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The Continuous Plankton Recorder survey and the North Atlantic Oscillation: Interannual- to Multidecadal-scale patterns of phytoplankton variability in the North Atlantic Ocean

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Abstract

At interannual to multidecadal time scales, much of the oceanographic and climatic variability in the North Atlantic Ocean can be associated with the North Atlantic Oscillation (NAO). While evidence suggests that there is a relationship between the NAO and zooplankton dynamics in the North Atlantic Ocean, the phytoplankton response to NAO-induced changes in the environment is less clear. Time series of monthly mean phytoplankton colour values, as compiled by the Continuous Plankton Recorder (CPR) survey, are analysed to infer relationships between the NAO and phytoplankton dynamics throughout the North Atlantic Ocean. While a few areas display highly significant ($p < 0.05$) trends in the CPR colour time series during the period 1948–2000, nominally significant ($p < 0.20$) positive trends are widespread across the basin, particularly on the continental shelves and in a transition zone stretching across the Central North Atlantic. When long-term trends are removed from both the NAO index and CPR colour time series, the correlation between them ceases to be significant. Several hypotheses are proposed to explain the observed variability in the CPR colour and its relationship with climate in the North Atlantic.

Keywords: Phytoplankton; North Atlantic Oscillation; Climate; North Atlantic Ocean; Continuous Plankton Recorder

Contents

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1. Introduction

The North Atlantic Oscillation (NAO) is the dominant mode of low-frequency climate variability in the North Atlantic Ocean (Hurrell, 1995). While the causes of this climatic mode remain uncertain (Hurrell, 1995; McCartney, 1997; Sutton & Allen, 1997; Hurrell, Kushnir, & Visbeck, 2001), descriptive and modelling studies have shown that the NAO impacts oceanic (Hurrell, 1995; Dickson, Lazier, Meincke, Rhines, & Swift, 1996; Dickson, 1997; Hurrell & Van Loon, 1997) and terrestrial climates (Hurrell, 1995; Hurrell & Van Loon, 1997) on interannual to multidecadal time scales. Marine and terrestrial ecosystems respond to NAO-induced changes in the coupled ocean-atmosphere system. The present study investigates the relationship between the NAO and the spatial and temporal variability of phytoplankton in the North Atlantic Ocean.

The Continuous Plankton Recorder (CPR) survey, overseen by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS), has measured the abundance and variability of over 450 zooplankton and phytoplankton taxa, as well as a visual index of phytoplankton colour, in the North Atlantic Ocean over the last 60 years (Warner & Hays, 1994). While numerous researchers have investigated zooplankton and phytoplankton variability in Northwest (Jossi & Goulet, 1993; Greene & Pershing, 2000; Conversi, Piontkovski, & Hameed, 2001; Sameoto, 2001) and Northeast Atlantic shelf ecosystems (Planque & Taylor, 1998; Stephens, Jordan, Taylor, & Proctor, 1998; Reid & Planque, 1999) using the CPR survey data, relatively few studies have examined phytoplankton variability across the entire North Atlantic Ocean (but see Colebrook, 1979).

In this study, we examine the statistical relationship between two time series, the NAO index and CPR colour throughout much of the North Atlantic Ocean. We explore connections among the results of this analysis, our current understanding of long-term phytoplankton trends, and oceanographic as well as meteorological conditions. Where possible, we incorporate satellite-derived sea surface temperature (SST) imagery from the Advanced Very High Resolution Radiometer (AVHRR) and nitrate data from the National Oceanographic Data Center (NODC) World Ocean Atlas (http://www.cdc.noaa.gov/cdc/data.nodc.woa94.html), in order to suggest physical mechanisms that might explain the observed relationships between the NAO and phytoplankton variability.

2. Methods

Measures of phytoplankton ‘colour’ made on CPR samples were averaged for 41 Standard Areas, which cover much of the North Atlantic Ocean (Fig. 1). Data were collected by the CPR, an instrument that is towed at a nominal depth of 10 m behind merchant and ocean weather ships. Warner and Hays (1994) have provided a detailed description of the CPR’s design and operation, which we briefly describe here. Sea-water enters through the opening of the CPR, is filtered though a continuous strip of silk, and then exits through the rear. A propeller, which is turned by the flow of water past the instrument, draws the fine silk mesh across the opening at a known rate. The filtering silk is returned to a laboratory at SAHFOS where CPR colour values of 0, 1, 2, or 6.5 are assigned, based on a qualitative assessment of the ‘greenness’

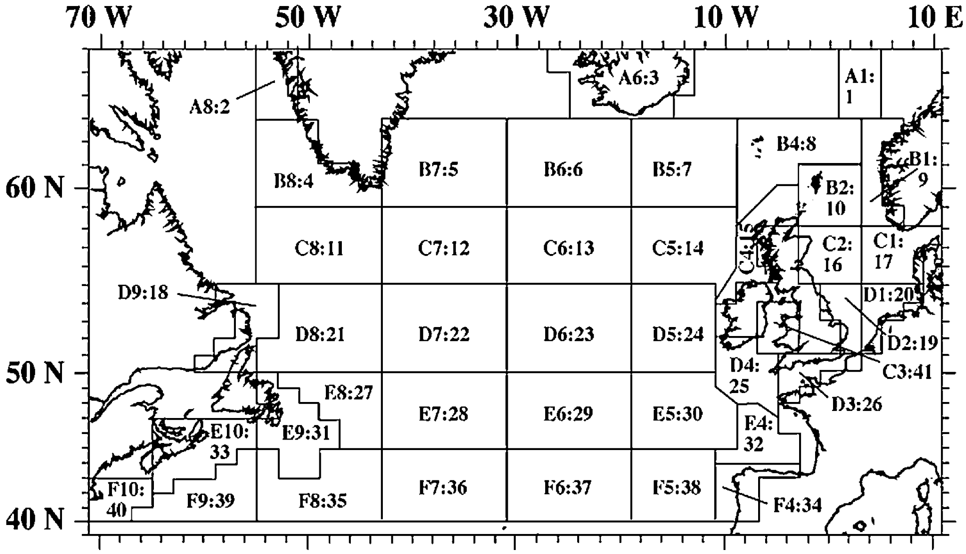

Fig. 1. CPR Standard Areas (SAHFOS name: area number).

of the silk. SAHFOS provided us with monthly means of CPR colour and information about the number of data points used to calculate the monthly mean for each of the 41 Standard Areas during the period 1948–2000. It should be noted that data coverage is not regular in time or space. Measurements are concentrated in areas adjacent to the British Isles, Iceland, and along the trans-Atlantic shipping routes, and are relatively sparse in the northern subtropical gyre and Labrador Sea (Fig. 2).

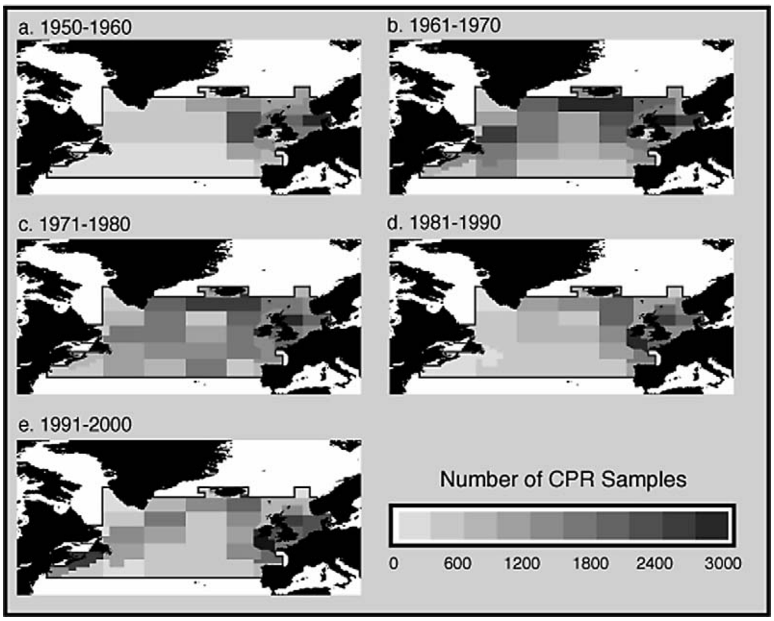

Fig. 2. CPR data distributions during the periods a) 1950–1960, b) 1961–1970, c) 1971–1980, d) 1981–1990, and e) 1991–2000. Data are concentrated around the British Isles, Iceland, and along trans-Atlantic ship routes.

