

# Synoptic scale analysis of mechanisms driving surface chlorophyll dynamics in the North Atlantic

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**Abstract.** Several hypotheses have been proposed for the onset of the spring phytoplankton bloom in the North Atlantic. Our main objective is to examine which bottom-up processes can best predict the annual increase in surface phytoplankton concentration in the North Atlantic by applying novel phenology algorithms to ocean colour data. We construct indicator fields and time series which, in various combinations, provide models consistent with the principle dynamics previously proposed. Using a multimodel inference approach, we investigate the evidence supporting these models, and how it varies in space. We show that, in terms of bottom-up processes alone, there is a dominant physical mechanism, namely mixed layer shoaling, that best predicts the interannual variation in the initial increase in surface chlorophyll across large sectors of the North Atlantic. We further show that different regions are governed by different physical phenomena, and that wind-driven mixing is a common component with either heat flux or light as triggers. We believe these findings to be relevant to the ongoing discussion on North Atlantic bloom onset.

## 1 Introduction

About half of global primary production is performed by marine phytoplankton. Phytoplankton production fuels marine ecosystems and the harvesting of marine living resources, as well as playing an important role in global carbon cycling (Field et al., 1998). In many parts of the world's oceans, marine primary production undergoes a distinct seasonal cycle, with the major part of production occurring in the spring bloom (Longhurst, 1995; Martinez et al., 2011; Platt et al., 2010). This seasonal cycle is particularly apparent in the North Atlantic (Yoder et al., 1993), where it imprints seasonal variations in species abundance and annual routines (*e.g.* spawning, migration) throughout the ma-

rine food web from zooplankton (Gaard, 2000; Gislason and Silva, 2012; Heath et al., 2000), to fish (Trenkel et al., 2014; Badcock and Merrett, 1976) and marine mammals (Pauly et al., 1998). In the North Atlantic, the progression of primary production throughout the year, and its variation between years, is commonly used as a proxy for ecosystem state (Townsend et al., 1994; Frajka-Williams and Rhines, 2010; Lévy et al., 2005). The North Atlantic spring bloom is an important biological event and has attracted considerable attention during the last decades (Behrenfeld, 2010; Chiswell et al., 2013; Platt et al., 2003).

Phenology is the term used to describe the study of the timing of annual recurring biological events, such as the observed “greening” of the surface ocean, an indicator of bloom initiation. Phenology provides a staple for understanding the cascading fluctuations throughout the food web. To achieve this, a good phenology metric should be accurate, precise, and sensitive to the underlying environmental processes, both physical or biological (Ferreira et al., 2014). Much of the recent interest in spring bloom dynamics (Behrenfeld, 2010; Chiswell et al., 2013) concerns the mechanisms that influence different characteristics of the annual cycle.

Chlorophyll concentration is, arguably, the most important ecological variable setting the pace of life in temperate and high latitude seas. In this study, we use surface chlorophyll concentrations as derived from satellite ocean colour to detect spring bloom initiation (Cole et al., 2012; Sasaoka et al., 2011; Behrenfeld et al., 2013b; Brody et al., 2013). We thus assume that the chlorophyll concentration at the surface represents that of the surface mixed layer (Evans and Parslow, 1985). While we note that some aspects of bloom dynamics are more properly described by integrating phytoplankton biomass over the mixed layer (Brody and Lozier, 2014; Behrenfeld, 2010), it is the surface chlorophyll that is the most readily accessible via the highly-resolved (both spatially and temporally) ocean colour products.

There are essentially three environmental processes that can change the surface chlorophyll concentration: phytoplankton growth (through light and nutrients); loss terms (*e.g.* respiration, grazing, coagulation and sinking); and dilution (through mixed layer deepening). These processes are particularly important during two key phases of the seasonal cycle: 1) events that lead to an increase in phytoplankton biomass – bloom initiations, and 2) conditions that halt the net increase in biomass – the peak of the bloom. Phytoplankton biomass will increase whenever the growth rate exceeds the loss rate (Sverdrup, 1953). This picture, with regards the distinction between biomass and surface chlorophyll concentration, is somewhat complicated by dilution; a deepening mixed layer dilutes the concentration but has no effect on the biomass, a process that has repercussion on the feeding success and thus population dynamics of grazers. However, a shoaling mixed layer has no direct influence on the concentration but remove biomass to some extent. These processes and their implications for phytoplankton, the resources they rely on, and their grazers, have been carefully considered in recent re-analyses of spring bloom dynamics (Behrenfeld et al., 2013a; Lindemann and John, 2014).

It is also fair to say that the annual trajectory of phytoplankton biomass and surface phytoplankton concentration follow different dynamics (Chiswell et al., 2013).

While we recognise that phytoplankton biomass variation is an important aspect of spring bloom dynamics, in this paper, we examine which fundamental physical processes may best predict the timing of the increase in surface phytoplankton concentrations. Furthermore we do so since ocean surface colour is a readily available synoptic scale observable spanning many years of measurements. The interannual variability in bloom timing is evaluated in terms of how much the increase in surface layer chlorophyll is advanced or delayed compared to the day of climatological maximum rate of increase.

### 1.1 Mixed layer shoaling

Over the years, several theories have been put forwarded which, in one way or the other, try to model the growth and loss rates in terms of fundamental processes (Table 1 and Figure 1). The classic application of the growth-loss view of bloom initiation is in regards to when photosynthetic production of organic matter surpasses respiration (Sverdrup, 1953), where respiration refers to all losses and is constant. This hypothesis is commonly referred to as the “critical depth hypothesis”, which states that a bloom begins when the surface mixed layer shoals to a depth above the critical depth (where integrated production equals losses). The shoaling of the mixed layer means that individual phytoplankton cells remain longer in the euphotic zone (Siegel et al., 2002; Sverdrup, 1953; Chiswell, 2011; Platt et al., 1991). By extension, this suggests that the light intensity integrated over the mixed layer is the most relevant factor driving phytoplankton blooms in the North Atlantic. Here, we term this hypothesis the “critical depth model” (Table 1).

### 1.2 Active mixing

Mixed layer shoaling, however, is not the only process which can increase the residence of primary producers in the well-lit surface ocean. Similar effects can be driven by periods of low surface mixing (Townsend et al., 1992). This has led to a series of alternative interpretations, which highlight active mixing (specifically the lack thereof) as a key ingredient (Townsend et al., 1994; Huisman et al., 1999; Taylor and Ferrari, 2011a).

One of the first quantitative studies (Townsend et al., 1994) examined the combined effects of wind-driven mixing and light: the hypothesis being that blooms can occur during periods when light is low but increasing and turbulent mixing reduced. These conditions can be met well before the surface mixed layer begins to shoal. We call this the “critical light exposure model” (Table 1).

This type of reasoning can also lead to considering only the competing effects of stratification by solar heating, and destratification by wind-driven mixing. This view encapsulated the key elements of the “critical turbulence model” (Huisman et al., 1999, 2002), where brief interludes in mixing and heating produce a stable layer in which phytoplankton cells are retained within the euphotic layer.

Thus, a balance between heat-flux and wind-driven mixing may explain North Atlantic phytoplankton seasonality (Table 1).

