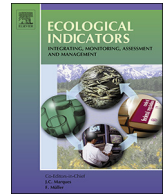




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Original Articles

Regional differences and inter-annual variability in the timing of surface phytoplankton blooms in the Labrador Sea

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ARTICLE INFO

Keywords:

Phytoplankton bloom
 Marine bioregions
 Labrador Sea
 Ocean color remote-sensing
 Physical forcing
 Inter-annual variability
 Sub-polar North Atlantic

ABSTRACT

The annual phytoplankton bloom is an important marine event and its inter-annual variability can be used to monitor changes in the pelagic ecosystem. In this context, the use of a bio-regionalization analysis to objectively identify ocean areas that differ in their biological characteristics and environmental conditions may be useful to disentangle the functioning of the ecosystem. In this work, satellite surface chlorophyll-*a* concentration observations were used to obtain a bio-regionalization of the Labrador Sea (LS). Specifically, bioregions were defined using a K-means cluster analysis applied on the satellite time-series of chlorophyll-*a* concentration. Finally, the resulting biologically regionalization was used in conjunction with simulated data from a state-of-the-art ocean circulation model (NEMO) to investigate difference in spring bloom timing response across the Labrador Sea (LS). Chlorophyll-*a* seasonal cycle in the LS varies markedly between two neighboring but distinct bioregions: the north ($> 60^\circ\text{N}$) and the south ($< 60^\circ\text{N}$). The north LS blooms earlier (\sim early-mid April) and more intensely, while the south LS blooms later (\sim May) and its duration may persist all summer long. In the southern LS bioregion, the maximum phytoplankton growth rate (i.e., the initiation of the surface spring bloom) coincides closely with the timing of the first cooling-to-heating shift in air-sea heat fluxes. In this area, the bloom timing tends to precede the shoaling of the mixed-layer depth and the vernal development of the upper ocean stratification. In the southern bioregion, the cooling-to-heating shift in air-sea heat fluxes provided a more suitable indicator for the spring bloom initiation. Meanwhile, in the northern LS bioregion, the early onset of the spring bloom is related to the seasonal evolution (i.e., shoaling) of the mixed-layer depth and precedes the cessation of wintertime cooling. Over the northern bioregion, freshwater exchanges may suppress vertical mixing while the air-sea fluxes are still negative (i.e., ocean cooling). Given the heterogeneity of the LS basin, this study emphasizes the importance to consider the bioregion-specific differences in the upper ocean physical-biological interactions.

1. Introduction

Various oceanic regions are characterized by strong seasonal variations in phytoplankton abundance. In these regions, the transition from winter to spring is characterized by a rapid and intense phytoplankton growth (Henson et al., 2006) that is easily recognizable by ocean-color satellite sensors through the increase in surface chlorophyll-*a* concentration (Siegel et al., 2002), a key diagnostic pigment for all phytoplankton groups (Huot et al., 2007). One of these ocean regions is undoubtedly the North Atlantic, a strongly seasonal ocean characterized by intense spring phytoplankton blooms (Siegel et al., 2002). In the North Atlantic, the pronounced seasonal growth cycle of phytoplankton has been the subject of many interdisciplinary works. In particular, much attention has been given to changes in the timing of

the spring bloom (e.g., Gonzalez Taboada and Anadon, 2014; Henson et al., 2009), which can result in the decoupling of phenological relationships in the pelagic food chain (Edwards and Richardson, 2004; Friedland et al., 2016) and represents a critical factor for the seasonality of the biological carbon pump (Sanders et al., 2014). The bloom timing by determining when food sources are available to both fish and marine birds, plays thus a large role in maintaining food web interactions and commercial fisheries (Racault et al., 2014). In this connection, understand what exactly causes the spring blooms to occur and monitoring their spatial patterns is of fundamental importance.