The CPR colour values provide qualitative monthly measures of relative phytoplankton abundance in the different regions, but these data cannot easily be related to absolute quantitative values. Edwards, Reid and Planque (2001) reported that it was unknown if the variations in these colour indices corresponded more closely to fluctuations in primary production or to changes in phytoplankton biomass, an issue that cannot be resolved without a better understanding of loss terms, such as grazing. However, despite the uncertainty surrounding the interpretation of the CPR colour data, previous studies have demonstrated that the data are a good indicator of phytoplankton variability in time and space (Reid, Edwards, Hunt, & Warner, 1998; Edwards et al., 2001; Sameoto, 2001). The length of the time series together with the broad spatial coverage of the CPR survey allow us to monitor long-term fluctuations in the relative abundances of phytoplankton throughout the North Atlantic Ocean, which can then be compared to fluctuations in the NAO.

The NAO index, a measure of climate variability over the North Atlantic Ocean, is calculated as the normalised difference in winter sea-level pressures between Stykkisholmur in Iceland and Lisbon in Portugal (Hurrell, 1995). There is a strong pressure gradient between Iceland and Portugal during positive phases of the NAO, and a weak gradient during its negative phases. The NAO index was predominantly negative from 1950–1970 and predominantly positive from 1970 to the present. A notable exception during the current positive phase was a sharp reversal to a negative value in the winter of 1995–1996, which was followed by a switch back to strongly positive values by 1998 (Fig. 3).

Phytoplankton abundance in the North Atlantic Ocean exhibits a high degree of seasonality (Colebrook, 1979). Climatological mean seasonal cycles, weighted by the number of samples used to calculate each monthly mean of CPR colour, were constructed for each sector with the following equation:

$$(\text{Climatological monthly mean})_m = \frac{\sum^{y} (\text{monthly mean})_{y,m} \times (n)_{y,m}}{\sum^{y} (n)_{y,m}} \quad (1)$$

where y is a given year, m is a given month, and n is the number of samples used to calculate the monthly

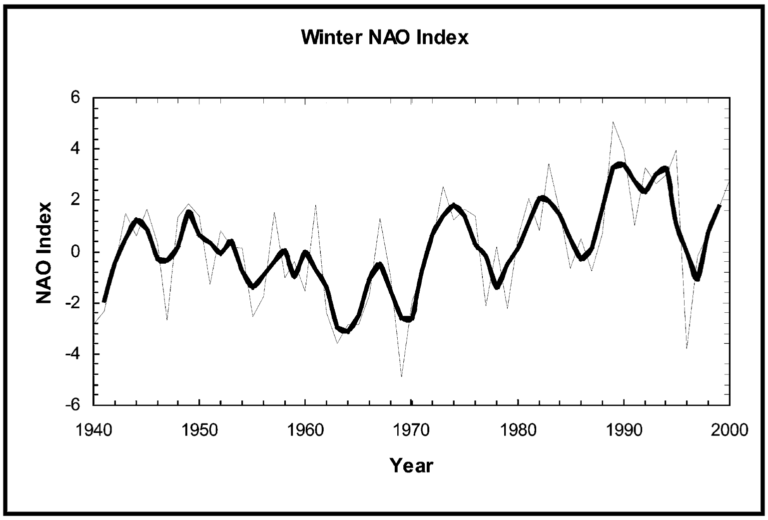

Fig. 3. Winter (December–March) NAO index during the period 1940–2000. The bold line represents the NAO index smoothed [using three-year running averages]. The 1950s to 1970s were predominantly negative and the 1970s to 2000 were predominantly positive. The time series exhibits a significant (p = 0.04), positive (r^2 = 0.13) trend over the period.

mean colour. Time series of monthly colour anomalies for each ocean zone were constructed by subtracting the monthly mean colour from the corresponding climatological mean value as follows:

$$(\text{monthly anomaly})_{y,m} = (\text{monthly mean})_{y,m} - (\text{climatological monthly mean})_{m} \quad (2)$$

where y is a given year and m is a given month. A weighted mean, similar to that calculated using Eq. (1), was then used to create time series of the yearly mean of monthly colour anomalies; these anomalies are henceforward referred to as time series of the yearly mean colour anomaly. Using calculations of the yearly mean from the monthly anomaly data prevents data from samples taken during periods of extremely high or low phytoplankton abundance from overly biasing the means.

This study utilises time series analysis to characterise the regional relationships between phytoplankton abundance and the NAO. As we sought to understand this relationship at interannual to multidecadal time scales, different methods of analysing the time series were used. First, we looked at the long-term trends in the time series of the yearly mean colour anomaly during the survey period by fitting a first-order (linear) model to the data. Secondly, we conducted lagged regressions between time series of the NAO index and the yearly mean colour anomaly in order to assess the total amount of variance in CPR colour that can be explained by the NAO; we called these time series 'unadjusted'. Thirdly, we removed the long-term trends in the time series of the NAO index and the yearly mean colour anomaly and conducted lagged regressions; we called these time series 'detrended'. Detrending the time series allowed us to determine the correlation in high-frequency variability between the time series.

Linear trends in each of the 41 time series of the yearly mean colour anomaly are represented by the following equation:

$$L(y) = a + b(y) \quad (3)$$

where y is a given year and $L(y)$ represents the estimated mean colour anomaly in year y; coefficients a and b, the intercept and slope, respectively, are estimated from the data using the least-squares method. For each region, a time series of yearly mean colour anomaly versus time regression was conducted to determine if the slope of the linear fit differed significantly from zero. While analysis of long-term trends can yield information about possible decadal variability in phytoplankton abundance, other methods must be utilised if we want to look at higher-frequency variability.

Time series of the unadjusted yearly mean colour anomaly in the 41 Standard Areas and of the NAO index were regressed to assess zero, one, two, and three-year lagged correlations. The presence of autocorrelation in the time series violates a basic assumption of independence in the data necessary for conducting unbiased hypothesis testing. We calculated the detrended time series by subtracting the first-order linear fit (Eq. (3)) from the anomaly data to remove this long-term component of autocorrelation:

$$(\text{Detrended yearly mean anomaly})_{y} = (\text{yearly mean anomaly})_{y} - L(y) \quad (4)$$

where y is a given year. The NAO time series was detrended in an analogous manner. The resulting detrended NAO and colour time series were regressed to assess zero, one, two, and three-year lagged correlations.

A method was developed to evaluate the significance of spatial correlation patterns resulting from each of the three analyses outlined above. If we assume that there is no relationship between the unadjusted time series of the NAO index and the yearly mean colour anomaly, and that the phytoplankton dynamics in adjacent ocean sectors behave independently, then conducting 41 regression analyses between the time series at the 20% probability level would yield, on average, eight areas of nominally significant correlation by random chance alone. Because it is unlikely that plankton time series in adjacent ocean sectors behave independently, many more than eight sectors of nominally significant correlation ($p=0.20$) could occur. To distinguish between chance occurrence of significant correlation (spurious structure) and actual significance (spatial structure), we conducted a resampling test for field significance corresponding to each of the three analyses outlined above (see Livezy & Chen, 1983; Wilks, 1995).

Below, we describe how the re-sampling test was conducted to determine the field significance of the regressions of the unadjusted NAO index versus the yearly mean colour anomaly time series. Under the null hypothesis, H_o, there is no relationship between the two time series. Using the moving-blocks bootstrap methods described by Wilks (1997), we constructed a new time series of the NAO index (of similar time length) by randomly selecting 4-year blocks from the NAO-index time series. If, for example, the time series were 60 years long, then 15 randomly selected blocks of four years would comprise the new time series. This effectively randomises the relationship between the time series of the NAO index and colour while retaining the short-term ($<$ 4 years) autocorrelations within the NAO index. The colour time series for each sector is not modified; therefore the spatial correlation between sectors remains intact. Regressions between the randomised NAO index and unmodified colour time series were conducted in each sector and the number of positive (+r) and negative ($-$r) nominally significant ($p < 0.20$) sectors were noted. This was repeated 10,000 times, each time re-randomising the NAO index to create the relevant null distributions (Fig. 4). From these distributions, which represent the number of positive (Fig. 4(a)) or negative (Fig. 4(b)) nominally significant areas of correlation resulting solely by chance, we can assess the significance of the observed spatial structure.