95 More recently, Taylor and Ferrari (2011b) have shown that blooms may be detected much earlier than the shoaling of the mixed layer depth, and it has been proposed that blooms can be initiated as soon as deep convection ceases (Taylor and Ferrari, 2011a). That is, as soon as the ocean experiences a net inward heat flux. In this context, the timing of the transition from net cooling to net warming is a key element linked to the variability phytoplankton seasonality. We term this the “critical heat flux model” (Table 1).

### 100 **1.3 Other processes not considered**

There have been theories also focusing on specific regional effects. For instance, Mahadevan et al. (2012) were able to link bloom onset to eddy-driven stratification, prior to net warming. Fronts were also found to trigger high-latitude blooms by reduced mixing, which explains high chlorophyll levels in light-limited regions (Taylor and Ferrari, 2011b). Other studies (Frajka-Williams and Rhines, 105 2010; McGillicuddy et al., 2007; Garçon et al., 2001) have also linked spring bloom initiation to off-shore advection, eddy-induced upwelling or river runoff. Finally, oceanic convection has been found responsible for a significant vertical transport, thus maintaining a winter stock of phytoplankton in the deep mixed layer that can potentially re-seed the spring bloom (Backhaus et al., 1999, 2003).

Behrenfeld (2010) adopted a different approach by not assuming constant top-down controls, suggesting the “dilution-recoupling hypothesis”. This is a concept that is implicit in Evans and Parslow (1985)’s model. Behrenfeld (2010)’s hypothesis proposes that a vertically integrated biomass increases in mid-winter with the increase of day length (as a proxy for spring), even when the mixed layer depth is at its deepest, and reaches its maximum with the recoupling of grazers due to stratification. Unfortunately, as also noted by Behrenfeld (2010), data on top-down controls are not available 115 at the spatial and temporal resolutions necessary to deeply understand the complex structure of North Atlantic phytoplankton seasonality.

### **1.4 When and why does a surface bloom start?**

As noted by Cole et al. (2015), assessing the drivers of bloom initiation variability may lead to 120 the understanding of what started the bloom in the first place. Despite all of the above mentioned hypotheses, there is still no clear consensus regarding a single main driver of North Atlantic spring blooms. Additionally, the spatial application of these theories may not hold true in smaller regions, where local forcing plays a more important role. Nonetheless, the key process, and common to all hypotheses of surface bloom initiation, is based on the spring stabilization of the water column, 125 where both light and nutrients are at sufficient levels: whether by mixed layer shoaling (Sverdrup, 1953), or by weakening turbulent mixing (Huisman et al., 1999, 2002; Taylor and Ferrari, 2011a;

Townsend et al., 1994; Taylor and Ferrari, 2011b). Their main differences reside in the physical proxy for bloom initiation: what physical indicator best predicts bloom timing?

130 While there are a number of metrics that can be used to delineate bloom initiation Yoder and Kennelly (2003); Siegel et al. (2002); Rolinski et al. (2007), our goal to seek a metric that can be credibly related to the processes proposed above, *i.e.* those that relate to the preconditioning of the water column prior to surface bloom initiation. In this, any metric that uses the bloom peak (such as the popular 5 % above annual median), or seasonally integrated chlorophyll, will be handicapped because it inherently takes into account not only what starts the bloom, but also what terminates it  
135 some weeks or months later. Therefore, we construct a phenology metric that is not confounded by the bloom peak, does not require winter values, and is a straightforward indicator of the greening of the surface ocean as observed from space. Our metric is based on the maximum increase in surface concentration, a point that we believe to be more closely connected to the physical factors leading to the bloom than other commonly used metrics.

140 We construct four models based on the literature on the subject by using a range of physical mechanisms from satellite observations and modeled data, and describe key processes observed in the North Atlantic (Table 1 and Figure 1). In each case, we make the models as simple as possible - capturing the essential process dynamics in terms of at most two observable/estimated fields only.

We use the Information Theoretic (IT) approach to investigate which hypothesis for surface blooms  
145 has the most support within the North Atlantic. The IT approach is a very useful tool when comparing different models. In particular, it provides a rigorous framework for evaluating the evidence in support of competing models. It does so by defining *a priori* a set of “multiple working hypotheses” rather than a single alternative to the null hypothesis. The IT approach is then followed by expressing each hypothesis in quantitative terms that represent their strength of evidence to be further used in  
150 the model selection (Burnham et al., 2011).

We conduct our study by only focusing on bottom-up controls that may trigger a North Atlantic phytoplankton surface bloom, and thus neglect the effect of top-down controls (grazing, (Behrenfeld, 2010; Evans and Parslow, 1985; Irigoien et al., 2005)). Information on top-down controls is not available at the spatial and temporal coverage needed to assess mesoscale physical forcing.  
155 In addition, as Chiswell (2011) shows, the seasonal cycle of surface chlorophyll differs from the vertically-integrated chlorophyll. Behrenfeld (2010)’s “dilution-recoupling hypothesis” applied to vertically-integrated chlorophyll blooms, while the other hypotheses (Sverdrup, 1953; Siegel et al., 2002; Platt et al., 1991; Huisman et al., 1999; Huisman and Sommeijer, 2002; Huisman et al., 2002; Townsend et al., 1994; Taylor and Ferrari, 2011a, b) can be applied to surface chlorophyll. Our aim  
160 is to compare the latter ones, in which it is assumed that surface blooms only take off when the surface waters stabilise.

## 2 Material and Methods

### 2.1 Information Theoretic (IT) Approach

The main aspects of the IT framework (Burnham et al., 2011; Burnham and Anderson, 2002; Akaike, 165 1973) in the context of our study include (1) identifying plausible mechanistic hypotheses, and (2) a strong reliance on the quantitative evidence of factor(s) affecting a response variable, rather than a formal assessment of the statistical significance of such factor(s). In our study, (1) is expressed through mathematical descriptions of the different hypotheses to be tested (see Table 1 and Section 2.2), while (2) is covered by ranking the spatial evidence of the models using the concept of model 170 selection and multimodel inference (see Burnham et al. (2011) and Section 2.5).

### 2.2 Physical mechanisms

We are particularly interested in knowing how much information from raw data is correlated to surface chlorophyll. Raw data refers to the original data in their simplest form, without pre-processing. Therefore, we quantitatively translate the fundamental physical processes that can be used to predict 175 a phytoplankton surface bloom in the North Atlantic into simple and straight-forward models (Table 1 and Figure 1).

**Critical depth** - A bloom initiates if the mixed layer depth (*MLD*) shoals below the critical depth, so light (*PAR*) becomes available to phytoplankton cells (Figure 1a) (Sverdrup, 1953; Siegel et al., 2002; Platt et al., 1991). Therefore, *PAR* integrated over the *MLD* translates the light 180 available within the euphotic depth for phytoplankton to grow.

**Critical turbulence** - A bloom initiates if there is a balance between buoyancy (heat flux, *HF*) and wind-driven mixing (*MIX*, Figure 1b) (Huisman et al., 1999; Huisman and Sommeijer, 2002; Huisman et al., 2002).

**Critical light exposure** - A bloom initiates if wind-driven mixing (*MIX*) is at a level that allows 185 light (*PAR*) availability (Figure 1c) (Townsend et al., 1994).