Traditionally, the onset of the sub-polar North Atlantic phytoplankton blooms has been attributed to changes in the mixed-layer depth: in open ocean/deep water the bloom begins when the mixed-layer shoals (from winter to spring) to a depth shallower than a critical

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depth at which the phytoplankton net growth becomes positive (i.e., the growth of phytoplankton exceeds autotrophic respiration). The progressive shoaling of the mixed-layer depth helps phytoplankton to remain and accumulate in the brighter surface layer. Later, in late spring or early summer, nutrients become exhausted in the euphotic zone, the growth slows and the loss due to increasing grazing pressure reduces the phytoplankton abundance to a lower level. This classical explanation for the occurrence of the spring bloom represents the so-called “critical depth hypothesis” (Sverdrup, 1953). Nowadays, the Sverdrup’s critical-depth hypothesis remains the most cited and widely accepted theory and it has been used to investigate the timing of the spring bloom over high latitude regions (e.g., Henson et al., 2006). However, contemporary studies have agreed (Mahadevan et al., 2012), challenged (Behrenfeld, 2010; Boss and Behrenfeld, 2010) or merely refined the Sverdrup’s model by testing if reduction in turbulent mixing within the mixed layer (rather than the decrease in the mixed layer itself) can create the appropriate conditions for the bloom onset (Chiswell, 2011; Taylor and Ferrari, 2011). Overall, in the North Atlantic the bloom onset variability has been studied extensively and it has been related to several physical drivers. For instance, large-scale climate indices such as the North Atlantic Oscillation have been linked to changes in the timing of the sub-polar bloom (Henson et al., 2009; Zhai et al., 2013).

In the Labrador Sea (LS), a sub-polar sea that connects the North Atlantic with the Arctic Ocean, few studies have investigated the bloom onset variability and its ecological significance. More specifically, satellite observations in conjunction with numerical model (Frajka-Williams and Rhines, 2010; Wu et al., 2008a), shipboard observations (Head et al., 2000) and hydrographic-based studies (Frajka-Williams et al., 2009) have identified a north-to-south progression in the spring bloom initiation. In the northern region (north of $\sim 60^\circ\text{N}$) of the LS the bloom starts earlier, and it is usually shorter but more intense compared to the central-southern region of the basin. This reversed geographical pattern represents a distinctive feature if compared to the North Atlantic where spring blooms tend to follow a general northward progression (Siegel et al., 2002). The early bloom in the north LS was related to the shallower mixed layer associated with Arctic-derived low-salinity waters. Instead, the initiation of the spring bloom in the central-southern LS was linked to the formation of the seasonal thermal stratification established by surface warming (Frajka-Williams and Rhines, 2010; Wu et al., 2008a). Recently, the difference in the bloom temporal variations was redefined based on climatological ocean-color observations (Lacour et al., 2015): the spring bloom starts when the depth of the mixed layer shoals and regulates the phytoplankton’s time exposure to sunlight. Overall, the spring bloom onset in both regions occur when the mean photosynthetically available radiation (PAR) over the mixed layer reach the same threshold of $2.5 \text{ mol photon m}^{-2} \text{ d}^{-1}$, suggesting that light-mixing regime was the main driver of the bloom onset in the whole LS basin (Lacour et al., 2015).

All these studies, using the critical depth hypothesis showed that over the LS the onset of the spring bloom is highly sensitive to the light availability and the depth of the mixed layer. However, Townsend et al. (1994) reported blooms in North Atlantic waters weeks before the shoaling of the mixed layer. The authors suggested that in presence of a very calm period (i.e., relaxation of atmospheric forcing), a near-surface bloom could occur without stratification. Recent observations showed evidence for widespread winter (January–March) phytoplankton blooms in a large part of the North Atlantic sub-polar gyre triggered by prolonged periods of calm (Lacour et al., 2017). Probably, these periods of calm combined with the phytoplankton cells ability to control buoyancy can maintain phytoplankton stock in the upper water column (Lindemann and St. John, 2014). Numerical simulations also suggest that a net positive phytoplankton population growth in a deep mixed layer is possible when turbulence levels are not too strong and/or possibly close to a critical threshold to maintain phytoplankton in the well-lit zone (Ghosal and Mandre, 2003; Huisman et al., 2002).

