see that the behaviour is driven by a mixture of natural oscillations and the recent climate warming trend and that the importance of these factors has strong variation across space and species.

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