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Climate change-related regime shifts have altered spatial synchrony of plankton dynamics in the North Sea

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Abstract

During the 1980s, the North Sea plankton community underwent a well-documented ecosystem regime shift, including both spatial changes (northward species range shifts) and temporal changes (increases in the total abundances of warmer water species). This regime shift has been attributed to climate change. Plankton provide a link between climate and higher trophic-level organisms, which can forage on large spatial and temporal scales. It is therefore important to understand not only whether climate change affects purely spatial or temporal aspects of plankton dynamics, but also whether it affects spatiotemporal aspects such as metapopulation synchrony. If plankton synchrony is altered, higher trophic-level feeding patterns may be modified. A second motivation for investigating changes in synchrony is that the possibility of such alterations has been examined for few organisms, in spite of the fact that synchrony is ubiquitous and of major importance in ecology. This study uses correlation coefficients and spectral analysis to investigate whether synchrony changed between the periods 1959–1980 and 1989–2010. Twenty-three plankton taxa, sea surface temperature (SST), and wind speed were examined. Results revealed that synchrony in SST and plankton was altered. Changes were idiosyncratic, and were not explained by changes in abundance. Changes in the synchrony of *Calanus helgolandicus* and *Para-pseudocalanus* spp appeared to be driven by changes in SST synchrony. This study is one of few to document alterations of synchrony and climate-change impacts on synchrony. We discuss why climate-change impacts on synchrony may well be more common and consequential than previously recognized.

Keywords: cospectrum, North Sea, plankton, power spectrum, regime shift, synchrony

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Introduction

Population dynamics are influenced by climate fluctuations, and there is ever-growing evidence that global change-related alterations to climate fluctuations also alter population dynamics. For instance, Saitoh *et al.* (2006) described a shift in the dynamics of the grey-sided vole (*Clethrionomys rufocanus*) during the 1970s, corresponding to the timing of a regime shift in Pacific climate (Hare & Mantua, 2000). García-Carreras *et al.* found links between changes in the spectral colors of climatic fluctuations and the spectral colors of population fluctuations (García-Carreras & Reuman, 2011). García-Carreras & Reuman (2013) and Lawson *et al.* (2015) argued that changes in other statistical aspects of environmental time series can be at least as important for populations as changes in more commonly studied mean environments.

In the North Sea, several studies have demonstrated that a climate change-induced ecosystem regime shift occurred in the 1980s. The ecosystem shifted from a cooler to a warmer state (Beaugrand, 2004; Beaugrand & Ibañez, 2004), altering relationships between species and large-scale climate variables such as the North Atlantic Oscillation (NAO) and Northern Hemisphere Temperature (NHT) (Reid *et al.*, 2001; Beaugrand & Reid, 2003; Beaugrand, 2004, 2012; Lindley *et al.*, 2010), and resulting in increases in phytoplankton biomass and shifts in community composition (Beaugrand, 2003). In particular, a change in the dominant copepod species occurred, from *Calanus finmarchicus* to *C. helgolandicus* (Planque & Fromentin, 1996). Increases in decapod and echinoderm larvae and a decrease in bivalve larvae also occurred (Kirby *et al.*, 2008). Changes similar to some of these have also been

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detected in the North Pacific (Venrick *et al.*, 1987; Hays *et al.*, 2005). Reid *et al.* (2016) showed recently that the 1980s regime shift formed part of a major change in the Earth's biophysical systems triggered by the combined effects of anthropogenic warming and a volcanic eruption.

Although climate-induced changes in spatial patterns and temporal dynamics such as those described above are well documented, possible changes in aspects of spatiotemporal dynamics such as metapopulation synchrony have not been investigated in the North Sea and are much less studied generally. Filling that gap is the main goal of this study. Metapopulation synchrony is defined as correlated fluctuations in the abundances of geographically distant populations. Synchronized climatic drivers of populations can induce synchrony in the populations, a process called the Moran effect. This is one of the main causes of synchrony (Moran, 1953; Lande *et al.*, 1999; Liebhold *et al.*, 2004; Engen & Saether, 2005). Hence, changes in climatic drivers may cause changes in synchrony.

It is important to study synchrony and potential changes in synchrony for several reasons. First, synchrony has been observed across large geographic areas and in diverse taxa including plankton (general examples: Moran, 1953; Hanski & Woiwod, 1993; Paradis *et al.*, 1998; Koenig, 1999; Lande *et al.*, 1999; Liebhold *et al.*, 2004; Engen *et al.*, 2005; Vasseur & Fox, 2007, 2009; plankton examples: Perry *et al.*, 2004; Vasseur & Gaedke, 2007; Batchelder *et al.*, 2012; Ottesen *et al.*, 2013). Second, synchrony is ecologically important in part because metapopulations exhibiting more synchrony can have an increased risk of extinction (Heino *et al.*, 1997). Third, synchrony can also influence regional ecosystem functioning (Bjørnstad *et al.*, 2002; Beaugrand *et al.*, 2003; Stenseth *et al.*, 2004; Haynes *et al.*, 2013): asynchronous local population fluctuations negate each other in the regional average population and hence have limited influence on regional functioning measures, but synchronization can result in large-scale outbreaks or shortages (Micheli *et al.*, 1999; Earn *et al.*, 2000; Vasseur & Gaedke, 2007; Keitt, 2008; Ciesla, 2011).

Synchrony in plankton may be additionally important to study because higher trophic levels in marine systems aggregate energy, which ultimately comes from plankton, over wide spatial and temporal scales. Plankton populations influence the survival and breeding success of higher predators of economic and conservation importance (Davis *et al.*, 1991; Menden-Deuer & Grünbaum, 2006), including cod (Beaugrand *et al.*, 2003), haddock (Platt *et al.*, 2003), tuna (Fiedler & Bernard, 1987), marine mammals (Weise *et al.*, 2006), penguins (Boersma *et al.*, 2009), and other seabirds (Rindorf *et al.*, 2000). Spatial patchiness, and therefore synchrony in plankton, affects consumer–resource particle encounter rates, and can thereby also affect nutrient cycling and carbon export to deep ocean layers (Goldthwait *et al.*, 2004; Ballantyne *et al.*, 2011; Prairie *et al.*, 2012). Consequences of changes in synchrony for these processes may be complex (Powell & Okubo, 1994; Grünbaum, 2002; Franks, 2005; Ballantyne *et al.*, 2011).

