

## Physical controls of variability in North Atlantic phytoplankton communities

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### Abstract

The structure of marine phytoplankton communities in the North Atlantic Ocean varies considerably on seasonal, interannual, and longer timescales in response to environmental change. However, the causes of ecological variability on interannual and longer timescales remain uncertain. Here, using a half-century of observations, we compare changes in atmospheric forcing (surface wind speed and heat fluxes) and ocean surface properties (sea surface temperature, mixed layer depth, thermal stratification, and turbulent kinetic energy) with variability in total phytoplankton biomass and the abundances of diatoms and dinoflagellates, as measured by the Continuous Plankton Recorder survey. On seasonal timescales, there is a clear connection between observed changes in the physical environment and the phytoplankton assemblages. Strong turbulence, deep mixed layers, and weak stratification decrease diatom abundance in the subpolar gyre, but increase diatoms in the subtropical gyre, a pattern broadly consistent with growth limitation of phytoplankton in high and low latitudes by light and nutrients, respectively. In contrast, dinoflagellates prosper in stratified, weakly turbulent conditions in sampled portions of the subpolar and subtropical gyres. On interannual to multidecadal timescales, however, the links between observed ecological and physical changes are much weaker. The physical mechanisms that differentiate the fates of diatoms and dinoflagellates on seasonal timescales do not appear to control their longer-term variability, perhaps because year-to-year variability in the phytoplankton assemblages is greater than in the physical drivers. This suggests that other biological (e.g., zooplankton grazing, chaos in the plankton) or physical mechanisms (e.g., changes in ocean circulation) may play important regulatory roles.

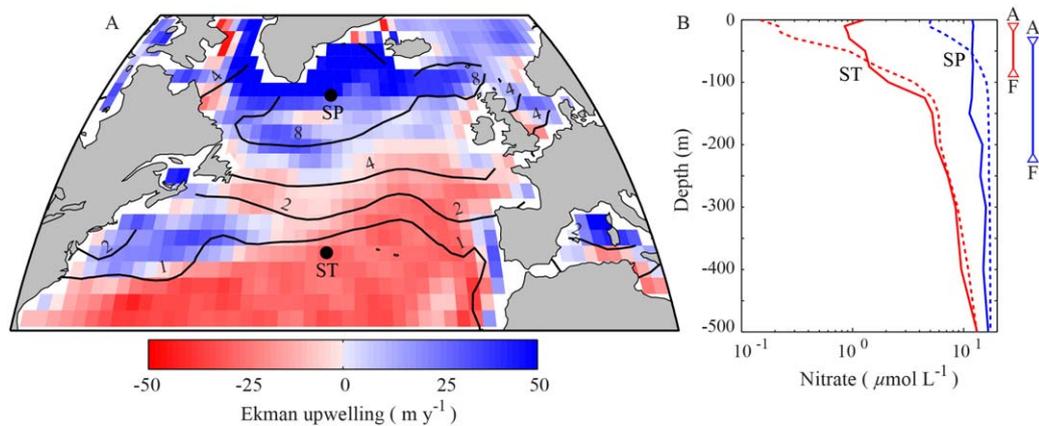
The structure of North Atlantic phytoplankton communities varies in response to changes in ocean surface conditions and atmospheric forcing (Sverdrup 1953; Margalef 1978; Taylor et al. 1993). These ecological changes are important because they have the potential to affect the broader marine food web, global biogeochemical cycles, and the climate system (Falkowski et al. 1998; Henson et al. 2012). Although the physical drivers of seasonal changes in North Atlantic phytoplankton communities are relatively well studied (Sverdrup 1953; Follows and Dutkiewicz 2002), if still debated (Behrenfeld 2010; Taylor and Ferrari 2011), considerably less is known about how and why phytoplankton communities have varied on interannual to multidecadal timescales. Do the same physical mechanisms that guide seasonal ecological change govern ecological variability on longer timescales? In particular, how

do subtropical and subpolar gyre communities and distinct phytoplankton assemblages, such as diatoms and dinoflagellates, respond to the physical forcing?

To address these questions, we examine and compare a half-century of concomitant phytoplankton assemblage, atmospheric forcing, and surface oceanographic observations taken in the subtropical and subpolar North Atlantic. The Continuous Plankton Recorder (CPR) survey has sampled greater than 100 common diatom and dinoflagellate species over the North Atlantic subpolar and northern subtropical gyres since 1958, and provides an internally consistent and unparalleled view of surface ecological variability (Richardson et al. 2006). Although the CPR data have known limitations associated with sampling procedures (e.g., Richardson et al. 2006; Barton et al. 2013), they offer temporal, spatial, and taxonomic coverage not possible with any other dataset, and therefore, offer a unique and crucial perspective of how marine phytoplankton assemblages shift through time and space (Edwards and Richardson 2004; Leterme et al. 2005; Hinder et al. 2012). We consider long-term records of phytoplankton color index

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**Fig. 1.** (A) Ekman upwelling velocity ( $w_{ek}$ ;  $\text{m y}^{-1}$ ) in downwelling ( $w_{ek} < 0$ ) subtropical and upwelling ( $w_{ek} > 0$ ) subpolar gyres in the North Atlantic. The black contours indicate the annual mean nitrate concentration at the surface ( $\mu\text{mol L}^{-1}$ ). (B) Mean nitrate concentration ( $\mu\text{mol L}^{-1}$ ) with depth in the subtropical (red lines, 'ST' on map) and subpolar (blue lines, 'SP' on map) gyres for August (dashed line) and February (solid line). MLDs in February (F, deeper) and August (A, shallower) are shown at right. Ekman upwelling velocity is calculated using NCEP/NCAR annual mean wind stress data (Kalnay et al. 1996). Monthly mean nitrate data are taken from the World Ocean Atlas (Garcia et al. 2010) and averaged over a  $5^\circ \times 5^\circ$  area.

(PCI), a proxy for total surface phytoplankton biomass, and the total abundances of diatoms and dinoflagellates, two key phytoplankton functional groups with strongly contrasting ecological niches and contributions to marine biogeochemical cycles (Henson et al. 2012; Irwin et al. 2012). By decomposing the observed ecological variability into seasonal, interannual to multidecadal (variations longer than one year, but less than the  $\sim 50$ -year long record), and a long-term trend component (comparable to the  $\sim 50$ -year record), we assess which physical mechanisms act as key drivers at each timescale, their regional relevance, and their importance to diatom and dinoflagellate abundance. The primary physical drivers that are believed to shape phytoplankton community structure include wind forcing and surface buoyancy fluxes from the atmosphere, which then alter the physical environment (turbulent kinetic energy [TKE] in the mixed layer, sea surface temperature [SST], mixed layer depth [MLD], and upper water column stratification). These key physical drivers potentially impact the light and nutrients experienced by phytoplankton in the ocean surface (Sverdrup 1953; Follows and Dutkiewicz 2002) but also the interactions and imbalances between predators and prey (Behrenfeld 2010; Behrenfeld and Boss 2014). The goal of our analysis is to evaluate and assess the statistical links between each phytoplankton metric (PCI, abundance of diatom and dinoflagellates) and likely physical drivers for different timescales across the northern subtropical and subpolar North Atlantic Ocean.

### Contrasting dynamics and habitats in subpolar and subtropical gyres

The CPR survey covers portions of the North Atlantic subpolar and subtropical gyres, and allows the environmental controls of phytoplankton assemblages to be assessed in a consistent manner. Here, we highlight key differences between

the gyres, in terms of circulation, nutrient supply, and light availability, as the contrasts provide a guiding framework for interpreting the results of our study.

In the subtropical North Atlantic, prevailing surface wind stress patterns drive Ekman downwelling and deepen the nutricline (Fig. 1). The water column is stably stratified, and aside from entrainment due to seasonal or episodic mixing events and horizontal transports of nutrients (Williams and Follows 1998; Williams et al. 2000; Palter and Lozier 2008), the supply of nutrients to the surface euphotic zone is weak. Although light is generally abundant at these latitudes, the limited supply of nutrients leads to low phytoplankton biomass and to assemblages dominated by picoplankton and flagellates, with larger cells such as diatoms being relatively scarce (Tarran et al. 2006; Ward et al. 2012). Population growth by photoautotrophs is typically balanced by grazing (Lessard and Murrell 1998), and much of the primary production in the ocean surface is fueled by nutrients remineralized locally within the surface layer (Azam et al. 1983).

In these relatively stratified waters, seasonality in atmospheric forcing mediates the entrainment flux of nutrients (Fig. 1B) and leads to changes in the phytoplankton community. For example, at the Bermuda Atlantic Time Series station (BATS;  $31^\circ 50' \text{ N}$ ,  $64^\circ 10' \text{ W}$ ) and the European Station for Time-series in the Ocean, Canary Islands (ESTOC;  $29^\circ 10' \text{ N}$ ,  $15^\circ 30' \text{ W}$ ), located on opposite sides of the North Atlantic gyre but at similar latitudes, increased surface winds and cooling in winter drive deeper mixing and entrainment of nutrients, spurring a contemporary surface increase in chlorophyll and primary production (Steinberg et al. 2001; Neuer et al. 2002). Weaker winds and surface warming in spring and summer re-stratify the water column, leading to lower primary production at the surface. In accord with this view, Follows and Dutkiewicz (2002) found that spatial variations

in the strength of the winter/spring bloom in the subtropical region within a given year are positively correlated with the magnitude of TKE inputs by wind mixing and surface cooling.

In contrast to the subtropics, the prevailing winds over the subpolar North Atlantic drive Ekman upwelling, making deep nutrients relatively accessible to phytoplankton (Fig. 1). Strong winds and surface cooling in winter deepen the mixed layer and entrain nutrients to the surface, whereas during summer the supply is generally weaker due to increased stratification (Williams et al. 2000). In addition, surface nutrients here are augmented by seasonal induction of nutrients from the nutricline (Williams et al. 2006). At this latitude, however, light supply is highly seasonal and limits phytoplankton growth in winter. With abundant nutrients, ample light, and weak grazing pressure in late winter, spring, or early summer, phytoplankton populations grow rapidly (Sverdrup 1953; Behrenfeld 2010; Taylor and Ferrari 2011), but ultimately decline as nutrients are exhausted, cells aggregate, die, or sink from the water column, and predators graze down phytoplankton (Sarthou et al. 2005). Follows and Dutkiewicz (2002) found that spatial variations in the strength of the spring or summer bloom in the subpolar region are negatively correlated with the magnitude of TKE inputs by wind mixing and surface cooling. Although larger phytoplankton cells and their predators are conspicuous features of subpolar bloom conditions (Ward et al. 2012), relatively small cells and flagellates, but fewer large cells, dominate stratified summer conditions (Barton et al. 2013).

