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

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Abstract

Several hypotheses have been proposed for phytoplankton bloom onset in the North Atlantic. The physical properties driving phytoplankton seasonality can also be used as indicators of the greening of the oceans. Our main objective is to examine which bottom-up processes can best predict changes in the growing phase of phytoplankton surface blooms 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 multi-model 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 (mixed layer shoaling) best predicting the North Atlantic phytoplankton surface chlorophyll. 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 for 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 marine 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

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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 greening of the ocean (timing of bloom initiation). Phenology estimates provide 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 (physical or biological) (Ferreira et al., 2014). Whereas some studies estimate spring bloom phenology metrics based on proxies of primary productivity such as chlorophyll concentration (Yoder and Kennelly, 2003; Siegel et al., 2002; Rolinski et al., 2007; Greve et al., 2005; Ferreira et al., 2014), others focus on the physical drivers that are recreated during fall and winter (mixing, low light, high nutrients) (Evans and Parslow, 1985; Sverdrup, 1953; Lindemann and John, 2014) and propagated into spring and summer conditions (stratification, high light, low nutrients). A spring bloom is thus not an isolated biological event, but rather an annual recurring cycle that emerges from the combination of favourable environmental processes (Evans and Parslow, 1985).

Chlorophyll concentration is, arguably, the most important ecological variable setting the pace of life in temperate and high latitude seas. Several studies have been using satellite ocean colour (surface chlorophyll concentration) to detect spring bloom initiation (e.g. Cole et al., 2012; Sasaoka et al., 2011; Behrenfeld et al., 2013b; Brody et al., 2013). In this study, we use surface chlorophyll concentration as a measure of the greening effect of the ocean. We thus assume that the chlorophyll concentration at the surface represents that of the mixed layer depth (Evans and Parslow, 1985). While we note that bloom dynamics are more properly described by integrating phytoplankton biomass over the mixed layer, it is the surface chlorophyll that is the most readily ac-

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cessible via the highly-resolved (both spatially and temporally) ocean colour products. In addition, during spring, it is possible to detect a bloom from the fluctuations both in surface chlorophyll and in vertically integrated biomass.

There are essentially four environmental processes that can change the surface chlorophyll concentration: phytoplankton growth (through light and nutrients); loss terms (e.g. respiration, sinking, grazing, and other potential loss terms such as coagulation); and dilution (through mixed layer deepening). These processes are particularly important during two key phases of the seasonal cycle: (1) an initial increase in production (the growing phase), and (2) a peak in production (Fig. A1). Growth and loss terms have been recognised to describe a phytoplankton bloom by Sverdrup (1953): phytoplankton biomass will increase whenever the growth rate exceeds the loss rate. This definition of a phytoplankton bloom is true throughout the year. However, not all processes are present during the growing phase (grey area in Fig. A1). Even though a balance between growth and grazing is crucial to bloom initiation (Behrenfeld, 2010), the rate of cell division during the growing phase is mainly dependent on light and nutrients. During the growing phase, the surface chlorophyll concentration increases while the mixed layer is shoaling. Therefore, surface chlorophyll can only vary due to growth or losses.

In this paper, we examine which fundamental physical processes may best predict the timing of spring surface phytoplankton blooms in the North Atlantic during the growing phase. 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 Fig. 1). The classic application of the growth-loss view of bloom initiation is in regards to when photosynthetic production of organic matter surpasses respira-

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tion losses (Sverdrup, 1953). In Sverdrup (1953)'s work, respiration refers to all losses and is constant. His hypothesis is commonly referred to as the "critical depth hypothesis", which states that a bloom occurs when the surface mixed layer shoals to a depth above the critical depth (when phytoplankton growth 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).

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More recently, Taylor and Ferrari (2011b) have shown that blooms may be detected much earlier than the shoaling of the mixed layer depth. Taylor and Ferrari (2011a) proposed the hypothesis that blooms can be initiated as soon as deep convection ceases. 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 in the North Atlantic phytoplankton seasonality. We term this the “critical heat flux model” (Table 1).