The potential for secular trends or regime shifts in synchrony driven by changes in climatic drivers has seldom been examined in any system. Ranta *et al.* (1997ab, 1998) demonstrated complex periodic changes in measures of synchrony for lynx populations and other populations and using models, but this was apparently due to details of dynamics rather than being a secular trend in the nature or causes of synchrony. Viboud *et al.* (2006) showed that strength of synchrony in influenza epidemics varied through time, but the pattern was not associated with climate. Cazelles *et al.* (2005) showed associations between changing synchrony in dengue epidemics and El Niño. Ojanen *et al.* (2013) showed an apparent secular trend in synchrony of populations of Glanville fritillary butterflies. Post & Forchhammer (2004) showed changes in caribou synchrony linked to changes in the NAO. Sheppard *et al.* (2015) demonstrated that large-scale changes in the synchrony of winter climatic variables, related to the NAO, caused major changes in the synchrony of aphid phenology across Britain. And Allstadt *et al.* (2015) showed changes in gypsy moth synchrony related to changes in climatic synchrony. These studies make plausible the idea of Post & Forchhammer (2002) that changes in population synchrony may be another important and common consequence of climate change. However, examples such as these showing changes in synchrony are rare compared with the many studies of synchrony that do not examine changes; more studies of changes in synchrony are needed.

To analyze synchrony and changes in synchrony, we use both standard correlation-based methods and spectral methods. Techniques such as Mantel correlograms (Oden & Sokal, 1986) and spline correlograms (Bjørnstad & Falck, 2001) are commonly employed to describe the relationship between synchrony and distance between sampling locations, and are based on correlation coefficients between time series at all pairs of sampling locations. We also apply cospectral methods. Spectral methods decompose time series into their harmonic components, indicating which frequencies are contributing most to the variance of a signal or the covariance between signals, and therefore allow the decomposition of total synchrony according to the frequencies, or timescales, at which it occurs. Synchrony on one timescale can occur independently of synchrony on another timescale, and these differences can obscure detection of synchrony by standard correlation-based methods because the correlation methods compute total synchrony on all timescales (Fig. 1; Keitt, 2008; Sheppard *et al.*, 2015). In addition, long-timescale synchrony may be more important than short-timescale synchrony, as it is more likely to affect longer lived consumers. Timescale-specific approaches to synchrony exist (e.g., Grenfell *et al.*, 2001; Viboud *et al.*, 2006; Vasseur & Gaedke, 2007; Keitt, 2008; Sheppard *et al.*, 2015), but have rarely been applied. We believe that this underuse has limited our ability to understand changes in synchrony as well as their causes and consequences (Sheppard *et al.*, 2015).

To meet our overall research goal of investigating potential changes in synchrony over the North Sea regime shift, we will address the following specific questions. (i) Has average synchrony of plankton dynamics between locations in the North Sea changed over the regime shift? (ii) Has the way in which synchrony declines with geographic distance changed as a result of the regime shift, and specifically have long-range and short-range synchrony changed? (iii) Has the frequency-specific structure of synchrony changed over the regime shift, and specifically have high-frequency and low-frequency synchrony been altered? As plankton are the main basis of the marine food web and synchrony is ecologically important, but changes in synchrony are seldom studied, our study is important both in its examination of an important system and as an example of a more general phenomenon.

Materials and methods

Datasets

We used data from the Continuous Plankton Recorder (CPR) database of the Sir Alister Hardy Foundation for Ocean Science (SAHFOS), focusing on the region 52°N–60°N latitude and 4°W–8°E longitude because data were most extensive in that region during the periods before and after the regime shift of the 1980s. The CPR database includes spatiotemporal population data from the North Sea and North Atlantic that now span more than 80 years for some taxa. A sampling

