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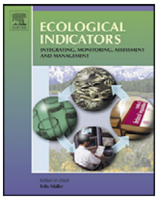

Phytoplankton phenology in the global ocean

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ABSTRACT

In recent years, phytoplankton phenology has been proposed as an indicator to monitor systematically the state of the pelagic ecosystem and to detect changes triggered by perturbation of the environmental conditions. Here we describe the phenology of phytoplankton growth for the world ocean using remote-sensing ocean colour data, and analyse its variability between 1998 and 2007. Generally, the tropics and subtropics present long growing period (≈15–20 weeks) of low amplitude (<0.5 mg Chl m^{-3}), whereas the high-latitudes show short growing period (<10 weeks) of high amplitude (up to 7 mg Chl m^{-3}). Statistical analyses suggest a close coupling between the development of the growing period and the seasonal increase in insolation in the North Atlantic and Southern Ocean. In the tropics and subtropics, variability in light is low, and the growing period is controlled by nutrient supply occurring when mixing increases. Large interannual variability in the duration of the growing period is observed over the decade 1998–2007, with positive anomalies following the major 1997–1998 El Niño-La Niña events, and generally negative anomalies from 2003 to 2007. Warmer Sea-Surface Temperature (SST) over the duration of the growing period is associated with longer duration at high-latitudes indicating an extension of the growing period over summer months. The opposite is observed in the tropics and subtropics, where the duration is shorter when the SST is warmer, indicating increased stratification. Positive phases of North Atlantic Oscillation and Southern Annular Mode and negative phases of Multivariate El Niño-Southern Oscillation index (El Niño conditions), associated with enhanced water mixing and nutrients supply, generally sustain longer growth. On the basis of the results, perspectives are drawn on the utility of phenology as an organising principle for the analysis of pelagic ecosystem.

1. Introduction

In the global ocean, phytoplankton growth conditions are controlled by regional and seasonal changes in physical forcings (such as sea-surface temperature, winds, cloud cover and precipitations), which are in turn forced by climatic patterns. Large-scale climate patterns are characterised by indices of climatic modes such as the Multivariate El Niño Southern Oscillation (ENSO) index, the North Atlantic Oscillation and the Southern Annular Mode. Properties of the pelagic ecosystem are affected by the variability of such climatic modes, through changes in phytoplankton abundance and community composition (Chavez et al., 1999; Lomas and Bates, 2004; Leterme et al., 2005), integrated primary production (Bates, 2001; Turk et al., 2001; Behrenfeld et al., 2001, 2006), grazer abundance and community composition (Beaugrand and Reid, 2003; Chiba et al., 2008), and higher trophic level community composition (Chavez et al., 2003).

To allow regional and interannual comparison of the effect of changes in physical forcing or climatic modes on the pelagic ecosystem, ecological indices have been developed. Ecological indices are quantitative metrics of the pelagic ecosystem introduced as objective alternatives to more subjective concepts such as ecosystem health, vigour and resilience (Platt and Sathyendranath, 2008). The indices must therefore be comparable between years and sites because of the large spatial and temporal variability in the annual cycle of phytoplankton biomass. One systematic approach to characterise the phytoplanktonic ecosystem is to quantify phytoplankton phenology. Phenology relates to the study of the timing of periodic biological events as influenced by the environment (Schwartz, 2003). The development of phytoplankton population is treated as the phytoplankton growing period. Phenologically important phases of the phytoplankton growth include: (1) the

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time of initiation b_i; (2) the time of maximum amplitude b_t; (3) the time of termination b_e; and (4) the duration b_d.

Remotely sensed data (especially ocean-colour and Sea Surface Temperature), available continuously since 1997 at high spatial (1 km) and temporal resolution (daily), allow to monitor closely the annual cycle of phytoplankton biomass (estimated in chlorophyll units) along with changes in temperature. Analysis of large-scale, interannual and decadal variability in phytoplankton phenology is then possible, but has been investigated to date at only the local to regional scale. In the North Atlantic, the latitudinal progression of the spring bloom was shown to follow the increase in insolation and the time of bloom initiation to extend over almost 5 months, from January in the subtropics to May in the subpolar region (Siegel et al., 2002). Interannual variability in the timing of initiation of the spring bloom in the Irminger Basin and in the Japan Sea was related to the preceding winter's average wind speed and net heat flux (Henson et al., 2006; Yamada and Ishizaka, 2006). Decadal (1997–2009) estimations of the timing of peak chlorophyll *a* showed significant trends toward earlier bloom in boreal North Pacific and in part of the Arctic, whereas in the North Atlantic, blooms showed a delay in the trend (Kahru et al., 2011). The particularly strong periodicity in the bloom timing in the subpolar region of the North Atlantic correlated positively with the North Atlantic Oscillation (NAO) index (Henson et al., 2009). A considerable degree of interannual and spatial variability was observed in the timing of events in the North-West Atlantic Shelf (Platt et al., 2009; Zhai et al., 2011). For the pelagic ecosystem, the variability in timing of onset has a critical importance to the survival and recruitment of fish and invertebrate populations (Platt et al., 2003; Edwards and Richardson, 2004; Koeller et al., 2009).