1.3 Fronts, eddies, advection and convection

There have been theories also focusing on locations with specific characteristics. 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, 2010; McGillicuddy et al., 2007; Garçon et al., 2001) have also linked spring bloom initiation to offshore 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).

1.4 Grazing

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, 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 at the spatial and temporal

resolutions necessary to deeply understand the complex structure of North Atlantic phytoplankton seasonality.

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. The key process, and common to all hypotheses looking at surface blooms, is based on the spring restratification, 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, b; Townsend et al., 1994). Their main differences reside in the proxy for bloom initiation: what physical indicator best predicts bloom timing?

The Information Theoretic (IT) approach is a very useful tool when comparing different models. In particular, it provides the evidence in support of the considered models, 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 the model selection (Burnham et al., 2011); rather than using test statistics and their associated significance levels.

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 Fig. 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 IT approach to investigate which hypothesis for surface blooms has the most support within the North Atlantic.

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. In addition, as Chiswell (2011) shows, the seasonal

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cycle of surface chlorophyll differs from the vertically-integrated chlorophyll. Behrenfeld (2010)'s dilution-recoupling hypothesis applies to vertically-integrated chlorophyll blooms, while the other hypotheses (Sverdrup, 1953; Siegel et al., 2002; Platt et al., 1991; Huisman et al., 1999, 2002; Huisman and Sommeijer, 2002; Townsend et al., 1994; Taylor and Ferrari, 2011a, b) apply to surface chlorophyll. Our aim 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 Physical mechanisms

We are particularly interested in knowing how much information from raw data (in their simpler form) is correlated to surface chlorophyll. Therefore, we quantitatively translate the fundamental physical processes that can be used to predict a phytoplankton surface bloom in the North Atlantic into simple and straight-forward models (Table 1 and Fig. 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 (Fig. 1a) (Sverdrup, 1953; Siegel et al., 2002; Platt et al., 1991). Therefore, PAR integrated over the MLD translates the light 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, Fig. 1b) (Huisman et al., 1999, 2002; Huisman and Sommeijer, 2002).

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

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

2.2 Data sets

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) and model estimations for the variables where satellite data was not available (wind stress, heat flux and mixed layer depth).

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.

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 sys-

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tem for the North Atlantic and Arctic Ocean with a resolution of approximately 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 kg m^{-1} , as in Petrenko et al. (2013) from 1998 to 2010.

Light intensity integrated to the mixed layer (PAR_{MLD}) was defined as the Photosynthetically Active Radiation (PAR) integrated to the MLD, using the K_d , following the equation by Irwin et al. (2012):

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

where PAR is measured at the surface.

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: $|\text{WS}|^{\frac{3}{2}}$, which is proportional to the power exerted by the wind on the surface ocean.

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 interpolation to match the spatial resolution of the other data sets.

New studies (e.g. Brody and Lozier, 2014) have been incorporating Behrenfeld (2010) concept by using an integrated chlorophyll metric to look at bloom initiation

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in the North Atlantic. Instead, we decided to use an anomaly of surface chlorophyll because it is a more relevant measure in regards to higher trophic levels. In order to use an integrated chlorophyll field, we would need to use modelled mixed layer depth, which is incorporated in one 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 avoiding contamination from 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 time series for each $1/4^\circ$ as follows. We estimated the climatology of CHL by using a Generalized Additive Model (GAM) with a penalized cyclic cubic regression spline of the day of year. The year of each seasonal cycle (from 1998 to 2010) was fit with a normal random effect (spline with a penalized ridge penalty). The fits for each year and $1/4^\circ$ were then averaged to produce a climatology for each $1/4^\circ$ (darkred line in Fig. 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 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 penalized cubic regression spline of the day of year over a 30-day window around RP_0 (grey area in Fig. 2) as follows: $RPA = \frac{\Delta_{CHL}}{g}$. We only estimated RPA for positive values of g , i.e. for time steps when chlorophyll concentration is increasing. We thus estimated how 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. low seasonality).