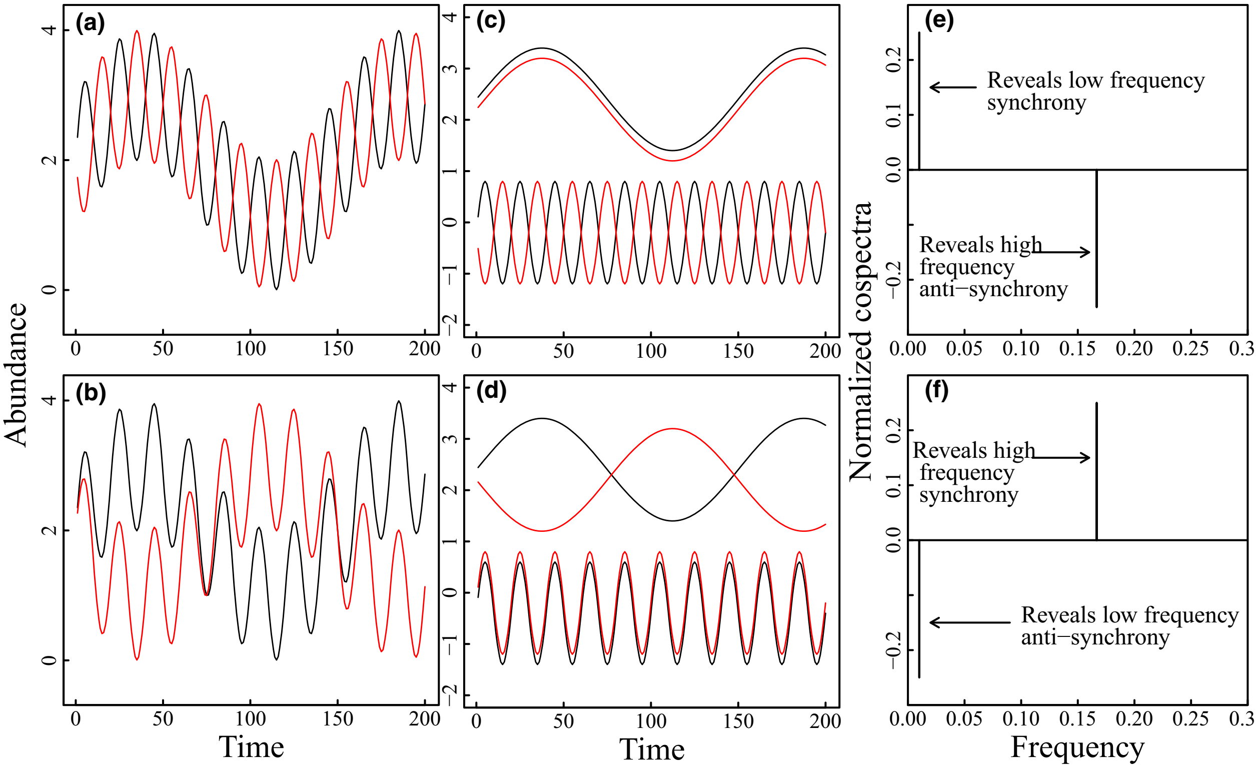

Fig. 1 Idealized illustration of how synchrony can differ on different timescales. (a) Time series are synchronous on long timescales and antisynchronous on short timescales. (b) Time series are antisynchronous on long timescales and synchronous on short timescales. (c, d) Breakdown of the individual frequencies that sum to form the time series in a and b, respectively. Standard correlation coefficients between time series are 0 for both (a) and (b), misleadingly suggesting lack of synchrony. Note that corresponding normalized cospectra (e, f; see Methods) reveal that positive synchrony at one frequency is masked by negative synchrony at the other. In practice, exact cancellation is unlikely, but asynchrony at some frequencies may strongly conceal important synchrony at other frequencies.

device is towed behind available ships at about 7 m depth. Water is filtered through a moving band of silk with a mesh size of approximately 270 μm (Batten *et al.*, 2003). On return to the laboratory, the silk is laid out on a bench for visual estimation of chlorophyll as Phytoplankton Color (Raitsos *et al.*, 2013). The silk is then cut into sections representing samples of 3 m^3 of seawater over 10 nautical miles. Phytoplankton and zooplankton taxa are then identified and counted, typically on alternate samples. Minimal changes have been made to the sampling device and analysis procedure over the study's history, to ensure consistency (Batten *et al.*, 2003). The resulting database contains estimates of the abundance of >500 taxa of plankton on a large number of 10 nautical mile transects (samples) taken at monthly intervals (typically) all over the North Sea, over the period of the survey (Reid *et al.*, 2003). For a more detailed description of the survey, see Batten *et al.* (2003) and Beaugrand *et al.* (2003).

We examined 22 phytoplankton and zooplankton taxa plus the Phytoplankton Color Index (PCI). Taxa were selected because they were common enough to yield data suitable for the intended analyses, and because they were known to be important in North Sea ecosystem dynamics or were relevant to human concerns such as harmful algal blooms or fisheries. Phytoplankton include both diatoms and dinoflagellates such as the nuisance bloom-forming species of the genera *Pseudo-nitzschia* and *Ceratium*. Zooplankton include the copepod species *C. finmarchicus* and *C. helgolandicus*, important prey species for exploited fish (Prokopchuk & Sentyabov, 2006; Heath & Lough, 2007). The PCI is an estimate of the 'greenness' of a sample as one of four categories (0–3, recorded in the database as 0,1,2, and 6.5) (Batten *et al.*, 2003). PCI 2 has approximately twice the amount of color (assayed with dilution factors) and PCI 3 has 6.5 times the color of PCI 1 (Colebrook & Robinson, 1965). The PCI is known to correlate well with fluorometer and satellite measures of chlorophyll (Batten *et al.*, 2003; Raitsos *et al.*, 2013). A list of taxa is given in Table 1.

Sea Surface Temperature (SST) and wind speed data are from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) (Woodruff *et al.*, 1987). SST and wind speed data were obtained for the same area of the North Sea as for plankton. SST and wind speed were used because of their well-known effects on growth rates and bloom patterns, wind effects occurring through the influence of wind-caused thermocline mixing events on nutrient availability in the surface ocean. Data on SST were also examined for a region that stretched across the North Atlantic, 45°N–60°N and 60°W–8°W, to examine long-distance environmental synchrony.

Change in synchrony using correlation

Data were aggregated into 1° by 1° grid cells and 83 annual time series were produced. Annual data were split into two time periods of equal length on either side of the 1980s, 1959–1980 and 1989–2010 chosen for equal length and data availability. For each period, time series were linearly detrended. For each biological or environmental variable and for each period separately, correlations between all pairs of time series with at least 10 overlapping values were calculated. A maximum distance of 600 km was used between pairs of time series in the North Sea, and a limit of 1700 km was used in the North Atlantic region, because few pairs were available and estimates of synchrony were poor at greater distances.

To obtain a visual picture of how synchrony depends on distance between sampled locations, spline correlogram methods (Bjørnstad *et al.*, 1999; Bjørnstad & Falck, 2001) were used both before the regime shift and afterward. These methods use a smoothing spline to produce a continuous estimate of correlation as a function of distance, with confidence bands determined by bootstrapping.

To establish whether changes in synchrony across the regime shift were statistically significant, we examined, for the North Sea data, average changes in overall synchrony in the distance range 0–600 km (called the 'regional' distance category), as well as average changes in synchrony in the distance categories 0–300 km ('near') and 300–600 km ('far'). To accomplish this, the correlation matrix of the 1959–1980 period was subtracted, element by element, from the correlation matrix of the 1989–2010 period. Entries of this difference matrix still correspond to pairs of sampling locations, and therefore each entry in the difference matrix has a corresponding associated distance (the distance between the sampling locations used for that entry). The mean of all entries in the difference matrix for which this distance was in the category 0–600 km was computed, as well as the means of entries with associated distances in the categories 0–300 km and 300–600 km separately. We then shuffled time series data between the former and latter periods 10 000 times, computing the mean differences in synchrony between the two correlation matrices for each randomization (for distance categories 0–600 km, 0–300 km, and 300–600 km separately; these quantities were calculated exactly in the same way as for the unshuffled data). We calculated the fraction of randomizations for which changes in synchrony were less than changes computed for the actual data. Each of the 10 000 shuffles was applied in the same way to time series in all locations. So the total correlation coefficient between a pair of time series in different locations calculated across all years (1959–1980 and 1989–2010 combined) would have been the same for all randomizations, although any differences in correlation from the 1959–1980 period to the 1989–2010 period were destroyed. This is consistent with the null hypothesis being tested that no changes in synchrony occurred across the regime shift. Variables for which fewer than 2.5% of randomizations exhibited changes in synchrony less than that of the real data putatively showed a significant decrease in synchrony from before the regime shift to after it. Conversely, variables for which more than 97.5% of randomizations exhibited changes in synchrony less than that of the real data showed a significant increase in synchrony from before the regime shift to after it. Type I error rate was controlled by further randomization methods. Methodological details are online in Appendix S1.

