

ANNUAL CYCLES OF ECOLOGICAL DISTURBANCE AND RECOVERY UNDERLYING THE SUBARCTIC ATLANTIC SPRING PLANKTON BLOOM

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Key Points (3):

1. Satellite- and model-derived annual cycles in subarctic Atlantic plankton properties reveal blooms as consequences of subtle imbalances of food web equilibria.
2. Late autumn/early winter deepening of the mixed layer plays a critical role in bloom initiation, with deeper winter mixing yielding larger water column inventories of phytoplankton.
3. Climate-driven reductions in winter mixing may dampen subarctic Atlantic plankton cycles.

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Abstract

Satellite measurements allow global assessments of phytoplankton concentrations and, from observed temporal changes in biomass, direct access to net biomass accumulation rates (r). For the subarctic Atlantic basin, analysis of annual cycles in r reveal that initiation of the annual blooming-phase does not occur in spring after stratification surpasses a critical threshold, but rather in early winter when growth conditions for phytoplankton are deteriorating. This finding has been confirmed with *in situ* profiling float data. The objective of the current study was to test whether satellite-based annual cycles in r are reproduced by the Biogeochemical Element Cycling - Community Climate System Model and, if so, to use the additional ecosystem properties resolved by the model to better understand factors controlling phytoplankton blooms. We find that the model gives a similar early onset time for the blooming phase, that this initiation is largely due to the physical disruption of phytoplankton-grazer interactions during mixed layer deepening, and that parallel increases in phytoplankton specific division and loss rates during spring maintain the subtle disruption in food web equilibrium that ultimately yields the spring bloom climax. The link between winter mixing and bloom dynamics is illustrated by contrasting annual plankton cycles between regions with deeper and shallower mixing. We show that maximum water column inventories of phytoplankton vary in proportion to maximum winter mixing depth, implying that future reductions in winter mixing may dampen plankton cycles in the subarctic Atlantic. We propose that ecosystem disturbance-recovery sequences are a unifying property of global ocean plankton blooms.

1. Introduction

High-latitude oceans experience strong seasonal variability in environmental conditions and can express large-amplitude plankton cycles with major seasonal blooms [Longhurst, 2007]. While representing less than one-third the global area occupied by the permanently-stratified tropical and subtropical biomes, these high-latitude regions support many of the Earth's productive fisheries and play a critical role in the ocean-atmosphere exchange of CO₂ [Takahashi *et al.*, 2009; Chassot *et al.*, 2010]. Potential impacts of climate warming on high-latitude marine ecosystems are thus an issue of significant ecological concern.

The subarctic Atlantic is a classic example of a seasonally-varying plankton ecosystem, with a late-spring climax in phytoplankton concentration that is amongst the most conspicuous biological events annually recorded by global satellite ocean observations (Figure 1a). Initiation of this bloom is traditionally viewed as occurring when springtime solar radiation levels are sufficiently high and surface layer mixing depths are sufficiently shallow that phytoplankton division rates can first overcome grazing and other losses [Sverdrup, 1953; Siegel *et al.*, 2002]. This 'bottom-up' view thus focuses on resources regulating phytoplankton specific cell division rates, rather than factors influencing loss rates.

One of the challenges in understanding bloom initiation is that historic field data in the subarctic Atlantic have been temporally biased, favoring the late spring period of maximum phytoplankton concentration. Without adequate coverage of the late-autumn to early-spring transition period, it is difficult to effectively evaluate the bloom initiation event - i.e., the point in time when phytoplankton specific division rates first overcome loss rates [Sverdrup, 1953].

Satellite measurements continuously monitor global plankton populations, but retrieved properties are largely limited to standing stocks. However, temporal changes in stocks permit one of the only direct satellite assessments of an ecological *rate*; the net population accumulation rate, r (i.e., the specific rate of change in biomass). By evaluating annual cycles in satellite-observed r , *Behrenfeld* [2010] showed that mixed layer biomass first begins accumulating in the subarctic Atlantic in late-autumn or early-winter when growth conditions for phytoplankton are deteriorating and approaching their worst. These findings challenged traditional ‘bottom-up’ notions of the bloom by showing that initiation occurs when phytoplankton specific division rates (μ) are declining (rather than increasing) and that, throughout the blooming period, changes in μ are not reflected by similar changes in r . It was therefore proposed that bloom dynamics reflect subtle disruptions in the balance between phytoplankton division and loss rates and that these disruptions are initiated largely by physical dilution effects during mixed layer deepening. This view was termed the ‘dilution-recoupling hypothesis’ [*Behrenfeld*, 2010].

To further test the satellite-based results, *Boss and Behrenfeld* [2010] examined two years of optical profiling float data from the subarctic Atlantic (blue star in Figure 1a). These *in situ* data confirmed the earlier finding that mixed layer biomass begins accumulating during autumn/winter mixed layer deepening (i.e., prior to springtime restratification) and demonstrated that satellite retrievals of net population accumulation rates are not compromised by uncertainties in phytoplankton vertical structure over the blooming phase of the annual cycle.

Objectives of the current study were two-fold. First, we wished to evaluate whether key features in the annual cycle of subarctic Atlantic phytoplankton observed by satellite [*Behrenfeld*, 2010] are reproduced by an established global-scale ocean ecosystem model.

For this exercise, we employed the Biogeochemical Element Cycling - Community Climate System Model (BEC-CCSM) [Doney *et al.*, 2009a] and divided the satellite and model data for the subarctic Atlantic basin into fourteen 5° latitude by 10° degree longitude bins (Fig. 1a). Twelve of these bins are identical to those used in *Behrenfeld* [2010]. Our second objective, assuming the first evaluation proved successful, was to use the detailed characterization of ecosystem interactions in the BEC-CCSM to further investigate the underpinnings of the subarctic Atlantic bloom, from initiation to climax, in the context of its temporal evolution as a coupled physical-ecological system.

Our analysis shows that the BEC-CCSM gives an early-winter onset for the blooming phase of the annual cycle that is similar to satellite results. This initiation is strongly influenced by the physical disruption of phytoplankton-grazer interactions associated with a rapidly deepening mixed layer. We find that the extent of this disruption is proportional to the depth of winter mixing, implying that reduced winter mixing associated with climate warming may dampen high-latitude plankton cycles. During the restratification period, improvements in light conditions help prolong the bloom through the spring by allowing phytoplankton specific division rates to slightly outpace rapidly increasing loss rates. Our results emphasize that phytoplankton blooms cannot be interpreted as a simple consequence of a single growth-regulating factor such as light, but rather are expressions of slight ecosystem imbalances that are tightly coupled with variability in the physical environment.

2. Methods

For this study, treatment of satellite data and binning over the subarctic Atlantic basin were nearly identical to that in *Behrenfeld* [2010] and only minor modifications were made to the BEC-CCSM.

The following sections provide a brief overview of our methods and describe any changes made from previous analyses. Additional details on methods can be found in the cited publications and in the auxiliary material accompanying this manuscript.

2.1 Satellite data analysis

Seasonal cycles in North Atlantic phytoplankton were investigated using 8-day resolution remote sensing data from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) [McClain, 2009]. Our analysis deviates from that of *Behrenfeld* [2010] in that: (1) the satellite time series was extended to the period January 1998 to December 2007, (2) we added 2 North Atlantic bins (B-04 and B-11; Figure 1a) that were not included in the earlier study, and (3) the SeaWiFS data employed in the current study were from an additional 2011 reprocessing of the full SeaWiFS data set (see <http://oceancolor.gsfc.nasa.gov>). As in the earlier study, the 5° latitude by 10° degree longitude bins are defined to avoid continental margins (except bin B-11) and to minimize the influence of advection (relative to processes occurring within a bin) between 8-day periods while still capturing spatial variability in phytoplankton seasonal properties. The lowest latitude bins (B-01 to B-04) lie between 40°N and 45°N. In the northern-most bins (B-08 to B-14), satellite data are unavailable for a few weeks each year during midwinter due to high solar zenith angles and low illumination. For orientation in figure 1a, the site of the Joint Global Ocean Flux Study - North Atlantic Bloom Experiment (JGOFS-NABE) [Ducklow and Harris, 1993] is indicated by a white star, the North Atlantic Bloom 2008 study (NAB08) [Mahadevan *et al.*, 2012] is marked by a pink star, and the profiling float study of *Boss and Behrenfeld* [2010] is shown by a blue star.