**Critical heat flux** - Bloom initiation is associated with the date when net warming starts ( $0\text{ }HF$ ), which is related to wind-driven mixing (*MIX*), and increases the time of phytoplankton in the euphotic layer (Figure 1d) (Taylor and Ferrari, 2011a, b).

### 2.3 Data sets

190 In order to gather the information necessary to formulate the models for the North Atlantic domain, we used satellite observations (chlorophyll concentration, attenuation coefficient and photosynthetically active radiation), model estimations for the variables where satellite data was not available (mixed layer depth), and model and observational merged data (wind stress and heat flux).

We used products derived from the European Node for Global Ocean Colour (GlobColour Project, <http://www.globcolour.info/>). The GlobColour Project blends observational data from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS), the Moderate Resolution Imaging Spectroradiometer (MODIS-AQUA), and the Medium Resolution Imaging Spectrometer (MERIS) instruments by using the Garver-Siegel-Maritorena (GSM) algorithm (Maritorena et al., 2002) to generate a merged, global ocean colour product. Combining the three sensors increases the data coverage in both time and space, thus providing significantly elevated spatio-temporal coverage (Maritorena et al., 2010), making it a common choice for phenology studies (Cole et al., 2012; Kahru et al., 2011). For this study, we chose to use daily,  $1/4^\circ$  level 3 mean chlorophyll concentration ( $CHL$ ) and attenuation coefficient ( $K_d$ ) products (based on the analysis performed by Ferreira et al. (2014)), from 1998 to 2010 inclusive, thus providing a total of 13 years of data.

Photosynthetically active radiation ( $PAR$ ) was obtained from the SeaWifs data center (<http://oceancolor.gsfc.nasa.gov/>). We used daily, 9 km resolution product from 1998 to 2010. These data were further gridded onto  $1/4^\circ$  using linear interpolation to match the spatial resolution of the other data sets.

Light intensity integrated to the mixed layer ( $PAR_{MLD}$ ) was defined as  $PAR$  integrated to the  $MLD$ , using the  $K_d$ , following the equation by Irwin et al. (2012), and also used by Cole et al. (2015):

$$PAR_{MLD} = \frac{PAR}{K_d \times MLD} (1 - e^{-K_d \times MLD}) \quad (1)$$

, where  $PAR$  is measured at the surface.

Mixed layer depth ( $MLD$ ) data were obtained from TOPAZ 4 reanalysis (Sakov et al., 2012). The TOPAZ system is a coupled ocean-sea ice data simulation system for the North Atlantic and Arctic Ocean with a resolution of 12-16 km, and is the main forecasting system for the Arctic Ocean in Copernicus (<http://www.myocean.eu>) and the Norwegian contribution to the Global Ocean Data Assimilation Experiment (GODAE). It uses the Hybrid Coordinate Ocean Model (HYCOM, <http://hycom.org/hycom/>) (Bleck, 2002). HYCOM is coupled to a EVP sea ice model (Hunke and Dukowicz, 1997) and a thermodynamic module (Drange et al., 1996). The model assimilates sea surface temperature, altimetry, ice concentration, ice drift, and available *in situ* measurements with the ensemble Kalman Filter (Evensen, 2003). The model daily output is binned onto a  $1/4^\circ$  regular grid. The  $MLD$  is calculated using a density criteria with a threshold of  $0.01 \text{ kg.m}^{-1}$ , as in Petrenko et al. (2013) from 1998 to 2010.

Wind stress ( $WS$ ) is the stress exerted by the wind on the sea surface. We used  $WS$  as a proxy for wind-driven mixing ( $MIX$ ) (Simpson et al., 1981; Taboada and Anadón, 2014). Therefore,  $MIX$  was estimated by using:  $|WS|^{3/2}$ , which is proportional to the power exerted by the wind on the surface ocean and the turbulent kinetic energy used in Brody and Lozier (2014)'s calculations of the mixing length scale. We acknowledge that Brody and Lozier (2014) may be a model that best

230 represents the fundamental dynamics, but for the sake of simplicity and using an index closer to the original data, we decided to use our above defined *MIX*.

Both *WS* and heat flux (*HF*) data were gathered on a spatial resolution of  $1.875^\circ \times 1.905^\circ$  from the National Centers for Environmental Prediction (NCAR) and the National Center for Atmospheric Research (NCEP) (Kalnay et al., 1996). These data sets were further gridded onto  $1/4^\circ$  using linear  
235 interpolation to match the spatial resolution of the other data sets.

All data sets started on October 1, 1997. We only focused on latitudes north of  $40^\circ\text{N}$  due to the fact that lower latitudes have a less well-defined seasonal cycle (Follows and Dutkiewicz, 2011; Brody and Lozier, 2014).

## 2.4 Metrics

240 New studies (*e.g.* (Brody and Lozier, 2014)) have been incorporating Behrenfeld (2010)'s concept by using an integrated chlorophyll metric to look at bloom initiation in the North Atlantic. We decided to use an anomaly of surface chlorophyll because it is a more relevant measure in regards to higher trophic levels and is one we believe is closer to bloom preconditioning. In order to use an integrated chlorophyll field, we would need to use modelled mixed layer depth, which is incorporated in one  
245 of the models we are testing.

Our metric, the rate of change phenology anomaly (*RPA*), is an index of how advanced or delayed (anomaly) the spring surface bloom is each year. This has the advantage of not depending on the maximum chlorophyll concentration (an indicator of the peak of the bloom), which occurs in many other metrics used in the literature (Siegel et al., 2002; Sharples et al., 2006). We estimated an *RPA*  
250 time series for each  $1/4^\circ$  as follows. We estimated the climatology of *CHL* by using a Generalized Additive Model (GAM), which is essentially an average of the GAMs applied to each seasonal cycle (from 1998 to 2010). The fits for each year and  $1/4^\circ$  were averaged to produce a climatology for each  $1/4^\circ$  (darkred line in Figure 2). We then calculated the day of maximum increase in *CHL* in the climatology - climatological bloom ( $RP_0$ ) and the climatological maximum rate of increase in  
255 *CHL* ( $g$ ). Lastly, we estimated the rate of change phenology anomaly (*RPA*) for each year and each  $1/4^\circ$  by using a GAM with a smoothing spline on the values withing a 30-day window around  $RP_0$  (grey area in Figure 2) as follows:  $RPA = \frac{\Delta CHL}{g}$ . We set a threshold of at least 3 *CHL* values must exist withing the 30-day window for the *RPA* method to work. We only estimated *RPA* for positive values of  $g$ , *i.e.* for time steps where chlorophyll concentration is increasing. We thus estimated how  
260 delayed or advanced the bloom is in comparison with the climatological bloom. The output is the *RPA* in days, which is an indicator of changes in surface chlorophyll. We further apply a spatial kriging with a maximum radius of 250 km to fill in the the pixels where the method cannot be used, *e.g.* due to missing data around the date of interest (thus a threshold of at least 3 values) or low seasonality. However, low seasonality is a problem that applies further south of our model domain

265 (Taboada and Anadón, 2014; Demarcq et al., 2012). The percentage of pixels where no the method cannot be determined by the RPA method is  $22 \pm 11$  %.