2.3 Analysis

All data sets started on 1 October 1997. We only focused on latitudes north of $40^\circ N$ due to the fact that lower latitudes have a less well-defined seasonal cycle (Follows and Dutkiewicz, 2011; Brody and Lozier, 2014). We used the IT approach (Burnham et al., 2011) to examine the evidence supporting each mechanism within the North Atlantic

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(Table 1). 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_{MLD}, MIX and HF. We also use 0HF for when HF becomes positive (start of net warming) and remains positive for at least 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.

We investigated the spatially dependent ranking of the models (Table 1 and Fig. 1) using the IT approach. This approach uses the Akaike Information Criterion (AIC) (Burnham et al., 2011). We used AICc, which is AIC with a greater penalty for finite samples, due to the short time series (13 years). The Akaike weight (based on the AICc) is thus a value between 0 and 1. 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). Based on the weight of each model, we could select the most supported model for each 1/4° pixel.

3 Results

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

The spatial distribution of winning hypotheses shows no systematic pattern with regards to basin, depth, or latitude (Fig. 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 (results not shown): no systematic pattern.

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 the 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 ones observed off Newfoundland are observed in the spatial distribution of Akaike weights (Figure B1). 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 Fig. 3: for instance, offshore of Newfoundland.

A pixel-wise multimodel inference approach also allows the quantification of the number of occurrences of each of the four alternative hypotheses as the winning (Fig. 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 (30 d PAR_{MLD}, 30 d PAR, 30 d MIX, 30 d HF, 0 HF) within the four hypotheses (Fig. 1), we built single-variable models using each component as variable for each 1/4° pixel (Fig. 4). The most frequent winning physical component based on the Akaike weights is HF. 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

The phenology of spring bloom characteristics (e.g. initiation, peak, magnitude) is thought to be controlled by a number of mechanisms including bottom-up and top-down processes. Here, we specifically set out to test various bottom-up processes that can be used as indicators of the growing phase of phytoplankton surface blooms (grey

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area in Figure A1), 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 with what limits the bloom amplitude as with what starts it in the first place. Instead, we seek to explain what bottom-up processes determine the interannual variability of the growing phase. By quantifying each physical mechanism independently, we observe that, even though there is no clear loosening mechanism in the North Atlantic domain, Sverdrup (1953)'s classical theory (critical depth) still dominates; i.e. it has a superior evidence supporting the interannual variability of timing across the greatest range of space in the North Atlantic (Fig. 3).

Even though the critical depth hypothesis is the most successful model within the North Atlantic domain (Fig. 3), its corresponding parameter (the light intensity available integrated to the mixed layer, PAR_{ml}) comes in fourth place in the single parameter inter-comparison, with a spatial distribution with no clear pattern (Fig. 4). This finding may be due to two reasons. First, 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. Second, 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_{ml} 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 (Fig. 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

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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 of the mixed layer shoaling over the active mixing mechanism, but not everywhere.

In a similar approach, 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 climatological mixing length scales, which inhibits both mesoscale processes and interannual variability to 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 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 Fig. 4). These findings suggest that spring bloom seasonality in these regions may be driven by periods of reduced active turbulent mixing, increasing exposure to light (Huisman et al., 1999, 2002; Huisman and Sommeijer, 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. 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.

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The explanatory power of the hypotheses that assume the mechanism of active mixing (critical turbulence; critical light exposure and critical heat flux) is fairly evenly distributed (Fig. 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 Figs. 3 and 4, where the critical depth model is a clear winner in the model inter-comparison, but only scores average when tested against individual 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 (Fig. 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 subsequent 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. 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 (Fig. 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 (Fig. 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, 2002); Huisman and Sommeijer (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

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(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 Fig. 5a and c). 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. First, we based the critical depth hypothesis on Sverdrup’s classical theory, thus only accounting for PAR_{mid}. This makes the model inherently simpler. The other three hypotheses use two parameters separately, and are therefore somewhat handicapped (higher penalty

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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 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 PARmld alone showed to be inherently superior (with a much stronger signal) than the combined MLD and PAR model, thus we chose to keep our interpretation of the critical depth hypothesis using PARmld. This underscores the point that physical reasoning can come a long way in improving model predictions.

