



Shutdown of convection triggers increase of surface chlorophyll

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ABSTRACT

The long-standing explanation of the triggering cause of the surface increase of phytoplankton visible in spring satellite images argues that phytoplankton biomass accumulation begins once the mixed layer depths become shallower than a 'critical depth'. However, a series of recent studies have found evidence for phytoplankton increase in deep mixed layers, and several hypotheses have been proposed to explain this early increase. In this manuscript it is suggested that the surface concentration of phytoplankton increases rapidly in a 'surface bloom' when atmospheric cooling of the ocean turns into an atmospheric heating at the end of winter. The hypothesis is supported by analysis of satellite observations of chlorophyll and of heat fluxes from atmospheric reanalysis from the North Atlantic.

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1. Introduction

Satellite images show that the subpolar North Atlantic turns green every spring in response to an explosive surface increase of freely drifting microscopic algae, called phytoplankton. The primary production during this 'spring bloom' is of considerable interest to oceanographers, because it is the first link of the area's food chain and contributes significantly to global photosynthesis and ocean carbon uptake (Takahashi et al., 2009). It is generally believed that the increase in surface chlorophyll coincides with the onset of the spring bloom, when growth from photosynthesis first outweighs losses, driving primary production (e.g. Siegel et al., 2002). However Behrenfeld (2010) cautioned that net biomass increase may start earlier in the season without a signature in the surface phytoplankton concentration, if ocean turbulence rapidly mixes the new phytoplankton down into the deep ocean. We will therefore refer to changes in ocean color as the *surface spring bloom* to distinguish them from the proper spring bloom which represents the net increase of phytoplankton biomass throughout the entire water column. In this paper we test the hypothesis that surface spring blooms are associated with a change in air–sea heat fluxes and begin when winter cooling of the ocean switches to spring warming, thereby reducing vertical mixing of phytoplankton.

The prevailing view is that the surface greening coincides with the spring bloom (e.g. Follows and Dutkiewicz, 2002; Siegel et al., 2002) and its onset can be explained with the "critical depth" hypothesis (Gran and Braarud, 1935; Riley, 1946; Sverdrup, 1953). Like terrestrial

plants, phytoplankton need sunlight and nutrients (carbon, phosphorus, nitrogen, silica, iron, etc.) to grow. This constrains phytoplankton production, because the euphotic layer, the surface layer of the ocean with sufficient light for photosynthesis, is often stripped of nutrients by previous phytoplankton growth. According to the critical depth hypothesis, winter cooling and winds churn the upper ocean and bring nutrient-rich waters to the surface, but this benefit is outweighed by the downward mixing of phytoplankton below the euphotic layer. As spring approaches, cooling and winds wane, resulting in a shallowing of the mixing layer. Meanwhile, the day length and solar insolation levels increase. The active mixing layer reaches a "critical depth" when phytoplankton experience sufficient light levels that their growth balances the losses due to consumption by zooplankton, respiration, sinking, etc. When the mixing layer shoals above this critical depth, the phytoplankton population starts growing, creating a bloom. If the phytoplankton concentration increases uniformly in a shallowing mixing layer, the surface concentration will necessarily increase. Therefore, the spring bloom and surface spring bloom coincide under this hypothesis. A deficiency of the hypothesis is that it cannot be rigorously tested against observations because of the difficulty of measuring the depth of the mixing layer and the biological parameters required to compute the critical depth (Siegel et al., 2002).

Since the early 1950s (Sverdrup, 1953), the depth of the mixed layer, where density is nearly homogeneous, has been used as a proxy for the active mixing layer—measurements of the mixing layer require sophisticated turbulence probes, while the mixed layer can be more easily estimated by taking routine vertical profiles of temperature and salinity to compute density. However, the mixed layer proxy is imperfect. It

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does indeed track a layer that has been mixed, but the mixing may not be active anymore. The mixed layer takes days to weeks to develop a near-surface vertical density gradient (restratification) once vertical mixing subsides as a result of a drop in air–sea surface fluxes or through instabilities of surface currents that cause warm water to slide over cold water (Boccaletti et al., 2007; Taylor and Ferrari, 2011a). On the other hand, the surface phytoplankton concentration can increase as soon as vertical mixing subsides. Several authors have reported the occurrence of phytoplankton blooms in mixed layers deeper than the critical depth from shipboard measurements of temperature, salinity, and phytoplankton concentration (Boss and Behrenfeld, 2010; Dale and Heimdal, 1999; Townsend et al., 1992).

Alternatively we argue that phytoplankton increase at the ocean surface, as seen from satellites, starts when vertical mixing subsides. In the subpolar North Atlantic, wintertime vertical mixing is primarily driven by surface cooling through convection, particularly away from coastal regions where winds are also important. Hence, we put forward the hypothesis that the surface bloom begins when ocean cooling subsides at the end of winter and turns into surface heating, resulting in a shutdown of vertical convection and a reduction in mixing. We refer to this scenario as the convection shutdown hypothesis. Waniek (2003) and Taylor and Ferrari (2011b) have confirmed that the timing of the shift from cooling to heating in air–sea heat fluxes is a very robust indicator of surface blooms in numerical and mathematical models of the North Atlantic bloom. There have also been observational reports of blooms starting when the heat flux changed sign (Koeve et al., 2002). The goal of this paper is to test the convection shutdown hypothesis using 8 years of satellite measurements over the whole subpolar North Atlantic.