Change in synchrony using spectral methods

For the North Sea region, spectral analysis used different time series from the correlation analysis as there were years

Table 1 Randomization results indicating changes in synchrony from the period 1959–1980 to the period 1989–2010, for regional average synchrony and for the 0–300 km (near) and 300–600 km (far) distance categories, and also for high (greater than 0.2 cycles yr^{-1}) and low (less than 0.2 cycles yr^{-1}) frequencies (see Methods).

Species	Regional	Near	Far	Low	High
Phytoplankton					
Phytoplankton Color	0.114	0.159	0.088	0.192	0.288
Diatoms					
Thalassiosira sp.	0.972	0.996*$^{\uparrow}$	0.653	0.903	0.887
Proboscia alata	0.042	0.010*$^{\downarrow}$	0.219	0.493	0.013*$^{\downarrow}$
Rhizosolenia styliformis	0.270	0.236	0.389	0.148	0.095
Pseudo-nitzschia delicatissima	0.912	0.716	0.970	0.741	0.847
Pseudo-nitzschia seriata	0.022*$^{\downarrow}$	0.115	0.009*$^{\downarrow}$	0.233	0.267
Dinoflagellates					
Ceratium macroceros	0.591	0.346	0.853	0.878	0.480
Ceratium fusus	0.974	0.985*$^{\uparrow}$	0.910	0.902	0.809
Ceratium furca	0.857	0.935	0.653	0.720	0.402
Ceratium tripos	0.521	0.100	0.891	0.138	0.704
Zooplankton					
Copepods					
Euphausiids	0.336	0.349	0.319	0.304	0.691
Acartia sp.	0.580	0.366	0.726	0.704	0.225
Calanus stages I-IV	0.035	0.039	0.153	0.352	0.606
Oithona sp.	0.949	0.961	0.866	0.686	0.785
Para-pseudocalanus spp.	0.564	0.548	0.565	0.002*$^{\downarrow}$	0.594
Pseudocalanus sp.	0.316	0.326	0.385	0.266	0.528
Calanus helgolandicus	0.087	0.177	0.058	0.004*$^{\downarrow}$	0.854
Calanus finmarchicus	0.021*$^{\downarrow}$	0.029	0.034	0.098	0.970
Centropages typicus	0.006*$^{\downarrow}$	0.000*$^{\downarrow}$	0.171	0.172	0.428
Metridia lucens	0.364	0.807	0.019*$^{\downarrow}$	0.082	0.340
Temora longicornis	0.627	0.574	0.627	0.816	0.237
Meroplankton					
Decapod larvae	0.051	0.077	0.102	0.060	0.492
Echinoderm larvae	0.917	0.743	0.970	0.304	0.688
Environmental					
SST	0.029	0.017*$^{\downarrow}$	0.038	0.006*$^{\downarrow}$	0.843
Wind	0.119	0.088	0.153	0.238	0.358
Probability of Type 1 error	0.035*	0.009*	0.135	0.027*	0.460

Values are fractions of 10 000 randomizations that showed a change in synchrony less than shown by the data, so values less than 0.025 indicate a decrease in synchrony during the regime shift and values greater than 0.975 indicate an increase. These values are marked with a *, with arrows indicating the direction of change. The final row contains the results of controlling for type I error, numbers indicating the probability of obtaining as many species or more showing significant changes by chance alone if there were no changes in synchrony across the regime shift. Methodological details are online in Appendix S1.

missing from several of the 1° by 1° grid cell time series. This was not a problem for the correlation analysis, and using time series from 1° by 1° cells allowed the best spatial coverage for that analysis. However, spectral analysis using standard periodogram methods requires complete time series, so instead two CPR transect routes (called A and C in Richardson *et al.*, 2006) across the North Sea were used (Fig. 2). These are routes traversed regularly by ships participating in the CPR survey, so they were sampled intensively through the entirety of the two periods 1959–1980 and 1989–2010. Plankton and environmental data that fell within the two transects were aggregated into 19 annual time series for the periods 1959–1980 and 1989–2010, each time series representing a box 20 nautical miles by 1.5 degrees (longitude for A and latitude for C; Fig. 2 shows the boxes). Four time series from transect C were discarded due to missing data. A maximum distance of 600 km was again used.

In contrast to the transect data used for spectral analysis of North Sea data, but like the correlation analysis, spectral analysis of SST in the North Atlantic used 1° by 1° grid cells. Distances up to a maximum of 1700 km were used, because SST data were sufficient when only those cells with complete time series over both periods were included.