Recently, vertical profiles from different Biogeochemical-Argo (BGC-Argo) floats that sampled the waters of the subpolar North Atlantic revealed unequivocally that phytoplankton populations start growing in early winter but at very weak rates (Mignot et al., 2018). However, the period of explosive population growth (i.e., the so-called spring bloom phase) is not observed until spring, when atmospheric cooling subsides and the mixed layer shoals (Mignot et al., 2018).

While the weak accumulation of phytoplankton in winter has no surface signature (Ferrari et al., 2015; Mignot et al., 2018) the onset and magnitude of the spring bloom can be intercepted and monitored by satellite remote sensing of ocean color measures. Recently, Ferrari et al. (2015) used satellite data to show that over the subpolar North Atlantic the cooling-to-heating shift in air-sea heat fluxes (the so-called convection shutdown hypothesis) is a robust indicator of surface blooms. Using the air-sea heat fluxes to estimate when the mixing layer shoals, the authors demonstrated that the spring bloom onset is triggered by a reduction in turbulent mixing due to an increase in net warming at the end of winter.

Although previous studies have examined the role of convective mixing in spring blooms of the North Atlantic, none of these specifically focus on the LS (e.g., Ferrari et al., 2015), one of the few marine regions where open-ocean deep convection occurs. The goal of this study is therefore to test for the first time if the shutdown of winter convective mixing could be, on an inter-annual scale, a more suitable predictor for the spring bloom onset within the heterogeneous LS, a basin which hosts pronounced seasonal growth cycles of phytoplankton. Additionally, this study also investigates the role of the upper-ocean stratification in triggering the surface spring bloom. To achieve the aforementioned objectives, we used a biogeographic-based approach (based on satellite-derived ocean color observations) in conjunction with simulated data from a state-of-the-art ocean general circulation model to identify region-specific physical determinants for the spring bloom initiation. The rationale is that spurred on by a dominant forcing mechanism, interactions among algal growth dynamics and the physical environment may vary across sub-regional spatial scales. Therefore, the best way to compare timing of events is to use a cross-region and inter-annual analysis. Knowing the role of blooms in drawing down atmospheric carbon dioxide and its importance in food web interactions, a better understanding of the mechanisms governing the timing of the LS’s spring bloom is of particular relevance.

2. Methods and data

2.1. Satellite Chlorophyll-*a* time series

The area lying between 67°N – 52°N and 65°W – 42°W was selected to study the inter-annual variability in phytoplankton bloom onset over the LS (Fig. 1A). Daily time series (from 1998 to 2015) of surface satellite-derived chlorophyll-*a* (mg m^{-3}) at 25 km ($\sim 0.25^\circ$) of spatial resolution were obtained from the GlobColour Project (<http://hermes.acri.fr>). The surface chlorophyll-*a* values are gathered by using the Garver-Siegel-Maritorena (GSM) model (Maritorena et al., 2002) combining, when possible, data from different sensors (i.e., SeaWiFS, MERIS, MODIS and VIIRS), and ultimately providing a merged product with elevated spatiotemporal coverage (Maritorena et al., 2010). The GlobColour dataset is a common and appropriate choice for phytoplankton phenology studies despite data gaps due to cloud cover (e.g., Cole et al., 2015). Additionally, the dataset performs relatively well when compared with the SeaWiFS Bio-optical Archive and Storage System (SeaBASS) database and other *in situ* datasets (see Cole et al., 2015, and the references therein).

In order to facilitate comparison with the model output time-series (see Section 2.4), the daily images of chlorophyll-*a* were averaged on a pixel-by-pixel basis (by using the geometric mean that is less affected by extreme value than the arithmetic mean) to create a 10-day composite time-series. The latter, was useful to minimizing data gaps while

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