The paper is organized as follows. We introduce the data sets used in the analysis in Section 2. The data are used to test the convection shutdown hypothesis in Section 3. Section 4 confirms that freshwater fluxes and winds are of secondary importance in driving deep mixing in the subpolar North Atlantic and can therefore be ignored, at leading order, in the analysis. Section 5 compares and contrasts the convective shutdown hypothesis with the critical depth hypothesis. Finally we discuss the implications of our results for understanding ocean productivity.

2. Data and methods

To test the convection shutdown hypothesis, we analyzed timeseries of the net air–sea heat flux and chlorophyll concentration from the North Atlantic for the years 2003–2010. The heat flux and chlorophyll concentration are readily available on a global scale from remote-sensing products, unlike the mixed layer depth and the biological parameters—phytoplankton cellular growth, respiration and consumption rates—which are needed to directly test the critical depth hypothesis and can only be obtained from fragmentary and difficult shipboard measurements.

Chlorophyll concentrations were inferred from measurements of ocean color from the NASA MODIS-Aqua satellite using the algorithm OC3M described in Feldman et al. (1989) and O'Reilly et al. (2000)—the algorithm returns chlorophyll-*a*, a specific form of chlorophyll used in oxygenic photosynthesis. Although chlorophyll concentration depends on other factors in addition to phytoplankton abundance, it has been used successfully to study phytoplankton biomass especially at the end of winter when concentrations are low (Henson et al., 2009). The data, downloaded from <http://oceandata.sci.gsfc.nasa.gov/MODISA/Binned>, was already averaged over 8-day intervals and was further processed by averaging in 1°×1° degree latitude, longitude bins. The analysis was carried out using data for the period from 2003 to 2010. The rate of chlorophyll increase in each bin was computed as the 8-day rate of change in surface chlorophyll divided by the 8-day average chlorophyll concentration, i.e. $Chl^{-1} \times dChl/dt$ where *Chl* is the averaged chlorophyll concentration. Years with less than 50% data

coverage between January and June, due to cloud coverage in a particular bin, were not included in the analysis to guarantee that there were sufficient data points to identify the onset of the surface bloom.

The net air–sea heat flux was obtained from the daily ECMWF ERA-Interim reanalysis. The air–sea heat flux from this product was estimated based on a bulk algorithm with atmospheric conditions from a 4D-var data assimilation model with sea-surface temperatures from the OSTIA analysis (Dee et al., 2011; Donlon et al., 2007). In order to facilitate comparison with the chlorophyll concentration, and to reduce scatter in the data, the heat flux timeseries were averaged over 8 days in the same 1°×1° bins as the MODIS-Aqua data. The 8-day average is further supported by the analysis of Taylor and Ferrari (2011b), who find that the growth rate of phytoplankton populations responds only to heat flux changes on timescales longer than a few days; transient reversals from cooling to heating associated with the daily cycle and high frequency storms are too short to result in an appreciable population growth.

The ERA-Interim surface fluxes were used, because they capture the seasonal and interannual variability, as well as the spatial structure, of the net heat flux over the North Atlantic (Balmaseda et al., 2010). Balmaseda et al. (2008) reported that the ERA-Interim surface fluxes, when used to initialize the ocean component of the ECMWF seasonal forecasting system, had a consistent positive impact on the skill of the seasonal forecast. However no uncertainty estimates were provided for the ERA-Interim surface fluxes. Therefore we repeated the key calculation leading to Fig. 3, but using the surface heat flux from a different reanalysis by the National Centers for Environmental Prediction Global Ocean Data Assimilation System (Kanamitsu et al., 2002) downloaded from <http://iridl.ldeo.columbia.edu>. The results were essentially identical to the ones presented in the next section building confidence in the surface flux products.

3. The convection shutdown hypothesis

A map of the whole 45–61°N and 10–50°W analysis region in the North Atlantic is indicated by a black box in Fig. 1. Coastal areas, where cooling is not the main driver of vertical mixing, were omitted from the analysis by excluding regions where the water depth is less than 1000 m. The sudden increases in phytoplankton biomass associated with the surface spring bloom in the subpolar waters are highlighted by the large seasonal variations in chlorophyll concentrations in this region (Fig. 1). As an illustration, the timeseries of chlorophyll concentration (black lines and circles in Fig. 2) and the 8-day averaged heat flux (red curve in Fig. 2) are shown for three arbitrary 1°×1° areas centered at 25.5°W, 57.5°N, at 37.5°W, 53.5°N and at 31.5°W, 51.5°N respectively (indicated by black stars in Fig. 1). The timeseries are shown for an arbitrary subset of 3 years 2004–2006. The seasonal cycle in heat flux is visible in the large negative values (cooling) in winter, favoring convective mixing, and positive values (heating) in summer. The surface spring bloom is visible as an abrupt increase in chlorophyll concentration each spring and it coincides closely with the timing of the first shift from cooling to heating in most years when there is chlorophyll data.