The precise mechanisms that lead to the dramatic subpolar phytoplankton bloom have been the subject of renewed interest. The traditional view, termed the critical depth hypothesis, holds that phytoplankton bloom in spring as the MLD shoals above the critical depth, the depth at which phytoplankton net growth becomes positive (Sverdrup 1953). Two recent studies have extended this idea to differentiate between the depth of the mixed layer and the depth of active mixing, as defined by local wind and buoyancy forcing (Taylor and Ferrari 2011; Brody and Lozier 2014). The depth of active mixing can be much shallower than the mixed layer, implying that phytoplankton can bloom near the surface even when the mixed layer is still deep. An intriguing alternative to these “bottom up” perspectives places greater emphasis on the “top down” regulatory role of zooplankton grazing, and is termed the disturbance-recovery hypothesis (Behrenfeld 2010; Behrenfeld and Boss 2014). In this view, it is the decoupling of predator and prey mediated by physical disturbance and differential generation lengths, rather than light and nutrient availability, that primarily underpins seasonal changes in the phytoplankton. Although the sparsely sampled and coarsely resolved CPR data are not ideally suited for understanding the timing and initiation of spring blooms, to the extent that is possible we will look for

evidence of these mechanisms in the North Atlantic CPR data

## Methods

### Analysis of CPR data

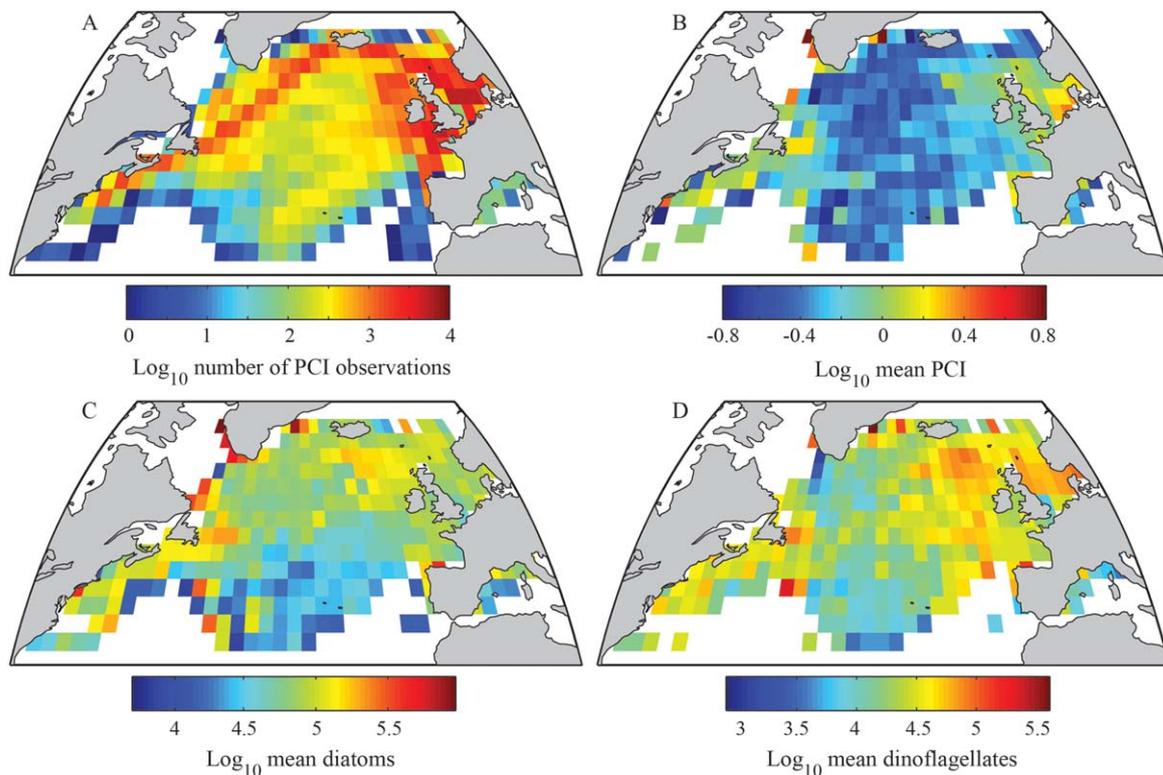
We calculate a monthly mean PCI for the years 1958–2006, using all available raw CPR tow data within each  $2.5^\circ \times 2.5^\circ$  grid in our study domain. The PCI is a proxy for total phytoplankton biomass, and has been found to compare favorably with satellite-derived estimates of chlorophyll *a* (Raitsoo et al. 2005). We also calculate monthly mean integrated diatom and dinoflagellate abundance by summing the abundances of all surveyed diatom and dinoflagellate taxa that have been sampled consistently over the whole period (for a list of taxa, see Barton et al. 2013). The integrated diatom and dinoflagellate abundance includes many, but not all, taxa within each group, and the PCI reflects all phytoplankton captured in the CPR mesh, not just diatoms and dinoflagellates. We use the term “assemblage” when referring to a subset of all phytoplankton species. The density of data samples varies in time and space, with the greatest number of samples taken in the northeast North Atlantic and along shipping routes (Fig. 2). Beyond the monthly averaging and spatial regridding, we deliberately have not smoothed or gap-filled any of the time series data to retain faithfully the character of the original, raw data. We have also conducted our analyses with data gridded to  $1.25^\circ$  and  $5.0^\circ$  resolution, and find the study results insensitive to this resolution choice. The  $2.5^\circ$  resolution is a compromise between having enough data in each grid cell for meaningful statistics and retaining resolution.

A simple framework is next outlined for decomposing variability in the phytoplankton time series at each grid cell into a range of different timescales, from seasonal to multi-decadal. The noise associated with the CPR survey sampling is estimated and signal-to-noise ratios (SNRs), which compare variance in phytoplankton and noise time series, are calculated. Our approach is demonstrated with PCI data from the western English Channel, a relatively well-sampled region (Fig. 3).

At a given location and time  $t$ , the observed phytoplankton data,  $P_t$ , can be decomposed into a climatological mean seasonal cycle ( $P_t^{\text{Season}}$ ), a long term trend ( $P_t^{\text{Trend}}$ ), phytoplankton variability on interannual to multidecadal timescales ( $P_t^{\text{Var}}$ ), and sampling noise ( $P_t^{\text{Noise}}$ ):

$$P_t = P_t^{\text{Season}} + P_t^{\text{Trend}} + P_t^{\text{Var}} + P_t^{\text{Noise}} \quad (1)$$

The climatological seasonal cycle,  $P_t^{\text{Season}}$ , is the mean of all available data,  $P_t$ , for a given grid cell for a given month of the year (Fig. 3A, inset). The seasonal cycle is subtracted from  $P_t$  to yield monthly anomalies,  $P'_t$  (Fig. 3B), from which we calculate the long-term trend,  $P_t^{\text{Trend}}$  (Fig. 3B). The linear trend over the record is estimated using the nonparametric



**Fig. 2.** (A)  $\text{Log}_{10}$  total number of raw CPR samples taken within each  $2.5^\circ \times 2.5^\circ$  grid cell during 1958–2006.  $\text{Log}_{10}$  annual mean (B) PCI, (C) total diatoms, and (D) total dinoflagellates.

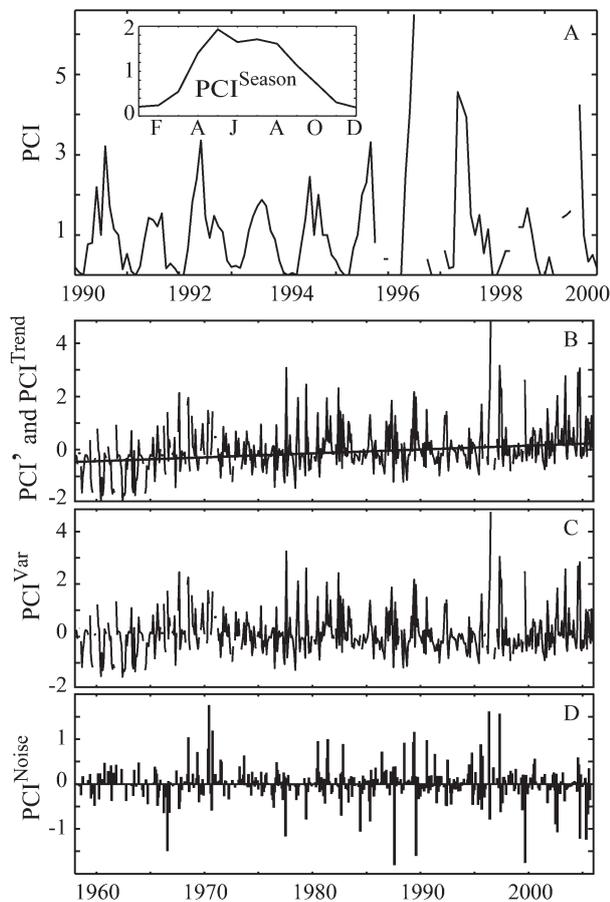
Theil-Sen approach, which reduces the sensitivity to large outliers (Theil 1950), a common feature in the anomaly time series.  $P_t^{\text{Var}}$  is the residual after subtracting  $P_t^{\text{Trend}}$  from the monthly anomalies,  $P'_t$ , and includes ecological variability on interannual to multidecadal timescales. Only significant ( $p < 0.05$ ), non-zero trends are subtracted when calculating  $P_t^{\text{Var}}$ . We also examined log-transformed CPR time series, but found the final results did not differ appreciably from the non-log-transformed data.

Lastly, the SNR for each phytoplankton time series is calculated to assess whether observed variability in the phytoplankton time series exceeds what might occur from variable sampling density. Our approach here assumes that measurement errors in the CPR survey are random and small and that errors in the CPR time series are associated with sampling intensity. To estimate the sampling noise at time  $t$ ,  $P_t^{\text{Noise}}$  the standard error of all available raw data is calculated within each grid cell for each month during 1958–2006. A synthetic time series of noise is generated, and repeated 10,000 times, by multiplying the standard error by a randomly generated Gaussian white noise time series (with a mean of zero and standard deviation of one). The SNR is calculated as the variance in each phytoplankton time series divided by the variance in the noise time series,  $\sigma_{\text{Phy}}^2/\sigma_{\text{Noise}}^2$  (Fleming 2010). At each location,  $\sigma_{\text{Phy}}^2$  is the variance in each

phytoplankton time series— $P_t^{\text{Season}}$ ,  $P_t^{\text{Trend}}$ , and  $P_t^{\text{Var}}$ —and  $\sigma_{\text{Noise}}^2$  is the mean variance of 10,000 randomly generated noise time series. A large SNR ( $\text{SNR} > 1$ ) indicates that the variability in the phytoplankton time series is not likely a product of potential sampling biases.

#### Analysis of environmental data

The physical data for the North Atlantic basin are similarly decomposed using the framework (1), including surface wind speed ( $\text{m s}^{-1}$ ), total heat flux ( $H$ ;  $H > 0$  for fluxes out of the ocean;  $\text{W m}^{-2}$ ), depth-integrated TKE generation in the surface boundary layer ( $\text{m}^3 \text{s}^{-3}$ ), SST ( $^\circ\text{C}$ ), stratification ( $^\circ\text{C}$ ), and MLD (m). The SST is the temperature in the surface layer (0–13 m depth) obtained from the UK Met Office temperature and salinity reanalysis dataset (Smith and Murphy 2007), which combines historical and more recent Argo measurements of temperature and salinity with model covariance fields to produce a gap-free global dataset. Stratification is evaluated from the difference in temperature between the surface and 200 m, again using the temperature reanalysis data. The MLD is diagnosed using a potential density threshold method (De Boyer Montégut et al. 2004), where the MLD is defined as the depth at which the potential density changes by  $0.03 \text{ kg m}^{-3}$  from the surface layer. Potential density profiles were calculated from UK Met Office reanalysis temperature and salinity data.