We investigated the spatially dependent ranking of the models (Table 1 and Figure 1) using the IT approach. Thus, we constructed indicator fields and time series which, in various combinations, provide models consistent with the principle physical dynamics observed in the North Atlantic. We apply a centered moving average of 30 days. From now on, these indices will be referred to as 30d (30-day average) in front of *PAR*, *PAR<sub>MLD</sub>*, *MIX* and *HF*. We also use *0HF* for when *HF* becomes positive (start of net warming) and remains positive for seven consecutive days. We further applied an inverse distance weighted interpolation (using the weighted average of the values at the known pixels) to all thresholds to fill in the pixels where the thresholds could not be estimated. All pixels in waters shallower than 200 m were removed as coastal regions have higher associated biases (Maritorena et al., 2010) due to high turbidity and consequent different optical properties (McCain et al., 2006; Antoine et al., 1996; Longhurst et al., 1995; Sathyendranath et al., 2001).

## 2.5 Analysis

There are several model selection tools that can be used for comparing and ranking models. In our IT approach, we used the Akaike Information Criterion (AIC) (Burnham et al., 2011), which is based on the residual sum of squares (RSS) from each one that explain variability in the response. By comparing and ranking the evidence from different models, their relative importance can be quantified. Since we only aimed at assessing 13 years of data ( from 1998 to 2010), we used the AICc. The AICc is AIC corrected for small samples. Theoretically, as sample size increases, AICc converges to AIC. Another model selection unit is the Akaike weight, which can be either based on the AIC or the AICc. The Akaike weight is a value between 0 and 1 representing the weight mean probability of each model, *i.e.* the strength of evidence in support of each model.

Each model was dealt with as regressions as shown in Table 1. Based on the weight of each model, we could select the most supported model for each  $1/4^\circ$  pixel.

## 290 3 Results

From the four hypotheses considered (critical depth; critical turbulence; critical light exposure, and critical heat flux) within each  $1/4^\circ$  pixel, the one with the highest Akaike weight is selected as the winning hypothesis (Figure 3), where we see that the critical depth seems to be the most frequent winning hypothesis.

295 The spatial distribution of winning hypotheses shows no systematic pattern with regards to basin, depth, or latitude (Figure 3). We also ran this analysis with two other bloom timing metrics: 5 % above annual median (Siegel et al., 2002; Cole et al., 2012; Brody et al., 2013; Racault et al., 2012; Henson et al., 2010) and maximum increase in chlorophyll concentration (Rolinski et al., 2007;

Sharples et al., 2006; Wiltshire et al., 2008; Brody et al., 2013) and we found similar results: no  
300 systematic pattern (results not shown).

In spite of the general dominance of the critical depth hypothesis, there are, however, regions that  
show some coherency: the critical turbulence appears to be well supported mainly off Newfoundland;  
the critical heat flux is frequently observed in north of Iceland and in the Labrador Sea; the critical  
light exposure appears to have a wider distribution with very low frequencies. Similar features as the  
305 ones observed off Newfoundland are observed in the spatial distribution of Akaike weights (Figure  
A1). There are regions where the weights are close to 1, indicating that the corresponding models  
are clear winners. Some of these regions are the same as the ones observed in Figure 3: for instance,  
offshore of Newfoundland.

A pixel-wise multimodel inference approach also allows the quantification of the number of oc-  
310 currences of each of the four alternative hypotheses as the winning (Figure 3). There are no clear  
differences in the ranking units of the three less frequent hypothesis (0.15, 0.11 and 0.07), whilst the  
critical depth showed a higher ranking unit (0.67).

To better understand the effect of each physical component ( $30dPAR_{MLD}$ ,  $30dPAR$ ,  $30dMIX$ ,  
 $30dHF$ ,  $0HF$ ) within the four hypotheses (Figure 1), we built single-variable models (linear regres-  
315 sions) using each component as variable for each  $1/4^\circ$  pixel (Figure 4). The most frequent winning  
physical component based on the Akaike weights is  $30dHF$ . Its spatial distribution dominates off  
Newfoundland, in the subpolar gyre and intermediate gyre regions, and in the Bay of Biscay. Its  
dominance is however only slightly greater than the other physical components.

#### 4 Discussion

320 The phenology of spring bloom characteristics (*e.g.* initiation, peak, magnitude) is thought to be con-  
trolled by a number of mechanisms including bottom-up and top-down processes. Here we specif-  
ically set out to test various bottom-up processes that can be used as indicators of phytoplankton  
surface blooms, testing several simplified hypotheses across a broad extent of the North Atlantic.  
In this regard, spring surface bloom initiation is problematic in that defining it has as much to do  
325 with what limits the bloom amplitude as what starts it in the first place. Moreover, limiting factor(s)  
can be the ultimate switching mechanism needed for a bloom to start. Instead, we seek to explain  
what bottom-up processes determine the interannual variability of the the phase where the rate of  
surface chlorophyll increase reaches its maximum. By quantifying each physical mechanism inde-  
pendently, we observe that, even though there is no clear losing mechanism in the North Atlantic  
330 domain, Sverdrup (1953)'s classical theory (critical depth) still dominates; *i.e.* it has a superior evi-  
dence supporting the interannual variability of timing across the greatest range of space in the North  
Atlantic (Figure 3).

Most of the authors assessing bloom phenology focus on the initiation phase, but how long does this phase really lasts? Since we built a different metric (and even indicator, see difference in Ferreira et al. (2014)), a comparison of results is rather difficult. It is important to note that bloom initiation metrics, as suggested by Ferreira et al. (2014), fall within different phases of the bloom. Nevertheless, the most commonly used bloom initiation metrics may not be so different from our *RPA* metric. For instance, one of the most used phenology metrics, the 5 % above annual median (Siegel et al., 2002), usually falls within a date later than the initiation date and it is still considered an initiation metric. This could thus be considered a semantics issue. Additionally, the problem with this type of metrics still remains: they rely on the full cycle (or at least the peak) of chlorophyll concentration in order to be estimated. The ideal bloom phenology metric should be accurate, precise, and simultaneously sensitive to the underlying environmental processes, and should carefully reflect the question being asked (Ferreira et al., 2014). Therefore, the construction of a metric that is independent of the minimum and maximum chlorophyll values, and still respects all the above-mentioned issues, is valuable. Moreover, studies focusing in regions with, for instance, a high percentage of missing winter data, would benefit from this type of metrics.

Even though the critical depth hypothesis is the most successful model within the North Atlantic domain (Figure 3), its corresponding parameter (the light intensity available integrated to the mixed layer,  $PAR_{MLD}$ ) comes in fourth place in the single parameter inter-comparison, with a spatial distribution with no clear pattern (Figure 4). In a recent study, Cole et al. (2015) found that  $PAR_{MLD}$  is a consistent driver of spatial variability in the North Atlantic bloom, and a weak driver of inter-annual variability. Our finding may be due to two reasons. Firstly, the critical depth model may be handicapped, since it is based on second-level calculation (modeled data), therefore potentially misleading. A successful representation of Sverdrup's theory would require observations of temporally and spatially distributed mixed layer. Secondly, the success of the critical depth model stems primarily from its compact form where the underlying mechanism is integrated into a single variable. Since the Akaike weights are being penalised according the number of parameters, a compact form (only one parameter) may thus have an advantage over the models using more parameters. This observation is notable within regions where the critical depth dominates (*e.g.* north and south of Iceland), but  $PAR_{mld}$  was not the winning parameter. Instead, other parameters are more important (*e.g.*  $HF$ , heat flux).