Analogous re-sampling tests for field significance were also conducted for the other regression analyses described above. In all of the resampling tests, the colour time series remained unaltered to maintain the spatial correlation of the phytoplankton data. The field significance tests of the yearly mean colour anomaly time series versus time regressions, or the test for field significance of long-term trends, differed from the method described above in that time was randomised, rather than the NAO index. The field significance tests of detrended data regressions were similar to those done on the unadjusted data except that blocks of the detrended NAO index values were used to comprise the new, randomised NAO index. Positive and negative null distributions for all tests for field significance appear in Fig. 4. Note that Fig. 4 contains only the null distributions for field significance tests of unadjusted and detrended data regressions at a zero lag because null distributions at longer time lags are very similar.

We used data from other sources to assist us in interpreting the results of our time-series analyses. These results will be included in the discussion. AVHRR SST data were used to provide a climatological background for our arguments. The Pentad Climatology methodology of the Jet Propulsion Laboratory (JPL) for analysing AVHRR 9-km resolution SST data was used to determine the climatological position of the Gulf Stream and the North Atlantic Current. JPL used this method to calculate five-day climatologies for each location during 1985–2000. The five-day climatologies were averaged to create a yearly composite image. We also used the 1° gridded nitrate data in the NODC World Ocean Atlas as a climatological measure of nitrate variability with latitude and depth.

3. Results

The level of significance determines confidence in the results of a statistical test. While a *p*-value of less than 0.05 is conventionally accepted as the cut-off level for a significant result, this level is arbitrary. Because the colour time series are relatively short and noisy, and since this study is searching for general patterns of phytoplankton abundance over long time periods and broad spatial expanses in the North Atlantic Ocean, we are prepared to be less stringent in our interpretations of significance. For this reason, we refer to a test yielding a *p*-value less than 0.05 as ‘significant’ and a test yielding a *p*-value of less than 0.20 as ‘nominally significant’.

Widespread nominally significant positive trends in the time series of yearly mean colour anomaly are observed in the Northeastern Shelf, Northwestern Shelf and Central North Atlantic ecosystems (Fig. 5). Sea areas adjacent to the British Isles and Europe, with the exception of the Irish Sea, all exhibit nominally significant positive trends in colour during the survey period. The Northwestern Shelf sectors, including

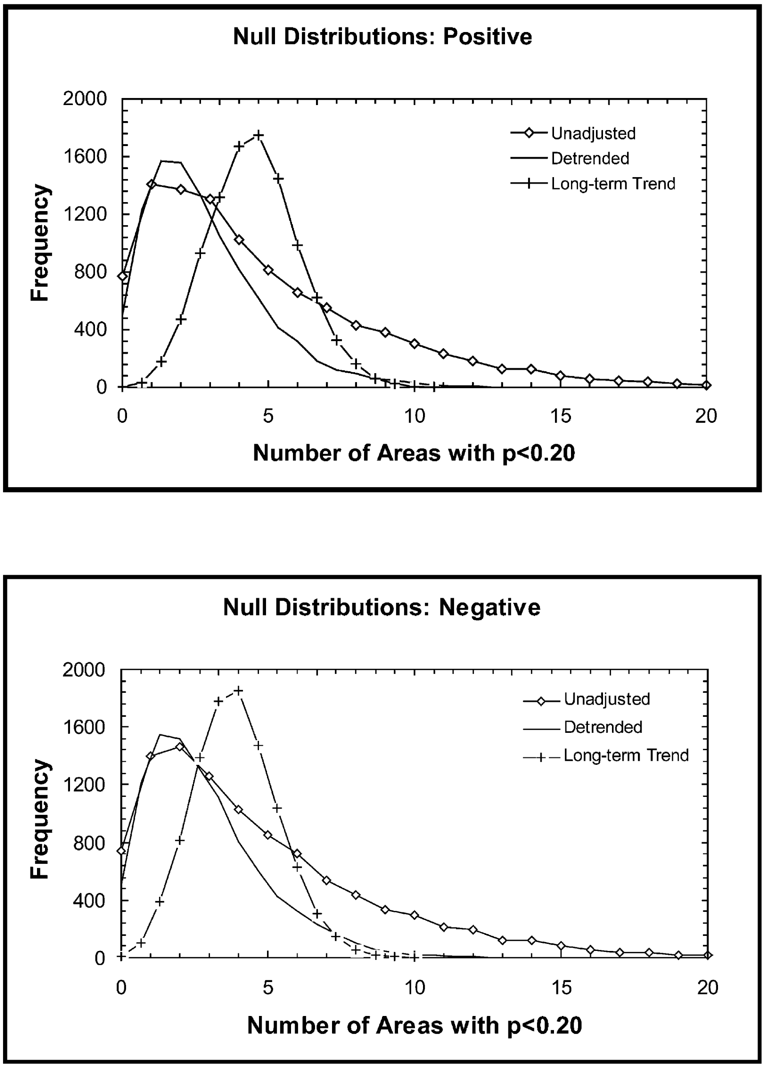

Fig. 4. Null distributions for tests of field significance. Null distributions representing the number of sectors exhibiting nominally significant ($p < 0.20$) areas of a) positive and b) negative long-term trends between the CPR colour and randomised-block year time series are shown with a solid line with a plus sign. Null distributions representing the number of sectors exhibiting nominally significant ($p < 0.20$) areas of a) positive and b) negative lag-zero correlations between the unadjusted CPR colour and randomised-block NAO index time series are shown with a solid line with a diamond. Null distributions representing the number of sectors exhibiting nominally significant ($p < 0.20$) areas of (a) positive and (b) negative lag-zero correlation between the detrended CPR colour and detrended randomised-block NAO index time series are shown with a solid line. Correlations at longer time lags are not shown because they are nearly identical to the lag-zero correlations.

Georges Bank, the Scotian Shelf and the Grand Banks, also exhibit nominally significant positive trends. A northeast–southwest band of sectors exhibiting nominally significant positive trends connects the two shelf areas. A few sectors exhibiting nominally significant negative trends occur in the far north and south of the survey area.

Spatial coherence in these patterns must be evaluated using the ‘moving-blocks bootstrap resampling test’ mentioned previously. Null distributions representing the number of sectors exhibiting nominally significant

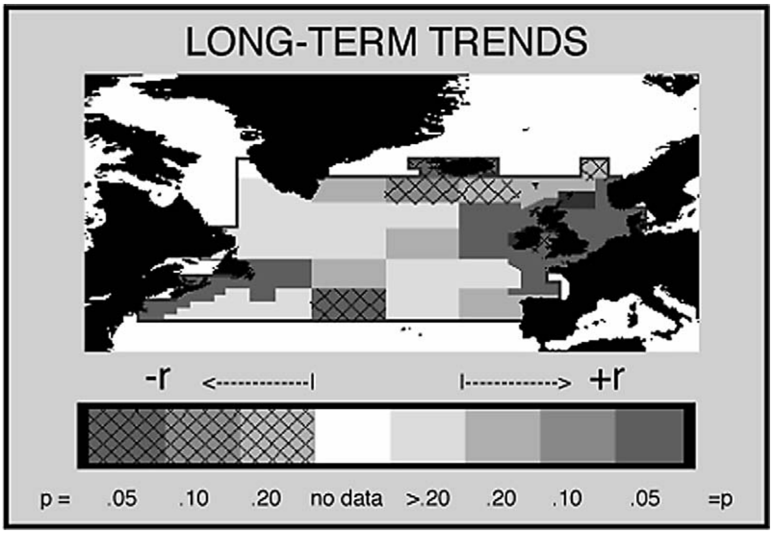

Fig. 5. Long-term linear trends in the yearly mean CPR colour-anomaly time series in the North Atlantic Ocean. A regression analysis of the CPR time series determined the significance of the trends. Nominally significant positive trends during the survey period are widespread across the North Atlantic Ocean, particularly around the British Isles and off the northeast coast of America.

positive and negative trends in the yearly mean colour anomaly vs. randomised-block year regression are shown in Fig. 4. Using the null distributions, we assessed the likelihood that the observed results were due to chance. 22 ocean sectors, primarily located within the band crossing the Central North Atlantic Ocean or within the two shelf areas, exhibit nominally significant positive trends (Fig. 5). Analysis of the positive null distribution (Fig. 4(a)) shows that an occurrence of 22 sectors of nominally significant, positive trends is exceedingly rare, as none of the 10,000 resampling tests yielded more than 22 sectors. The rejection level, defined as the fraction of resamplings yielding more nominally significant areas than observed, is a formal measure of the rareness of an observed spatial pattern. Low numbers indicate that the observed number of nominally significant positive results is extremely rare; a high rejection level indicates that the observed number is not unusual, and therefore indistinguishable from random chance. In the case described above, the rejection level approaches zero. It is, therefore, reasonable to conclude that the positive trends displayed in Fig. 5 represent spatial coherence, or field significance, rather than a chance result. The same method was also used to evaluate the field significance of nominally significant negative trends in Fig. 5. The areas of nominally significant negative trends are much less frequent and cannot be distinguished from random chance. Table 1 summarises the field significance tests outlined above.