**Fig. 3.** (A) Absolute value PCI time series in the western English Channel (49.4° N, 5° W) for 1990–2000, with climatological seasonal cycle ( $PCI^{Season}$ ) inset. (B) PCI monthly anomalies ( $PCI'$ ) with seasonal cycle subtracted and long term trend overlaid ( $PCI^{Trend}$ ), (C) detrended anomaly time series ( $PCI^{Var}$ ), and (D) estimate of sampling noise ( $PCI^{Noise}$ ) for 1958–2006. The example noise time series is created by multiplying the standard error by a randomly generated Gaussian white noise time series.

Sea surface wind and air-sea heat fluxes are taken from monthly mean NCEP/NCAR reanalysis data (Kalnay et al. 1996), and we have summed latent, sensible, longwave, and shortwave heat fluxes to get the total, net heat flux. Local mechanical forcing from the wind and penetrative convection from surface cooling generate TKE in the surface boundary layer, some of which is converted to potential energy (PE) by deepening the mixed layer and increasing its density. The dominant terms in the TKE budget are diagnosed following Niiler and Kraus (1977), and as applied by Follows and Dutkiewicz (2002):

$$\frac{dh}{dt} h \Delta b = m_1 u_*^3 + m_2 \frac{\alpha g h}{\rho C_p 2} H \quad (2)$$

where the rate of conversion of TKE to PE (first term) is sustained by the inputs of TKE from the wind (second term)

and penetrative convection from surface cooling (third term); here  $\Delta b$  is the change in buoyancy between the mixed layer and the thermocline ( $m s^{-2}$ ),  $g$  is gravity ( $m s^{-2}$ ),  $\alpha$  is the thermal expansion coefficient ( $K^{-1}$ ),  $C_p$  is heat capacity of water ( $J kg^{-1} K^{-1}$ ),  $h$  is MLD (m),  $u_*$  ( $m s^{-1}$ ) is frictional wind velocity ( $= \sqrt{|\bar{\tau}|/\rho}$ ),  $\bar{\tau}$  is surface wind stress ( $N m^{-2}$ ) from NCEP/NCAR monthly mean data, and  $\rho$  is density of seawater ( $kg m^{-3}$ ). Coefficients  $m_1$  and  $m_2$  define the amount of energy available for mixing;  $m_1$  is typically 1.25, whereas  $m_2$  is  $\sim 1.0$  during periods of surface warming and 0.15 in periods of surface cooling (Kraus 1988). Increasing TKE lowers the time-averaged light experienced by a phytoplankton cell, and is associated with entrainment of nutrients into the surface layer.

Finally, the connection between the ecosystem and physical variables is assessed using Kendall's  $\tau$  coefficient, which is less sensitive to outliers than the more traditional Pearson correlation.

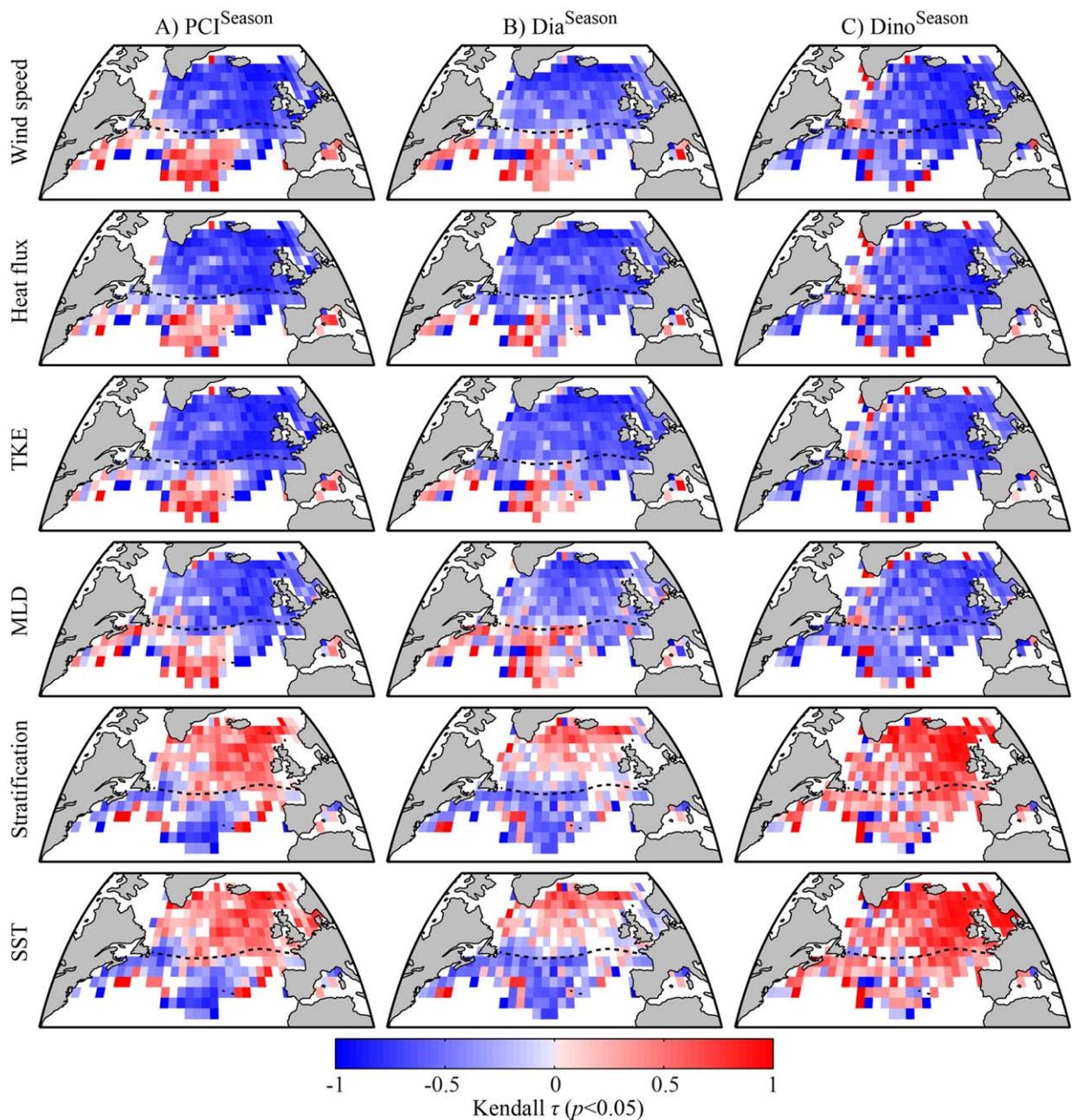
## Results

### Seasonal environmental change and biological responses

Our analysis confirms a cornerstone of biological oceanography: clear and widespread connections between seasonal cycles of key environmental drivers and seasonal cycles of total phytoplankton biomass and the abundance of diatoms and dinoflagellates in the North Atlantic (Margalef 1978; Taylor et al. 1993; Barton et al. 2013). Although these patterns have been previously described using a range of independent datasets, their robust signature and gyre-scale coherence lend confidence to the ability of the CPR survey to faithfully capture meaningful ecological patterns.

The seasonal analysis also highlights important differences in the mechanisms that regulate subtropical and subpolar PCI, as well as novel distinctions between the diatom and dinoflagellate assemblages. In the subpolar gyre, PCI is positively correlated with stratification and SST, but negatively correlated with surface wind stress, heat flux, TKE, and MLD (Fig. 4A). In contrast, in the subtropical gyre, PCI is negatively correlated with stratification and SST, but positively correlated with surface wind stress, heat flux, TKE, and MLD (Fig. 4A). Diatoms exhibit seasonal correlations with physical drivers that are similar to the total phytoplankton biomass (Fig. 4B). Dinoflagellates, by contrast, exhibit seasonal responses to physical drivers that are distinct from the total biomass and diatom abundance (Fig. 4C). Across the subpolar and subtropical gyres, dinoflagellates prosper during warm, stratified conditions, and their abundance is negatively correlated with surface wind speed, cooling, turbulence, and deeper mixed layers.

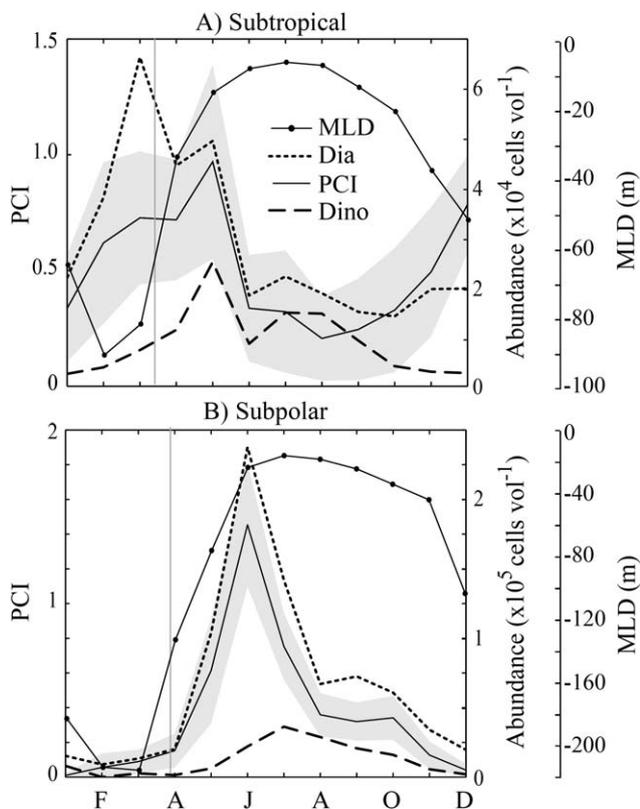
We provide additional context for these correlations by showing the climatological seasonal cycles of PCI, diatom abundance, dinoflagellate abundance, and MLD (with scale inverted to show negative depths) for a subtropical and



**Fig. 4.** Kendall's  $\tau$  correlation between the climatological mean seasonal cycles of PCI (PCI<sup>Season</sup>; A), summed diatoms (Dia<sup>Season</sup>; B), and summed dinoflagellates (Dino<sup>Season</sup>; C) and, from top to bottom down each column, climatological seasonal cycles of surface wind speed, total heat flux, TKE generation, MLD, stratification, and SST. Only significant correlations ( $p < 0.05$ ) are shown. The dashed black contour shows the approximate boundary between the subpolar and subtropical gyres, as defined by the  $4 \mu\text{mol L}^{-1}$  mean annual surface nitrate contour. Nitrate data from the World Ocean Atlas 2009 (Garcia et al. 2010).

subpolar location (Fig. 5). In the northern subtropical location (Fig. 5A), mixed layers are relatively shallow but still seasonally variable, reaching a maximum depth in February. PCI peaks in May, but there is a robust fall bloom in this area, unlike the subpolar location. Diatoms bloom early in spring (March), decline through the summer, and show a very weak fall bloom. Dinoflagellates are generally more

abundant in warm season months, with maxima in May and July to August. Interestingly, the fall PCI bloom does not appear to be primarily driven by changes in diatom or dinoflagellate populations, implying that other taxa (e.g., small but captured cells, taxonomic groups, and species not sampled by the CPR survey or considered in this study) are responsible for the peak in PCI here. In the subpolar location



**Fig. 5.** Climatological seasonal cycles of PCI (solid line), diatom abundance (dotted line), dinoflagellate abundance (dashed line), and MLD (solid line with filled circles; scale inverted to show negative depths) in subtropical (A) and subpolar (B) locations noted in Fig. 1 (averaged over a  $10^\circ \times 10^\circ$  area). The vertical gray line shows when heat fluxes switch from cooling to heating the ocean surface in spring. We have included in shaded gray the 95% confidence interval for PCI ( $\pm 2\sigma$ , where  $\sigma$  is the monthly standard error).