To test the convection shutdown hypothesis quantitatively, it is useful to define a “convection shutdown time”, $t_Q = 0$, corresponding to the end of wintertime convection. Although high frequency variability was removed from the heat flux timeseries, there were still short intervals of less than 8 days when the heat flux became positive. Based on the modeling study of Taylor and Ferrari (2011b), we expected the phytoplankton concentration to increase very quickly (a few days) after the end of convective forcing. However, we did not expect to detect responses faster than 8 days, since the chlorophyll concentration is averaged over 8-day intervals. We therefore defined the convection shutdown time as the first time in each calendar year when the heat flux remained positive for more than 8 days. Comparing the convection shutdown time (dashed gray vertical lines in Fig. 2) with the chlorophyll

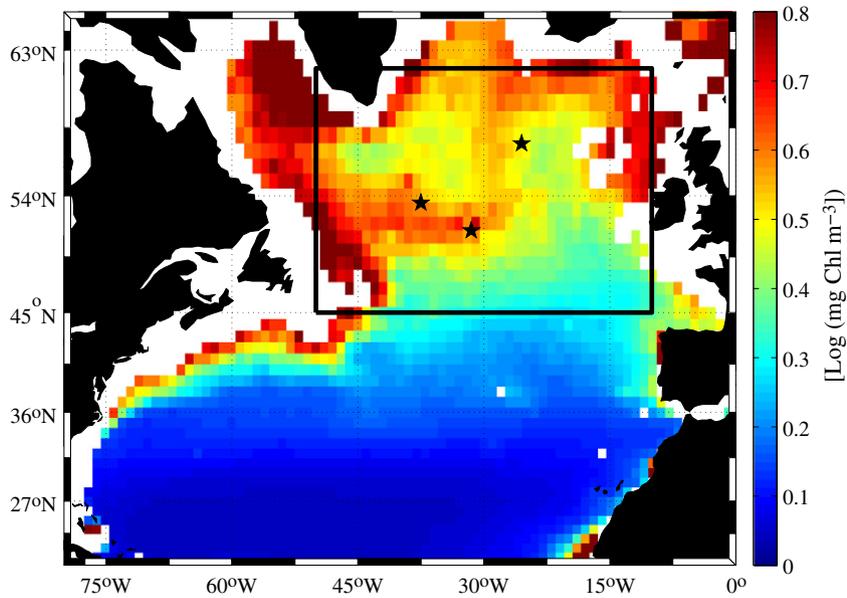


Fig. 1. Map of the standard deviation in chlorophyll concentration from MODIS Aqua for the 2003–2010 time period. For each $1^\circ \times 1^\circ$ area, the standard deviation is computed as the deviation from the 8-year averaged chlorophyll concentration to highlight regions with a strong seasonal signal. The black box indicates the region used for this study. A 1000 m bathymetry white mask obtained from ftp://topex.ucsd.edu/pub/global_topo_2min has been applied to eliminate coastal regions. The black asterisks represent the locations of the timeseries in Fig. 2.

concentration, it is apparent that large increases in chlorophyll concentration often closely coincide with the convection shutdown time.

The analysis is now extended to the whole $45\text{--}61^\circ\text{N}$ and $10\text{--}50^\circ\text{W}$ analysis region to provide a more systematic and quantitative test of the convection shutdown hypothesis. We calculated the chlorophyll increase rates at $t_Q = 0$ for the whole region shown in Fig. 1 and for the 8-year period between 2003 and 2010. The surface chlorophyll increase rate is used as a proxy for the net increase of surface phytoplankton and will be referred to as net surface increase rate. If the convection shutdown hypothesis has predictive skill, we should see large net surface increase rates near $t_Q = 0$. To test this hypothesis, for each of the 8 years and each of the $640\ 1^\circ \times 1^\circ$ areas within the analysis domain, we averaged the net surface increase rates in successive 8-

day intervals, centered at $t_Q = 0$. The net surface increase rate averaged over all years and locations (5120 points) as a function of the convection shutdown time is shown as a thick solid line in Fig. 3, along with the one standard deviation in gray. The average net surface increase rate at $t_Q = 0$ is $\approx 0.05\ \text{day}^{-1}$, much larger than at any other time. This value is about one standard deviation above zero, indicating that approximately 85% of the convection shutdown events are associated with positive net surface increase rates. The net surface increase rate at $t_Q = 0$ is much higher than the net surface increase rates in the 8-day intervals immediately before and after convection shutdown. A two-sample Kolmogorov–Smirnov test (Chakravarti et al., 1967) confirms that the net surface increase rate distributions at $t_Q = 0$ are different from any time before and after at the 95% confidence level.