Satellite products used as indices of phytoplankton abundance were surface chlorophyll concentration, [Chl] (mg m^{-3}), from the NASA standard OC4-V6 algorithm (the most familiar product to SeaWiFS users) and phytoplankton carbon concentration, [C_{phyto}] (mmol m^{-3}),

calculated using the particulate backscattering coefficient at 443 nm from the Garver-Siegel-Maritorena (GSM) algorithm [Garver and Siegel, 1997; Maritorena et al., 2002] and following the $[C_{\text{phyto}}]$ algorithm of Behrenfeld et al. [2005] and Westberry et al. [2008].

Depth-integrated carbon and chlorophyll inventories (i.e., ΣC_{phyto} and ΣChl), specific rates of biomass accumulation (r), and phytoplankton specific division rates (μ) were assessed following Behrenfeld [2010] and Boss and Behrenfeld [2010]. Briefly, ΣC_{phyto} and ΣChl were calculated as the product of measured surface concentration and the greater of MLD or euphotic depth (Z_{eu}), where Z_{eu} was calculated following Morel and Berthon [1989]. This assessment assumes uniform phytoplankton properties within an active mixing layer. This assumption is supported by *in situ* measurements during the late autumn-through-spring period when MLD exceeds Z_{eu} [Townsend et al., 1992; Ward and Waniek, 2007; Boss et al., 2008]. In the recent study of Boss and Behrenfeld [2010], two years of continuous profiling optical float data in the subarctic Atlantic showed that measured phytoplankton properties integrated through the mixed layer were closely approximated by the product of surface chlorophyll or carbon concentration and MLD over the autumn through spring period. This uniformity results from mixed layer transit times of a few days or less [Backhaus et al., 2003; D'Asaro, 2008]. In contrast to the autumn-through-spring period that is central to the current investigation of the subarctic Atlantic bloom, Z_{eu} typically exceeds MLD between roughly June and October (e.g., figure 4 in Behrenfeld [2010] and figure 3 in Boss and Behrenfeld [2010])). Under these conditions, phytoplankton properties below the mixed layer, but still within the euphotic zone, can be significantly different from those within the mixed layer. This situation can lead to errors when extrapolating surface properties to depth. However, this vertical structure in phytoplankton biomass has little impact on conclusions of the current study regarding the late autumn-through-spring blooming period.

As described in *Behrenfeld* [2010], understanding bloom dynamics requires an evaluation of the balance between phytoplankton division (μ) and loss (l) rates within the mixed layer. The difference between these two rates defines r (i.e., $r = \mu - l$), where a positive value for r indicates an increasing phytoplankton population and a negative value indicates a decreasing population.

When evaluating r from observed temporal changes in $[Chl]$ or $[C_{phyto}]$, it is important to consider whether the mixed layer is deepening or shoaling. Specifically, if light and nutrient conditions in the mixed layer allow μ to exceed l and the mixed layer depth is constant or shoaling, then phytoplankton concentration ($mg\ m^{-3}$) will increase over time. Under such conditions, the specific rate of biomass accumulation (r) can be calculated from two measures of biomass concentration (C_0, C_1) separated by a period of time ($\Delta t = t_1 - t_0$) following:

$$r = \ln(C_1/C_0)/\Delta t. \quad (1)$$

This scenario is similar to calculating μ for a laboratory phytoplankton culture where the volume of the culture is either held constant or decreases (for example, if samples are removed) between t_0 and t_1 . Equation 1, however, does not permit an accurate assessment of r if the mixed layer is deepening. Specifically, if we assume that light and nutrient conditions allow the same excess of μ over l (i.e., the same r) but that mixed layer deepening dilutes the phytoplankton population with plankton-free water from below, then the observed change in phytoplankton concentration from t_0 to t_1 will be smaller than the previous scenario (i.e., a fixed or shrinking volume) and may even decrease if the dilution effect is strong enough. Under these conditions, retrieval of r requires accounting for the change in volume (V) within which the phytoplankton population is suspended during t_0 to t_1 (i.e., V_0 and V_1 , respectively).

Thus, modifying equation 1 to account for the purely physical effects of dilution gives:

$$r = \ln[(C_1 V_1)/(C_0 V_0)]/\Delta t. \quad (2)$$

Application of equation 2 for the mixed layer deepening scenario is similar to calculating μ for a laboratory phytoplankton culture that is being diluted between t_0 and t_1 , with the extreme case being a chemostat culture where a rapidly growing population is held at a constant concentration by equally rapid dilution. If equation 2 is also applied to a phytoplankton population in a fixed or shoaling mixed layer (the earlier scenario), then the resultant values of r would not only reflect the balance between μ and l within the mixed layer, but would also include losses due to detrainment from the mixed layer (a purely physical process).

In summary, r is calculated from satellite data using equation 2 when the volume of the actively growing phytoplankton population is being expanded by mixed layer deepening and the newly entrained water is relatively phytoplankton free. This condition occurs in the subarctic Atlantic in the late autumn and winter when the MLD $> Z_{eu}$. During springtime mixed layer shoaling, equation 1 is used to assess r , which allows the ecological processes regulating the dynamic balance between mixed layer μ and l to be isolated from the purely physical effects of detrainment. Finally, in the summer and early autumn period where the mixed layer is deepening but still shallower than Z_{eu} , the newly entrained water from depth is not plankton free. If the phytoplankton concentration in the entrained deep water is equal to that in the mixed layer, then equation 1 can be used to assess r . As the actual phytoplankton concentration below the mixed layer is not known, this approach imparts an uncertainties in retrieved r , but this uncertainty has no impact on our conclusions regarding the winter-spring bloom in the subarctic Atlantic.

In summary, r was calculated from 8-day resolution SeaWiFS data for each North Atlantic bin following:

$$r = \ln(\Sigma C_{\text{phyto}-1} / \Sigma C_{\text{phyto}-0}) / \Delta t, \text{ if MLD is deepening and } > Z_{\text{eu}}, \quad (3)$$

$$r = \ln([C_{\text{phyto}-1}] / [C_{\text{phyto}-0}]) / \Delta t, \text{ if MLD is shoaling or } < Z_{\text{eu}}, \quad (4)$$

where $[C_{\text{phyto}-0}]$ and $\Sigma C_{\text{phyto}-0}$ are phytoplankton carbon concentration and inventory, respectively, at t_0 , $[C_{\text{phyto}-1}]$ and $\Sigma C_{\text{phyto}-1}$ are phytoplankton carbon concentration and inventory, respectively, at t_1 , $\Delta t = t_1 - t_0 = 8$ days, and r is the average specific rate of biomass accumulation between time-points t_0 and t_1 . This approach is identical to that used in *Behrenfeld* [2010] and *Boss and Behrenfeld* [2010].

Phytoplankton specific division rates (μ) were calculated as water column-integrated daily net primary production (NPP) divided by ΣC_{phyto} . NPP was calculated from SeaWiFS data at 8-day resolution using the Vertically Generalized Production Model (VGPM) [*Behrenfeld and Falkowski*, 1997], where the maximum daily chlorophyll-specific light-saturated photosynthetic rate (P_{opt}^b) was described as an exponential function of SST [*Morel*, 1991; *Campbell et al.*, 2002; *Carr et al.*, 2006; *Behrenfeld*, 2010].

Our analysis also employed data on incident surface photosynthetically active radiation (PAR), sea surface temperature (SST), and mixed layer depth (MLD). PAR data are SeaWiFS cloudiness-corrected values. SST data are from the Moderate-resolution Imaging Spectrometer (MODIS) and the Advanced Very High Resolution Radiometer (AVHRR) (<http://web.science.oregonstate.edu/ocean.productivity>).

PAR and SST data are from the NASA Ocean Color website (oceancolor.gsfc.nasa.gov/). MLD values were from the Fleet Numerical Meteorology and Oceanography Center (FNMOC) model [Clancy and Sadler, 1992] and the Simple Ocean Data Assimilation (SODA) model, where MLD was defined as the first depth where density is 0.125 kg m^{-3} greater than the surface value. This MLD criterion does not account for short-term periods of low turbulence during the spring stratification period, but these transient events are not critical to bloom development [Mahadevan *et al.*, 2012] nor during convective deepening the mixed layer in the late-autumn, early-winter period of bloom initiation. The merged FNMOC and SODA data sets are described in detail and downloadable at www.science.oregonstate.edu/ocean.productivity. These MLD data are based on model estimates tuned to available *in-situ* data (i.e., they are ‘data-assimilating models’). As described below (see section 2.2), the BEC-CCSM also generates MLD estimates, but in this case the data are not tuned to *in situ* measurements. Nevertheless, spatial and temporal variations in MLD are similar to those from the data assimilating FNMOC and SODA estimates. All satellite-based properties requiring MLD estimates used FNMOC and SODA data, while all BEC-CCSM properties requiring MLD estimates used MLD data from the model. In the results section, MLD estimates from the data assimilating models are shown in figures 1b, 3b, and 5a, while MLD data from the BEC-CCSM are shown in figures 3b, 4a, and 5b.