(Fig. 5B), mixed layers are deepest in March, shoal rapidly through early summer, and then deepen again through late summer and fall. There is a robust spring bloom peaking in June and much more modest fall bloom of diatoms and PCI peaking in September. Dinoflagellates are most abundant in summer, with a maximum in July. These seasonal cycles of total biomass, diatoms, and dinoflagellates are broadly consistent with previous CPR studies (Barton et al. 2013) and satellite observations (D'Ortenzio et al. 2012).

### Multidecadal trends

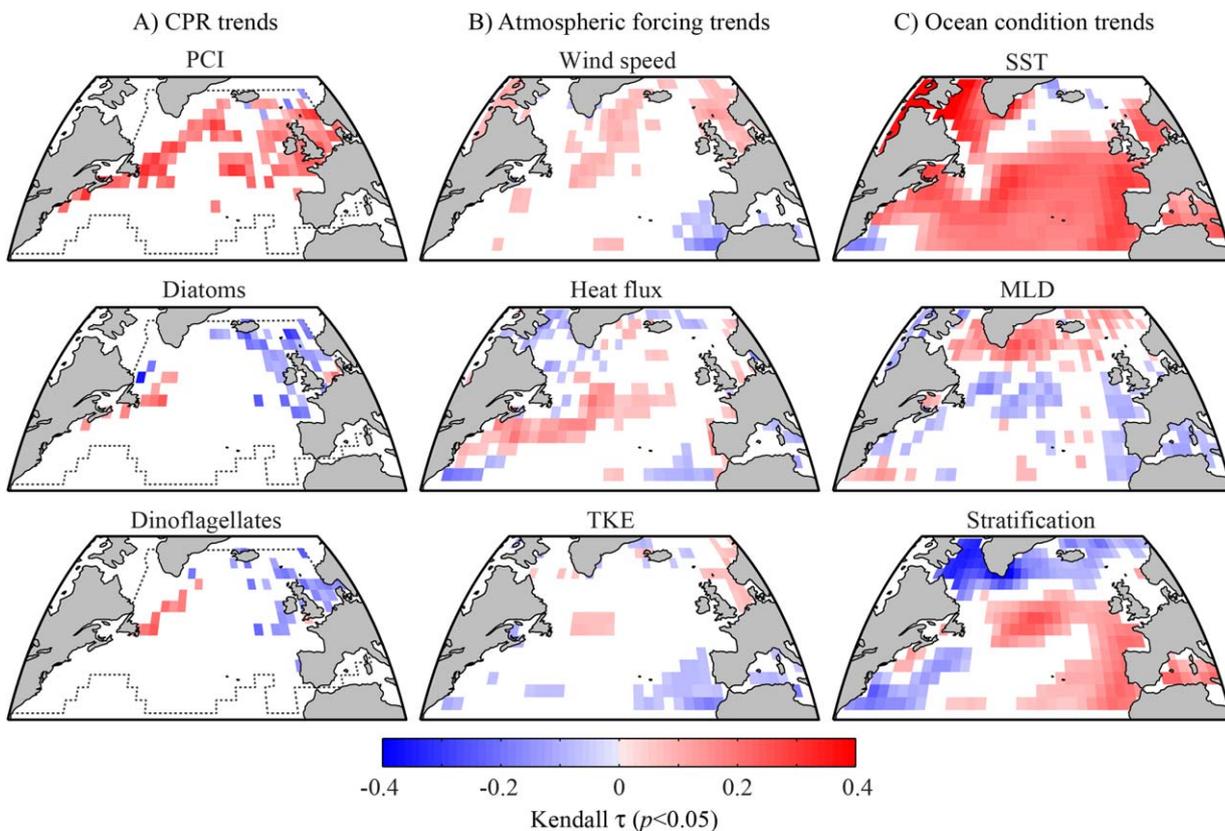
Between 1958 and 2006, phytoplankton biomass increased over a swath of the subpolar North Atlantic (Fig. 6A), a pattern that has been previously reported and linked to climate variability (Barton et al. 2003). A few isolated areas exhibited a decline in PCI, but for most areas there has been no significant trend. The abundances of diatoms and dinoflagellates have decreased in the northeast Atlantic but have not significantly changed elsewhere (Fig. 6A). Hinder et al. (2012), sampling only the most common taxa in this region, reported a

strong decline of dinoflagellates, but little change in diatoms. The contrast in the northeast Atlantic between increasing PCI but decreasing diatoms and dinoflagellates is striking, as it is generally believed that periods and places with greater chlorophyll or biomass also have proportionally more large phytoplankton cells, such as diatoms and dinoflagellates (Chisholm 1992). It is also interesting that the increase in PCI in the central North Atlantic does not appear to be driven by an increase in diatoms or dinoflagellates. The mismatch between PCI and diatom and dinoflagellate assemblage trends implies that other types of phytoplankton are varying independently from diatoms and dinoflagellates. However, the CPR survey does not fully resolve these other taxa.

During this same period, there has been a long-term increase in wind speed over the central subpolar gyre, the North Sea, and northeast Atlantic, with a decline in waters off of Spain and North Africa (Fig. 6B). Surface heat loss increased along the path of the Gulf Stream and North Atlantic Current, with some enhanced heat input elsewhere (recall that  $H > 0$  implies a flux out of the ocean). Trends in mixed layer TKE have less spatial coherence, but there is an area of decreasing turbulence near Spain and North Africa (Fig. 6B), in the same vicinity as the weakened winds. SST in much of the subtropical and subpolar North Atlantic has warmed strongly, yet much of the region of increasing PCI has not shown significant surface warming (Fig. 6C). These SST trends are consistent with other observational studies (Deser et al. 2010). At the same time, mixed layers have deepened in waters near Greenland and Iceland but have shoaled in the central North Atlantic on the intergyre margin and in the northeast Atlantic near Europe (Fig. 6C). The spatial pattern of trends for stratification is nearly the reverse, with decreased stratification in the Labrador Sea and near Greenland, but increased stratification in the central and northeast North Atlantic (Fig. 6C). Although it is impossible to rule out or prove a connection between slow-moving environmental and ecological change based on these data alone, none of the long-term trends in atmospheric forcing or ocean conditions examined here correspond closely to the spatial patterns seen in the multidecadal biological trends.

### Interannual to multidecadal variability

Although there is strong correlation between observed physical and PCI time series in the North Atlantic (Fig. 7A), this correlation is largely a consequence of seasonal variations (Fig. 7B). After the seasonal cycles (e.g., Fig. 4) and linear trends (e.g., Fig. 6) have been removed from PCI time series, there is little connection between ecological variability and physical forcing occurring on interannual to multidecadal timescales (Fig. 7C). A similar pattern is true for both diatoms and dinoflagellates (data not shown). The apparent insensitivity of the phytoplankton assemblages to interannual to multidecadal variability in the environment can be seen at a subtropical and subpolar location in the North



**Fig. 6.** Linear trends, indicated by the Kendall's  $\tau$  coefficient, in (A) CPR metrics, (B) atmospheric forcing, and (C) surface ocean conditions over 1958–2006. Only significant correlations ( $p < 0.05$ ) are shown. The dashed black perimeter in the biological trends at left indicates where CPR data are available.

Atlantic, where there is no correlation between  $\text{PCI}^{\text{Var}}$ ,  $\text{Dia}^{\text{Var}}$ ,  $\text{Dino}^{\text{Var}}$ , and  $\text{MLD}^{\text{Var}}$  (Fig. 8). For example, the phytoplankton assemblage in the subpolar North Atlantic (Fig. 8B) does not appear to track the deepening of the mixed layer from the 1970s to 1990s, associated with a change in the North Atlantic Oscillation (NAO) phase from negative to positive.

The lack of a clear connection between physical forcing and ecological change on interannual to multidecadal timescales, however, does not preclude significant ecological variability on these timescales. After subtracting the seasonal cycles and trends from the PCI time series, there is strong PCI variability that exceeds our estimates of sampling noise, as indicated by signal to noise ratios that are generally greater than one (Fig. 9; the same is true for diatoms and dinoflagellates; data not shown). Thus, there is considerable variability occurring on these timescales that is not easily or simply linked to the principal physical drivers considered in this study. The variance in phytoplankton and physical time series at each timescale provides further context for the lack of correlation: year-to-year variability in the plankton assemblage is considerably greater than in the physical drivers (Table 1).

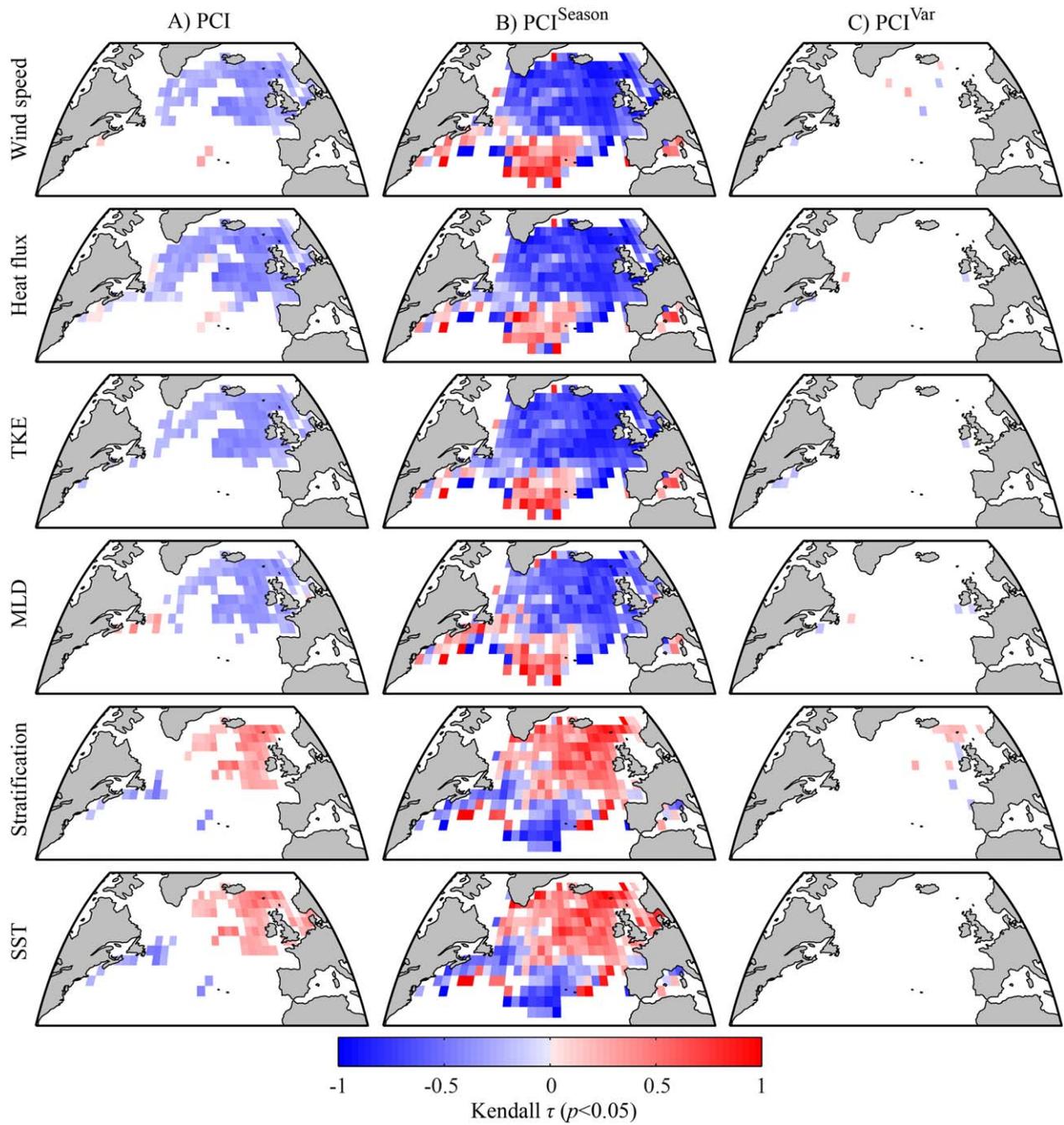
Our analyses focus on monthly relationships between atmospheric forcing and oceanographic conditions and the