The lag-zero regression of the yearly mean colour anomaly time series with the NAO index reveals a

Table 1
Summary of field significance tests for sectors exhibiting nominally significant, (a) positive and (b) negative trends in Fig. 5. A low rejection level indicates that the occurrence of patterns observed in Fig. 5 represents actual spatial structure

Trend	#Areas of $+r$, $p < 0.20$	#Tests with fewer $+r$, $p < 0.20$ areas	Rejection level
$+r$	22	10,000	<0.001
$-r$	6	5003	0.500

northeast–southwest band of sectors exhibiting nominally significant positive correlations (Fig. 6(a)). This band parallels that seen in the previously discussed trend data (Fig. 5). The band persists for a time lag of one year (Fig. 6(b)), but becomes insignificant and disappears at two- and three-year time lags (Fig. 6(c)–(d)). There are few sectors of nominally significant negative correlations. Numerous Northwest and Northeast Shelf sectors exhibit nominally significant positive correlations at zero-, one-, two-, and three-year time lags (Fig. 6). Tests for field significance, the positive, lag-zero null distributions for which are shown in Fig. 4(a), indicate that the widespread occurrence of sectors with nominally significant positive correlations at multiple time lags in Fig. 6 represents actual spatial structure rather than chance occurrences. The sectors of nominally significant negative correlations in Fig. 6 are much less frequent and cannot be distinguished from random chance. These arguments are summarised in Table 2.

The data used in regression analyses of the unadjusted time series violate the assumption of independence. By removing the long-term trends from the unadjusted data and regressing the detrended data, we reduce this violation, although autocorrelations at time scales shorter than the decadal still remain. The detrended

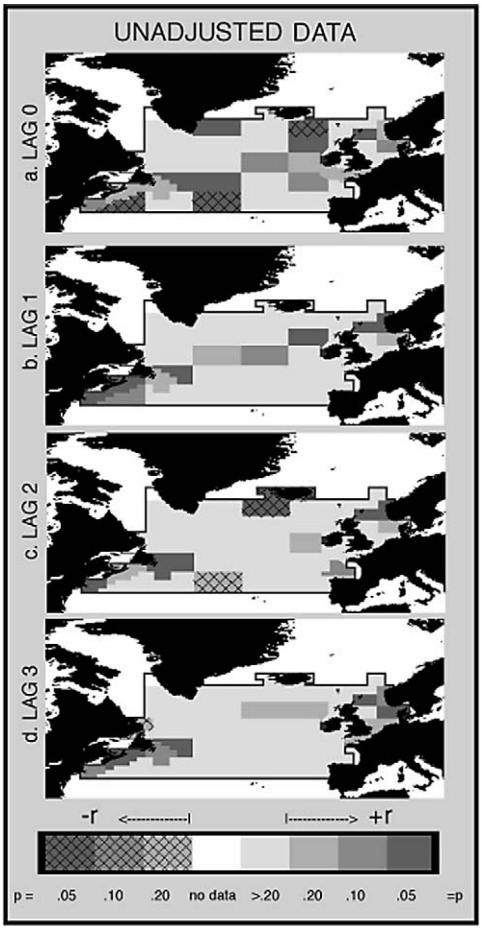

Fig. 6. Results of (a) lag-zero, (b) lag-one, (c) lag-two, and (d) lag-three regressions between the NAO index and the yearly mean CPR colour anomaly time series. Negative correlation coefficients are cross-hatched, positive coefficients are not. Darker shades of grey are more significant (smaller p value). A band of sectors exhibiting significant positive correlations is distributed across the North Atlantic Ocean at lag zero, but disappears at longer time lags. The correlation remains strong at longer time lags on the continental shelves.

Table 2
Summary of field significance tests for sectors exhibiting nominally significant, (a) positive and (b) negative correlation at lags zero, one, two, and three years in Fig. 6(a)–(d). A low rejection level indicates that the occurrence of patterns observed in Fig. 6 represents actual spatial structure

(a) Positive areas Lag	#Areas of $+r$, $p < 0.20$	#Tests with fewer $+r$, $p < 0.20$ areas	Rejection level
0	14	9602	0.040
1	11	9055	0.095
2	9	8403	0.160
3	12	9280	0.072
(b) Negative areas Lag	#Areas of $-r$, $p < 0.20$	#Tests with fewer $-r$, $p < 0.20$ areas	Rejection level
0	4	3517	0.648
1	0	0	1.000
2	3	3517	0.648
3	1	739	0.926

time series regressions have the potential to resolve the relationships between the high-frequency variability in the NAO index and the colour time series. Contrary to the occurrence of patterns in the other regression maps (Figs. 5 and 6), the detrended regressions at time lags of zero, one, two, and three years reveal a random scattering of nominally significant positive and negative sectors (Fig. 7). Tests for field significance, the null distributions for which are shown in Fig. 4, show that the patterns in Fig. 7 cannot be distinguished from random chance. Therefore, we conclude there is no evidence for a correlation between the time series of the detrended NAO index and the yearly mean colour anomaly in the North Atlantic Ocean. Table 3 summarises this result.

4. Discussion

Much of the North Atlantic Ocean, particularly the continental-shelf areas and a narrow band within the Central North Atlantic, exhibited an increase in the CPR colour index during the period 1948–2000. Phytoplankton are sensitive to changes in their physical environment, and so it is likely that these trends have come about through some dynamic oceanographic or meteorological process. In the discussion of our results, we offer several physical hypotheses to explain the observed patterns of phytoplankton variability.

The NAO index was used to characterise the behaviour of the NAO and its relationship with phytoplankton production in the North Atlantic. We used this index because it is a useful measure of climate in the North Atlantic Ocean and accounts for a large portion of the variability observed there. However, no statistical relationship was found between high-frequency variability in the CPR colour and the NAO index time series. The NAO index exhibited a significant, positive ($r^2 = 0.13$, $p = 0.004$) increase during the period 1948–2000 (Fig. 3). This long-term trend in the NAO index is similar to the positive phytoplankton trends observed in many areas. While numerous studies of oceanic and atmospheric dynamics have suggested a link with the NAO, we stress that making an association between the CPR colour and the NAO index time series may result in erroneous conclusions because both are relatively short and contain long-term trends. This problem particularly applies to analysing the colour time series. Conclusions based on trends in the relatively short colour time series are speculative and must be interpreted cautiously. Neverthe-

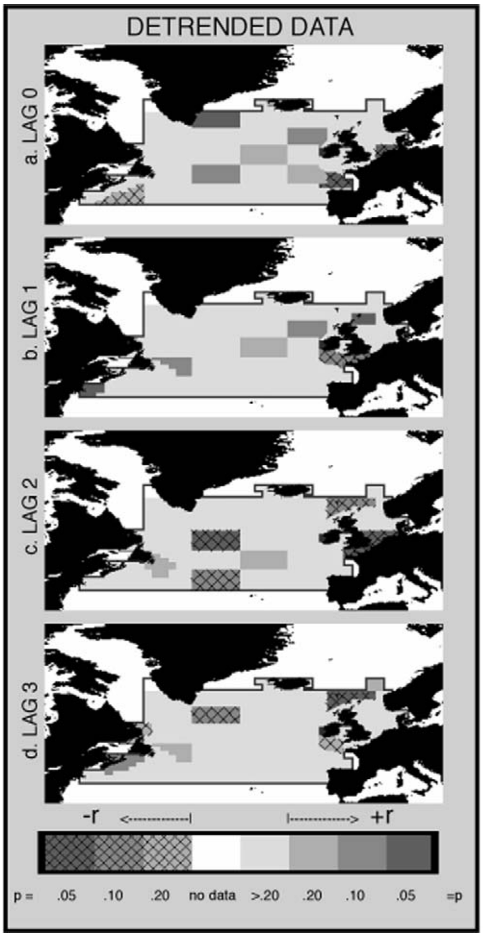

Fig. 7. Results of (a) lag-zero, (b) lag-one, (c) lag-two, and (d) lag-three regressions between the detrended NAO index and the detrended yearly mean CPR colour anomaly time series. Negative correlation coefficients are cross-hatched, positive coefficients are not. Darker shades of grey are more significant (smaller *p* value). No coherent spatial pattern appears.

less, these analyses do provide a reasonable means to generate hypotheses linking long-term trends in phytoplankton and NAO-dependent physical factors.