Several different methods have been developed to investigate phytoplankton phenology and especially to estimate the time of initiation b_i from *in situ* and remotely sensed observations of chlorophyll concentration in marine or freshwater ecosystems. Generally, the choice of method has depended on the shape of the phytoplankton growth (exponential or not) and the sampling frequency. Conventionally, the methods involve: (1) estimating the inflexion points (Rolinski et al., 2007; Wiltshire et al., 2008); (2) fitting a density function such as the Weibull or Gaussian distribution (Platt et al., 2003, 2009; Yamada and Ishizaka, 2006; Rolinski et al., 2007) or the Generalised Linear Model (Vargas et al., 2009); or (3) defining a fixed or relative threshold chlorophyll level (Siegel et al., 2002; Fleming and Kaitala, 2006; Henson et al., 2006; Platt et al., 2009; Zhai et al., 2011). The relative threshold method is particularly suitable for work on a global scale because it encompasses the large variability of shapes in the phytoplankton growth. Using interannual remotely sensed chlorophyll data, Siegel et al. (2002) proposed the median chlorophyll plus 5% as a reasonable index for bloom initiation for the North Atlantic. In this region, the authors observed little quantitative differences in the resulting computation when varying the threshold from 1 to 30%. Henson et al. (2006) applied the median plus 5% threshold in the Irminger Basin. They demonstrated basin-scale coherence in b_i and the timing of mixed-layer stratification. Thomalla et al. (2011) also applied the median plus 5% threshold to examine the regional characteristics of the seasonal cycle of phytoplankton biomass in the Southern Ocean. After fitting a shifted-Gaussian curve to the chlorophyll data on the Scotian Shelf, Platt et al. (2009) and Zhai et al. (2011) defined a relative threshold for initiation as the time when the amplitude of the fitted curve reached 20% of the maximum amplitude of the Gaussian. In the present study, the relative threshold of Siegel et al. (2002) (i.e. median plus 5%) is selected because of its pertinence on global scale and its direct applicability to remotely sensed chlorophyll data. The termination of the growing period is estimated using the same threshold as the initiation. The growing period can therefore be approximated as the duration during which the chlorophyll concentrations remain above the threshold. The phytoplankton growth is characterised by more or less rapid and intense changes in biomass and presents different shapes throughout the global ocean. The most rapid and intense increase in biomass are defined as the bloom (Sverdrup, 1953; Cushing, 1959; Yoder et al., 1993) and occur at high-latitude and upwelling regions. These regions, and especially in the Northern Hemisphere, have been the main focus in the literature on phytoplankton phenology (Ji et al., 2010). Phenology remains to be assessed in the less productive, but not less important, permanently stratified regions representing 74% of the global ice-free ocean (Behrenfeld et al., 2006). Here, a decade of remotely sensed ocean-colour data from 1998 to 2007 are used to: (1) describe the regional and interannual variability in phytoplankton phenology for the global ocean; and (2) explore the relationships between the phenology of phytoplankton growth and the changes in climate and physical conditions.

Table 1
Ecological and physical indices developed and adapted from Platt and Sathyendranath (2008). Indices are derived from remotely sensed radiances in the visible (ocean colour) and infra-red (SST) spectra.

Index	Label	Units
Initiation of growing period	b_i	week
Timing of maximum amplitude	b_t	week
Termination of growing period	b_e	week
Duration of growing period	b_d	weeks
Amplitude of growing period	b_a	mg m^{-3}
Average chlorophyll *a* over duration	b_s	mg m^{-3}
PAR at initiation of growing period	l_i	mol photon m^{-2} d^{-1}
PAR at termination of growing period	l_e	mol photon m^{-2} d^{-1}
Average PAR over duration	l_d	mol photon m^{-2} d^{-1}
SST at initiation of growing period	t_i	°C
SST at termination of growing period	t_e	°C
Average SST over duration	t_d	°C

2. Data and methods

2.1. The remotely sensed data

NOAA Optimum Interpolation Sea-Surface Temperature (SST) V2 weekly data products were downloaded on a one-degree global grid from the National Oceanic-Atmospheric Administration/Office of Oceanic and Atmospheric Research/Earth System research Laboratory at http://www.cdc.noaa.gov/ for the period 1998–2007.

The Sea-viewing Wide Field-of-view Sensor (SeaWiFS) weekly level 3 data of chlorophyll *a* and Photosynthetically Active Radiation (PAR) with a global area coverage at 9-km resolution were retrieved from http://oceancolor.gsfc.nasa.gov/ for the period 1998–2007. The reprocessing of 2009 for SeaWiFS data was used. To estimate the timing of various ecological events, gaps were eliminated from the time series. Missing values were filled by interpolating spatially adjacent values (average of 3 × 3 pixels on the 9-km grid), when these were available. Any remaining missing values were filled by interpolating temporally adjacent values (average of previous and following weeks), when these were available. Otherwise the value was not filled. A 3-week running mean was applied to remove small peaks in chlorophyll *a*. To remain coherent with the spatial resolution of the SST data, chlorophyll and PAR data were then averaged to one-degree resolution.

2.2. Ecological and physical indices

The ecological indices considered in this paper are summarised in Table 1. The timings of initiation (b_i) and termination (b_e) of the phytoplankton growth were detected as the weeks when the chlorophyll concentration in a particular year rose above the long-term median value plus 5% and later fell below this same