phytoplankton assemblages. However, we have also investigated whether environmental changes in winter could have subsequent ecological impacts throughout the growing season. We find no widespread and robust correlation between the maximum depth of winter mixing and the maximum (or the average) phytoplankton biomass (PCI) throughout the growing season (defined here as January through August; data not shown).

We have also diagnosed the correlations between the NAO index and each of the physical and ecological time series across the North Atlantic, using monthly time series and the winter NAO index (December to March). There are strong and significant correlations between the NAO and each of the physical variables considered in our study, as has been reported elsewhere (Marshall et al. 2001). However, similar to Barton et al. (2003), we find no widespread, significant link between the winter NAO index and PCI or diatom and dinoflagellate assemblages (data not shown).

## Discussion

In the following discussion, we first consider the empirical evidence for how atmospheric forcing and ocean surface



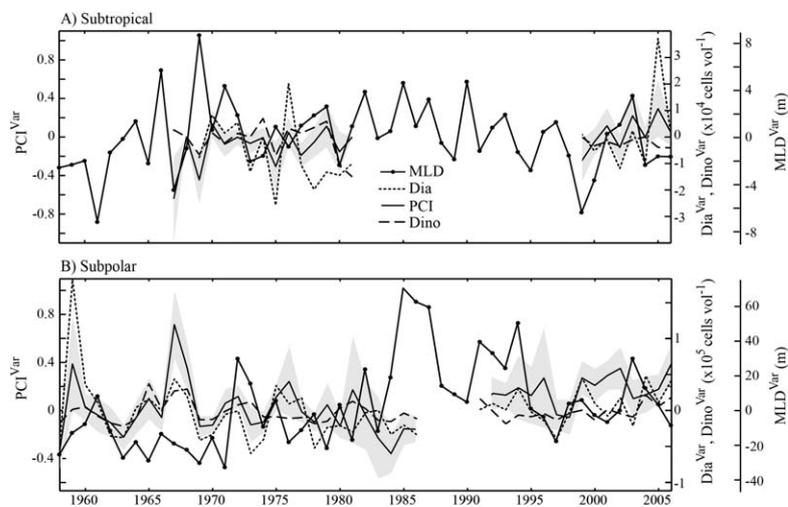
**Fig. 7.** Kendall's  $\tau$  correlation between absolute value (PCI; A), climatological mean seasonal cycle ( $\text{PCI}^{\text{Season}}$ ; B), and detrended PCI anomaly ( $\text{PCI}^{\text{Var}}$ ; C) time series and corresponding surface wind speed, total heat flux, TKE generation, MLD, stratification, and SST time series. Only significant correlations ( $p < 0.05$ ) are shown. Data in column B are the same as Fig. 3A, but are repeated to show the progression and strength of correlation at each timescale.

conditions control phytoplankton assemblages on seasonal timescales, highlighting mechanistic differences in the behavior of the subpolar and subtropical gyres and the responses of diatoms and dinoflagellates. We then examine possible explanations for why there is no obvious link between physical and ecological change on interannual to multidecadal timescales in the North Atlantic, and discuss

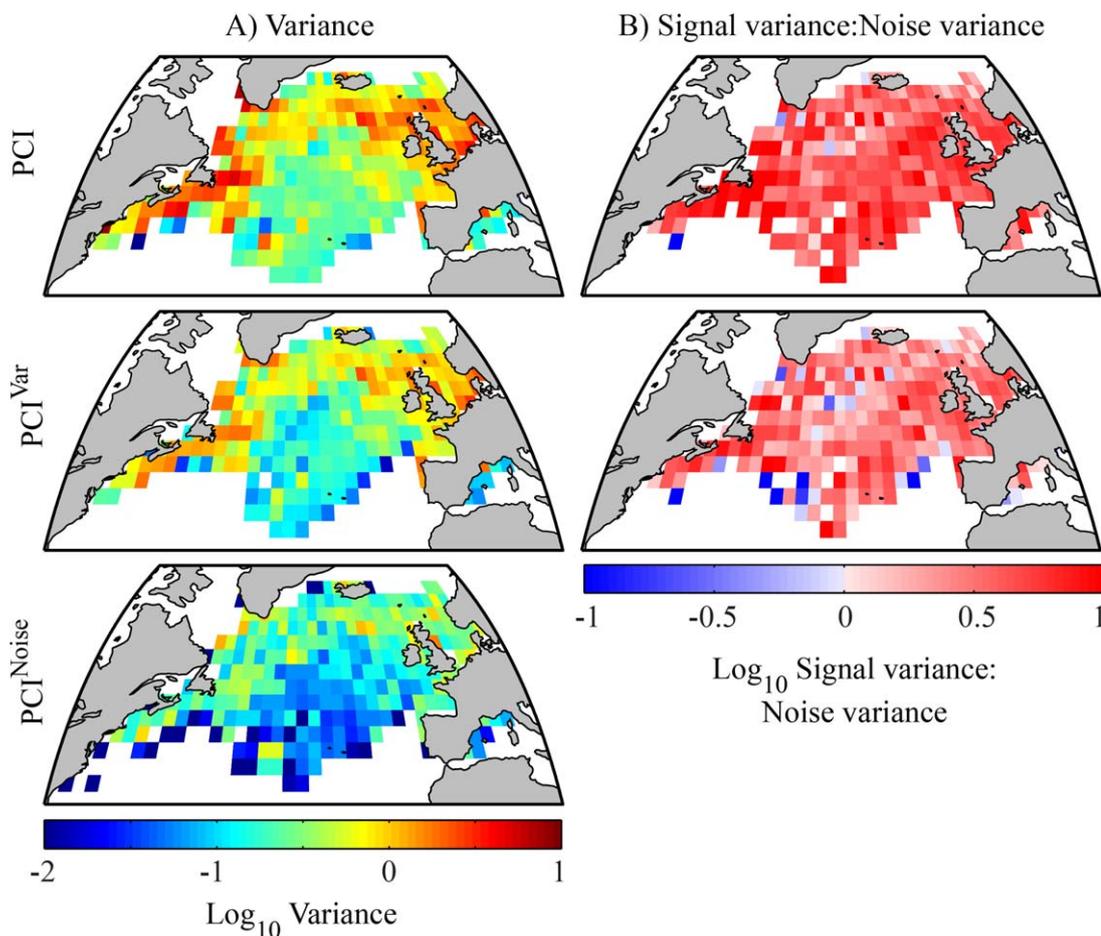
several key physical and biological processes that may play important, and as yet, unresolved roles.

#### Seasonal forcing of total phytoplankton biomass in subtropical and subpolar habitats

Our analysis broadly reaffirms the paradigm that the seasonal changes in phytoplankton biomass (PCI) in the subpolar



**Fig. 8.** Detrended anomaly time series (indicated by the “Var” superscript) for PCI (solid line), diatom abundance (dotted line), dinoflagellate abundance (dashed line), and MLD (solid line with filled circles) in subtropical (A) and subpolar (B) locations noted in Fig. 1 (annually averaged over a 10° × 10° area). Positive MLD anomalies indicate deeper MLDs. We have included in shaded gray the 95% confidence interval for PCI ( $\pm 2\sigma$ , where  $\sigma$  is the standard error of all anomalies within the region over a year).



**Fig. 9.** (A) Signal variance for absolute value (PCI; top) and detrended PCI anomaly (PCI<sup>Var</sup>; middle) time series, normalized by the noise variance (PCI<sup>Noise</sup>; bottom) to calculate the signal to noise ratio (B). Signal variance and SNR are presented in log<sub>10</sub> units; values greater than one (i.e., 10<sup>0</sup>) indicate ecological variability above and beyond our estimate of CPR sampling noise.

**Table 1.** Pooled variance for ecological and physical time series describing the original observations (Absolute values; PCI), the long-term trend ( $PCI^{\text{Trend}}$ ), the seasonal cycle ( $PCI^{\text{Season}}$ ), and the detrended anomalies ( $PCI^{\text{Var}}$ ). The pooled variance is a weighted, spatial average of the temporal variance at each location, where the weights are the number of monthly observations. Values have been normalized by the pooled variance in the seasonal cycle, such that seasonal cycle values are one and values are unitless. Values greater than one indicate greater variance than in the seasonal cycle

	Absolute values	Long-term trend	Seasonal cycle	Detrended anomalies
PCI	3.039	0.130	1.000	1.999
Diatoms	3.374	0.274	1.000	2.345
Dinoflagellates	4.771	0.093	1.000	3.450
Wind speed	1.602	0.002	1.000	0.599
Heat flux	1.122	0.001	1.000	0.120
SST	1.053	0.004	1.000	1.048

and subtropical North Atlantic are constrained by the availability of light and nutrients, respectively, as mediated by seasonal changes in atmospheric forcing (Sverdrup 1953; Follows and Dutkiewicz 2002). In the subpolar gyre, strong winds, cooling, and deep mixing tend to decrease phytoplankton biomass, whereas stratification and warmer SSTs are correlated with increased phytoplankton biomass (Figs. 4, 5). In the northern subtropical gyre, strong winds, cooling, and deep mixing lead to increased PCI, whereas stratification and warmer SSTs lead to decreased PCI (Fig. 4, 5). In the northern subtropical regions covered by the CPR survey (Fig. 5A), there is also a robust autumn bloom driven by deepening mixed layers and entrainment of nutrients (Colebrook 1982).