All of the four alternative hypotheses are expressed as simple interpretations of what potentially drives the surface blooms in the North Atlantic at the mesoscale (Figure 1). The models are constructed so as to be as simple as possible, using at most two physical observables (light intensity, light intensity integrated over the mixed layer depth, wind-driven mixing and heat flux) in various forms. Each model is based on one of the two classes of mechanisms discussed in the introduction: mixed layer shoaling (critical depth) or active mixing (critical turbulence, critical light exposure and critical heat flux). Our study shows the strength of the critical depth model and indicates a dominance

370 of the mixed layer shoaling over the active mixing mechanism, but not everywhere. In a similar ap-  
proach, Brody and Lozier (2014) found contrasting results. Their study does not support the theory  
that phytoplankton growth is triggered by shoaling of the seasonal thermocline. However, Brody and  
Lozier (2014) tested a different range of theories by using a one-dimensional approach of climato-  
logical mixing length scales, which inhibits both mesoscale processes and interannual variability to  
375 be assessed.

In our study, even though the critical depth hypothesis is the winner (most spatially frequent), the  
spatial distribution of the winning model shows regions where the mixed layer shoaling mechanism  
seems not to be supported. For instance, there is a dominance of the critical turbulence and critical  
light exposure models in the Bay of Biscay. This may be due to the high degree of upwelling in this  
380 region; hence the failure of critical depth hypothesis to predict surface bloom dynamics. Another  
example occurs east of Newfoundland, where the critical turbulence and critical heat flux hypotheses  
dominate. Both of these hypotheses have wind-driven mixing as a common parameter. In addition,  
heat flux and light intensity are also key individual drivers in this region (as confirmed in Figure 4).  
These findings suggest that spring bloom seasonality in these regions may be driven by periods of  
385 reduced active turbulent mixing, increasing exposure to light (Huisman et al., 1999; Huisman and  
Sommeijer, 2002; Huisman et al., 2002; Taboada and Anadón, 2014)]. The region off Newfoundland  
is also very energetic (high physical forcing), highly influenced by the subpolar gyre, and serves as  
a path for the northward movement of the Gulf Stream waters. Even though we do not assess 3D  
processes in our study, they may still help the understanding of the dynamics of the North Atlantic  
390 system. The failure of critical depth to explain the bloom dynamics in this region may be due to  
subduction of cold waters from the subpolar gyre and the warm waters from the North Atlantic drift.  
This may explain why the critical turbulence and the critical heat flux were dominating in the region  
east of Newfoundland and into the central North Atlantic.

The explanatory power of the hypotheses that assume the mechanism of active mixing (critical  
395 turbulence; critical light exposure and critical heat flux) is fairly evenly distributed (Figure 3). These  
three hypotheses seem to operate with a switch-on mechanism, *i.e.* a number of conditions has to  
be met for bloom growth, and any one may be the critical condition that triggers the growth spurt.  
This interpretation is supported by comparing Figures 3 and 4, where the critical depth model is a  
clear winner in the model inter-comparison, but only scores average when tested against individ-  
400 ual parameters. In this case, the limiting conditions appear to be either light intensity or heat flux  
(since all three have wind-driven mixing as a common parameter). Our results show that there is  
no clear winning hypothesis among these three active mixing models, but there is a bias towards  
mechanisms involving heat flux (Figure 4). This finding is supported by Taylor and Ferrari (2011a),  
where a bloom develops due to the start of net warming, weakening turbulent mixing, and subse-  
405 quent increase of the residence time of phytoplankton cells within the euphotic layer. In order for  
this to happen, a standing stock of phytoplankton cells needs to exist *a priori*. The “seed stock” is

the left overs from the previous year that have been surviving all winter at depth due to convection. As suggested by Backhaus et al. (2003, 1999); Chiswell (2011), deep convection spreads out the overwintering remnants, but, as soon as stratification comes in, those lucky enough to be in the surface start to bloom. From our results (Figure 3), we confirm that heat flux (*i.e.* cooling and heating of the ocean surface) is the dominant mechanism. Thus, in regions where the critical depth is not the winning model, the active mixing mechanism (either triggered by light intensity or heat flux) seems to play an important role.

The second most common physical property was wind-driven mixing (Figure 4) and is the common parameter in the models concerning the active mixing mechanism. In the past, the importance of wind-driven mixing has been shown by Huisman et al. (1999); Huisman and Sommeijer (2002); Huisman et al. (2002), and confirmed by Taylor and Ferrari (2011a, b). The first group of authors stresses a balance between wind-driven mixing and sinking rates, so that an intermediate mixing allows both enough surface nutrient replenishment, and sufficient average light exposure. Recently, Taboada and Anadón (2014) suggested that wind forcing (wind stress as a proxy for wind surface mixing) played a key role in bloom timing and magnitude (see their Figures 5a and 5c). The results shown by these authors are based on single-parameter hypotheses (not including heat flux) and confirm that spring blooms are triggered by different physical properties in different mesoscale regions. Our results are thus in agreement, where wind stress is found as a common parameter within the North Atlantic domain.

Winds have essentially two effects: turbulent mixing (Backhaus et al., 2003; Townsend et al., 1994) which is only shallow (around 50 m in mid-latitudes), and surface cooling which promotes deep convection (Backhaus et al., 2003). Together with the cessation of convective overturn, wind stress decreases during the spring. Deep mixing is therefore no longer active, and there is a shift from a deep-mixed regime to a shallow light-driven regime. However, it is important to note that the depth of the mixed layer is not the same as the depth of vertical mixing of plankton (Chiswell, 2011). These two depths only match when vertical mixing is at its limit (Taylor and Ferrari, 2011a). In the presence of low vertical mixing, a surface bloom can initiate even if critical depth conditions (Sverdrup, 1953) are not met, *i.e.* even if the thermocline is deeper than the critical depth. This mechanism is presented by Chiswell (2011) as the “stratification-onset model”, in which the author contends that the critical depth hypothesis is valid during autumn and winter, when the deepening thermocline may cease production due to downward mixing of plankton, but not in spring, since the upper layers are not well mixed in plankton. The model is consistent with the findings by Taylor and Ferrari (2011a), in which surface stratification results from cessation of convective overturn and low wind stress. Additionally, Chiswell (2011) distinguished between a surface bloom and a vertically-integrated bloom. In our study, we show that the critical depth hypothesis can still be used to predict phytoplankton spring surface blooms.