Second, 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 (Fig. 3), it is reasonable to expect similar high temporal 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.

Third, we also recognise that our study fails at assessing top-down mechanisms. A key hypothesis that has been attempted by Brody and Lozier (2014) is “dilution-recoupling hypothesis” (Behrenfeld, 2010). Brody and Lozier (2014) found no clear effect of seasonal thermocline on integrated 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 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 Sverdrup (1953) published the “critical depth hypothesis”. The discussion took a different direction 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 because data is more readily available than for top-down factors. The theories mentioned in the above sections (Fig. 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.

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 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 believe these findings to be relevant for the ongoing discussion on North Atlantic bloom onset.

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Appendix A

Figure A1 – Schematic figure showing the phytoplankton bloom initiation dynamics.

Appendix B

Figure B1 – Map of the Akaike weights of the winner model $1/4^\circ$ pixel.

5 *Acknowledgements.* The data outputs from this study can be obtained by contacting A. S. A. Ferreira at asofiaaferreira@gmail.com. GlobColor data were provided by accessing the GlobColour's FTP server available at ftp://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 a deliverable of the Nordic Centre for Research on Marine Ecosystems and Resources under Climate Change (NorMER), which is funded by the Norden Top-level Research Initiative sub-programme "Effect Studies and Adaptation to Climate Change". A. W. Visser acknowledges the Danish Council for Strategic Research and its support for the NAACOS project. The research leading to these results has received funding from the European Union 7th Framework Programme (FP7 2007-2013) under grant agreement number 308299 (NACLIM project).

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

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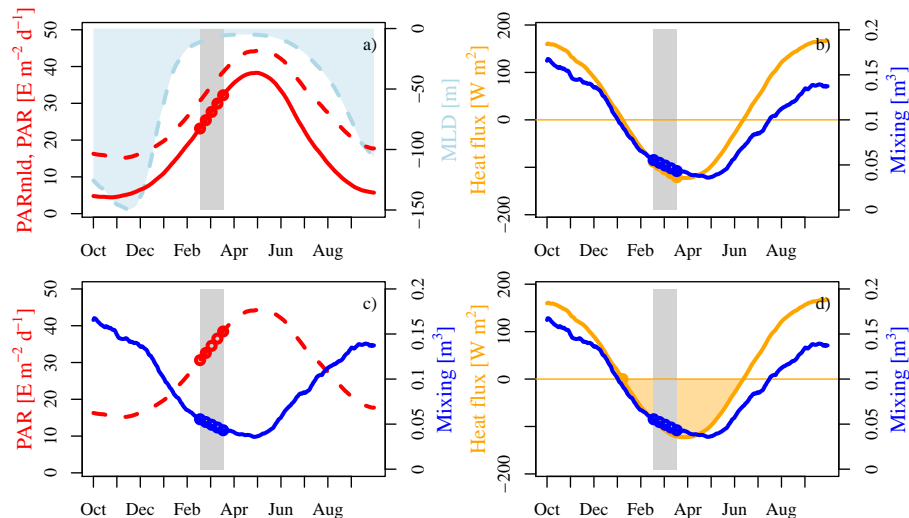


Figure 1. Definitions of each mechanism: **(a)** critical depth; **(b)** critical turbulence; **(c)** critical light exposure; **(d)** critical heat flux (Table 1). Grey vertical area: 30 days prior to the date of climatological maximum rate of change in chlorophyll concentration; open circles: average 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).