A *normalized cospectrum* was used to decompose synchrony between time series according to the frequencies, or timescales, at which it occurs. The normalized cospectrum is the frequency-specific decomposition of the Pearson correlation coefficient commonly used to describe synchrony. It gives

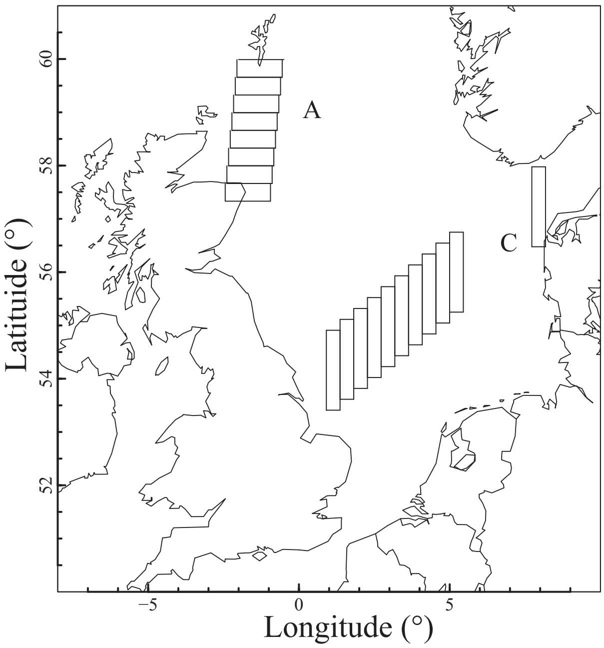

Fig. 2 Map of the North Sea showing transects A and C and boxes used for spectral analyses.

in-phase correlation between two time series as a function of frequency and, like the correlation coefficient, takes values between -1 and 1. So the input of the normalized cospectrum technique is two time series, and the output is a plot with x-axis showing frequency and y-axis showing in-phase synchrony between the time series at that frequency. Figure 1 gives idealized examples. The integral of the normalized cospectrum over all frequencies equals the correlation coefficient. The highest peaks in the normalized cospectrum correspond to frequency components that are most important in accounting for covariation in the time series. To obtain the normalized cospectrum of two time series, one starts with their cospectrum (a standard method, see Brillinger, 2001), and normalizes in a simple way: by dividing by the geometric mean of the variances of the time series. Because the integral of the cospectrum of two time series is their covariance, this normalization ensures that the integral of the normalized cospectrum of the time series is their Pearson correlation coefficient.

To obtain a visual picture of how synchrony depends on frequency and how this changed during the regime shift, plots of synchrony vs. frequency were produced. For each variable, and for the 1959–1980 and 1989–2010 periods separately, time series were linearly detrended prior to calculating the normalized cospectrum. Mean normalized cospectra over all distances were then calculated for each variable and for the two periods separately, with means over pairs of time series computed on a frequency-by-frequency basis. Bootstrapping with 10 000 resamplings was again used to produce confidence bands (Bjørnstad & Falck, 2001). Averages of mean normalized cospectra over high frequencies (frequencies >0.2 cycles per year) and low frequencies (≤ 0.2 cycles per year) were computed, 0.2 corresponding to a 5-year cycle.

To establish whether observed changes from before the regime shift to after it were significant, we examined differences in synchrony at low frequencies and high frequencies. For each variable, the three-dimensional normalized cospectrum array from the 1959–1980 period (location by location by frequency being the dimensions of the array) was subtracted from the normalized cospectrum array for the 1989–2010 period. The mean of this difference, computed frequency by frequency over all distances, was calculated. We then summed the resulting average changes over high frequencies (>0.2 cycles per year) and low frequencies (≤ 0.2 cycles per year) separately. To test if results were significant, we again employed randomization methods based on shuffling times between the two periods. Methodological details are online in Appendix S1. Analyses were performed using R 2.15.2.

Results

Using plots of correlation vs. distance, changes in synchrony from the 1959–1980 period to the 1989–2010 period were visually apparent for several plankton taxa (Fig. 3 for selected variables; Fig. S1 for the remaining variables). Plots showed decreasing synchrony with increasing distance, as expected, in all variables in both periods. Although some taxa showed little change between the two periods across all distances (e.g., Decapod larvae, Fig. 3c), several taxa showed an increase in synchrony from the earlier period to the later (e.g., *Ceratium furca*, Fig. 3a); and several others showed a decrease (e.g., *C. finmarchicus*, Fig. 3b). Both environmental variables showed a decrease in synchrony across the regime shift (SST, Fig. 3d; wind speed, Fig. S1).

Changes in synchrony across the regime shift, as measured using correlations, were often statistically significant. Three taxa showed significant changes in regional synchrony over the period of the regime shift (Table 1, column 'regional'); this was more taxa than would have been expected by chance if there was no change in synchrony (Table 1, column 'regional', last row). Four plankton taxa and SST showed significant changes in synchrony at short distances (0–300 km; Table 1, column 'near'), and a further two taxa showed significant changes at long distances (300–600 km; Table 1, column 'far'). For the 0–300 km results, this was more taxa than would have been expected by chance if there were no change in synchrony (Table 1, column 'near', last row). The 'near' and 'far' categories showed consistent changes – there were no variables with a significant increase in one category and a significant decrease in the other. But considering both distance categories separately was important because sometimes lack of strong change in one distance range made strong change over the other distance range undetectable when only change in regional synchrony was considered (Table 1).