Our findings have, however, assumptions that are worth considering. Firstly, we based the critical  
445 depth hypothesis on Sverdrup's classical theory, thus only accounting for *PAR<sub>mld</sub>*. This makes the  
model inherently simpler. The other three hypotheses use two parameters separately, and are there-  
fore somewhat handicapped (higher penalty due to higher number of parameters) when compared to  
the critical depth. We believe that this type of study would improve if similar combinations would be  
450 found for the remaining hypotheses: critical turbulence, critical light exposure and critical heat flux.  
For this reason, we tried to use a two-parameter approach (considering *MLD* and *PAR* separately)  
for the critical depth hypothesis, so that the four models would have the same number of parameters,  
and thus the AICc weights would be comparable. The critical depth explained by *PAR<sub>mld</sub>* alone  
showed to be inherently superior (with a much stronger signal) than the combined *MLD* and *PAR*  
455 model, thus we chose to keep our interpretation of the critical depth hypothesis using *PAR<sub>mld</sub>*. This  
underscores the point that physical reasoning can come a long way in improving model predictions.

Secondly, we recognise that our study assumes that the same mechanism predicts surface bloom  
timing at a given location for the entire time frame (from 1998 to 2010). However, it is conceivable  
that different mechanisms may be best predictors in different years. Considering the high variability  
in the spatial distribution of the models (Figure 3), it is reasonable to expect similar high temporal  
460 variability. In the same way we observe that different mechanisms dominate in different regions,  
intuitively, one can assume that different mechanisms will also dominate in different years. Indeed,  
given the scatter in winning models, it is entirely conceivable that bloom timing is governed by a  
limiting factor; that multiple conditions have to be met, any one of which may be the trigger in any  
given year or location.

465 Thirdly, we also recognise that our study fails at assessing top-down mechanisms. A key hypothe-  
sis that has been attempted by Brody and Lozier (2014) is "dilution-recoupling hypothesis" (Behren-  
feld, 2010). Brody and Lozier (2014) found no clear effect of seasonal thermocline increases on inte-  
grated chlorophyll increases. However, as they noted, in order to successfully study this hypothesis,  
one would require temporally and spatially distributed data on grazing pressure and encounter rates  
470 between grazers and phytoplankton. Since such highly-resolved data sets are not available, top-down  
mechanisms cannot be properly assessed at this time.

## 5 Conclusions

The complexity of spring bloom dynamics in the North Atlantic has been discussed since Sver-  
drup (1953) published the "critical depth hypothesis". The discussion took a different direction  
475 when Behrenfeld (2010) suggested a top-down control of the phytoplankton seasonal cycle with  
the "dilution-recoupling hypothesis". Various studies followed the same line of thought (Behrenfeld  
et al., 2013c, a, b; Irigoien et al., 2005). However, bottom-up factors are still the most studied (Siegel  
et al., 2002; Huisman et al., 1999; Townsend et al., 1994; Taylor and Ferrari, 2011a), especially be-

cause data is more readily available than for top-down factors. The theories mentioned in the above  
480 sections (Figure 1) do not necessarily disagree with this reasoning. Instead, each one adds a missing  
element necessary to fully understand spring bloom dynamics (Lindemann and John, 2014). Even  
though satellite observations have provided great insight over the last decades, the picture is still  
one of complexity. Our study thus confirms that a single hypothesis for what drives a North Atlantic  
spring bloom may be too simplistic.

485 A consensus is yet to be developed regarding the onset of spring phytoplankton blooms in the  
North Atlantic. Every theory published in the literature claims to best predict the timing of the spring  
bloom. However, one cannot adopt a single hypothesis simply because all of the theories seem to  
apply, either at shorter temporal or spatial scales. By revisiting four of the main hypotheses on the  
subject, we are able to confirm that phytoplankton surface bloom dynamics in the highly-variable  
490 North Atlantic are far too complex to be driven by the same mechanism in all places and in all  
years. We show that, in terms of bottom-up processes alone, there is a dominant physical mechanism  
(mixed layer shoaling) that best predicts the growing phase of North Atlantic phytoplankton blooms  
at the mesoscale ( $1/4^\circ$ ). However, some regions show coherent patterns, supporting the idea that  
there are distinct physical phenomena driving spring surface blooms, rather than a single one. We  
495 believe these findings to be relevant for the ongoing discussion on North Atlantic bloom onset.

## Appendix A: Appendix A

Figure A1 - Map of the Akaike weights of the winner model.

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500 ftp.acri.fr/, supported by EU FP7 MyOcean and ESA GlobColor projects, using ESA ENVISAT MERIS, NASA  
MODIS and SeaWiFS data. *PAR* was obtained from the SeaWifs data center available at <http://oceancolor.gsfc.nasa.gov/>. *MLD* was obtained from the Hybrid Coordinate Ocean Model (HYCOM) available at <http://hycom.org/hycom/>. *WS* and *HF* were obtained from the Earth System Research Laboratory, Physical Sciences Division, and are available at <http://www.esrl.noaa.gov/psd/data/gridded/tables/daily.html>. This paper is  
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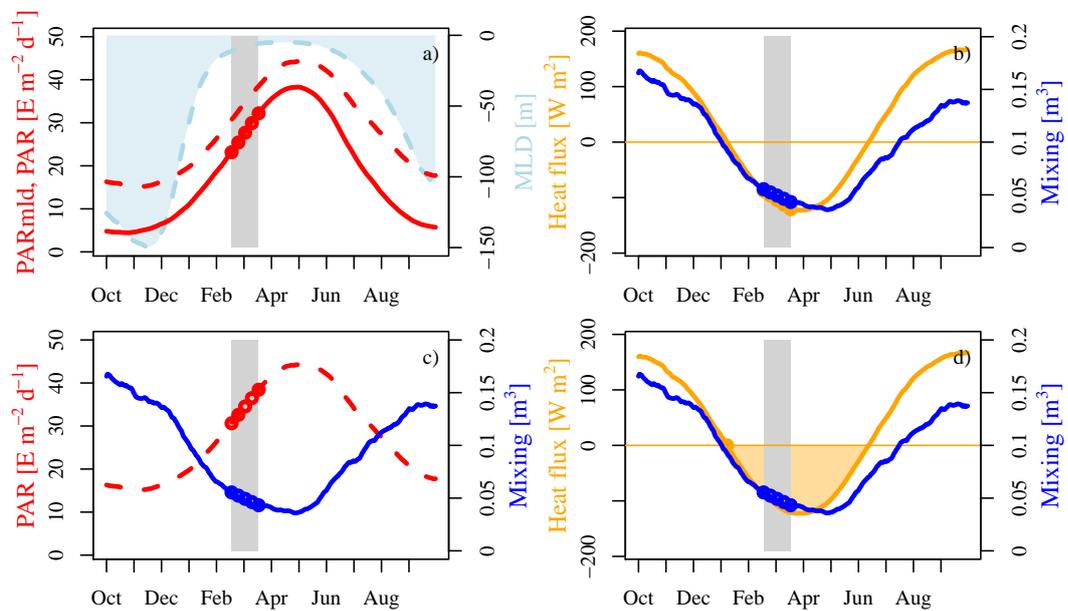
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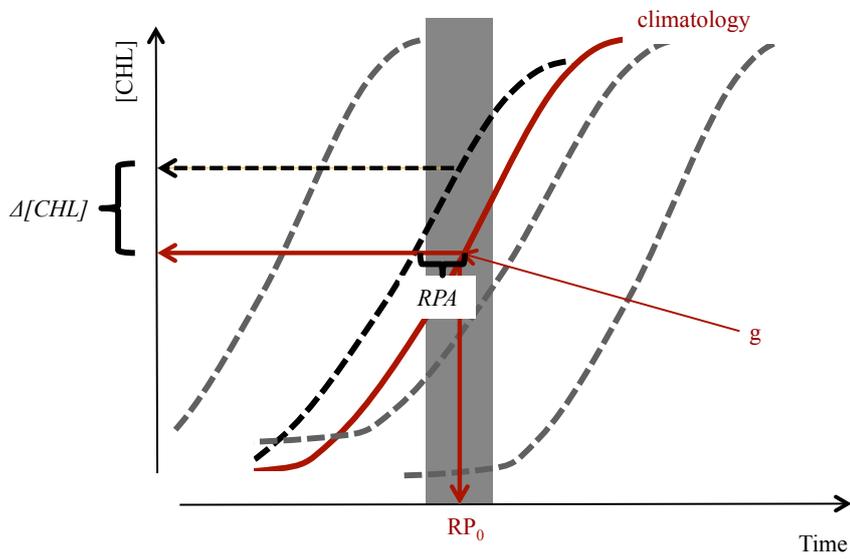
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**Table 1.** Models to explain the Rate of change Phenology Anomaly (RPA) were built based on published theories regarding the bloom onset Sverdrup (1953); Siegel et al. (2002); Huisman et al. (1999); Townsend et al. (1994); Taylor and Ferrari (2011a). These are indicators of physical processes observed in the North Atlantic.