For the purpose of this discussion, we will look at how three primary factors influencing phytoplankton growth and abundance, namely light, nutrients, and temperature, are affected by the advection of water masses and by water-column stratification. Advection of water masses with distinct temperature and nutrient properties can change the physical environment of phytoplankton. Superimposed on these water-mass properties, mixed-layer processes influence the light conditions that an algal cell experiences. The critical-depth concept suggests that when the depth of mixing, D_m, shoals above the critical depth, D_{cr}, net phytoplankton growth will occur (Sverdrup, 1953). The opposite effect, a deepening of D_m relative to D_{cr}, can limit phytoplankton growth. Because the growth of a phytoplankton population is sensitive to regional physical conditions (Siegel, Doney, & Yoder, 2002), it is important to consider how environmental factors influence the upper layer of the ocean. Hypotheses addressing phytoplankton variability during the CPR survey period should address both advection and mixed-layer processes.

The discussion of results is presented for three oceanographic regions: Northeast Shelf (areas B1, B2,

Table 3
Summary of field significance tests for sectors exhibiting nominally significant, (a) positive and (b) negative correlation at lags zero, one, two, and three years in Fig. 7(a)–(d). A low rejection level indicates that the occurrence of patterns observed in Fig. 7 represents actual spatial structure

(a) Positive areas Lag	#Areas of $+r$, $p < 0.20$	#Tests with fewer $+r$, $p < 0.20$ areas	Rejection level
0	5	6329	0.367
1	5	6335	0.367
2	2	1662	0.834
3	2	1530	0.847
(b) Negative areas Lag	#Areas of $-r$, $p < 0.20$	#Tests with fewer $-r$, $p < 0.20$ areas	Rejection level
0	3	3200	0.680
1	2	1659	0.834
2	6	7014	0.299
3	4	4784	0.522

C1, C2, C3, C4, D1, D2, D3, D4), Northwest Shelf (areas F10, E10, and E9), and Central North Atlantic (all other areas not included in the two shelf regions). The reasons for making these regional divisions are twofold: 1) to separate open-ocean areas from shelf areas, and 2) to recognise the inherent differences between the climatic and oceanographic processes in the Northwest and Northeast Atlantic.

4.1. Northeast Shelf

Edwards, Reid and Planque (2001) provided several explanations for multidecadal variability of phytoplankton in the North Sea. They observed, much as shown by the results of this study, a long-term increase in phytoplankton abundance during the survey period. Here, we summarise their arguments explaining phytoplankton variability in the North Sea and attempt to generalise the discussion to include other Northeast shelf areas.

In continental-shelf waters near the British Isles, the spring phytoplankton bloom begins after stratification (Colebrook, 1979). Dickson, Kelley, Colebrook, Wooster, and Cushing (1988a) hypothesised that increased northerly winds in spring during the period 1950–1970 inhibited water column stratification. This delayed spring phytoplankton blooms and reduced the total seasonal abundance in waters adjacent to the British Isles. The observed 1950–1980 decline of phytoplankton (Dickson, Kelley, Colebrook, Wooster & Cushing, 1988a) coincided with colder than normal temperatures over Europe (Van Loon & Williams, 1976; Moses, Kiladis, Diaz, & Barry, 1987). The analysis of North Sea SST data by Edwards et al. (2001) showed a relatively cool period during the mid-1970s to mid-1980s. The advection of the Great Salinity Anomaly (described by Dickson, Meincke, Malmberg, & Lee, 1988b), with its cold low-salinity signature extending to depths of at least 500 m, into seas around the British Isles in the late 1970s would seem to be consistent with the observed drop in SST. However, Dickson et al. (1988b) found the salinity anomaly hard to discern in the Celtic Sea and English Channel, meaning that its effect on stratification in these areas was probably minimal. Colder atmospheric and oceanic temperatures, combined with an increase of northerly winds, tend to destabilise the water-column and deepen the mixed layer, delaying water-column stratification in spring. In addition to inhibiting stratification, Edwards et al. (2001) suggested that a reduced inflow of water from the North Atlantic Ocean during the late 1970s and early 1980s (noted by Turrell, Henderson, Slesser, Payne, & Adams, 1992) limited the availability of nutrients in the North Sea. It is, therefore, likely that during the 1950s to mid-1980s phytoplankton growth around the British Isles was inhibited by reduced water-column stratification and lower nutrient availability.

During the early 1980s, Europe entered a phase of relatively warm atmospheric temperatures that has frequently been linked with the NAO (Hurrell, 1995; Hurrell & Van Loon, 1997; Hurrell, Kushnir & Visbeck, 2001). Earlier stratification of the water-column, aided by warmer atmospheric conditions over seas adjacent to the British Isles and Europe, presumably favoured an earlier spring bloom and greater annual standing stocks. Reid, Borges & Svendsen (2001) and Edwards et al. (2001) both documented a marked increase in North Sea SST beginning in the late 1980s. This increase was particularly strong during the growing season from April to August. The increase in temperature was accompanied by advection of nutrients into the North Sea from the North Atlantic (Reid, Borges & Svendsen, 2001). These nutrient-rich North Atlantic waters have higher salinity and density than waters from the North Sea and therefore would be found below the surface. While these nutrient-rich waters might not be available to phytoplankton after the onset of stratification in spring, during winter or as a result of tidal mixing in the North Sea these nutrients will be brought to the surface, thus fertilising an early spring phytoplankton bloom. These conditions favourable for phytoplankton growth are likely to have been associated with the pronounced increase in phytoplankton abundance observed in the central North Sea and in waters west of Ireland (Reid, Edwards, Hunt & Warner, 1998; Edwards et al., 2001). The results of this study suggest that the positive trends in phytoplankton abundance observed in the North Sea may be widespread throughout the Northeast Shelf areas.

The observed long-term changes in the CPR colour index in the Northeast Shelf sectors (Reid, Edwards, Hunt & Warner, 1998; Edwards et al., 2001) suggest that an indirect relationship with the NAO may exist (Edwards et al., 2001). While we found no relationship between the high-frequency variability in the colour and NAO index time series, we did observe a longer-term trend in the CPR colour index similar to the trend in the NAO index. Edwards et al. (2001), synthesising data provided by Dickson and Turrell (2000), pointed out that the multi-decadal NAO signal has been increasing over the last century and a half; the 1950s and 1960s had the longest period of negative index values, and the 1980s and 1990s the longest period of positive index values. If much of the variability in oceanographic and meteorological variables observed on the Northeast Shelf can be explained by the NAO, then we should expect there to be decadal persistence of the physical factors associated with increasing NAO signal amplification. Given the shortness of the time series relative to multi-decadal variability, we stress that at present the NAO cannot be firmly associated with changes observed in the colour time series.

Finally, we would be remiss if we did not consider the potential impact of increased nutrient input from European rivers into the Northeast Shelf waters (Richardson, 1997). This increased input of nutrients from rivers could have spurred some of the phytoplankton growth observed during the survey period. However, Edwards et al. (2001) suggested that eutrophication and subsequent phytoplankton growth are largely confined to near-shore waters that are not well covered by the CPR survey. Extending their line of reasoning, we conclude that the physical processes described previously provide a more likely explanation for the observed colour-patterns in the open ocean and outer shelf areas than the input of nutrients from continental rivers.