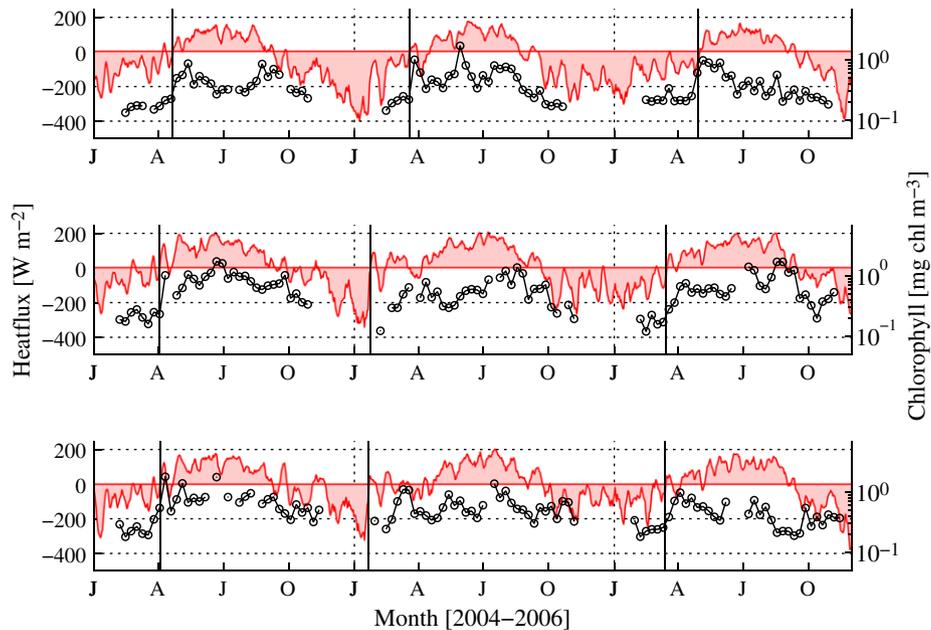


Fig. 2. Timeseries of chlorophyll-a from MODIS Aqua (black dots and lines), ERA-interim air-sea heat flux (red lines and patches) at the three locations indicated by black stars in Fig. 1 for 3 years 2004–2006. The three $1^\circ \times 1^\circ$ areas are centered at $25.5^\circ\text{W}, 57.5^\circ\text{N}$ (upper panel), at $37.5^\circ\text{W}, 53.5^\circ\text{N}$ (middle panel) and $31.5^\circ\text{W}, 51.5^\circ\text{N}$ (lower panel). High rates of chlorophyll-a increase at the surface are associated with $t_Q = 0$, the time when the heat flux changes sign (dash-dotted line).

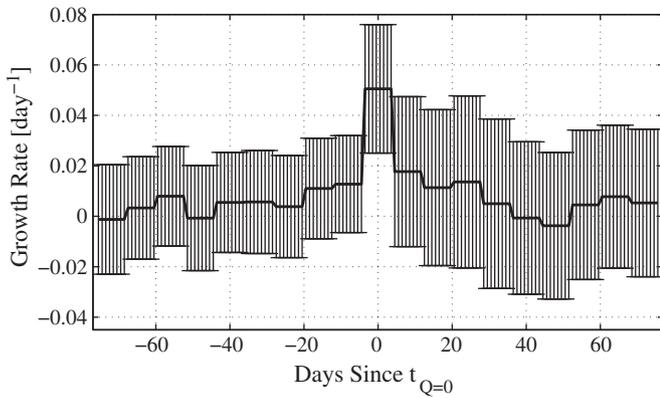


Fig. 3. Net increase rate of chlorophyll from MODIS Aqua 2003–2010. The net surface increase rate is computed as the rate of change in the mean chlorophyll in 8-day intervals divided by the 8-day average chlorophyll concentration. Net increase rates are computed for each $1^\circ \times 1^\circ$ area in the black boxed region shown in Fig. 1 for the 8-year period. The net surface increase rates, averaged over all areas and each year as a function of the convection shutdown time, are shown as a thick solid line and the vertical bars indicate the one standard deviation about the average. The average net surface increase rate at $t_Q = 0$ is much larger than at any time before or after.

These results imply that the convection shutdown hypothesis is a robust indicator of the timing of the surface spring bloom detected via remote sensing in the region considered.