The CPR data offer unique perspectives on the applicability of the “top-down” disturbance-recovery mechanism across contrasting ocean regimes. In the northern subtropical areas (Fig. 5A), phytoplankton bloom strongly in winter or spring while mixed layers are deepest, and increase well in advance of the switch from cooling to heating at the ocean surface. Thus, we argue that the best explanation for seasonal dynamics here is the seasonal entrainment of nutrients, rather than the critical depth (Sverdrup 1953) or disturbance-recovery hypotheses (Behrenfeld and Boss 2014). In subpolar seas, PCI begins increasing while the mixed layer is deepest and light is still low (Fig. 5B), consistent with the disturbance-recovery hypothesis. However, rapid shoaling of the mixed layer and a switch from cooling to warming the ocean surface precede the period of greatest PCI increases in these latitudes (Fig. 5B), consistent with a more traditional biophysical view of how subpolar spring phytoplankton blooms proceed (Sverdrup 1953; Taylor and Ferrari 2011; Brody and Lozier 2014). However, we note that the MLD may not be the appropriate metric for gauging phytoplankton exposure to light: Brody and Lozier (2014) demonstrated

that the depth of active mixing is shallower than the MLD prior to the onset of stratification. Thus, although we find tentative support for both the critical depth hypothesis and “top-down” disturbance-recovery mechanism in the subpolar North Atlantic, the coarsely sampled and averaged CPR survey data and the lack of mixing length data preclude further speculation on the precise triggers and timing of phytoplankton.

### Contrasting seasonal responses of diatoms and dinoflagellates

Diatoms and dinoflagellates are significant components of the phytoplankton community in the North Atlantic, and have different life histories, physiologies, and trophic strategies (Sarhou et al. 2005). The traditional view of their ecology, formalized by Ramon Margalef’s mandala paradigm, holds that diatoms prefer turbulent, nutrient-rich conditions, and dinoflagellates calm, nutrient-poor conditions (Margalef 1978; Irwin et al. 2012). Our present analysis and increasing knowledge of how diatom and dinoflagellate traits determine their fitness under different environmental conditions (Ward et al. 2011; Irwin et al. 2012; Barton et al. 2013) allow us to update and refine this paradigm to account for differences between subtropical and subpolar systems.

In the downwelling, nutrient-limited subtropical gyre, increasing turbulence and mixing increases diatom abundance, as expected, whereas in the upwelling, light-limited subpolar gyre, the opposite is generally true (Fig. 4). Diatoms are largely photoautotrophic, nonmotile phytoplankton that require silica to form their covering frustules. For a given cell size, diatoms are able to grow relatively quickly, compared with other taxa, and have high affinities for nitrate and phosphate (Edwards et al. 2012). They can also tolerate low and variable light conditions (Depauw et al. 2012). These traits are thought to enable diatoms to form conspicuous blooms in relatively turbulent, nutrient rich conditions at high latitudes (Rynearson et al. 2013) and low latitude upwelling systems in the North Atlantic (Taylor et al. 2012). However, where light may be limiting, such as in the high latitudes in spring and winter, increasing turbulence may exacerbate light limitation. Thus, while pulses of nutrients (Schartau et al. 2010) and increased uptake of nutrients due to turbulence favor diatoms (Barton et al. 2014), and support classical Margalef’s mandala paradigm, we have shown here that this perspective should be refined on seasonal timescales to be specific to the dynamics within each gyre.

The relationship between seasonal environmental change and dinoflagellate dynamics is quite different from that of diatoms (Fig. 4). Generally speaking, diatom abundance peaks before dinoflagellates in seasonal ecological succession (Barton et al. 2013). In both the subtropical and subpolar gyres, strong winds, surface cooling, turbulence, and deep mixing are negatively correlated with dinoflagellate abundance, whereas increasing stratification and SST coincide with increases in dinoflagellate abundance. Dinoflagellates

tend to have relatively low nutrient affinities and growth rates (Edwards et al. 2012), and are, thus, not generally opportunistic bloom formers like diatoms (with the notable exception of harmful algal blooms; Smayda 1997). Most, if not all, dinoflagellates are either mixotrophic (exhibiting both photosynthetic and heterotrophic modes of nutrition) or heterotrophic (Barton et al. 2013). Mixotrophy is thought to be favored in resource-poor conditions (Ward et al. 2011), such as in stratified summer conditions in the North Atlantic. Heterotrophic dinoflagellates appear to be most abundant during stratified summer conditions characterized by an abundance of small prey cells (Barton et al. 2013). Finally, dinoflagellates are motile, yet their ability to swim effectively to maximize exposure to light, nutrients, and prey is negatively impacted by strong turbulence and shear (Durham et al. 2009), which may help explain the widespread negative correlation with turbulence. Taken together, these traits help explain the strong and basin-wide negative correlation of dinoflagellates with winds, cooling, turbulence, and mixing, as well as the positive connection with stratification and SST (Fig. 4).

The strong contrasts between diatoms and dinoflagellates highlight an important point: there is no single, universal mechanism that drives the seasonal cycles and blooms of all phytoplankton species. Not only does the importance of different physical mechanisms vary across the ocean and through time (e.g., Fig. 4) but also the range of phytoplankton species traits and complexity of predator-prey interactions implies that links between environmental forcing and population change should be distinct for groups of similar phytoplankton. The seasonal ecological succession of phytoplankton species in marine and freshwater systems illustrates the complex variations present in the microbial community (Taylor et al. 1993), and these patterns almost certainly cannot be explained without considering differences among species, as we have highlighted here.

#### **Ecological variability on interannual and longer timescales**

There is considerable variability in North Atlantic phytoplankton assemblages occurring on interannual and longer timescales (Figs. 6–8, Table 1), yet it is not easily or directly linked to variability in ocean surface wind speed, heat fluxes, turbulence, MLD, stratification, or SST (Fig. 7). Although a linear response is not expected, we speculate that the lack of sensitivity in the phytoplankton to long-term environmental variability may arise because the year-to-year variability in the phytoplankton assemblages is greater than in the physical drivers (Table 1). Our results for the North Atlantic do not preclude the possibility of particular phytoplankton species (there are many species not sampled by the CPR survey, and we have aggregated over many species), other functional groups (e.g., coccolithophores or picoplankton), or specific regions being directly impacted by the physical variables

that we have examined. However, the lack of robust and widespread correlations between the usual physical drivers and CPR-observed ecological variability suggests that the drivers of long-term ecological change in the North Atlantic may be more complex and uncertain than previously reported. Here, we place our results in the context of previous studies arguing for and against causal links from atmospheric forcing and resulting ocean conditions to marine phytoplankton community variability, and suggest other physical and biological mechanisms that may ultimately explain the observed ecological variability in the North Atlantic.

In the subtropical North Atlantic, it has generally been argued that changes in local atmospheric forcing from year to year influence surface phytoplankton biomass and community structure. For example, in their analysis of in situ data from BATS (data from 1990 to 1996) and satellite chlorophyll data from 1998 to 2000 throughout the subtropical North Atlantic, Follows and Dutkiewicz (2002) found that years with stronger winds and surface cooling had stronger spring phytoplankton blooms. Several other satellite-based studies have found a decrease in spatially integrated subtropical primary production or an increase in the spatial extent of the oligotrophic regions (low chlorophyll), which they attributed to increasing water column stratification associated with warming of ocean surface waters (Behrenfeld et al. 2006; Irwin and Oliver 2009). At BATS, interannual variability in primary productivity, total chlorophyll-*a*, and particulate carbon export are negatively correlated with the NAO index (Lomas et al. 2010), with positive NAO phases in this region being characterized by weaker winds and heat fluxes but higher surface temperatures (Marshall et al. 2001). Although model studies indicate that changes in atmospheric forcing linked to contrasting states of the NAO should influence the vertical supply of nutrients at BATS (Oschlies 2001), it has proven difficult to explain how the NAO impacts the phytoplankton community at BATS. For example, the NAO and MLD do not appear to be significantly correlated at BATS (Lomas et al. 2010).

Moreover, several recent studies have not found a strong link between interannual variations in stratification and phytoplankton dynamics (Lozier et al. 2011; Dave and Lozier 2013). By pairing chlorophyll observations and primary production estimates with nearby hydrographic profiles throughout the oligotrophic regions of the global ocean, these studies have shown that phytoplankton variability is strongly linked to water column stratification on seasonal timescales, yet there is to date no observed linkage between interannual variations in subtropical phytoplankton communities and interannual variability in local stratification. Instead, they argue that stratification changes to date may be insufficient to provide this linkage and/or variations in broader scale oceanographic processes, such as Ekman and geostrophic transports of nutrients, may help explain this

variability (Williams and Follows 1998; Palter and Lozier 2008; Ayers and Lozier 2010). It is possible that the stratification-phytoplankton link will become more apparent as climate warms in the coming century (Bopp et al. 2013). However, our analysis of northern subtropical CPR data supports these more recent studies questioning the direct link between local stratification changes and phytoplankton dynamics observed in the North Atlantic subtropical region over the past several decades.

In North Atlantic subpolar gyre, we also argue that the evidence for a link between local atmospheric forcing and the phytoplankton assemblage variability occurring on interannual and longer timescales is equivocal. Stronger surface winds and deeper mixed layers associated with positive phases of the NAO have been found to favor diatoms over dinoflagellates in the pelagic northeast North Atlantic, whereas dinoflagellates were more abundant in negative NAO conditions, characterized by weaker winds and shallower mixed layers (Henson et al. 2012). In a study of primarily continental shelf waters, Hinder et al. (2012) found a long-term increase in the relative abundance of diatoms vs. dinoflagellates, and linked this change to increases in wind and SST. Leterme et al. (2005) found that the winter NAO index was positively correlated with PCI and diatom abundance in the central North Atlantic during the spring bloom period (April to June), possibly in support of the hypothesis that deeper mixed layers should favor diatoms (Henson et al. 2012).

However, it is unclear how broadly these processes apply throughout the subpolar gyre. For example, CPR data from the northeast Atlantic indicate a negative correlation between diatoms and the NAO index in May and a positive correlation between dinoflagellates and the NAO index in April and May (Leterme et al. 2005), seemingly in contrast with the mechanism outlined above for the central North Atlantic. Moreover, Follows and Dutkiewicz (2002) found no year-on-year connection between atmospheric forcing and satellite-measured surface chlorophyll concentration throughout the subpolar gyre or in observations from Ocean Weather Station "India" (59° N, 19° W). Much as within the subtropical gyre, these links may become clearer as the climate changes in the coming century (Bopp et al. 2013). Yet our analyses of historical observations imply that interannual variations in phytoplankton assemblages are not neatly explained by local atmospheric forcing and oceanographic conditions, suggesting that other mechanisms may have been important. But what might these mechanisms be? In the following, we speculate on the potential roles of ocean circulation, zooplankton predation, and chaos in the plankton assemblages, and suggest that testing the importance of each potential alternative explanation should be the subject of future research.