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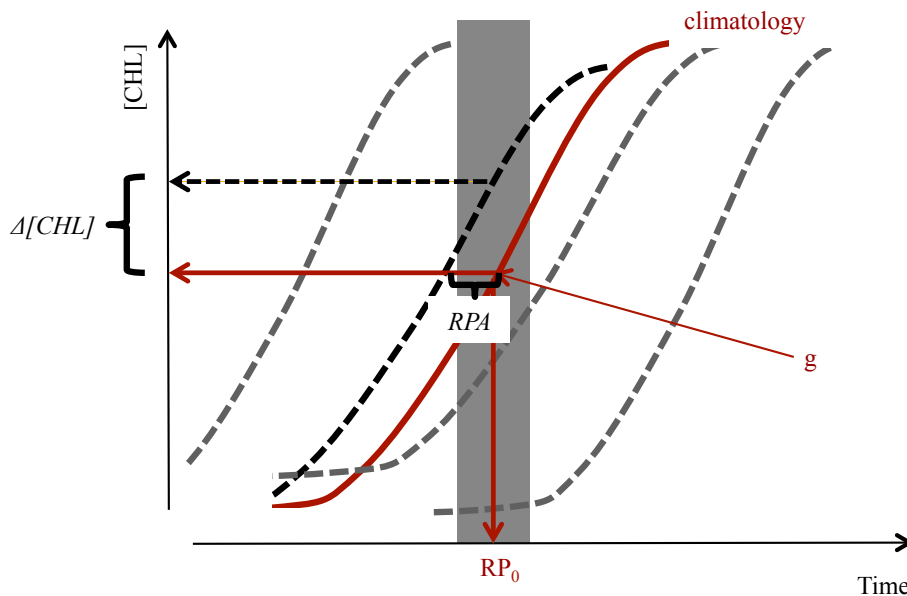


Figure 2. Calculation of the rate of change phenology anomaly (RPA). Each seasonal cycle (dashed, grey and black lines) is used to estimate the climatology (darkred line). The day of maximum increase (RP_0) in chlorophyll concentration (CHL) is used as a reference to estimate how delayed or advanced 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 (Δ CHL). The RPA thus represents the time difference in days of each year seasonal cycle.

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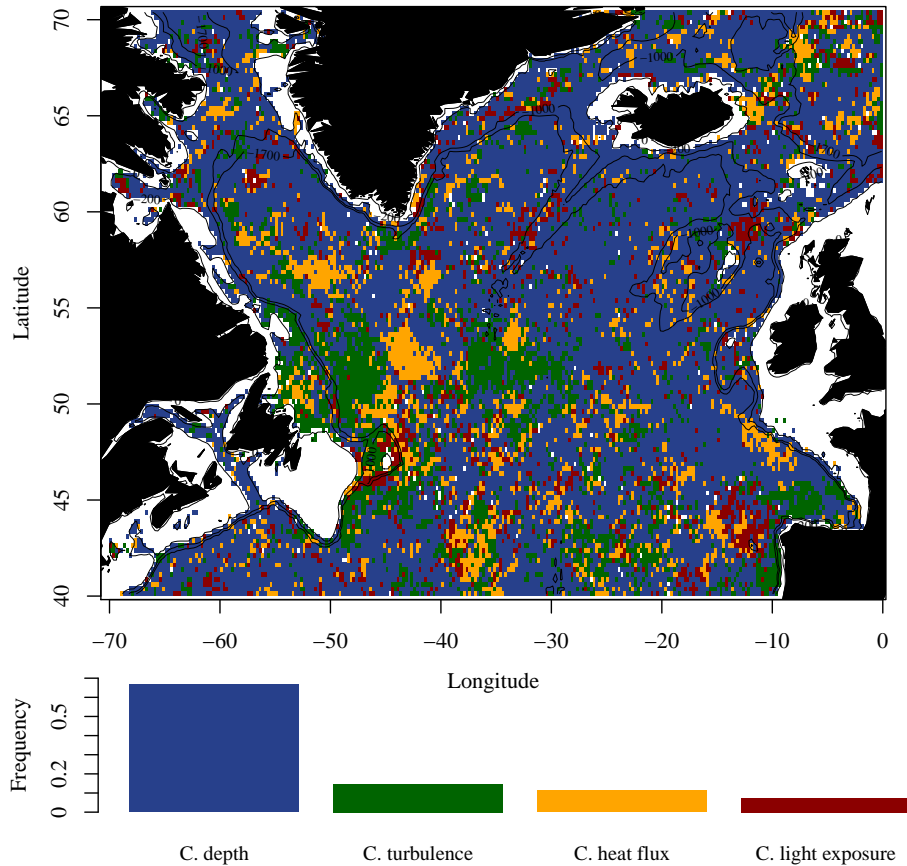