2.2. The Hindcast Global Ocean Ecosystem-Biogeochemistry Simulation

2.2.1 Ecosystem-Biogeochemistry Module

The Biogeochemical Element Cycling-Community Climate System Model (BEC-CCSM) [Doney *et al.*, 2009a] is cast as a set of three-dimensional, time-varying advection diffusion equations for a suite of tracers, C:

$$\frac{\partial C}{\partial t} + \nabla \cdot (\bar{v}C) - \nabla \cdot (K \nabla C) = RHS_{bio}^C \quad (5)$$

The physical transport is partitioned into resolved advection and parameterized eddy mixing terms. All of the ecological-biogeochemical source/sink terms and surface and sediment fluxes are grouped into the right hand side term, RHS_{bio} . The marine ecosystem module incorporates multi-nutrient limitation (N, P, Si, and Fe) on phytoplankton division and specific phytoplankton functional groups [Moore *et al.*, 2002; Moore *et al.*, 2004]. Model equations and parameters are provided in Table S1 in the auxiliary material.

There are fourteen main model compartments: small pico/nano-plankton, diatoms, diazotrophs, zooplankton, suspended and sinking particulate detritus, and dissolved nitrate, ammonia, phosphorus, iron, silicate, oxygen, dissolved inorganic carbon, and alkalinity. The pico/nanoplankton size class is designed to replicate the rapid and highly efficient nutrient recycling found in many subtropical, oligotrophic (low nutrient) environments. Diatoms model a larger, bloom-forming size class. Phytoplankton division rates are determined by available light and nutrients using a modified form of the *Geider et al.* [1998] dynamic growth model.

Photoacclimation is parameterized with dynamically adaptive Chl:C ratios. The diazotrophs fix all required nitrogen from N_2 gas. Calcification is parameterized as a fraction of the pico/nanoplankton production and described as a function of temperature and nutrients adapted for coccolithophores. Size-structure effects are included by varying key zooplankton (e.g., partitioning of fecal pellets between suspended and sinking detritus), depending on the food source [Lima and Doney, 2004]. Many of the biotic and detrital compartments contain multiple elemental pools, in addition to carbon, to track flows through the ecosystem. The model has one adaptive zooplankton class that grazes on phytoplankton and large detritus.

The biogeochemistry module [Doney *et al.*, 2009b] is based on an expanded version of the Ocean Carbon Model Intercomparison Project biotic model [Najjar *et al.*, 2007]. The module includes full carbonate system thermodynamics and air-sea CO₂ and O₂ fluxes. Gas transfer velocities are computed from the 6-hourly NCEP winds (<http://www.cdc.noaa.gov/cdc/reanalysis/reanalysis.shtml>) using the quadratic wind speed relationship of Wanninkhof [1992]. A dynamic iron cycle is incorporated with atmospheric dust deposition, water-column scavenging, and a continental sediment source [Moore *et al.*, 2006a; see also Moore and Braucher [2008] for a discussion on refinements of continental sediment source]. Denitrification is simulated in oxygen minimum zones following Moore and Doney [2007], and subsurface particle remineralization is parameterized by incorporating the mineral ballast arguments of Armstrong *et al.* [2002]. Our 3-D implementation of the ecosystem model equations and parameters follow those of Moore *et al.* [2004] with the following modifications: (1) incorporation of water column denitrification [Moore *et al.*, 2006a], (2) adjustments in iron dynamics and scavenging parameters [Moore *et al.*, 2006a; Moore and Braucher, 2008], and (3) inclusion of a temperature dependence for the phytoplankton linear mortality coefficient following a Q10 functional form [Eppley, 1972]:

$$\ell(T) = \ell(T_{ref}) 2.0^{0.1(T-T_{ref})} \quad (6)$$

The same form and parameter value is used for the temperature dependence of modeled phytoplankton and zooplankton growth and zooplankton mortality. The phytoplankton mortality temperature dependence was added to improve the simulated phytoplankton seasonal cycle compared to the results reported in Doney *et al.* [2009b].

2.2.2 Atmospheric Forcing and Ocean Physical Hindcasts

The Parallel Ocean Program (POP) is a z-level, hydrostatic, primitive equation model integrated here with a resolution of 3.6° in longitude, 0.8° to 1.8° in latitude, and 25 vertical levels (CCSM-3 low resolution ocean model, *Yeager et al.* [2006]). Effects of mesoscale eddy transport are parameterized according to *Gent and McWilliams* [1990]. The *Large et al.* [1994] K-Profile Parameterization is implemented in the vertical to capture surface boundary-layer dynamics and interior diapycnal mixing. The historical simulation (1958-2006) is integrated with air-sea heat, freshwater, and momentum fluxes derived from a bulk flux forcing method using atmospheric forcing data from Co-ordinated Ocean-Ice Reference Experiments, Corrected Interannual Forcing Version 2 available from (<http://data1.gfdl.noaa.gov/nomads/forms/mom4/COREv2.html>) [*Large and Yeager*, 2009]. *Doney et al.* [2007] present a quantitative skill assessment of the ocean physical solutions in terms of interannual variability of temperature, sea surface height, and circulation. Mineral aerosol deposition to the ocean is simulated using a 3-D atmospheric chemical transport model [*Luo et al.*, 2003; *Mahowald et al.* 2003] based on National Centers for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) reanalysis [*Kistler et al.*, 2001].

Initial conditions for the 3-D ocean nutrient and inorganic carbon variables are prescribed from data based climatologies (e.g., *Key et al.*, [2004]). The ecological-biogeochemical simulation is spun-up for several hundred years, prior to initiating the interannual varying forcing, using a repeat annual cycle of physical forcing and dust deposition. The model ecosystem components converge to a repeat annual cycle within a few years of spin-up. The full interannual variability in physics is initiated in a model year equivalent to calendar year 1958 and then integrated forward through 2006.

Projections of future changes in ocean mixed layer depth for the 21st century are derived from the Community Climate System Model version 4 (CCSM4), a fully-coupled global climate model consisting of land, atmosphere, ocean, and sea-ice components [Gent *et al.*, 2011]. State information and fluxes are exchanged between components daily via a coupler. The full system conserves mass and energy. The ocean component of CCSM4 is the Parallel Ocean Program version 2 (POP2), a z-level, hydrostatic, primitive equation model integrated with a nominal horizontal resolution of $1^\circ \times 1^\circ$ and 60 vertical levels with grid spacing of 10 m in the upper 160 m increasing to 250 m at depth [Danabasoglu *et al.*, 2012]. Mesoscale eddy transport is parameterized according to Gent and McWilliams [1990] (GM), with a depth and time varying GM coefficient. Interior diapycnal mixing and boundary layer dynamics are represented using K-Profile Parameterization of Large *et al.* [1994]. The 21st century CCSM4 simulations are integrated following the protocol from the Climate Model Intercomparison Project CMIP5 [Taylor *et al.*, 2009], with prescribed atmospheric CO₂ from a high emissions scenario (RCP8.5). RCP stands for Representative Concentration Pathways, which are based on specified global radiative forcing levels (in this case +8.5 W/m² by 2100). Socio-economic and emissions scenarios have been constructed to match each RCP [Moss *et al.* 2010].

3. Results

3.1 Annual phytoplankton cycles in the subarctic Atlantic

The most dramatic attribute of a bloom is the high abundance of phytoplankton occurring at the final stage of the event, which is often quantified by the surface chlorophyll concentration (e.g., Figure 1a). These climax concentrations, however, are a consequence of phytoplankton accumulation over a prolonged ‘blooming-phase’.

Here, we define the blooming-phase of the annual cycle as the entire period of accumulating mixed layer phytoplankton biomass (i.e., positive values of r) leading up to the spring bloom climax.