First, ocean circulation, including Ekman and geostrophic currents, has the capacity to impact surface phytoplankton communities by mediating the three-dimensional transport

of nutrients. For example, along the northern flank of the subtropical gyre, strong winter winds generate a southward Ekman flux of subpolar nutrients into the subtropics (Williams and Follows 1998; Ayers and Lozier 2010). In the subpolar gyre, by contrast, horizontal Ekman fluxes generally remove nutrients from the euphotic zone. As the winds across the North Atlantic are marked by spatially coordinated, low frequency variability (e.g., NAO), this mechanism may play a role in structuring phytoplankton communities on interannual to decadal timescales, particularly at the intergyre boundary and margins. Geostrophic currents have also been shown to affect nutrient supply: geostrophic flow advects relatively nutrient-poor waters toward the subpolar gyre (Williams and Follows 1998; Williams et al. 2011), while nutrients are imported to the subtropical gyre via the upper limb of the meridional overturning circulation (Williams et al. 2006; Palter and Lozier 2008). Additionally, eddy mixing along the intergyre boundary has been shown to deliver nutrients from the subpolar to the subtropical basin (Bower et al. 1984). Therefore, interannual to decadal changes in the strength and geometry of the gyre circulations, as have been observed in the North Atlantic (Hátún et al. 2005), are expected to impact the horizontal delivery of nutrients to the euphotic zone. Thus, we suggest that future studies of phytoplankton variability consider the ecological significance of broad scale changes in the three-dimensional ocean circulation.

Although our focus has been largely on "bottom-up" processes, zooplankton predation clearly plays an instrumental role in regulating phytoplankton assemblages. Mechanisms that disrupt the balance between predator and prey over longer timescales would make it more difficult to detect direct "bottom up" links between atmospheric and oceanographic forcing variability and phytoplankton assemblages. For example, growth rates of zooplankton and phytoplankton have different sensitivities to temperature (Rose and Caron 2007); many larger zooplankton, such as copepods, have multiple developmental stages and relatively long generation times that are dependent on temperature (Kiørboe and Hirst 2008); and many zooplankton have overwintering strategies (e.g., diapause in copepods) or dormant phases (e.g., dinoflagellate cysts) that may be cued by environmental conditions (Hairton et al. 1990). Finally, as the environment changes through time, predator and prey species ranges and phenologies may change at different rates (Beaugrand et al. 2002; Edwards and Richardson 2004). Each of these mechanisms has the potential to alter the relative balance of top-down and bottom-up regulation of phytoplankton assemblages, yet our limited understanding of their impacts on long-term variability in phytoplankton assemblages precludes an assessment of their impact on the observations we report here (Chen et al. 2012).

There is also growing appreciation of the importance of chaos in plankton communities, resulting possibly from

resource competition or predator-prey dynamics (Benincà et al. 2008; Kenitz et al. 2013). The presence of chaos, although still unsubstantiated in open ocean phytoplankton communities, would make detecting links between physical forcing and ecological change even more difficult.

### Summary and wider implications

Large seasonal changes in atmospheric forcing and ocean surface conditions shape, to a great degree, the seasonal cycles of phytoplankton biomass, but also the relative abundance of phytoplankton species. These ecological changes in the phytoplankton are felt throughout the marine food web, and help define the strength and efficiency of the ocean's biological pump. At the same time, there are real variations in the North Atlantic phytoplankton assemblages occurring on interannual to multidecadal timescales. Explanations for this variability have often focused on longer-term variability in the same physical mechanisms (i.e., changes in atmospheric forcing and ocean surface conditions) that shape seasonal change in the phytoplankton community (Barton et al. 2003; Behrenfeld et al. 2006; Irwin and Oliver 2009).

Here, however, we have carefully examined a well vetted, decades-long observational record of the subpolar and subtropical North Atlantic phytoplankton assemblage, and found that interannual to multidecadal changes in atmospheric forcing and surface oceanographic properties do not clearly or simply explain the historical variations in the North Atlantic phytoplankton assemblage. The lack of sensitivity in the phytoplankton to long-term variability in local atmospheric forcing and ocean conditions may arise, in part, because the year-to-year variability in the phytoplankton assemblage is much greater than in the physical drivers. It is also possible that other ecological (e.g., zooplankton grazing, chaos in the plankton) and physical mechanisms (e.g., ocean circulation) may play crucial, and as yet, poorly understood roles in driving observed ecological changes. For example, several recent studies have considered how changes in ocean circulation impact phytoplankton biomass or chlorophyll in the Pacific (Ayers and Lozier 2010; Rykaczewski and Dunne 2010) and Atlantic Oceans (Hátún et al. 2009; Johnson et al. 2013), but considerably uncertainty remains. Thus, our work indicates that the traditional "bottom up" view that focused solely on local changes in atmospheric forcing and ocean conditions may not be sufficient to understand how phytoplankton communities respond to changing climates, both in the historical record and in anthropogenic climate change scenarios.

### References

- Ayers, J. M., and M. S. Lozier. 2010. Physical controls on the seasonal migration of the North Pacific transition zone chlorophyll front. *J. Geophys. Res.* **115**: C05001. doi:10.1029/2009jc005596
- Azam, F., T. Fenchel, J. G. Field, J. S. Gray, L. A. Meyer-Reil, and T. F. Thingstad. 1983. The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* **10**: 257–263. doi:10.3354/meps010257
- Barton, A. D., Z. V. Finkel, B. A. Ward, D. G. Johns, and M. J. Follows. 2013. On the roles of cell size and trophic strategy in North Atlantic diatom and dinoflagellate communities. *Limnol. Oceanogr.* **58**: 254–266. doi:10.4319/lo.2013.58.1.0254
- Barton, A. D., C. H. Greene, B. C. Monger, and A. J. Pershing. 2003. The continuous plankton recorder survey and the North Atlantic Oscillation: Interannual-to multi-decadal-scale patterns of phytoplankton variability in the North Atlantic Ocean. *Prog. Oceanogr.* **58**: 337–358. doi:10.1016/j.pocean.2003.08.012
- Barton, A. D., B. A. Ward, R. G. Williams, and M. J. Follows. 2014. The impact of fine-scale turbulence on phytoplankton community structure. *Limnol. Oceanogr. Fluids Environ.* **4**: 34–49. doi:10.1215/21573689-2651533
- Beaugrand, G., P. C. Reid, F. Ibañez, J. A. Lindley, and M. Edwards. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* **296**: 1692–1694. doi:10.1126/science.1071329
- Behrenfeld, M. 2010. Abandoning Sverdrup's critical depth hypothesis on phytoplankton blooms. *Ecology* **91**: 977–989. doi:10.1890/09-1207.1
- Behrenfeld, M. J., and E. S. Boss. 2014. Resurrecting the ecological underpinnings of ocean plankton blooms. *Ann. Rev. Mar. Sci.* **6**: 167–194. doi:10.1146/annurev-marine-052913-021325
- Behrenfeld, M. J., and others. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* **444**: 752–755. doi:10.1038/nature05317
- Benincà, E., and others. 2008. Chaos in a long-term experiment with a plankton community. *Nature* **451**: 822–825. doi:10.1038/nature06512
- Bopp, L., and others. 2013. Multiple stressors of ocean ecosystems in the 21st century: Projections with CMIP5 models. *Biogeosciences* **10**: 3627–3676. doi:10.5194/bgd-10-3627-2013
- Bower, A. S., H. T. Rossby, and J. L. Lillibridge. 1984. The Gulf Stream—Barrier or blender? *J. Phys. Oceanogr.* **15**: 24–32. doi:10.1175/1520-0485(1985)015<0024:TGSOB>2.0.CO;2
- Brody, S. R., and M. S. Lozier. 2014. Changes in dominant mixing length scales as a driver of subpolar phytoplankton bloom initiation in the North Atlantic. *Geophys. Res. Lett.* **41**: 3197–3203. doi:10.1002/2014gl059707
- Chen, B., M. R. Landry, B. Huang, and H. Liu. 2012. Does warming enhance the effect of microzooplankton grazing on marine phytoplankton in the ocean? *Limnol. Oceanogr.* **57**: 519–526. doi:10.4319/lo.2012.57.2.0519
- Chisholm, S. W. 1992. Phytoplankton size. In P. G. Falkowski and A. D. Woodhead [eds.], *Primary productivity and biogeochemical cycles in the sea*. Plenum Press.

- Colebrook, J. M. 1982. Continuous plankton records: Seasonal variations in the distribution and abundance of plankton in the North Atlantic Ocean and the North Sea. *J. Plankton. Res.* **4**: 435–462. doi:10.1093/plankt/4.3.435
- D’Ortenzio, F., D. Antoine, E. Martinez, and M. Ribera d’Alcalá. 2012. Phenological changes of oceanic phytoplankton in the 1980s and 2000s as revealed by remotely sensed ocean-color observations. *Glob. Biogeochem. Cyc.* **26**: GB4003. doi:10.1029/2011gb004269
- Dave, A. C., and M. S. Lozier. 2013. Examining the global record of interannual variability in stratification and marine productivity in the low-latitude and mid-latitude ocean. *J. Geophys. Res.* **118**: 3114–3127. doi:10.1002/jgrc.20224
- De Boyer Montégut, C., G. Madec, A. Fischer, A. Lazar, and D. Iudicone. 2004. Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology. *J. Geophys. Res.* **109**. doi:10.1029/2004jc002378
- Depauw, F. A., A. Rogato, M. Ribera d’Alcalá, and A. Falciatore. 2012. Exploring the molecular basis of responses to light in marine diatoms. *J. Exp. Bot.* **63**: 1575–1591. doi:10.1093/jxb/ers005
- Deser, C., A. S. Phillips, and M. A. Alexander. 2010. Twentieth century tropical sea surface temperature trends revisited. *Geophys. Res. Lett.* **37**: L10701. doi:10.1029/2010GL043321
- Durham, W. M., J. O. Kessler, and R. Stocker. 2009. Disruption of vertical motility by shear triggers formation of thin phytoplankton layers. *Science* **323**: 1067–1070. doi:10.1126/science.1167334
- Edwards, K. F., M. K. Thomas, C. A. Klausmeier, and E. Litchman. 2012. Allometric scaling and taxonomic variation in nutrient utilization traits and maximum growth rate of phytoplankton. *Limnol. Oceanogr.* **57**: 554–566. doi:10.4319/lo.2012.57.2.0554
- Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**: 881–884. doi:10.1038/nature02808
- Falkowski, P. G., R. T. Barber, and V. Smetacek. 1998. Biogeochemical controls and feedbacks on ocean primary production. *Science* **281**: 200–206. doi:10.1126/science.281.5374.200
- Fleming, S. W. 2010. Signal-to-noise ratios in geophysical and environmental time series. *Environ. Eng. Geosci.* **16**: 389–399. doi:10.2113/gseegeosci.16.4.389
- Follows, M., and S. Dutkiewicz. 2002. Meteorological modulation of the North Atlantic spring bloom. *Deep Sea Res.* **49**: 321–344. doi:10.1016/S0967-0645(01)00105-9
- Garcia, H. E., and others. 2010. World Ocean Atlas 2009, V. 4: Nutrients (phosphate, nitrate, silicate), p. 398. *In* S. Levitus [ed.], NOAA Atlas NESDIS.
- Hairston, N. G., T. A. Dillon, and B. T. De Stasio. 1990. Field test for the cues of diapause in a freshwater copepod. *Ecology* **71**: 2218–2223. doi:10.2307/1938634
- Hátún, H., A. B. Sando, H. Drange, B. Hansen, and H. Valdimarsson. 2005. Influence of the Atlantic subpolar gyre on the thermohaline circulation. *Science* **309**: 1841–1844. doi:10.1126/science.1114777
- Hátún, H., and others. 2009. Large bio-geographical shifts in the north-eastern Atlantic Ocean: From the subpolar gyre, via plankton, to blue whiting and pilot whales. *Prog. Oceanogr.* **80**: 149–162. doi:10.1016/j.pocean.2009.03.001
- Henson, S., R. Lampitt, and D. Johns. 2012. Variability in phytoplankton community structure in response to the North Atlantic Oscillation and implications for organic carbon flux. *Limnol. Oceanogr.* **57**: 1591–1601. doi:10.4319/lo.2012.57.6.1591
- Hinder, S. L., G. C. Hays, M. Edwards, E. C. Roberts, A. W. Walne, and M. B. Gravenor. 2012. Changes in marine dinoflagellate and diatom abundance under climate change. *Nat. Clim. Change* **2**: 271–275. doi:10.1038/nclimate1388
- Irwin, A. J., A. M. Nelles, and Z. V. Finkel. 2012. Phytoplankton niches estimated from field data. *Limnol. Oceanogr.* **57**: 787–797. doi:10.4319/lo.2012.57.3.0787
- Irwin, A. J., and M. J. Oliver. 2009. Are ocean deserts getting larger? *Geophys. Res. Lett.* **36**. doi:10.1029/2009gl039883
- Johnson, C., M. Inall, and S. Häkkinen. 2013. Declining nutrient concentrations in the northeast Atlantic as a result of a weakening Subpolar Gyre. *Deep Sea Res. I.* **82**: 95–107. doi:10.1016/j.dsr.2013.08.007
- Kalnay, E., and others. 1996. The NCEP/NCAR 40-Year Reanalysis Project. *Bull. Am. Met. Soc.* **77**: 437–471. doi:10.1175/1520-0477(1996)077<0437:tnyrp>2.0.co;2
- Kenitz, K., R. G. Williams, J. Sharples, Ö. Selsil, and V. N. Biktashev. 2013. The paradox of the plankton: Species competition and nutrient feedback sustain phytoplankton diversity. *Mar. Ecol. Prog. Ser.* **490**: 107–119. doi:10.3354/meps10452
- Kjørboe, T., and A. G. Hirst. 2008. Optimal development time in pelagic copepods. *Mar. Ecol. Prog. Ser.* **367**: 15–22. doi:10.3354/meps07572
- Kraus, E. B. 1988. Merits and defects of different approaches to mixed layer modeling, p. 37–50. *In* J. C. J. Nihoul and B. M. Jamart [eds.], Small scale turbulence and mixing in the ocean. Elsevier.
- Lessard, E. J., and M. C. Murrell. 1998. Microzooplankton herbivory and phytoplankton growth in the northwestern Sargasso Sea. *Aquat. Microb. Ecol.* **16**: 173–188. doi:10.3354/ame016173
- Leterme, S. C., M. Edwards, L. Seuront, M. J. Attrill, P. C. Reid, and A. W. G. John. 2005. Decadal basin-scale changes in diatom, dinoflagellates, and phytoplankton color across the North Atlantic. *Limnol. Oceanogr.* **50**: 1244–1253. doi:10.4319/lo.2005.50.4.1244
- Lomas, M. W., and others. 2010. Increased ocean carbon export in the Sargasso Sea linked to climate variability is countered by its enhanced mesopelagic attenuation. *Biogeosciences* **7**: 57–70. doi:10.5194/bg-7-57-2010
- Lozier, M. S., A. C. Dave, J. B. Palter, L. M. Gerber, and R. T. Barber. 2011. On the relationship between stratification