4.2. Northwest Shelf

While several CPR studies have investigated zooplankton variability in the Northwest Atlantic shelf provinces (Jossi & Goulet, 1993; Greene & Pershing, 2000; Conversi et al., 2001; MERCINA, 2001; Sameoto, 2001; MERCINA, 2003), relatively few have focused on phytoplankton. This is not for lack of survey data, but perhaps for lack of complete datasets. In addition to the SAHFOS CPR survey in these areas, the National Marine Fisheries Service (NMFS) maintains a CPR survey in the Gulf of Maine, which runs along a transect from Boston, Massachusetts, to Yarmouth, Nova Scotia. Although the NMFS survey follows SAHFOS protocol, it is not located within the SAHFOS survey area and does not extend as far back in time. These differences complicate comparison between the two surveys. Using data collected and processed by NMFS, Pershing (2001) found no significant relationship between the CPR colour time series and the NAO index in the Gulf of Maine during the period 1961–1999. However, he did observe a positive long-term trend in the CPR time series. Although not co-located with the NMFS Gulf of Maine transect, the present study reports positive long-term trends in the CPR colour but no correlation between the detrended CPR colour and NAO index time series on the Northwest Shelf (Figs. 5 and 7). The occurrence of positive trends on the Northwest Shelf can be interpreted as an increase in phytoplankton abundance from the 1960s to the 1990s, because the SAHFOS CPR data were collected primarily in this sector during the 1960s and 1990s (see Fig. 2 for data distribution).

We offer the following hypotheses to explain the decadal-scale variability of the CPR colour index observed in this region. Oceanographic conditions on the Northwest Shelf, which are strongly influenced by remote convection and deep-water formation in the Labrador Sea, have exhibited considerable change during the CPR survey period (Petrie & Drinkwater, 1993; Pickart, McKee, Torres, & Harrington, 1999; Loder, Shore, Hannah, & Petrie, 2001; Smith, Houghton, Fairbanks, & Mountain, 2001). The ocean-atmosphere dynamics in the Labrador Sea are closely related to the NAO (Dickson, Lazier, Meincke, Rhines & Swift, 1996; Dickson, 1997). The shallow, baroclinic Labrador Current (LC) flows southward from the Labrador Sea around the Tail of the Grand Banks and into the Northwest Shelf provinces. Mixing between the cold, fresh LC coastal water and the warm, salty North Atlantic Central Water (NACW) results in the formation of Labrador Slope Water (LSW) and Warm Slope Water (WSW) (Gatien, 1976). LSW, composed primarily of LC water, is colder, fresher, and closer to shore than the WSW (Gatien, 1976). WSW, composed largely of NACW, is warmer and saltier than the LSW (Gatien, 1976). Petrie and Yeats (2000) found that the WSW is relatively enriched in nitrate compared to the LSW. High LC transport extends the distribution of LSW southward as far as the Middle Atlantic Bight, while low LC transport causes the distribution of LSW to recede northward to the Laurentian Channel (Gatien, 1976; Petrie & Drinkwater, 1993; MERCINA, 2001; Drinkwater, Petrie & Smith, 2002).

The NAO's dramatic change of phase in winter 1995–1996 allowed oceanographers to observe how the ocean responds to a large NAO phase shift, with the episode serving as a natural oceanographic experiment. During the positive NAO conditions preceding the episode, deep convection and increased deep-water formation in the Labrador Sea reduced the southwestward flow of the shallow LC around the Tail of the Grand Banks and enhanced the southward flow of the Deep Western Boundary Current (DWBC) (Petrie & Drinkwater, 1993; Dickson, Lazier, Meincke, Rhines & Swift, 1996; Dickson, 1997). During the negative NAO winter of 1995–1996, convection decreased and shoaled as a result of weaker storm activity and decreased heat loss in the Labrador Sea. The DWBC transport decreased and the shallow LC transport around the Tail of the Grand Banks increased, resulting in increased formation of cold, nutrient-poor LSW (MERCINA, 2001; Smith, Houghton, Fairbanks & Mountain, 2001; Drinkwater et al., 2002). LSW reached the Scotian Shelf and Gulf of Maine two years after this brief negative NAO phase and displaced the warmer, more nutrient-rich WSW. Production of LSW declined with the return to a positive phase of the NAO in 1997, thus ending the supply of cold slope water to the Gulf of Maine and Scotian Shelf. The cold LSW remnants in the Gulf of Maine began to mix and lose their cold-water signature in the summer of 1998, two years after the intensely negative NAO winter (MERCINA, 2001; Drinkwater et al., 2002).

Monitoring of the NAO phase shifts during the period 1996–1999 has improved our understanding of the oceanographic responses to thermohaline processes in the Labrador Sea and the subsequent changes in southward transport of subarctic water masses. During the 1950s and 1960s a negative NAO state prevailed, while positive NAO conditions occurred during the 1980s and 1990s, with, as described above, a corresponding reversal in oceanographic status. Drawing from this discussion of physical oceanographic responses of the Northwest Shelf to the NAO, two physical variables, namely temperature and nitrate availability, emerge which may help to explain the observed trends in the CPR colour index.

The positive trend in the NAO index during recent decades has been associated with positive trends in the surface (Conversi, Piontkovski & Hameed, 2001) and subsurface (Greene & Pershing, 2000; MERCINA, 2001) temperatures of the Northwest Shelf. Both temperature increases could explain the observed positive trend in the CPR colour index. In the absence of nutrient limitation, warmer SSTs often favour phytoplankton growth physiologically as well as by enhancing stratification and thus the availability of light for photosynthesis (Eppley, 1972). Less often appreciated are the potential effects of changing subsurface temperatures. Using a simple one-dimensional mixing model coupled with a light-dependent phytoplankton-growth model, Pershing (2001) found that an increase in Gulf of Maine bottom-water temperatures could result in a non-linear process of water-column stratification during spring, which subsequently could accelerate initiation of the vernal phytoplankton bloom. Since bottom waters in the region's deep shelf basins are derived from mixtures of WSW and cool LSW, and since such mixtures can vary with NAO-induced changes in slope-water circulation patterns (Loder et al., 2001; MERCINA, 2001; Smith, Houghton, Fairbanks & Mountain, 2001), the above model provides a plausible, if somewhat subtle, mechanism linking the NAO to phytoplankton production. These results suggest that NAO-induced surface and subsurface temperature changes can affect phytoplankton production not only through direct physiological mechanisms, but also through a variety of subtle biological and physical interactions.

The positive trend in the NAO index during recent decades may also be associated with changing nutrient conditions. Nitrate has been shown to be the limiting nutrient in the temperate North Atlantic Ocean (Dugdale & Goering, 1967; Eppley, Regner, & Harrison, 1979; Ryther & Dunstan, 1981). If nitrate is increased, one might therefore expect phytoplankton growth to be enhanced. During positive NAO conditions, the flow of the LC weakens, allowing the warmer, more nutrient-rich WSW to dominate the Northwest Shelf sectors. During negative NAO conditions, colder, nutrient-poor LSW dominates. A persistent positive phase of the NAO is likely to be accompanied by more nutrient-rich waters on the Northwest Shelf. While these proposed links between the NAO, temperature, and nitrate availability cannot account conclusively for the positive trend observed in the CPR colour time series, they do provide a consistent physical hypothesis relating multi-decadal variability in phytoplankton to climate.

4.3. Central North Atlantic

There have been few studies of CPR colour in the Central North Atlantic (but see Colebrook, 1979). This study finds areas of nominally significant, positive trend in CPR colour in the central North Atlantic Ocean, from Flemish Cap, east of Newfoundland, to the British Isles (Fig. 5). The oceanic transition zone between the subarctic and subtropical gyres, which is roughly co-located with the areas of positive trend, is marked by the Gulf Stream and North Atlantic Current system (Fig. 8). This area of the North Atlantic

Fig. 8. JPL Pentad Climatology (1985–2000) of the North Atlantic Ocean. Solid line represents approximate position of the Gulf Stream/North Atlantic Current (Position of current redrawn from Fratantoni (2001)). Numbers represent the approximate number of years necessary for an anomaly formed off the south-east United States coast to travel to that location (adapted from Sutton & Allen, 1997, Fig. 1b).

Ocean exhibits significant communication with upstream oceanographic processes and local long-term atmospheric forcing. Here, we discuss how oceanographic and atmospheric variables may explain the observed phytoplankton variability in the Central North Atlantic Ocean.