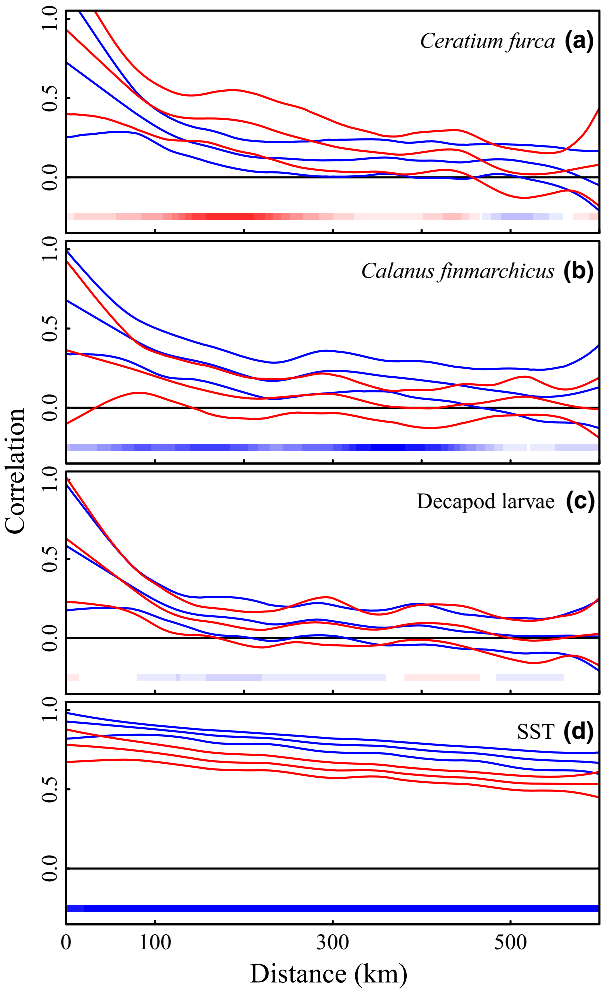

Fig. 3 Correlation vs. distance plots for plankton taxa and environmental variables for 1959–1980 (blue lines) and 1989–2010 (red lines). The colored bar indicates which band is higher, red meaning the later period and blue meaning the earlier period; white indicates that they are the same. Confidence bands are 95%. The point where the lower confidence line intersects with the *x*-axis indicates the distance at which synchrony has effectively declined to zero.

Time series were linearly detrended prior to correlation analysis to maintain consistency with spectral methods. Long-term trends may obscure synchrony from shorter term fluctuations (Buonaccorsi *et al.*, 2001), and the latter was the focus here, but detrending may also remove low-frequency synchrony of interest. Therefore, the first three columns of Table 1 were reproduced without detrending (Table S2). Results were the same in substance.

Spectral analysis revealed changes in the frequency distribution of synchrony, and changes were at low frequencies (Fig. 4 for selected variables; Fig. S2 for the remaining variables). *C. helgolandicus* (Fig. 4a),

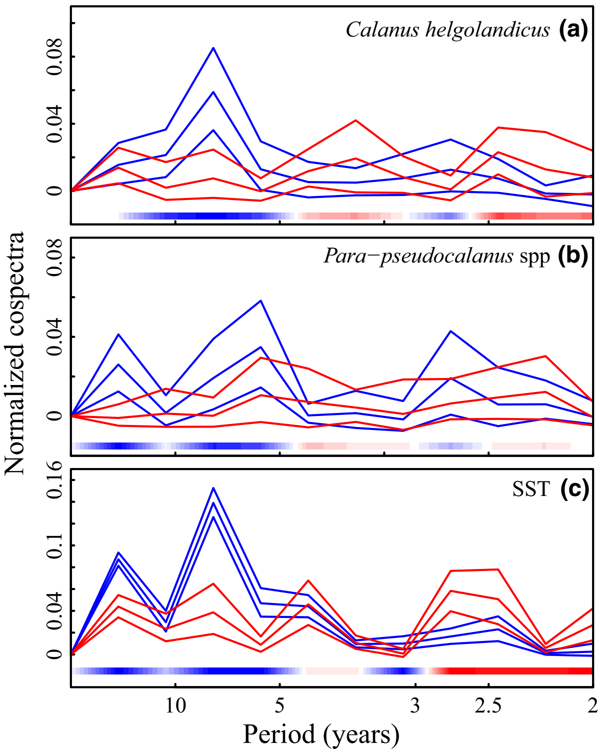

Fig. 4 Normalized cospectra averaged over all distances for time periods 1959–1980 (blue lines) and 1989–2010 (red lines). Confidence bands are 95%. The colored bar indicates which band is higher; red means the later period is higher, blue means the earlier period is higher, and white indicates that they are the same.

Para-pseudocalanus spp. (Fig. 4b), and SST (Fig. 4c) all had substantial peaks in their mean normalized cospectra at periods between 5 and 10 years before the regime shift, but the peaks were absent after the shift. Table 1 shows that these changes were significant. The putatively significant change seen in *Proboscia alata* at high frequencies could be a type 1 error, as seen in the final column of Table 1. The variables that showed significant changes at low frequencies did not show significant changes in aggregate across all frequencies (the 'regional' column in Table 1). This illustrates the importance of separating frequency bands – lack of change in one band can mask strong change in another band if bands are considered in aggregate.

Changes in synchrony were not confined to any particular taxonomic group: species of diatoms, dinoflagellates, and copepods all showed pronounced changes (Table 1). Only meroplankton showed no significant changes. Although phytoplankton species exhibited both increases and decreases in synchrony, the copepod species that showed a significant change all showed a decline. Environmental variables also show declines. Results suggest that changes in copepod synchrony may have been related to changes in environmental synchrony (see Discussion).

Variations in synchrony, such as the direction of change (increase vs. decrease), were not a statistical artifact due solely to changes in abundance patterns. For example, both *C. finmarchicus* and *C. typicus* showed a decrease in synchrony across the study period, but the abundances of these species showed opposite trends, with *C. finmarchicus* declining in the North Sea across the regime shift and *C. typicus* increasing (Fromentin & Planque, 1996; Beaugrand *et al.*, 2002).

SST results led us to investigate if changes seen in the North Sea extend across the North Atlantic. Figure 5a shows that short-range synchrony of SST did decrease over the period of the regime shift in the North Atlantic, as in the North Sea. However, at longer distances (longer than the distance across the North Sea), synchrony in the North Atlantic increased across the regime shift period. A similar result was found when just the Eastern Atlantic, off the shelf edge, was examined. The decline in low-frequency (5- to 10-year period) SST synchrony seen across the North Sea was not seen in the North Atlantic – instead there was an increase in low-frequency synchrony (Fig. 5b).

In the North Atlantic, SSTs showed a decline in synchrony over the regime shift at distances of less than 600 km and an increase at distances beyond 600 km; this reversal could not have been an artifact of coastal effects. The maximum distance considered in the North Atlantic was 1700 km, approximately half the East–West distance of the study area and not far enough to span the Atlantic. Thus, coastal points from opposite sides of the Atlantic were not compared.