- and primary productivity in the North Atlantic. *Geophys. Res. Lett.* **38**: L18609. doi:[10.1029/2011GL049414](https://doi.org/10.1029/2011GL049414)
- Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Ocean. Acta* **1**: 493–509.
- Marshall, J., and others. 2001. North Atlantic climate variability: Phenomena, impacts and mechanisms. *Int. J. Clim.* **21**: 1863–1898. doi:[10.1002/joc.693](https://doi.org/10.1002/joc.693)
- Neuer, S., and others. 2002. Differences in the biological carbon pump at three subtropical ocean sites. *Geophys. Res. Lett.* **29**. doi:[10.1029/2002GL015393](https://doi.org/10.1029/2002GL015393)
- Niiler, P. P., and E. B. Kraus. 1977. One-dimensional models of the upper ocean, p. 143–172. *In* E. B. Kraus [ed.], *Modeling and prediction of the upper layers of the ocean*. Pergamon.
- Oschlies, A. 2001. NAO-induced long-term changes in nutrient supply to the surface waters of the North Atlantic. *Geophys. Res. Lett.* **28**: 1751–1754. doi:[10.1029/2000gl012328](https://doi.org/10.1029/2000gl012328)
- Palter, J. B., and M. S. Lozier. 2008. On the source of Gulf Stream nutrients. *J. Geophys. Res.* **113**: C06018. doi:[10.1029/2007jc004611](https://doi.org/10.1029/2007jc004611)
- Raitsos, D. E., P. C. Reid, S. J. Lavender, M. Edwards, and A. J. Richardson. 2005. Extending the SeaWiFS chlorophyll data set back 50 years in the northeast Atlantic. *Geophys. Res. Lett.* **32**: L06603. doi:[10.1029/2005gl022484](https://doi.org/10.1029/2005gl022484)
- Richardson, A. J., and others. 2006. Using continuous plankton recorder data. *Prog. Oceanogr.* **68**: 27–74. doi:[10.1016/j.pocean.2005.09.011](https://doi.org/10.1016/j.pocean.2005.09.011)
- Rose, J. M., and D. A. Caron. 2007. Does low temperature constrain the growth rates of heterotrophic protists? Evidence and implications for algal blooms in cold waters. *Limnol. Oceanogr.* **52**: 886–895. doi:[10.4319/lo.2007.52.2.0886](https://doi.org/10.4319/lo.2007.52.2.0886)
- Rykaczewski, R. R., and J. P. Dunne. 2010. Enhanced nutrient supply to the California Current Ecosystem with global warming and increased stratification in an earth system model. *Geophys. Res. Lett.* **37**: L21606. doi:[10.1029/2010GL045019](https://doi.org/10.1029/2010GL045019)
- Rynearson, T. A., and others. 2013. Major contribution of diatom resting spores to vertical flux in the sub-polar North Atlantic. *Deep Sea Res. I* **82**: 60–71. doi:[10.1016/j.dsr.2013.07.013](https://doi.org/10.1016/j.dsr.2013.07.013)
- Sarthou, G., K. R. Timmermans, S. Blain, and P. Tréguer. 2005. Growth physiology and fate of diatoms in the ocean: A review. *J. Sea Res.* **53**: 25–42. doi:[10.1016/j.seares.2004.01.007](https://doi.org/10.1016/j.seares.2004.01.007)
- Schartau, M., M. R. Landry, and R. A. Armstrong. 2010. Density estimation of plankton size spectra: A reanalysis of IronEx II data. *J. Plankton Res.* **32**: 1167–1184. doi:[10.1093/plankt/fbq072](https://doi.org/10.1093/plankt/fbq072)
- Smayda, T. J. 1997. Harmful algal blooms: Their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnol. Oceanogr.* **42**: 1137–1153. doi:[10.4319/lo.1997.42.5\\_part\\_2.1137](https://doi.org/10.4319/lo.1997.42.5_part_2.1137)
- Smith, D., and J. Murphy. 2007. An objective ocean temperature and salinity analysis using covariances from a global climate model. *J. Geophys. Res.* **112**: C02022. doi:[10.1029/2005JC003172](https://doi.org/10.1029/2005JC003172)
- Steinberg, D. K., C. A. Carlson, N. R. Bates, R. J. Johnson, A. Michaels, and A. H. Knap. 2001. Overview of the US JGOFS Bermuda Atlantic Time-series Study (BATS): A decade-scale look at ocean biology and biogeochemistry. *Deep Sea Res. II* **48**: 1405–1447. doi:[10.1016/S0967-0645\(00\)00148-X](https://doi.org/10.1016/S0967-0645(00)00148-X)
- Sverdrup, H. 1953. On conditions of the vernal blooming of phytoplankton. *ICES J. Mar. Sci.* **18**: 287–295. doi:[10.1093/icesjms/18.3.287](https://doi.org/10.1093/icesjms/18.3.287)
- Tarran, G. A., J. L. Heywood, and M. V. Zubkov. 2006. Latitudinal changes in the standing stocks of nano- and picoeukaryotic phytoplankton in the Atlantic Ocean. *Deep Sea Res. II* **53**: 1516–1529. doi:[10.1016/j.dsr2.2006.05.004](https://doi.org/10.1016/j.dsr2.2006.05.004)
- Taylor, A. H., D. S. Harbour, R. P. Harris, P. H. Burkill, and E. S. Edwards. 1993. Seasonal succession in the pelagic ecosystem of the North Atlantic and the utilization of nitrogen. *J. Plankton Res.* **15**: 875–891. doi:[10.1093/plankt/15.8.875](https://doi.org/10.1093/plankt/15.8.875)
- Taylor, G. T., and others. 2012. Ecosystem responses in the southern Caribbean Sea to global climate change. *Proc. Natl. Acad. Sci. USA* **109**: 19315–19320. doi:[10.1073/pnas.1207514109](https://doi.org/10.1073/pnas.1207514109)
- Taylor, J. R., and R. Ferrari. 2011. Shutdown of turbulent convection as a new criterion for the onset of spring phytoplankton blooms. *Limnol. Oceanogr.* **56**: 2293–2307. doi:[10.4319/lo.2011.56.6.2293](https://doi.org/10.4319/lo.2011.56.6.2293)
- Theil, H. 1950. A rank-invariant method of linear and polynomial regression analysis. *Proc. R. Neth. Acad. Sci.* **LIII**: 1397–1412.
- Ward, B. A., S. Dutkiewicz, A. D. Barton, and M. J. Follows. 2011. Biophysical aspects of resource acquisition and competition in algal mixotrophs. *Am. Nat.* **178**: 98–112. doi:[10.1086/660284](https://doi.org/10.1086/660284)
- Ward, B. A., S. Dutkiewicz, O. Jahn, and M. J. Follows. 2012. A size-structured food-web model for the global ocean. *Limnol. Oceanogr.* **57**: 1877–1891. doi:[10.4319/lo.2012.57.6.1877](https://doi.org/10.4319/lo.2012.57.6.1877)
- Williams, R. G., and M. J. Follows. 1998. The Ekman transfer of nutrients and maintenance of new production over the North Atlantic. *Deep Sea Res. I* **45**: 461–489. doi:[10.1016/S0967-0637\(97\)00094-0](https://doi.org/10.1016/S0967-0637(97)00094-0)
- Williams, R. G., A. J. McClaren, and M. J. Follows. 2000. Estimating the convective supply of nitrate and implied variability in export production over the North Atlantic. *Global Biogeochem. Cycles* **14**: 1299–1313. doi:[10.1029/2000GB001260](https://doi.org/10.1029/2000GB001260)
- Williams, R. G., V. Roussinov, and M. J. Follows. 2006. Nutrient streams and their induction into the mixed layer. *Global Biogeochem. Cycles* **20**: GB1016. doi:[10.1029/2005gb002586](https://doi.org/10.1029/2005gb002586)

Williams, R. G., and others. 2011. Nutrient streams in the North Atlantic: Advective pathways of inorganic and dissolved organic nutrients. *Global Biogeochem. Cycles* **25**: GB4008. doi:[10.1029/2010gb003853](https://doi.org/10.1029/2010gb003853)

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