Figure 3. Selected model for each $1/4^\circ$ pixel (top), and relative frequency of each model (bottom). C. depth: critical depth; C. turbulence: critical turbulence; C. light exposure critical light exposure; C. heat flux: critical heat flux. Only pixels where the weight of the winning model is higher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

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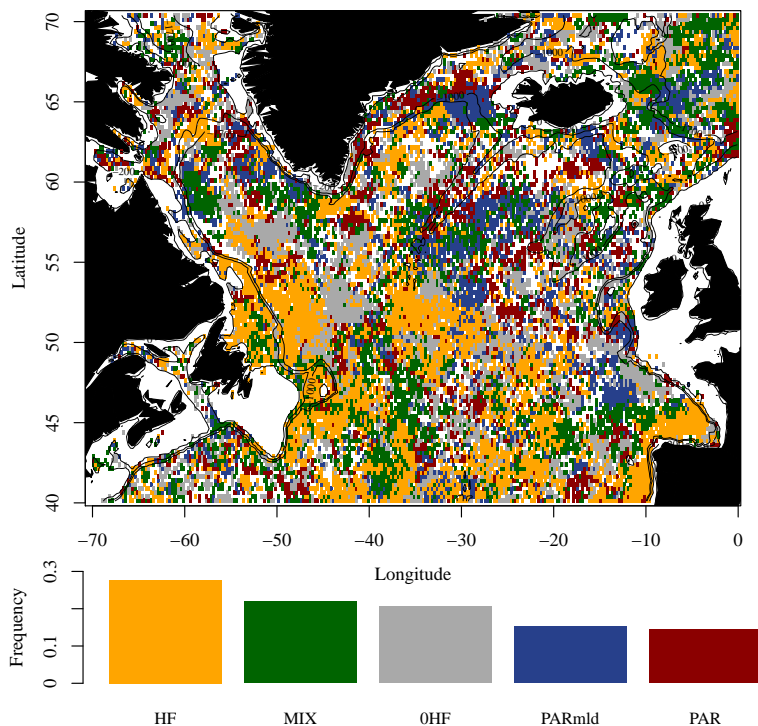


Figure 4. Selected variable for each $1/4^\circ$ pixel (top), and relative frequency of each single-variable model (bottom). PARmld: 30 d PAR_{MLD}; PAR: 30 d PAR; MIX: 30 d MIX; HF: 30 d HF and OHF: 0 HF. Only pixels where the weight of the winner model is higher than 30%, and the bottom depth exceeds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