Discussion

Nine of the 23 taxa and one of the two environmental variables we examined showed changes in synchrony over the regime shift, either in a distance category or in a frequency band or both. These results indicate that the climate change-driven North Sea regime shift of the 1980s, which was well documented in earlier work that only examined purely spatial or purely temporal aspects of plankton population dynamics (Reid *et al.*, 2001; Beaugrand, 2004; Alheit *et al.*, 2005; Lindley *et al.*, 2010), also affected spatiotemporal population patterns. Synchrony always decreased for copepod species, regardless of the distance category or frequency band considered. In contrast, some phytoplankton species in some distance categories or frequency bands increased in synchrony and others decreased. SST, but not wind speed, showed changes in synchrony across the regime shift. Some observed SST changes represent a phenomenon that is more widespread than even the North Sea: synchrony at distances of <600 km also decreased across the North Atlantic.

Two taxa, *C. helgolandicus* (a major prey item for exploited fish species) and *Para-pseudocalanus* spp., as well as SST, saw similar decreases in synchrony at about an 8-year period over the regime shift (Fig. 4). This suggests the possibility that changes in SST synchrony may have driven changes in synchrony in these taxa. This hypothesis is consistent with prior research in four respects. First, temperature modulates plankton variability in a wide range of ways (Beaugrand, 2009). Second, the NAO is known to affect plankton abundances (Fromentin & Planque, 1996; Piontkovski *et al.*, 2006; Beaugrand, 2012). It is also one of the major driving forces of aspects of climatic variability in the North Sea and North Atlantic, including SST, and therefore may be involved in the observed changes in both populations and SST synchrony. Changes in population synchrony have twice previously been attributed directly to changes in the synchrony of temperature-related environmental drivers, which were in turn shown to be due to changes in the NAO (Post & Forchhammer, 2004; Sheppard *et al.*, 2015). Third, previous studies have noted significant changes in both NAO and NHT

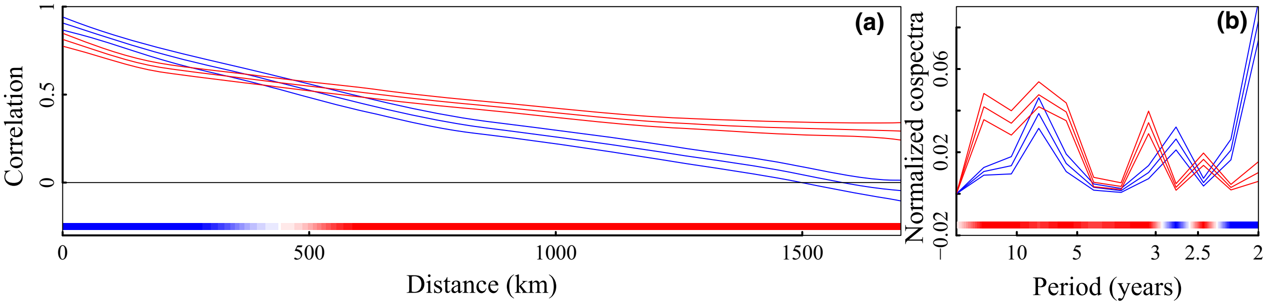

Fig. 5 Spline correlograms (a) and normalized cospectra averaged over all distances (b) for temperature time series for time periods 1959–1980 (blue lines) and 1989–2010 (red lines) for the larger geographic region of the North Atlantic (see Methods). Confidence bands are 95%. The colored bar indicates which band is higher; red means the later period is higher, blue means the earlier period is higher, and white indicates that they are the same.

anomalies over the period of the regime shift (Beaugrand, 2003; Beaugrand & Reid, 2003). Finally, synchrony of environmental drivers such as temperature is known to be a main cause of population synchrony (this is the Moran effect; Liebhold *et al.*, 2004). We recently proved a wavelet version of the classic Moran theorem (Sheppard *et al.*, 2015) that shows Moran effects can be frequency specific. Thus, a hypothesized mechanism for some of the frequency-specific patterns of synchrony we observed in the plankton, and changes therein, is frequency-specific Moran effects and changes in SST synchrony. This cannot be the only mechanism operating for all taxa considered because plankton synchrony does not always mirror SST synchrony exactly. Other environmental influences and dispersal may be important, but determining their relative importance and the means by which they combine is a difficult problem best saved for future work.

Changes through time in population synchrony have been detected previously in a few species (Ranta *et al.*, 1995, 1997b, 1998; Koenig, 2001; Post & Forchhammer, 2004; Ojanen *et al.*, 2013; Allstadt *et al.*, 2015; Sheppard *et al.*, 2015), but these studies are a small minority of all the studies of synchrony, and changes in synchrony and their causes are still poorly understood. Our results provide a valuable new example, and help suggest that, in fact, changes in synchrony might occur more frequently than is commonly recognized. We suggest above that the changes in synchrony we observed in *C. helgolandicus*, *Para-pseudocalanus* spp., and SST may relate to changes in the NAO and therefore may also relate to changes in synchrony in terrestrial systems, which have been attributed to the NAO (Post & Forchhammer, 2004; Sheppard *et al.*, 2015). The NAO affects climate and many species across a wide area (Ottersen *et al.*, 2001; Stenseth *et al.*, 2002; Post & Forchhammer, 2004). Moran effects are probably widespread (Lande *et al.*, 1999; Peltonen *et al.*, 2002; Liebhold *et al.*, 2004; Engen *et al.*, 2005), especially for winter climatic drivers in temperate regions (Grenfell *et al.*, 1998; Ottersen *et al.*, 2001; Post & Forchhammer, 2002, 2004; Stenseth *et al.*, 2004), and synchrony itself is ubiquitous (Liebhold *et al.*, 2004). Therefore, it is reasonable to hypothesize that changes in the NAO, and possibly also in other large climatic modes, may commonly cause changes, present but yet to be noticed, in the synchrony of many species.

The impacts of changes in population synchrony may also be more important than commonly recognized. They may have strong effects on higher trophic levels of ecosystems, and exploitative industries. In many hierarchical dynamical systems, synchrony between multiple signals is more important than the individual signals themselves. For instance, a neuron may fire when its input neurons fire simultaneously; and the electrical grid crashes only when demands of multiple users become synchronized, producing total-usage spikes. Only synchronous components of signals matter in the average signal that affects the next hierarchical level because nonsynchronous components cancel out in the aggregated signal that affects the next level. Complex ecosystems may be example systems of this type. In caricature, ecosystems include multiple trophic levels, with environmental and population-dynamical signals from lower levels often being spatially aggregated to affect higher levels and human concerns such as fisheries and agriculture. For instance, drought only affects an herbivore if rain is simultaneously scarce over much of its foraging area; predator populations are only harmed if prey are simultaneously scarce over a predator's whole foraging area; and human fish exploitation may only be reduced if fish populations decline synchronously over all fishing locations. Due to this kind of spatial averaging, synchrony of a species could be of primary importance to trophic levels above the species. Therefore, changes in synchrony brought about through climate change, for instance the changes in the North Sea that we have documented, may have substantial effects on higher trophic levels and exploiting industries.