The oceanic 'memory' for SST anomalies generated by wind mixing and convective processes is stored in subsurface waters over a period of several years (McCartney, 1997; Molinari, Mayer, Festa, & Bezdek, 1997). These anomalies are retained below the summer mixed-layer and propagated across the North Atlantic by oceanic circulation patterns (Hansen & Bezdek, 1996; Sutton & Allen, 1997). The thermohaline anomalies, once created and transported, have the ability to affect physical oceanography and climate in distant areas of the North Atlantic over periods of years to decades (Dickson, 1997; Sy, Rhein, Lazier, Koltemann, Meincke, Putzka et al., 1997). Sutton and Allen (1997) observed that SST anomalies, forming off the southeast coast of the United States, propagate along the path of the Gulf Stream and North Atlantic Current (Hansen & Bezdek, 1996), across the North Atlantic Ocean to the British Isles over a period of ~10 years. The approximate yearly position of the anomalies is displayed in Fig. 8. Within 3–7 years, an anomaly created off the North Carolina coast reaches the central North Atlantic. Moreover, there seems to be a degree of decadal variability to the anomalies. Sutton & Allen's (1997) Fig. 2a depicts warm anomalies propagating off the coast of the southeast United States and across the ocean during the period 1948–1965, and cold anomalies propagating in the same manner during the period 1965–1985. Kushnir (1994), using zonally averaged, normalised, and smoothed SST time series, found that the region between 40 and 60°N was anomalously warm in the 1930s to 1960s and was anomalously cool in the 1960s to 1980s. While changes in temperature can directly influence the growth of phytoplankton, anomalies on the scale described above, which were of the order of 0.5 °C, would not substantially affect the physiological growth of phytoplankton (see Eppley, 1972), but they may have an important impact on mixed-layer processes.

As mentioned above, nitrate is considered to be the limiting nutrient for phytoplankton growth in the temperate North Atlantic. Nitrate is removed from the surface waters by phytoplankton uptake and subsequent downward flux; it is replenished from deeper, more nutrient-rich waters by vertical mixing processes. Phytoplankton growth in arctic and subarctic regions follows the solar irradiance cycle (Longhurst, 1998), while growth in the southern regions is considered to be nutrient limited. The 1° gridded data in the NODC World Ocean Atlas show high concentrations of nitrate at higher latitudes and lower concentrations at lower latitudes (Fig. 9(a)). The transition zone between high and low concentrations of nitrate shows a slight trend from NE to SW and is centred on 50°N. The location is similar to the significant positive trend in CPR colour seen in Fig. 5. At this and similar latitudes, winter mixing drives the mixed layer to at least a few hundred metres and sometimes much more (Michaels & Knap, 1996; McCartney, 1997). Longitudinal depth profiles taken at 30°W, 40°W, and 50°W show surface nitrate concentrations increase north of 50°N and below the surface at 50°N (Fig. 9(a)–(d)). This increase in subsurface nitrate is not particularly strong immediately subsurface, but at depths of 100–200 m a noticeable increase occurs. The subsurface nitrate, even as deep as a few hundred metres, becomes available for phytoplankton production through strong winter mixing of the water column.

The NAO and atmospheric circulation patterns over the North Atlantic Ocean are closely related, primarily during the winter (Barnston & Livezy, 1987). One may recall that the NAO has shown a positive trend during the CPR survey period, and one should note that westerly winds over the North Atlantic Ocean intensified by as much as 8 m/s and shifted northward during the recent, predominantly positive NAO phase from the 1970s to the present (Hurrell, 1995). In contrast, during the previous, predominantly negative NAO phase during the 1960s, the winds were weaker and became more zonal in nature (Hurrell, 1995). The position of the storm tracks has shifted to the north during the positive NAO phase, whereas during the negative NAO phase the tracks crossed the North Atlantic further to the south (Rogers, 1990; Dickson, Lazier, Meincke, Rhines & Swift, 1996; Hurrell & Van Loon, 1997). Both west-wind stress and wind-stress curl associated with storminess mechanically mix and deepen the mixed layer, thus introducing

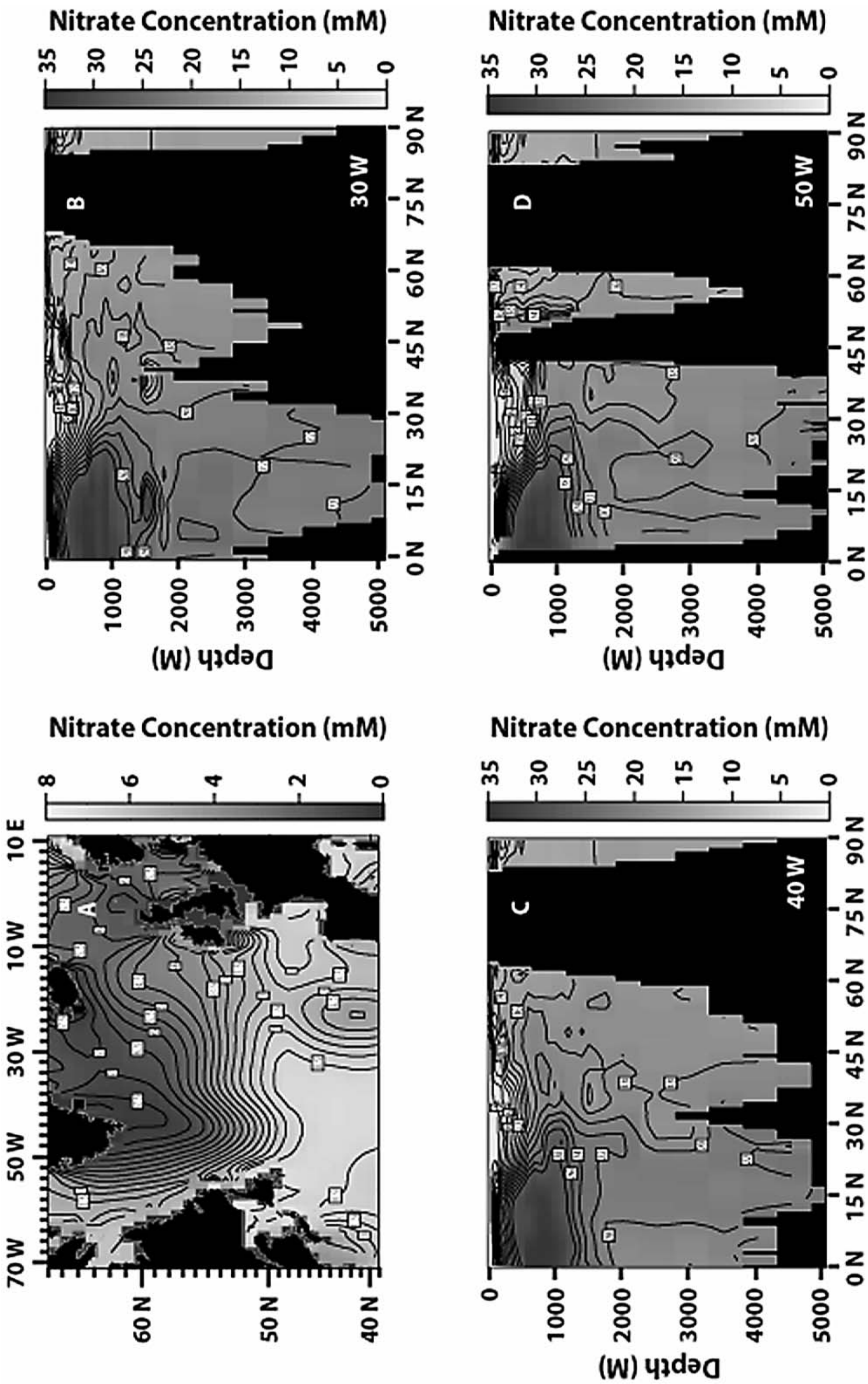

Fig. 9. Nitrate distribution in the North Atlantic Ocean. Units are in μ mol litre^{-1}. (a) Surface availability, (b) 30°W longitudinal section, (c) 40°W longitudinal section, and (d) 50°W longitudinal section.

nutrients to the surface. Not only does the wind mechanically mix the water column, but strong winds over the ocean also increase the loss of heat, further cooling the surface and increasing the depth of mixing. Hurrell (1995) noted this effect during the period 1981–1995, when the warm European climate brought about by increased westerly winds coincided with cooler SSTs in oceanic areas underlying the westerly belt. These observations of NAO-dependent wind and storm intensity enable us to interpret further the results of this study.