Key features of the blooming-phase include (1) the timing of and environmental conditions at initiation (when r first becomes positive), (2) changes in vertically-integrated chlorophyll inventories (ΣChl ; mg m^{-2}) and surface chlorophyll concentrations ($[\text{Chl}]$; mg m^{-3}), and (3) the relationship between r and μ over the duration of the blooming period.

As an illustration of basic patterns in phytoplankton stocks for the subarctic Atlantic, Figure 1b shows the annual cycle in satellite-derived $[\text{Chl}]$ (solid black symbols) from the bin encompassing the JGOFS-NABE site (i.e., B-05; Figure 1a). Surface $[\text{Chl}]$ is lowest between roughly December and February when incident photosynthetically active radiation (PAR) is minimal and the mixed layer depth (MLD) is deepest (blue and green lines, respectively, in Fig. 1b lower panel). Values of $[\text{Chl}]$ increase through spring to a maximum around June. The subsequent demise of the bloom may coincide with depletion of surface nitrate (Figure 1b, red line), silicate [Mahadevan *et al.*, 2012], or iron [Moore *et al.*, 2006b; Blain *et al.*, 2004; Nielsdóttir *et al.*, 2009] or may result from overgrazing [Banse, 1992, 2002] or viral infection [Suttle *et al.*, 1990; Bratbak *et al.*, 1993; Baudoux *et al.*, 2006; Vardi *et al.*, 2009; Bidle and Vardi, 2011].

The annual cycle of ΣChl (Fig. 1b open symbols) differs substantially from that of $[\text{Chl}]$ and begins increasing in late autumn when incident light is approaching its annual minimum and the MLD is still deepening (Fig. 1b, lower panel). ΣChl is maximum prior to significant nutrient draw-down and then reaches a minimum during the low-nutrient, stratified summer months (Fig. 1b).

Annual cycles in [Chl] and ΣChl similar to those shown in figure 1b are found for all 14 subarctic Atlantic bins (Figure S1 in the auxiliary material). The same basic patterns are also observed in annual cycles of satellite-based phytoplankton carbon concentration ($[\text{C}_{\text{phyto}}]$; mmol m^{-3}) and carbon inventories ($\Sigma\text{C}_{\text{phyto}}$; mmol m^{-2}) (Figure S2 in the auxiliary material). Within a given bin, strong correlations are found for the 10 year satellite time series between [Chl] and $[\text{C}_{\text{phyto}}]$ (e.g., Figure S3a in the auxiliary material) and between ΣChl and $\Sigma\text{C}_{\text{phyto}}$ (e.g., Figure S3b in the auxiliary material). Equivalent correlations were shown in figure 1b of *Behrenfeld [2010]*, along with an evaluation of intra-bin variability at 8-day resolution.

3.2 Subtle food web disequilibria underlie blooms

The specific rate of change in biomass (r) is defined by the difference between specific division and loss rates (i.e., $r = \mu - l$). In some regions of the tropical and subtropical oceans, μ and l are perpetually balanced and phytoplankton abundance remains stable throughout the year (i.e., $r \approx 0 \text{ d}^{-1}$) [*Behrenfeld et al.*, 2005]. It has long been recognized that imbalances between μ and l at higher latitudes can cause phytoplankton abundances to accumulate and decrease in large-amplitude annual cycles [e.g., *Riley et al.*, 1949; *Sverdrup*, 1953; *Evans and Parslow*, 1985; *Frost*, 1987; *Banase*, 1992, 2002; *Longhurst*, 2007], but few studies have evaluated complete annual cycles in μ , l , and r . Both satellite data and BEC-CCSM output allow inspection of temporal variability in these three key rate terms for the subarctic Atlantic.

For the BEC-CCSM, μ is calculated from modeled light, nutrient, and temperature fields and l is separated into losses due to zooplankton grazing (l_{grazing}) and non-grazing mortality (e.g., senescence, viral lysis, aggregate sinking) rates (*Doney et al.* [2009a]; Methods section 2.2, Table S1 in the auxiliary material).

For SeaWiFS data, r is calculated from observed changes in $[C_{\text{phyto}}]$ and ΣC_{phyto} [Behrenfeld, 2010; Boss and Behrenfeld, 2010; Methods section 2.1]. Satellite data also allow calculation of μ as the biomass-specific net primary production rate [Behrenfeld, 2010; Methods section 2.1], which subsequently allows l to be estimated as $\mu - r$.

Again using bin B-05 for illustration, comparison of satellite- and model-based data reveals that these two independent approaches yield nearly identical values for μ during the nutrient-enriched autumn-to-spring period that is critical to bloom development (Figure 2a). During this time, μ decreases until the maximum mixed layer depth (MLD) is reached in February (Figure 2a dashed green line) and then increases rapidly with subsequent mixed layer shoaling and continued increases in PAR. During summer and early autumn, the BEC-CCSM gives μ estimates that are notably lower than the satellite values, in part reflecting the challenge of characterizing biomass recycling during this low-nutrient period of the year. However, this summer-through-early autumn discrepancy between satellite- and model-based estimates of μ has no impact on our conclusions regarding primary processes influencing the annual blooming-phase.

Comparison of satellite- and model-based annual cycles in r reveals two particularly notable features (Figure 2b). First, the satellite-detected initiation of the blooming-phase prior to winter solstice (when r first becomes positive) is reproduced by the BEC-CCSM. In both cases, this initiation occurs while μ is still decreasing. Second, values of r may be at or near maximal in February (low light, deepest MLD) and then show little response to the large springtime increases in μ (e.g., compare Figure 2a and 2b). This early bloom initiation has also been observed in the field near the location of bin B-05 [Mumery et al., 2005].

In neither annual cycle of r is there any indication that mixed layer stratification in spring must surpass a critical threshold before μ can exceed l [Sverdrup, 1953].

Values of r are one to several orders of magnitude smaller than μ (Figure 2a,b). Thus, the seasonal cycle in phytoplankton losses, l , must be nearly identical to the seasonal cycle in μ , implying that the annual bloom results from only subtle disequilibria between two much larger and opposing rates [Evans and Parslow, 1985; Banse, 1992; Longhurst, 2007; Behrenfeld, 2010]. In other words, the bloom is a consequence of a residual difference. This imbalance can be examined through changes in the $r : \mu$ ratio, which reflects the fraction of phytoplankton production accumulating as biomass (a negative ratio marks decreasing biomass). As illustrated in figure 2c, the satellite-derived annual cycle in the $r : \mu$ ratio indicates a rapid increase in early winter, coincident with initiation of the blooming-phase. By midwinter, >10% of phytoplankton production may be accumulating as biomass (Figure 2c, red line). The $r : \mu$ ratio then takes a downturn and decreases until the end of the bloom. These blooming-phase changes in $r : \mu$ are closely reproduced in timing and magnitude by the BEC-CCSM (Figure 2c, green line). Both approaches thus show that a smaller and smaller fraction of total phytoplankton production accumulates as biomass as spring stratification proceeds (data to right of green dashed line in Figure 2c). It is this ‘recoupling’ between phytoplankton division and losses that constrains r to its relatively narrow range during the blooming-phase (Figure 2b), despite substantial springtime increases in μ (Figure 2a) (see additional discussion below).

Further inspection of BEC-CCSM data shows that seasonal changes in phytoplankton losses (l) are dominated by mortality to zooplankton grazing (Figure 2d).

This finding is consistent with a long history of modeling and field studies [e.g., *Evans and Parslow*, 1985; *Frost*, 1987; *Banse*, 1992, 2002; *Calbet and Landry*, 2004; *Landry and Calbet*, 2004; *Longhurst*, 2007; *Landry et al.*, 2011].

All ecosystem models are oversimplifications of natural systems. In the BEC-CCSM, for example, zooplankton vertical migration is not accounted for, a single zooplankton population is assumed to graze on all phytoplankton groups, grazing rates are assumed independent of phytoplankton species composition, no account is made for zooplankton life histories (e.g., seasonal hybernation), and a very simplistic description is used for zooplankton predation by higher trophic levels. Nevertheless, the reasonable correspondence between satellite and BEC-CCSM rates shown in figure 2 suggests that the model captures primary processes governing these annual cycles.