As a further test of the convection shutdown hypothesis, we extended the analysis to different latitudes. The convection shutdown hypothesis is supposed to hold only in the subpolar gyres, where winter growth is limited by light availability. Fig. 4 shows the chlorophyll increase rates as a function of $t_Q = 0$ for the same 8-year period and longitude band used in Fig. 3, but separately for each one latitude degree. The net surface increase rate peaks at $t_Q = 0$ only for latitudes between approximately 35°N and 60°N , i.e. in the subpolar latitude band where light limits winter phytoplankton growth. In the subtropical gyre, south of 35°N , growth is limited by the lack of nutrients at the surface. At these latitudes, vertical mixing promotes growth by supplying nutrients to the euphotic layer. The cessation of vertical mixing shuts down nutrient supply and suppresses growth. Consistently Fig. 4 shows that, south of 35°N , growth rates tend to be negative after $t_Q = 0$. It is less clear why the convection shutdown hypothesis fails north of 60°N . One possibility is that the data are too noisy due to extensive cloud coverage. It is also possible that at these high latitudes the day length is the dominant control on phytoplankton growth, because days become so short in winter. The seasonal increase of day length may therefore be more important for the surface bloom onset than any decrease in mixing.

It is worth remarking that an advantage of our analysis is that it avoided the cumbersome issue of defining the surface bloom onset

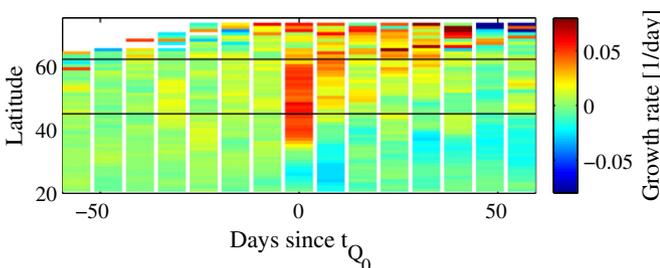


Fig. 4. Net increase rate of chlorophyll from MODIS Aqua 2003–2010, computed as in Fig. 3, but separately for each 1° latitude band between 20°N and 70°N . The analysis at each latitude is applied to the region between 10°W and 50°W . The net surface increase rates averaged along each longitude strip and each year as a function of the convection shutdown time, are shown in color. The average net surface increase rate at $t_Q = 0$ is much larger than at any time before or after between approximately 35°N and 60°N .

time. We tested whether the growth rate becomes positive when the heat flux changes sign at $t_Q = 0$, instead of asking whether the heat flux becomes positive when the surface bloom starts. Finding a robust definition of the bloom onset time remains an issue of debate. Some studies have argued that the surface bloom begins when the chlorophyll concentration exceeds some threshold, some preferred to pick the time when the chlorophyll growth rate first becomes positive, and others chose the time when the chlorophyll concentration becomes as large as some fraction of its maximum value (see Brody et al., 2013, for a comparison of the different definitions). Unfortunately the conclusions typically depend on the particular definition chosen leaving ample room for debate.

4. The role of evaporation, precipitation and winds

Turbulent mixing in the surface open ocean is typically driven by one of three forcings at the air–sea interface: cooling, evaporation, or winds. The hypothesis pursued in this work is that the North Atlantic surface bloom starts when turbulent mixing in the upper ocean weakens at the end of winter. The bloom onset can therefore be predicted, if a criterion is derived to identify the time when turbulent mixing wanes. In the convection shutdown hypothesis we implicitly assumed that, during winter, in the North Atlantic region shown in Fig. 1, cooling is the dominant driver of turbulent mixing and hence turbulent mixing stops when the air–sea heat flux switches from cooling to warming.

The relative importance of cooling and evaporation can be easily assessed. Both act to increase the density of surface waters thereby causing convection, i.e. turbulent sinking of waters. Using the ECMWF ERA-interim reanalysis we computed the density increase associated with cooling/warming versus evaporation/precipitation. We found that cooling is the dominant driver of convection in the subpolar North Atlantic and we therefore ignored the effect of evaporation and precipitation.

The relative importance of cooling and winds is generally harder to assess, but the problem is somewhat simpler in the region under consideration. In the subpolar North Atlantic, mixed layers are nearly always deeper than 200 m in winter (Kara et al., 2003), when the surface bloom begins. Mixed layers deeper than 200 m are typically generated by cooling–winds are less efficient at deep mixing than cooling. For example, Lozovatsky et al. (2005), using observations from the North Atlantic, found that wind-driven turbulence penetrates to a depth of $h \approx 0.44f^{-1} \sqrt{\tau/\rho_0}$ where f is the Coriolis frequency, τ is the wind stress, and ρ_0 is the surface density of seawater. To estimate how deep wind-driven mixing penetrates in the region under study, QuikSCAT winds, downloaded from http://podaac.jpl.nasa.gov/dataset/QSCAT_LEVEL_3, were averaged over $1^\circ \times 1^\circ$ latitude–longitude bins and over time using a weekly running average (JPL, 2001). The winds were averaged weekly to eliminate rapid daily fluctuations that are too fast for phytoplankton populations to respond. Fig. 5 shows the probability density function of wind stress for the 2003–2009 period (QuikSCAT stopped working in 2009.) Even for the strongest winds, vertical mixing penetrates at most down to ~ 100 m, much less than the typical winter mixed layer depth in the region shown in Fig. 1. D'Asaro (2014) points out that these scalings remain valid, even when considering the coupling between winds and surface gravity waves that leads to Langmuir turbulence. Hence cooling is expected to dominate deep mixing in winter.