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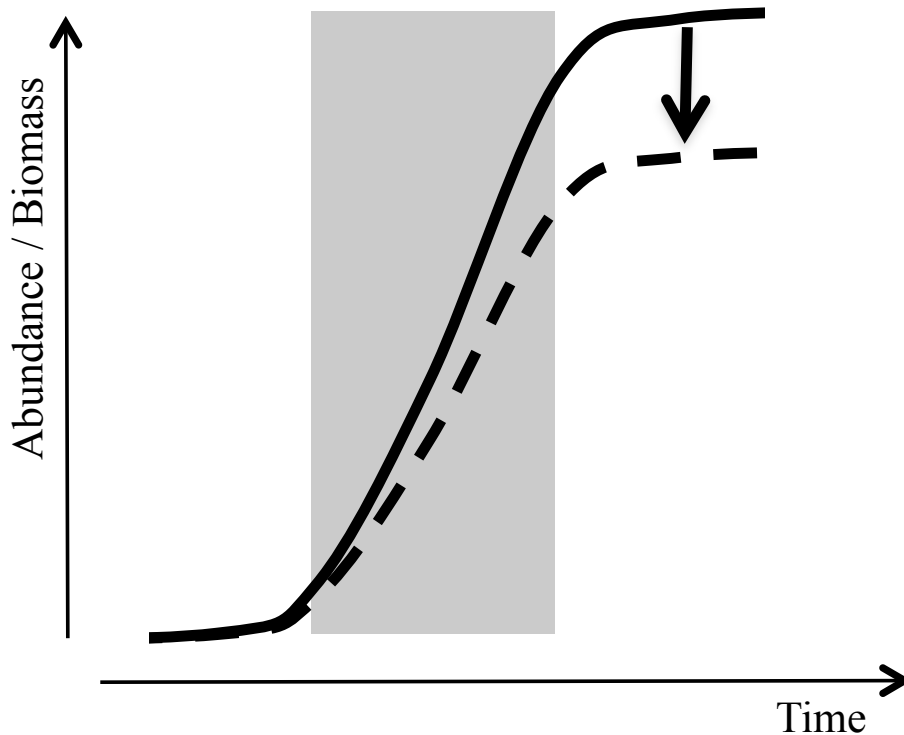


Figure A1. Seasonal cycle of the North Atlantic phytoplankton. In late winter, wind-driven mixing replenishes surface nutrients, but light is still low. During the spring, light becomes available, and phytoplankton abundance or biomass starts to increase (first production), enters its growing phase (grey area). In the first summer months, grazing by zooplankton can determine the extent of the peak of phytoplankton abundance or biomass (black arrow).

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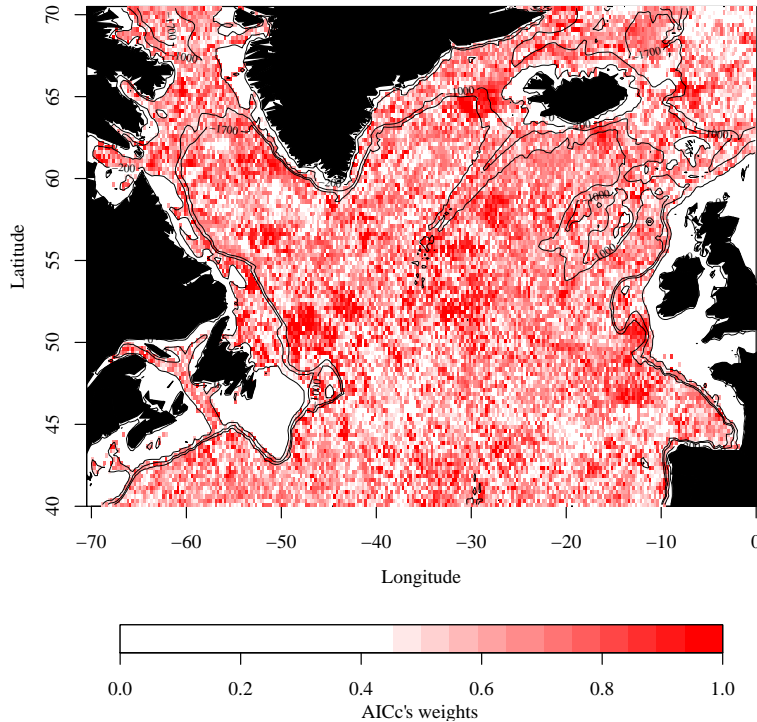


Figure B1. Akaike weights of the selected model for each $1/4^\circ$ pixel as in Fig. 2 in the main manuscript. Only pixels where the weight of the winner model is higher than 30%, and the bottom depth exceeds 200 m are used for the map.

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