One important relationship accounted for by the BEC-CCSM is that grazing losses are proportional to the product of predator-prey concentrations (i.e., $[C_{\text{phyto}}] \times [C_{\text{zoo}}]$) at low, non-saturating prey abundances (see Table S1 in the auxiliary material). As a result, the specific rate of grazing on phytoplankton scales with the grazer concentration (i.e., $l_{\text{grazing}} \propto [C_{\text{zoo}}]$) and the specific division rate of the grazer population scales with phytoplankton concentration (i.e., $\mu_{\text{zoo}} \propto [C_{\text{phyto}}]$). In the model, the observed summer through autumn decreases in phytoplankton concentration (Figure 1b) result in a reduction in μ_{zoo} , declining $[C_{\text{zoo}}]$, and a concomitant decrease in l_{grazing} (Figure 2d). This seasonal pattern in l_{grazing} is modulated to a substantial degree by mixed layer deepening, which entrains relatively plankton-free water from below [*Evans and Parslow*, 1985; *Behrenfeld*, 2010]. This 'dilution' effect of deep water entrainment does not directly impact the inventory (mg m^{-2}) of either phytoplankton or zooplankton, but it does decrease their concentrations (mg m^{-3}) and thus reduces both grazing efficiency and zooplankton growth.

If the impact of mixed layer deepening on l_{grazing} is sufficiently large, then r may become positive under conditions that are simultaneously decreasing μ . Figures 2b and 2c show this transition to positive r occurring in early winter when MLD is rapidly deepening and growth conditions for phytoplankton are deteriorating. In short, the model suggests that initiation occurs because changes in environmental conditions from autumn into winter have a greater impact on zooplankton grazing than phytoplankton division rates, even though μ is decreasing rapidly.

3.3 Deeper mixing and lower light enhance food web imbalances

The relationship between mixed layer deepening and imbalances between μ and l can be further explored by comparing plankton properties between bins with differing winter mixing depths. For such an analysis, it is beneficial to compare data between bins from the same latitudinal zone. This approach better isolates the effects of dilution, since annual cycles of incident PAR and sea surface temperature (SST) are similar (Figure 3a). In the subarctic Atlantic, the depth of winter mixing decreases from east to west within a latitudinal band, as shown in figure 3b for Bins B-05, B-06, and B-07 (blue, red, and green lines, respectively). These three bins are the northern-most bins with satellite coverage for all months. Satellite and model data show that the between-bin differences in MLD yield an east-to-west decreasing pattern in winter and early-spring $r : \mu$ (Figure 3c, e) and ΣChl (Figure 3d, f). In other words, deeper winter mixing causes larger imbalances between phytoplankton division and loss rates, such that a greater fraction of winter productivity accumulates as biomass in the east. However, deeper mixing also distributes the increasing phytoplankton population over a larger water volume, so initial biomass accumulation is expressed as an increase in ΣChl (Figure 3d, f), rather than $[\text{Chl}]$.

Another way of looking at this is that surface [Chl] fails to show the winter east-to-west increase expected from the purely physical effects of deeper (by 100's of meters) mixing in the east because of the simultaneous and countering ecological impacts of mixing on phytoplankton-grazer interactions.

The BEC-CCSM provides additional insights on the underlying ecology of the observed east-to-west patterns. Shallower mixing in the western bin (B-07) means that phytoplankton experience more sunlight each day during the winter and accordingly have higher specific division rates (μ) (Figure 3g; green line). In the east, winter μ values are lower because deeper mixing reduces daily light exposure (Figure 3g; blue and red lines). However, shallower mixing in the west also means that the dilution of phytoplankton and grazer populations is smaller, resulting in winter-through-spring grazing mortality that is proportionately higher (Figure 3h). This enhanced grazing counters the faster phytoplankton division rates in the west, giving a net result of lower peak values of ΣChl (Figure 3f).

The depth of convective mixing not only varies from east-to-west, but also from north-to-south (Figure 4a), along with daily light levels. Evaluation of basin-wide BEC-CCSM results indicates that deeper mixing and lower light consistently yield greater winter decoupling between phytoplankton division and grazing losses (i.e., $r : \mu$ ratio, Figure 4b) and, consequently, larger peak phytoplankton inventories (Figure 4c). Similar results are found for the satellite data (Figure S4 in the auxiliary material). Finally, winter mixing depth also varies from year to year. When annual maxima in MLD and ΣC_{phyto} are compiled for all regions and years, strong positive correlations are found between these two properties for both the satellite ($R = 0.75$) and model ($R = 0.84$) approaches (Figure 5).

Similar positive correlations are also observed between MLD and ΣChl maxima (Figure S5 in the auxiliary material), despite this broad compilation of data encompassing a wide range in SST and PAR conditions (Fig. S6 in the auxiliary material) that can potentially be associated with large changes in $\text{Chl}:\text{C}_{\text{phyto}}$ ratios.

3.4 The subarctic Atlantic ‘disturbance and recovery’ cycle

Disruption of predator-prey relations by early winter mixing is only one phase in the annual subarctic Atlantic plankton cycle. The blooming phase continues through spring and, after its climax, is followed by a prolonged period of declining biomass (i.e., negative r) (Figure 2b, 3c,e, 4b). Over this annual cycle, a variety of ‘bottom up’ factors can constrain phytoplankton division rates (μ). The relative importance of these different factors is largely inaccessible from remote sensing, but they are quantified in the BEC-CCSM. Figure 6 shows annual cycles in the severity of light, nitrogen, iron, phosphate, and silicate (diatoms only) limitation for the model ‘non-diatom’ and ‘diatom’ phytoplankton groups. The panels in figure 6 correspond to the 25°W to 35°W longitudinal band and are arranged top-to-bottom from 65°N to 40°N latitude (i.e., bins B-14, B-13, B-09, B-06, and B-02, respectively, as in Figure 1a). Also shown along the x-axis of each panel is a black triangle identifying the onset of the winter-spring blooming phase. For all bins, nutrients are the dominant limiting factor for μ in the summer, transitioning to light limitation in autumn. In each case, bloom initiation occurs after significant relaxation of nutrient limitation and typically before maximum light limitation. In other words, timing of the initiation event does not correspond to any particular feature in the bottom-up factors regulating μ , particularly for the non-diatom group that dominates during the early phase of the bloom (Figure 6, left column).

Nevertheless, bottom-up factors (especially light limitation) do play a role in modifying annual cycles of r .

As described above, light-driven decreases in μ and dilution of the phytoplankton population by mixed layer deepening drives a decrease in zooplankton concentration in autumn.

These impacts on the zooplankton community are sufficiently severe that eventually the decreases in l_{grazing} cause $l < \mu$, at which point the phytoplankton population begins to increase. If this increase were to result in an increase in $[C_{\text{phyto}}]$, the rise in food availability would stimulate a subsequent increase in zooplankton, thereby dampening any potential bloom. However, continued deepening of the mixed layer allows the increasing phytoplankton inventory (mg m^{-2}) to actually be associated with decreasing concentrations (mg m^{-3}), which accordingly further diminish (starve) the grazer population. This decoupling of μ and l continues at least until the annual maximum in MLD, at which point the $r : \mu$ ratio is at or near its annual maximum.

Cessation of mixed layer deepening is a turning point in the blooming phase because the excess of μ over l , which has existed for well over a month, now results in an increase in $[C_{\text{phyto}}]$. In other words, positive r now increases both phytoplankton concentration and inventory. As resolved by the BEC-CCSM, the increase in $[C_{\text{phyto}}]$ fuels an increase in grazer biomass and l_{grazing} (e.g., Figure 3h). If we could hold μ constant for the remainder of spring, this grazing response to increasing phytoplankton concentration would rapidly decrease r (i.e., $\mu - g [C_{\text{zoo}}]$ would get smaller with time). However, concurrent springtime MLD shoaling and rising PAR drive increases in μ that counter the growing losses to grazers, thereby perpetuating the bloom. Thus, the imbalance between l and μ initiated in early winter largely by physical processes (i.e., dilution) is sustained through spring by an interplay between concentration-driven increases in l and light-driven increases in μ .

The magnitude of this imbalance is regulated in part by the relative rate of change in l and μ (Figure 3g, h), but not the absolute value of μ (e.g., compare Figure 2a, b). Thus, r may be just as large in February and March (low μ) as it is in May and June (maximum μ) (e.g., Figure 2b).

The view that emerges from this description is a portrayal of the subarctic Atlantic bloom as an annually repeated ‘disturbance and recovery’ cycle, where predator-prey interactions are disrupted by environmental forcings and subsequently recovered by ecosystem feedbacks.