A second issue arises in considering the role of winds. We argued that cooling is the dominant driver of turbulent mixing in winter, but winds may well become important after time $t_Q = 0$, when cooling shuts off, because winds can maintain a vigorous turbulent mixing despite the end of surface cooling. If the depth of the wind-driven mixing is deeper than the critical depth, then the bloom onset can be delayed. To test the likelihood of such a scenario, we computed the probability density function of wind stress at $t_Q = 0$ (dashed line in Fig. 5.) The probability density function is very similar to that for the whole data set and shows that, according to the scaling in Lozovatsky et al. (2005), only 10%

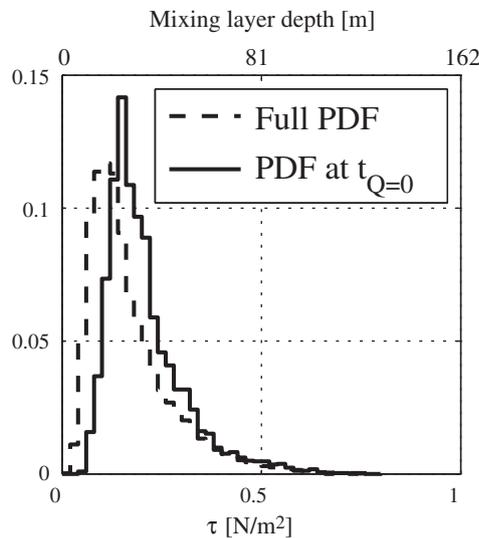


Fig. 5. Probability density function of daily wind stress for the region shown in Fig. 1 for the period 2003–2009 (continuous line) and for the times when the heat flux first changes sign, $t_{Q=0}$ (dashed line). The bottom horizontal axis shows the wind stress values, while the top horizontal axis shows the corresponding mixing layer depth calculated with the empirical formula in Lozovatsky et al. (2005). The probability density function is normalized so that their integral over all wind stresses is one.

of the time does wind-driven mixing penetrate below ~ 100 m, a typical value of critical depth for biological parameters representative of the North Atlantic (Henson et al., 2006). We conclude that winds do not typically arrest the development of the surface spring bloom in the North Atlantic. A similar conclusion was reached by Follows and Dutkiewicz (2002), who ran mixed layer models forced by observed winds and surface fluxes and concluded that winds played a minor role in driving mixing during the onset of the North Atlantic surface spring bloom. Whether similar conclusions hold for oceans other than the North Atlantic is instead unclear. For example, Chiswell (2011) detected a correlation between the weakening of winds and bloom onset in the Southern Ocean.

Last, but not least, it should be noted that our analysis applies only to surface blooms in the open ocean. It is not expected to apply in coastal regions where riverine flux of nutrients and turbulent interactions with the bottom boundary layer must also be considered. The relative importance of surface cooling in coastal areas deserves further study.

5. A comparison of the critical depth and the convection shutdown hypotheses

We argued that the critical depth hypothesis is very difficult to test experimentally. The main challenge is to measure accurately the critical depth which depends on poorly known biological parameters. Here we provide a quick primer of the critical depth hypothesis to discuss how it differs from the convection shutdown hypothesis and to test the two with data.

The critical depth hypothesis that the onset of the spring bloom depends on the mixed layer depth dates back to the seminal contributions of Gran and Braarud (1935), Riley (1946), and Sverdrup (1953). The argument goes that spring phytoplankton blooms are triggered when the mixed layer depth becomes shallower than the critical depth. Sverdrup defines the critical depth as “a surface mixing depth at which phytoplankton community growth is precisely matched by losses of phytoplankton biomass within this depth interval.” An approximate expression for the critical depth, H_c , is:

$$H_c \sim h_l \frac{\mu_0}{m}, \quad (1)$$

where μ_0 is the phytoplankton population growth rate at the surface in the absence of any biomass loss, h_l is the light extinction coefficient, and m is the biomass loss due to respiration, zooplankton grazing, sinking, viral lysis, and mortality (assumed to be constant with depth). According to the critical depth hypothesis, during winter the mixed layer is deeper than H_c , and primary production is limited by light exposure. In spring, when the mixed layer becomes shallower than H_c , light availability no longer prevents growth, and a bloom will develop as long as there are sufficient nutrients.

The critical depth hypothesis provides a very useful framework to study spring blooms, but it is extremely difficult to test quantitatively. The mixed layer depth can be estimated from vertical profiles of density which require in situ measurements. The critical depth depends on three parameters. The light extinction can be estimated in situ. The phytoplankton population growth rate at the surface μ_0 can be estimated for individual species in laboratory cultures, but a careful census of all species is needed to infer the overall community growth rate at a specific location. The loss rate is the sum of cellular respiration, zooplankton grazing, sinking, viral lysis, and mortality and it cannot be quantified accurately. The implication is that the critical depth model can never be tested in the Popperian sense of “attempting to falsify” it.