The effects of the breakdown of water-column stratification, as a result of wind mixing, on phytoplankton growth differ between regions of the North Atlantic Ocean (Siegel, Doney & Yoder, 2002). Michaels and Knap (1996) observed that in the subtropical North Atlantic convective mixing increased the nutrient and chlorophyll concentrations. Whereas in the subpolar gyre of the North Atlantic, the deepening of the mixed layer relative to the critical depth as a result of increased storminess lead to reductions in chlorophyll concentrations (Stramska et al., 1995). Dutkiewicz, Follows, Marshall & Gregg, (2001) developed a simple, two-layer bio-physical model to investigate the effect of wind mixing on chlorophyll concentrations in the North Atlantic Ocean. They found that high wind mixing during spring in the subtropics led to greater chlorophyll concentrations, whereas in subpolar regions it led to declines in chlorophyll concentrations. Here, we propose several hypotheses to explain the observed phytoplankton variability across the North Atlantic Ocean with due consideration of the largely latitudinal patterns in SST, wind, and nitrate patterns.

Our arguments are illustrated in Fig. 10, comparing 1970 to present (predominantly positive NAO; Fig. 10(a)) with 1950 to1970 (predominantly negative NAO; Fig. 10(b)). During the 1970s and up to the present, the band of intensified westerly winds, the nitrate transition zone, the zone of cool SST anomalies, and the band of nominally significant positive CPR trends were all co-located in the transition zone between the subtropical and subarctic regions of the North Atlantic. We hypothesise that during this period the strong westerlies and the associated loss of heat acted in concert to deepen the mixed layer of the transition zone, introducing more nitrate into the surface layer and increasing phytoplankton production. Subarctic areas north of this transition zone also experienced stronger winds and greater nitrate availability, but there the phytoplankton were unable to utilise the additional nitrate because of the unfavourable light conditions associated with enhanced deep mixing. This reasoning would explain why in those areas north of the transition zone we find no evidence of a positive long-term trend in CPR colour. Extending this line of reasoning further, winds were lighter in the subtropical areas south of this transition zone because of the

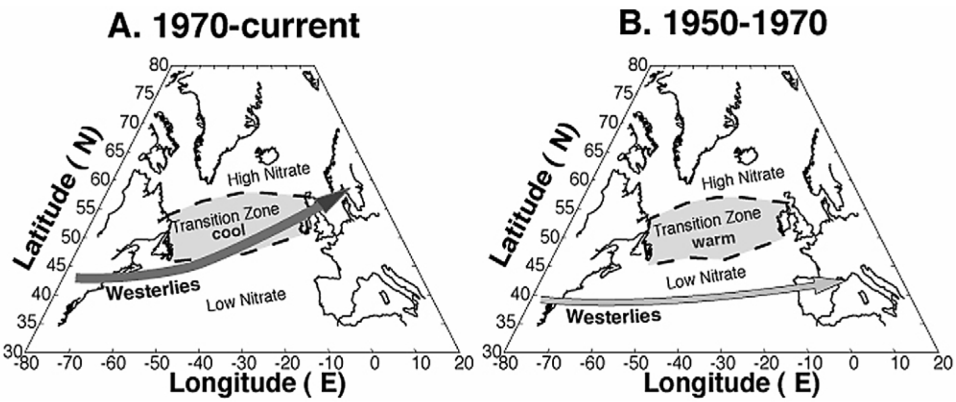

Fig. 10. Wind patterns, SST anomalies, and nutrient distribution over the North Atlantic Ocean during (a) the period 1970–present and (b) 1950–1970. Northern areas have high surface nitrate and southern areas have low surface nitrate. During the period 1970–present, strong wind mixing combined with negative SST anomalies tended to deepen the mixed layer and bring nitrate to the surface in the transition zone. During the period 1950–1970, weak wind mixing combined with positive SST anomalies increased stratification and nitrate limitation in the transition zone.

northward shift of the westerlies. The corresponding reduction in wind stress would enhance both stratification and nitrate limitation of phytoplankton production. This would then explain why these areas south of the transition zone also fail to exhibit evidence for a positive long-term trend in CPR colour. As the preceding arguments might suggest, there were indeed a few areas both north and south of the oceanic transition zone where nominally significant negative trends in CPR colour were observed (Fig. 5). Although the tests for field significance of these trends do not allow us to attach rigorous statistical confidence to them, their presence is consistent with our hypotheses.

In contrast to the predominantly positive NAO conditions during 1970 to present, the predominantly negative NAO conditions prevailing during 1950–1970 were characterised by a weakening and southward shift of the westerly winds (Fig. 10(b)). In the transition zone, the reduced wind stress would have enhanced both the stratification and nitrate limitation of phytoplankton production. This would explain why CPR colour values tended to be lower during this earlier period of predominantly negative NAO conditions. Although lacking rigorous statistical support, there are implications that the areas both to the north and to the south of the oceanic transition zone experienced higher phytoplankton production during this period (Fig. 5). This is consistent with the southward shift in the westerlies, which would not only result in more favourable light conditions for phytoplankton in the subarctic region but also enhance nitrate availability to phytoplankton in the subtropical region.

The above description of biological and physical coupling, linking wind stress, water-column stratification, light availability, nitrate availability and phytoplankton production, provides a consistent explanation for the spatially coherent patterns observed in the CPR colour/NAO correlation maps from the Central North Atlantic. While these linkages currently remain hypothetical, they suggest important directions for future research.

5. Conclusions

This study reports the observation of positive long-term trends in the CPR colour time series across the North Atlantic Ocean. Specifically, the continental shelf areas in both the Northeast and Northwest Atlantic, as well as a narrow transition zone between the subarctic and subpolar Central North Atlantic, all exhibited positive trends during the period 1948–2000. When the trends were removed from both the NAO and CPR time series, the residual time series showed no correlation. Our study sought to understand the observed phytoplankton variability by considering dynamic environmental conditions. The NAO, which is associated with a large part of the variability observed in numerous oceanographic and meteorological variables, also showed a positive trend during this period. While we have been careful not to over-interpret these long-term trends, we do suggest that they may indicate an association between long-term patterns of phytoplankton production and the NAO.

Over the Northeast Shelf, CPR colour has exhibited a positive trend during the survey period from 1948–2000; these results parallel those observed by other researchers. During the early part of the survey period, 1948–1970, it is likely that relatively cool SST and atmospheric conditions, together with increased northerly winds, inhibited water-column stratification. Reduced stratification, combined with lower nutrient availability, appears to have limited phytoplankton abundance. During the latter part of the survey period, 1970–2000, anomalously warm SST and atmospheric temperatures, as well as high nutrient availability, appear to have increased phytoplankton production.

As in the case of the Northeast Shelf, the Northwest Shelf has also exhibited a positive long-term trend in CPR colour from 1948–2000. The early part of the survey period, 1948–1970, was characterised by predominantly negative NAO conditions, the presence of relatively cold, nutrient-poor shelf waters, and lower values of the CPR colour index. When the phase of the NAO changed to predominantly positive in the 1970s, the shelf waters became warmer and richer in nutrients, and CPR colour values rose. Thus, NAO-dependent multidecadal variability in temperature and nutrient availability appear to provide the key to understanding long-term trends in the CPR colour index on both sides of the North Atlantic.

In the Central North Atlantic the observed positive long-term trend fell along the oceanic transition zone. To the north and south, light and nitrate availability, respectively, were the major limiting factors. Warmer SST and lower westerly wind velocities characterised this transition zone during the predominantly negative NAO period from 1948–1970, whereas colder SST and higher westerly-wind velocities characterised the predominantly positive NAO period from 1970–2000. We hypothesise that the combined effect of weaker winds, warmer SST, and enhanced stratification reduced nitrate availability in the euphotic zone. This may have inhibited phytoplankton growth during the early part of the CPR survey period. The converse appears to have happened during the later part. If stronger winds, colder SST, and increased mixing enhanced nitrate availability in the euphotic zone, then this would explain the higher CPR colour values observed.

While this descriptive study reveals several long-term patterns of phytoplankton variability, it can only provide tentative hypotheses about the physical processes underlying them. Future studies of regional phytoplankton dynamics in the North Atlantic Ocean should seek to link oceanographic, meteorological, and biological factors to observed changes in phytoplankton abundance. By investigating phytoplankton interannual to multidecadal variability, we add a new temporal component to our understanding of marine ecosystem dynamics in the North Atlantic Ocean.

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