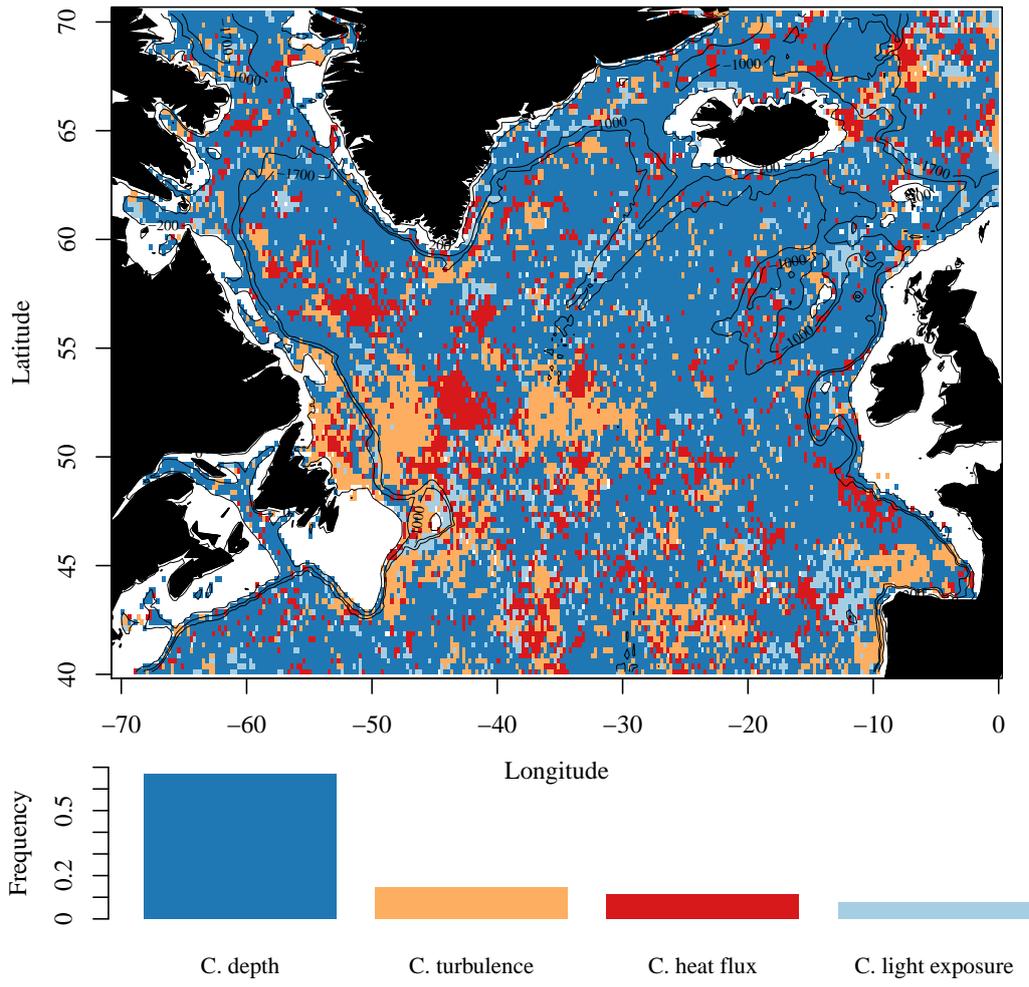
Name	Parameters	Mathematical expression	References
Critical depth	$PAR_{MLD}$ : light intensity ( $PAR$ ) integrated to the mixed layer depth ( $MLD$ )	$RPA \sim \alpha_1 30d PAR_{MLD} + \beta_1$	Sverdrup (1953); Siegel et al. (2002)
Critical turbulence	$HF$ : heat flux. $MIX$ : wind-driven mixing	$RPA \sim \alpha_{2a} 30d HF + \alpha_{2b} 30d MIX + \beta_2$	Huisman et al. (1999); Huisman and Sommeijer (2002); Huisman et al. (2002)
Critical light exposure	$PAR$ : light intensity. $MIX$ : wind-driven mixing	$RPA \sim \alpha_{3a} 30d PAR + \alpha_{3b} 30d MIX + \beta_3$	Townsend et al. (1994)
Critical heat flux	$HF$ : heat flux. $MIX$ : wind-driven mixing	$RPA \sim \alpha_{3a} 0 HF + \alpha_{3b} 30d MIX + \beta_3$	Taylor and Ferrari (2011a, b)