While the critical depth hypothesis cannot be falsified in general, because it is impossible to accurately measure the biological parameters that enter in the definition of the critical depth, we falsified one of its predictions: the onset of the spring bloom should coincide with a reduction in the mixed layer depth. Consider the $1^\circ \times 1^\circ$ area centered at 25.5°W , 57.5°N marked with the star further to the east in Fig. 1. The mixed layer depth in this region was determined by using daily density profiles from the Ocean Comprehensible Atlas (OCCA) for the global ocean for the years 2004–2006 (Forget, 2010). The OCCA state estimate combines a general circulation model, the MITgcm (Marshall et al., 1997a,b), with a variety of observations (including Argo float profiles, sea surface temperature, and altimetric data) in order to produce a quantitative depiction of the time-evolving global ocean state. We verified that the daily density profiles were consistent with co-located Argo float profiles.

Fig. 6 is equivalent to the upper panel of Fig. 2, except for the addition of the mixed layer depth in blue. The mixed layer is computed as the depth at which the density change from its surface value is $\Delta\rho = 0.03 \text{ kg m}^{-3}$. This is approximately the seawater density change resulting from a 0.2°C temperature change for the region under study. This definition has been recommended by Kara et al. (2000, 2003), who show that it tracks the depth of the layer where density is nearly homogeneous in daily profiles. Many other criteria are used in the literature and all have their limitations. Indeed, one point of our work is that any criterion for the onset of a spring bloom that relies on mixed layer depth will be plagued by the uncertainty of its computation.

Fig. 6 shows that only in 2005 the increase in chlorophyll concentration coincided with a decrease in mixed layer depth. In 2004 and 2006, the increase in chlorophyll concentration significantly preceded the decrease in mixed layer depth. In both years the mixed layer depth was still near its seasonal maximum at bloom onset. Since the critical depth hypothesis predicts a decrease in mixed layer depth preceding the bloom, it is unlikely to explain either of these blooms. The increase in chlorophyll concentration, instead, coincides closely with the timing of the first shift from cooling to heating.

A falsification of the critical depth hypothesis is not possible for the two other areas shown in the middle and lower panels in Fig. 2. In these region the winter mixed layers are not much deeper than a typical critical depth of order 100–200 m. So the uncertainties in both the definition of mixed layer depth and the calculation of the critical depth do not allow a stringent test of the critical depth hypothesis.

An additional complication in testing the critical depth hypothesis is that one should compare the critical depth with the depth of the active mixing layer. Direct measures of turbulent mixing are very hard to obtain and as a result the mixed layer depth is often used as a proxy

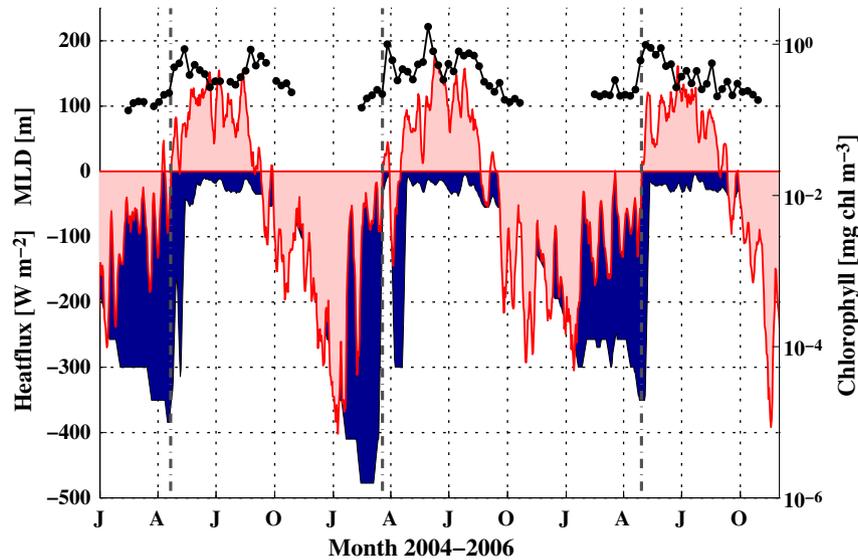


Fig. 6. Timeseries of chlorophyll-a from MODIS Aqua (black dots), ERA-interim air–sea heat flux (red), and mixed layer depth (blue) at the location of the black star furthest east in Fig. 1 for 3 years 2004–2006. High net surface increase rates are associated with $t_{Q=0}$, the time when the heat flux changes sign (dash-dotted line). The daily mixed layer depth timeseries is averaged over 8 days to be consistent with the other data. In 2 out of 3 years, the mixed layer depth is still very deep when chlorophyll starts growing at the end of winter.

for the mixing layer depth. However, the two can be quite different as explained in the introduction. The convective shutdown hypothesis overcomes this problem by using the air–sea heat flux to estimate when the mixing layer shoals at the end of winter. As discussed above, if wind-driven mixing does not penetrate below the critical depth, a shoaling of the mixing layer after the shutdown of convection can trigger a surface phytoplankton bloom. Since the convection shutdown hypothesis relies on a shoaling of the mixing layer, but not necessarily the mixed layer, it can be viewed as a generalization of the critical depth hypothesis.