Bloom initiation represents an important tipping point in this cycle, marking where concurrent but unequal autumn-to-winter decreases in grazing and phytoplankton division first cause l to become smaller than μ . This threshold is crossed earliest in our southern-most bins, where the relatively elevated daily light flux allows μ to exceed l after only modest dilution impacts on l_{grazing} (e.g., Figure 4b). With increasing latitude, light-driven decreases in μ are more substantial and thus require greater decreases in l_{grazing} for bloom initiation (Figure 7). In other words, the autumn-early winter period of phytoplankton decline is longer at higher latitudes and bloom initiation is delayed, although still occurring prior to mixed layer shoaling. The more severe reduction in grazers with increasing latitude is reflected by the increasing $r : \mu$ ratios within a given longitudinal band (Fig. 4b), and this greater impact on grazers contributes to the higher values of r in more northern bins during subsequent spring stratification (e.g., Figure 7). At extreme latitudes experiencing polar night, phytoplankton division ceases ($\mu = 0 \text{ d}^{-1}$) and bloom initiation must await a rise in sunlight. During this period, zooplankton mortality continues and, when phytoplankton growth finally does commence, μ and l can be strongly decoupled. This condition is best illustrated by our bin B-14, where delayed bloom initiation and severe predator-prey decoupling (black symbols in bottom panel of Figure 4b) results in the strongest spring peak in r (Figure 7).

Importantly, springtime values of μ for this bin do not exceed those for the lower latitude bins, thus re-emphasizing that the rate of increase in phytoplankton concentration (r) during stratification does not reflect the absolute value of μ , but rather an interplay between winter predator-prey decoupling and the relative rate of springtime increases in l and μ .

3.5 Winter losses and springtime detrainment

Despite being oversimplifications of natural systems, contemporary ecosystem models are nevertheless complex and sensitive to choices of model parameters. A primary conclusion from the current study is that early-winter ecosystem processes play a critical role in the subarctic Atlantic bloom. During this period, two terms of importance in the BEC-CCSM are the temperature-dependent phytoplankton linear mortality rate ($((T)$, Equation 6) and the temperature dependent maximum zooplankton growth rate ($Q_{10} = 2.0$; μ_{max} in Table S1 in the auxiliary material). To test the sensitivity of our results to these two key rates, we re-calculated annual cycles in r for μ_{max} with Q_{10} 's ranging from 0 to 3.5 and with $((T)$ assigned a fixed value of either 0 d^{-1} or 0.1 d^{-1} (Figure S7 in the auxiliary material). These sensitivity runs show that modeled annual cycles of r are relatively unaffected by either the choice of Q_{10} value for μ_{max} or by assigning $((T)$ a value of 0 d^{-1} . Increasing $((T)$ to 0.1 d^{-1} reduces winter phytoplankton stocks, and thus zooplankton, and consequently prolongs the winter decline in biomass and yields a blooming phase that is delayed compared to observations. Future modeling efforts will benefit from additional field measurements that better constrain winter phytoplankton (and zooplankton) mortality rates.

As detailed above in Section 2.1, annual cycles in r reported here include an accounting for dilution effects during mixed layer deepening and a removal detrainment effects during mixed layer shoaling. Only in this manner can the balance between phytoplankton division and loss rates within the mixed layer be accurately evaluated. *Behrenfeld* [2010; his Figure 3] illustrated the error in retrieved values of r that can result from neglecting dilution effects, which cause changes in phytoplankton concentration to under-represent population net accumulation rates in autumn and winter. While mixed layer deepening spreads the active phytoplankton population over a growing volume of water, mixed layer shoaling in spring does not have the opposite effect of concentrating phytoplankton. Instead, phytoplankton deeper in the water column are detrained from the euphotic zone during spring shoaling and are subsequently lost through sinking or grazing. One consequence of detrainment is that it contributes to the late spring convergence of phytoplankton concentrations between bins (Figure 3d, f, 4c). Specifically, MLDs across the subarctic basin shoal to similar depths during spring (e.g., Figure 3b, 4a), so a larger fraction of the wintertime phytoplankton inventory is lost (exported) to depth in areas of deeper winter mixing. With the BEC-CCSM, the significance of detrainment on total phytoplankton losses can be quantified by comparing annual cycles in r calculated using equations 3 and 4 with values calculated from phytoplankton inventories integrated to a fixed depth (e.g., annual maximum mixing depth) (Figure S8 in the auxiliary material). This comparison shows that inclusion of detrainment losses decreases values of r during the spring and results in annual cycles that consistently peak prior to mixed layer shoaling (i.e., mid-winter).

4. Discussion

The critical depth hypothesis formalized by *Sverdrup* in 1953 encapsulated concepts introduced by *Gran and Braarud* [1935] and was consistent with earlier modeling studies [e.g., *Riley et al.*, 1949] in that it recognized changes in phytoplankton biomass as reflecting a balance between phytoplankton specific division and loss rates. In *Sverdrup*'s treatment, though, phytoplankton 'respiration' per unit volume (which included all forms of phytoplankton losses) was assumed constant in time. This simplification had a major impact on the outcome of his analysis. Based on the choice of the 'respiration' rate, a unique mixed layer light condition emerges where the light-dependent phytoplankton division rate equals the 'respiration' rate. This specific point defines the 'critical mixing depth', before which phytoplankton biomass must be decreasing and after which the rate of biomass increase is proportional to subsequent increases in μ . Certainly, *Sverdrup* understood that phytoplankton loss rates were not constant in time, but if loss rates are allowed to change in proportion to μ , then the concept of a critical depth loses its value because, even in the middle of winter, net biomass accumulation (positive r) becomes possible so long as μ is positive and losses have been sufficiently diminished. The study of *Behrenfeld* [2010] demonstrated that, indeed, r can be positive throughout the winter.

Contemporary ocean ecosystem models, such as the BEC-CCSM, likewise build from the early work of *Riley et al.* [1949], but do not invoke a critical depth criterion. Instead, phytoplankton specific division rates are linked to regulating environmental factors (e.g., temperature, nutrients, light), zooplankton grazing is modulated by food availability, mortality, and often environmental properties (e.g., temperature), and attempts are made at mechanistically characterizing other phytoplankton loss processes (e.g., concentration-dependent aggregation leading to sinking).

As illustrated here, this treatment yields strong positive correlations between μ and l , which is consistent with many earlier modeling and field-based studies [e.g., *Halldal*, 1953; *Steemann Nielsen*, 1958; *Pollingher and Berman*, 1977; *Tilzer*, 1984; *Evans and Parslow*, 1985; *Frost*, 1987; *Strom and Welschmeyer*, 1991; *Banse*, 2002; *Longhurst*, 2007; *Calbet and Landry*, 2004; *Landry et al.*, 2011]. Covariation of μ and l has a potential to largely divorce variations in r from variability in μ . This independence of r from μ was an important theme in the study of *Evans and Parslow* [1985], where development of phytoplankton blooms was viewed as a consequence of slight modifications in predator-prey interactions unfolding over the annual cycle.

In *Behrenfeld* [2010], the transition from negative to positive r in early winter (while μ was still decreasing) was attributed to a disruption of predator-prey interactions by the dilution effects of mixed layer deepening. An equivalent effect was invoked in the studies of *Evans and Parslow* [1985] and *Marra and Barber* [2005]. Here, we more directly test the significance of the dilution effect by examining phytoplankton properties between bins with differing winter mixing depths. Our results indicate that this physical-ecological interaction plays a critical role in initiating the blooming-phase and governing the extent of winter-early spring decoupling between μ and l (as indexed by the $r:\mu$ ratio (e.g., Figure 3, 4)). By examining variability between bins and years, we also find a strong correspondence between winter MLD maxima and peak values of ΣC_{phyto} and ΣChl (Fig. 5, S5 in the auxiliary material). This result has a potentially significant implication. Specifically, forward projections of the BEC-CCSM have indicated that maximum winter mixed layer depths will become shallower over the next 100 years [*Danabasoglu et al.*, 2012; *Meehl et al.*, 2012], with average rates of change of 0.3 to 2.3 m y^{-1} when aggregated into our 14 regional bins (Figure S9 in the auxiliary material).