Changes in the synchrony of plankton may be an important example of the effects described above. Furthermore, different consumers of plankton may show different responses to changes in plankton synchrony depending on the spatial and temporal scales of individual foraging. Strong synchrony that occurs over a spatial extent that exceeds the migratory ability of an individual consumer, and that occurs on a timescale (period) that exceeds the required feeding frequency for survival or reproduction, will affect consumer population dynamics. This is because consumers in some areas and during some periods will lack prey and will be unable to wait out the period of scarcity or migrate to a location of prey abundance. In contrast, synchrony that occurs at high frequencies relative to consumer life history or that occurs over spatial extents smaller than migration distances is unlikely to affect consumers. Consumer species with different life spans and/or migratory propensities may therefore be affected differently by changes in plankton synchrony. For instance, if annual time series of plankton abundance are synchronized across the spawning grounds of a fish species, and synchrony occurs on timescales longer than the life span of the fish, then plankton could be unavailable to larvae for many years and the population may not persist. If plankton synchrony instead occurs on timescales less than the life span of the fish, recruitment may fail for some years, but adult fish will be able to live through the period of adversity to reproduce during the next period of plankton abundance. Although fish recruitment is a complex process influenced by many factors, it is believed that recruitment success is largely determined during the larval stage (Horwood *et al.*, 2000; Brander *et al.*, 2001). Food availability (zooplankton) plays an important role in the growth and survival of larval fish (Beaugrand *et al.*, 2003; Fiksen & Jørgensen, 2011).

These ideas relate to concepts explored in the literature on patchiness of plankton distributions (Kolmogorov, 1941, 1991; Platt, 1972, 1975; Steele, 1978; Therriault *et al.*, 1978; Mackas, 1984; Weber *et al.*, 1986; Powell & Okubo, 1994; Strutton *et al.*, 1997; Frank *et al.*, 2005; Ballantyne *et al.*, 2011; Prairie *et al.*, 2012), although different language is used there; the work of Grünbaum (2002) from that literature may facilitate future efforts to further illuminate possible consequences of changes in plankton for higher trophic levels. The spatial scale of synchrony should be similar to the characteristic size of plankton patches in snapshots of plankton spatial distributions described in the patchiness literature. Dominant timescales of synchrony should relate to patch durations. The work of Grünbaum (2002) identifies a so-called 'Frost number', which quantifies the ability of consumers to track (and thus exploit) the distribution of a patchy resource as it changes in time. The Frost number is $Fr = c^2T\tau/L^2$. Here $c^2\tau$ characterizes the effective speed of foraging behavior. When the distance scale, L, of resource patchiness is high (corresponding to large, widely separated patches, and to long-distance synchrony in our picture), the Frost number is low. Consumers must disperse over longer distances to track the resource, and thus the effective resource availability is lower. When the timescale, T, of changes in resource density is long (corresponding to long-lasting patches and long periods between patches, and to low-frequency synchrony in our picture), the Frost number is high, giving consumers more time to track and exploit resources.

Using the Frost number, Grünbaum (2002) considers a proof-of-concept dynamical model that can help capture the importance of the accessibility of resources because of their patchiness. The nature of resource patches has been shown to relate to resource–consumer encounter rates (Denman & Abbot, 1994; Prairie *et al.*, 2012) and to the population sizes of zooplankton consumers (Davis *et al.*, 1991; Menden-Deuer & Grünbaum, 2006). According to Prairie *et al.* (2012), 'Spatial heterogeneity in plankton distributions can affect grazing rates and trophic dynamics on much broader scales than those of the patches themselves.' The model of Grünbaum (2002) is a first effort to quantitatively understand the effects of observations such as these on consumer dynamics.

Synchrony of zooplankton taxa consistently decreased over the period of the regime shift whenever a significant change was observed, and these changes occurred at low frequencies but not high frequencies (Table 1). We hypothesize possible effects of such changes, all else being equal, using the Frost number. If decreases in low-frequency synchrony with no concomitant change in high-frequency synchrony correspond to a shorter average duration of resource patches (decreased T in the Frost number formula), then the Frost number decreases, corresponding to decreased resource availability for some consumers. We caution, however, that the Grünbaum model envisions consumer individuals moving to track resources. In our analysis, both time and distance scales are very large. Large organisms such as adult fish may be able to track an available resource on these scales, but consumer zooplankton and larval fish are probably reliant on ocean currents for movement on large scales. Long timescales of resource fluctuation may result in periods of resource scarcity, which exceed the ability of small organisms to survive such physically mediated 'foraging' and the Frost number and modeling choices of Grünbaum may not apply. We consider that further development of the Grünbaum model and other related models to help understand the trophic consequences of changes in synchrony for consumers of different life histories is an important avenue of future research.

Changes in synchrony that we observed were often specific to a distance range or a frequency band. These results suggest that synchrony and changes in synchrony may also differ by frequency band (Keitt, 2008; Sheppard *et al.*, 2015), a possibility supported by our frequency-specific Moran theorem (Sheppard *et al.*, 2015). Future work should therefore continue to take a frequency-specific perspective, as we did in this study.

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Author contributions

DCR designed and guided the research. ED carried out the research and wrote the first draft of the manuscript. LS provided technical guidance and assistance. PCR provided biological guidance and assistance. All authors edited the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Methodological details.
Figure S1. Correlation vs. distance plots for variables.
Figure S2. Average normalized cospectra for all variables.
Table S1. Total number of missing months in each season for each transect box.
Table S2. Same as Table 1, but without linear detrending.