6. Discussion and conclusions

Analysis of satellite observations of chlorophyll from the subpolar North Atlantic, between 35°N and 60°N, suggests that surface blooms develop when the atmospheric cooling of the ocean turns into an atmospheric heating at the end of winter. This supports our claim that the convection shutdown hypothesis is a robust indicator of the surface bloom onset, independent of biological parameters. However our analysis does not rule out other possible surface bloom triggers. Lévy et al. (1999), Taylor and Ferrari (2011a) and Mahadevan et al. (2012) proposed that in regions with large horizontal density gradients (fronts), restratification and a subsequent reduction in vertical mixing can trigger surface spring blooms before the end of wintertime convection. Evans and Parslow (1985) suggested that a decrease of grazing in winter can also trigger surface blooms when the mixed layers are deep. Later surface blooms are also possible. Strong wind-driven mixing can keep the turbulent mixing layer deeper than the critical depth after the end of winter convection, but this is rarely observed (Follows and Dutkiewicz, 2002). In this paper we ignored the seasonal changes in insolation on phytoplankton growth, because in the analysis region the heat flux typically changes sign when insolation is sufficient to allow photosynthesis (Marshall and Orr, 1928). Poleward of 60°N, however, low insolation appears to become a more important limiting factor than turbulent mixing. But, this far north, cloud coverage at the time of bloom onset is too pervasive to draw robust conclusions from ocean color data.

The recent work of Brody et al. (2013) supports the inference that surface blooms can be triggered by processes other than convection shutdown. They analyzed surface chlorophyll data like the ones used in this paper and reported both examples of blooms that start when

convection shuts off and when convection is still active. Our Fig. 3 shows that surface phytoplankton increase rates are very high through the subpolar North Atlantic when convection stops, an indication that convection shutdown is a trigger of surface blooms. The evidence of surface blooms that start when convection is still active confirms that other mechanisms can also be at play, but their overall importance on a basin scale has not yet been quantified. This would seem to be a worthwhile focus for future studies.

A more fundamental question is how often the first winter onset of phytoplankton growth has an expression in surface chlorophyll. Starting with Sverdrup (1953), it has been assumed that the first growth of phytoplankton in the season is associated with an increase in surface chlorophyll concentrations. However Yoshie et al. (2003) and Behrenfeld (2010) recently argued that blooms can also be triggered by the deepening of the mixed layer in early winter. Such blooms have no expression in surface chlorophyll at the onset. The hypothesis is that mixed layer deepening dilutes plankton concentrations. The effect of dilution is more significant on the grazing rate, because it depends on both the concentrations of phytoplankton and grazers, whereas the photosynthesis depends only on phytoplankton concentrations. The bloom therefore starts because of a decrease in grazing rate, rather than an increase in photosynthesis, and the overall increase in vertically integrated biomass is associated with a decrease in surface concentrations. Boss and Behrenfeld (2010) reported an example of a bloom with no initial expression in surface chlorophyll from bio-optical measurements from a float. However, even in this example, the bloom developed a surface signature later in the season, when mixing subsided. The difference from the traditional scenario is that there was a lag between the initial increase in vertically integrated biomass and the later increase of surface biomass. This suggests that the convection shutdown hypothesis predicts the onset of the surface bloom, regardless of whether the increase in surface biomass coincides with the increase of vertically integrated biomass. It remains an open question how much of the primary production in the North Atlantic is associated with blooms that have a surface expression at the onset versus blooms that start with no surface expression. Our analysis has only established that the surface increase in biomass seen from satellites is most often associated with a shutdown of convection for latitudes between 35°N and 60°N.

The influence of the air–sea heat flux on the timing of the North Atlantic surface blooms has important implications for our understanding

of the response of the local ecosystem to climate variability. The North Atlantic Oscillation is the dominant mode of winter climate variability in the region and modulates air–sea fluxes on interannual and decadal time-scales (Hurrell and Deser, 2009) and it has been shown to correlate with the timing of the surface bloom (Follows and Dutkiewicz, 2002). Long-term trends in air–sea fluxes have been attributed to anthropogenic climate change (Hurrell and Deser, 2006). Our analysis indicates that a long-term change in heat flux could shift the timing of the surface spring bloom. Since phytoplankton form the foundation of the marine food web, shifts in the timing of the surface spring bloom can strongly impact other species. For example, interannual variations in the timing of the surface spring bloom have been linked to the survival of fish larvae (Platt and Csar Fuentes-Yaco, 2003). While a full analysis of the bloom response to decadal and longer climate shifts is beyond the scope of this work, we established a clear connection between surface bloom timing and the air–sea heat flux, a core variable of climate studies.

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