Applying the relationships given in figure 5 to these projected changes in maximum MLD yields an average decrease in peak ΣC_{phyto} of 108 mmol C m⁻² by year 2100 (range for the 14 bins: 22 – 190 mmol C m⁻²), which is equivalent to a 40% reduction from current values (range: 10% - 66%). This simple calculation assumes that the response of subarctic Atlantic ecosystems to changes in winter MLD maxima remains consistent with present-day relationships. Nevertheless, the assessed change is certainly intriguing and warrants further analyses. It should also be noted that, while we observe strong correlations between maximum MLD and phytoplankton inventories, similar correlations are not found with climax phytoplankton concentrations (Figure S10 in the auxiliary material). This lack of correlation is in part due to the equalizing effects of detrainment discussed in Section 3.5, but also reflects the fact that the bloom climax occurs many months after the winter MLD maximum and thus is influenced by winter mixed layer nutrient loading, nutrient losses (export) during the prolonged stratification period, the balance between phytoplankton division rate and grazing rate, species succession (phytoplankton and zooplankton), and many other factors. Simulating this complexity remains a major challenge for ecosystem modeling and an important direction for model refinement.

Recorded changes in phytoplankton stocks allow net population accumulation rates, r , to be one of the only pelagic ecosystem rate-terms directly detected from space. Integrating over sufficient spatial scales minimizes uncertainties in r associated with advection. Furthermore, uncertainties in satellite-retrieved stocks (e.g., chlorophyll, phytoplankton carbon) should have minimal impacts on r estimates because the variability in optically-active constituents (e.g., pigments, colored dissolved organic matter) underlying stock algorithm errors [Siegel *et al.*, 2005a, b] is likely small during any eight-day period used in assessing r .

Satellite r data, along with stock and μ estimates, thus provide valuable observations for evaluating model output. Ecosystem models, in turn, provide important insights on underlying mechanisms for observed change. Nevertheless, these two data sources used in the current study fail to resolve many ecological complexities. For example, many large grazers hibernate at depth during winter [Longhurst and Williams, 1979; Miller, 2004; Longhurst, 2007] and zooplankton metabolism may be more sensitive to low temperatures than phytoplankton division rates [Rose and Caron, 2007; López-Urrutia, 2008; Taucher and Oschlies, 2011]. During restratification, we show that grazer responses to increasing phytoplankton abundance are important to the recoupling of l and μ , but major changes in species composition are also occurring during this period. Indeed the bloom in phytoplankton is not simply an accumulation of a few species, but rather encompasses a continuous succession of different species emerging briefly as dominant before residing again to the diverse background of secondary species [Sosik, 2010]. Larger zooplankton also re-emerge as significant components of the grazer population during spring restratification [Longhurst and Williams, 1979; Miller, 2004; Longhurst, 2007]. Additional studies are therefore needed to further evaluate the relative importance of these and many other processes occurring during the blooming-phase and to better understand mechanisms governing the dynamic taxonomic variability of marine ecosystems [Giovannoni and Vergin, 2012].

Since the early work of Gran and Braarud [1935], Riley *et al.* [1949], and Sverdrup [1953], interpretations of phytoplankton blooms have been continuously revised and refined. The Behrenfeld [2010] study re-invigorated the debate on factors controlling bloom initiation by using satellite data to de-emphasize bottom-up factors and refocus attention on physical processes disrupting predator-prey interactions.

Subsequent publications by *Chriswell* [2011], *Taylor and Ferrari* [2011], and *Mahadevan et al.* [2012] have argued again in favor of more traditional light-driven explanations for bloom initiation, but these studies do not address many of the issues raised by the earlier investigation. Here, we capitalize on basin-wide differences in light- and MLD conditions to further delineate the ecological underpinnings of annual plankton bloom cycles and their links to physical processes, while also noting a role for bottom-up factors in modulating these cycles. As in *Behrenfeld* [2010], our focus has once again been on the subarctic Atlantic, but our aim is to understand processes that transcend a single regional event and to build toward a more ‘general theory’ of phytoplankton blooms. To this end, the recently coined ‘dilution-recoupling hypothesis’ has here been restated and elaborated upon in the broader context of a ‘disturbance-recovery’ process. In the subarctic Atlantic, deep winter mixing and low light provide the necessary ecosystem disturbance to yield a bloom. Different sources of disturbance can play an equivalent role in bloom initiation in other regions of the global ocean, such as monsoon forcing in the Arabian Sea [*Marra and Barber* 2005], upwelling in coastal systems [*Cushing* 1959], and iron deposition in high-nutrient, low-chlorophyll waters [*Hamme et al.*, 2010]. In each case, a disturbance ‘opens a window’ for phytoplankton division to temporarily outpace losses, and in all cases subsequent ecosystem feedbacks tighten predator-prey coupling again to reclose this window over the course of the bloom.

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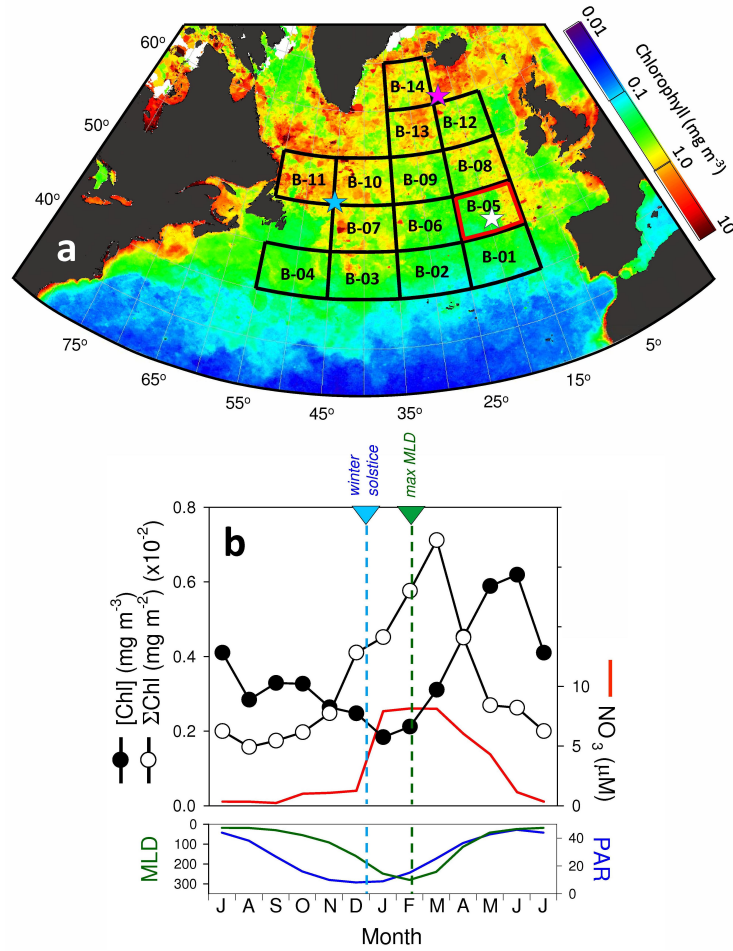


Figure 1. The subarctic Atlantic phytoplankton bloom. (a) Geographical location of the 14 regional bins. Background color shows satellite-based surface chlorophyll concentrations for June 2002, exemplifying a typical bloom. White star = location of JGOFS-NABE experiment. Pink star = location of NAB08 experiment. Blue star = location of Boss et al. (2010) float study. Red box = bin used to illustrate representative plankton properties in panel b and figure 2. (b) Satellite monthly mean (1997-2007) chlorophyll concentration ([Chl]; solid circle) and depth-integrated chlorophyll inventory (ΣChl ; open circle) for bin B-05. Red line = mean monthly climatological surface nitrate (right axis). Blue line, lower plot = surface incident PAR ($\text{mole photons m}^{-2} \text{d}^{-1}$). Green line, lower plot = MLD (m). Dashed vertical blue line = winter solstice. Dashed vertical green line = month of maximum MLD. Note that data are plotted beginning in July on the left to focus on the autumn-through-spring period critical to bloom development.