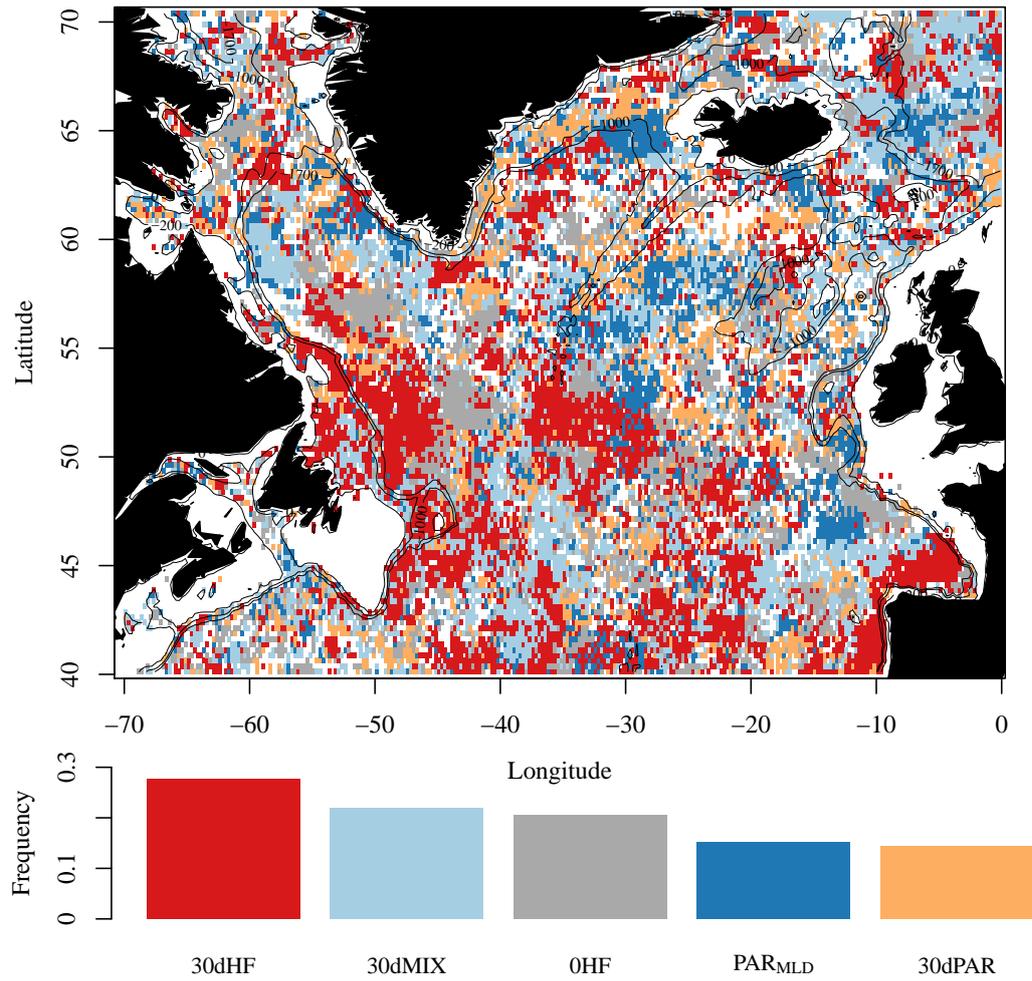
**Figure 1.** Definitions of each mechanism: a) critical depth; b) critical turbulence; c) critical light exposure; d) critical heat flux (Table 1). Grey vertical area: 30 days prior to the date of climatological maximum rate of change in chlorophyll concentration; open circles: average conditions during the 30 days. Lines show: mixed layer depth ( $MLD$ , light blue), photosynthetic active radiation ( $PAR$ , dashed red),  $PAR$  at the  $MLD$  ( $PAR_{MLD}$ , filled red), heat flux ( $HF$ , orange), and wind-driven mixing ( $MIX$ , dark blue).



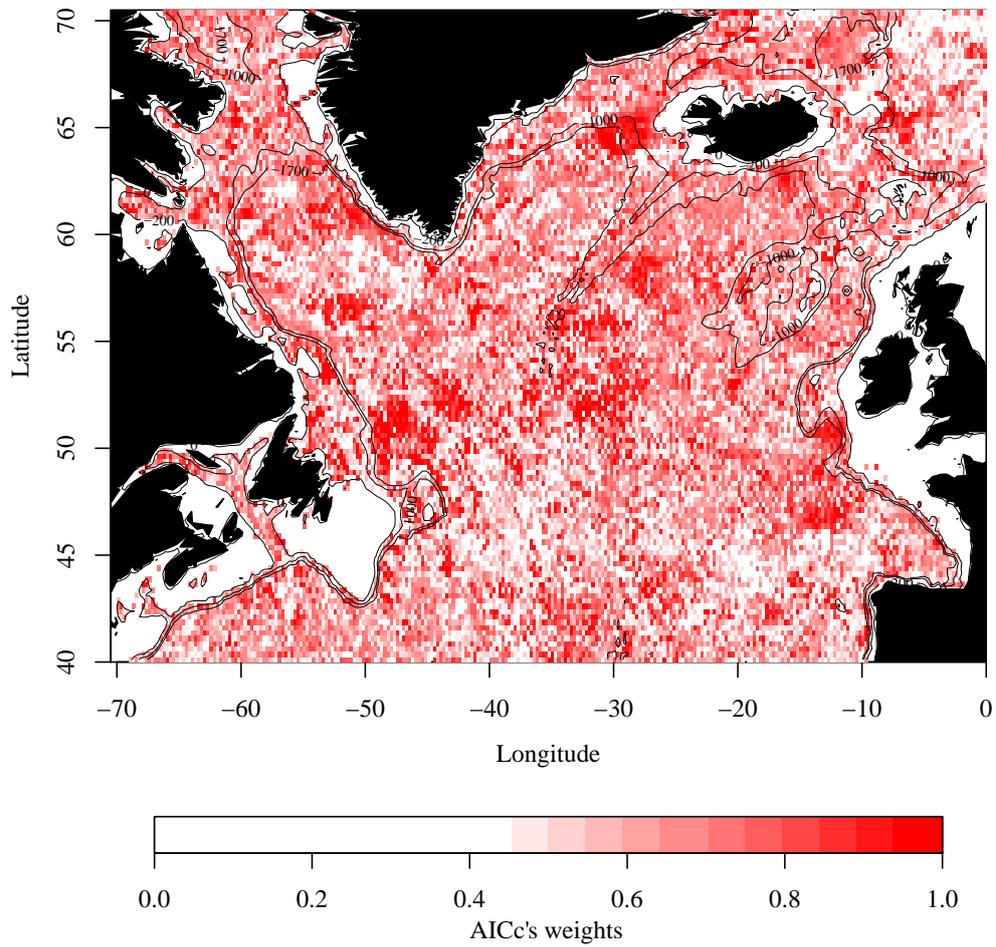
**Figure 2.** Calculation of the rate of change phenology anomaly ( $RPA$ ). Each seasonal cycle (dashed, grey and black lines) is used to estimate the climatology (darkred line). The day of maximum increase ( $RP_0$ ) in chlorophyll concentration ( $CHL$ ) is used as a reference to estimate how delayed or advanced each year surface bloom is. This is done by calculating the rate of increase ( $g$ ) at  $RP_0$  and the difference in the  $CHL$  on that day in the climatology and each year seasonal cycle ( $\Delta CHL$ ). The  $RPA$  thus represents the time difference in days of each year seasonal cycle.



**Figure 3.** Selected model for each  $1/4^\circ$  pixel (top), and relative frequency of each model (bottom). C. depth: critical depth; C. turbulence: critical turbulence; C. light exposure critical light exposure; C. heat flux: critical heat flux. Only pixels where the weight of the winning model is higher than 30 %, and the bottom depth exceeds 200 m are used for the map.



**Figure 4.** Selected variable for each  $1/4^\circ$  pixel (top), and relative frequency of each single-variable model (bottom). PAR<sub>MLD</sub>:  $30dPAR_{MLD}$ ; PAR:  $30dPAR$ ; MIX:  $30dMIX$ ; HF:  $30dHF$  and 0HF:  $0HF$ . Only pixels where the weight of the winner model is higher than 30 %, and the bottom depth exceeds 200 m are used for the map.



**Figure A 1.** Akaike weights of the selected model for each  $1/4^\circ$  pixel as in Figure 2 in the main manuscript. Only pixels where the weight of the winner model is higher than 30 %, and the bottom depth exceeds 200 m are used for the map.