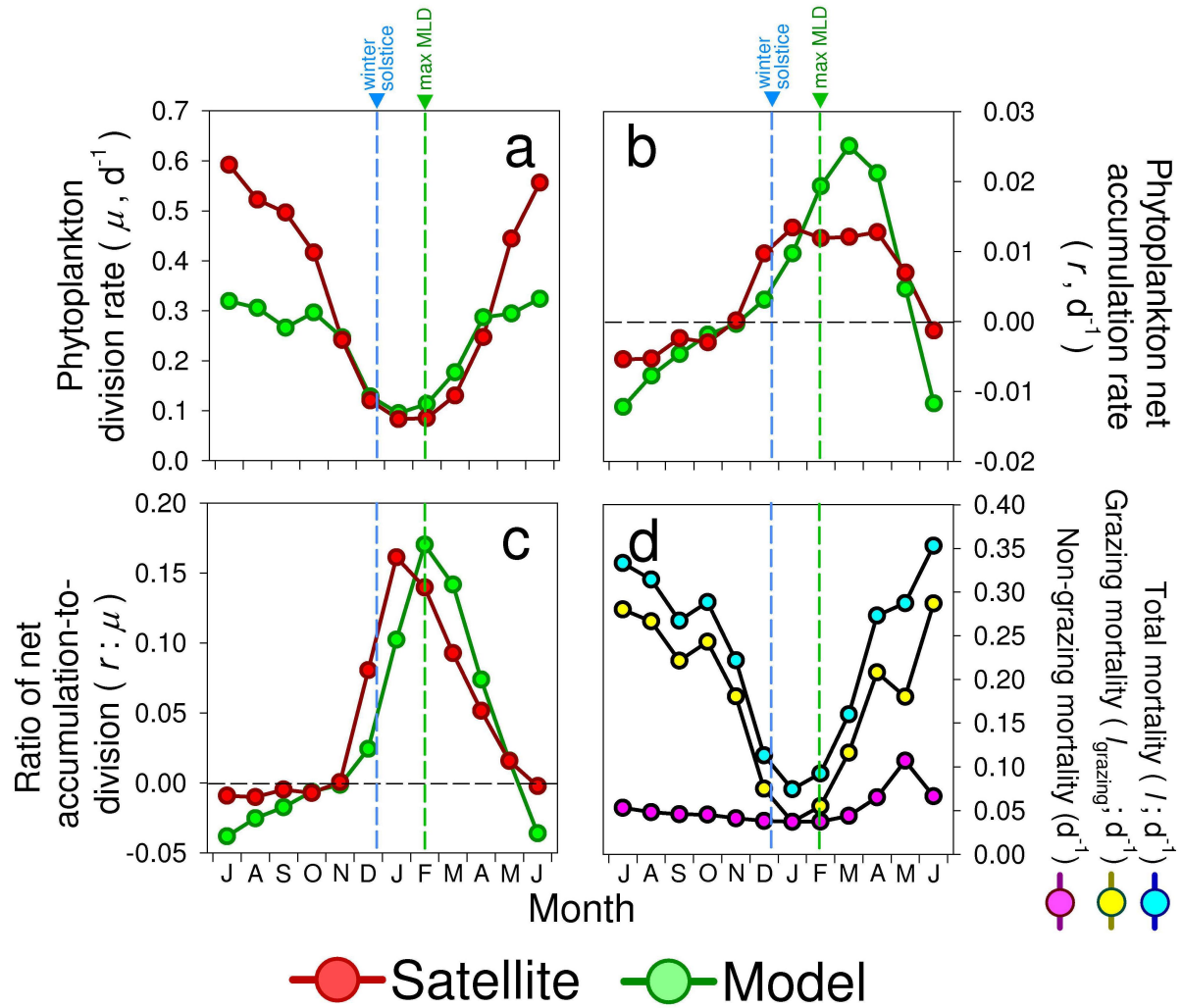


Figure 2. Satellite- (red) and model-based (green) annual cycles in key plankton properties of the subarctic Atlantic. (a) Phytoplankton specific division rate (μ). (b) Specific rate of accumulation in phytoplankton biomass (r). (c) Ratio of net accumulation rate to division rate ($r : \mu$). (d) BEC-CCSM-based phytoplankton mortality rates. Blue = total mortality (l). Yellow = grazing mortality (l_{grazing}). Pink = non-grazing mortality. Data in all plots are monthly mean values for bin B-05 over the period 1997–2007. Dashed vertical blue and green lines as in figure 1b. Data are plotted beginning in July on the left to focus on the autumn-through-spring period critical to bloom development.

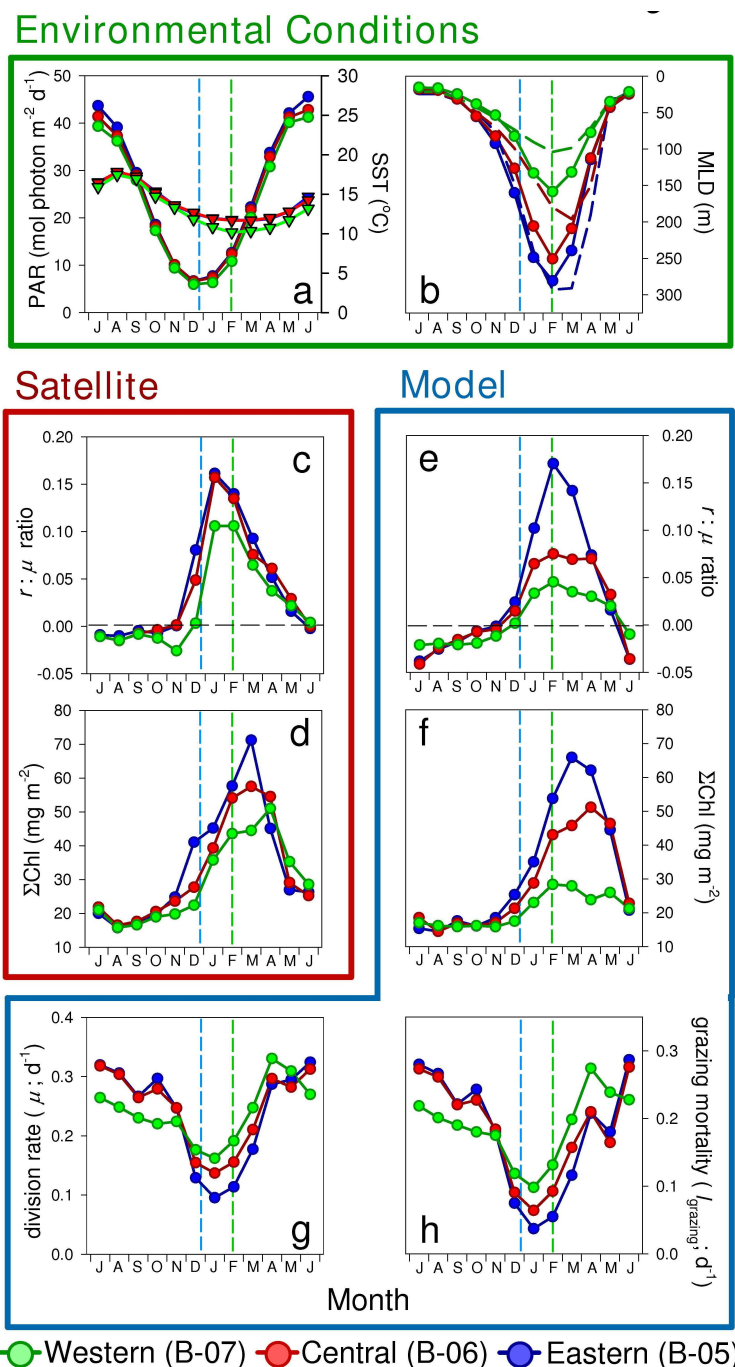


Figure 3. Longitudinal differences in subarctic Atlantic environmental (a-b) and plankton properties (c-h) for bins in the latitudinal zone of 45°–50° N (Figure 1a). Blue line = eastern-most bin (B-05). Red line = central bin (B-06). Green line = western-most bin (B-07). (a) Incident PAR (left axis; circles) and SST (right axis; inverted triangles). (b) Mixed layer depth (MLD) from (solid lines, circles) data assimilating models (see Methods) and (dashed lines) the BEC-CCSM. (c, d; red box) Satellite-derived plankton properties. (e-h; blue box) BEC-CCSM based plankton properties. (c, e) Ratio of phytoplankton specific net accumulation rate to division rate ($r : \mu$). (d, f) Depth-integrated chlorophyll (ΣChl). (g) Phytoplankton specific division rate (μ). (h) Grazing mortality rate (l_{grazing}). Data in all plots are monthly mean values for the period 1997–2007 and are plotted beginning in July on the left to focus on the autumn-through-spring period critical to bloom development. Dashed vertical blue and green lines as in figure 1b.

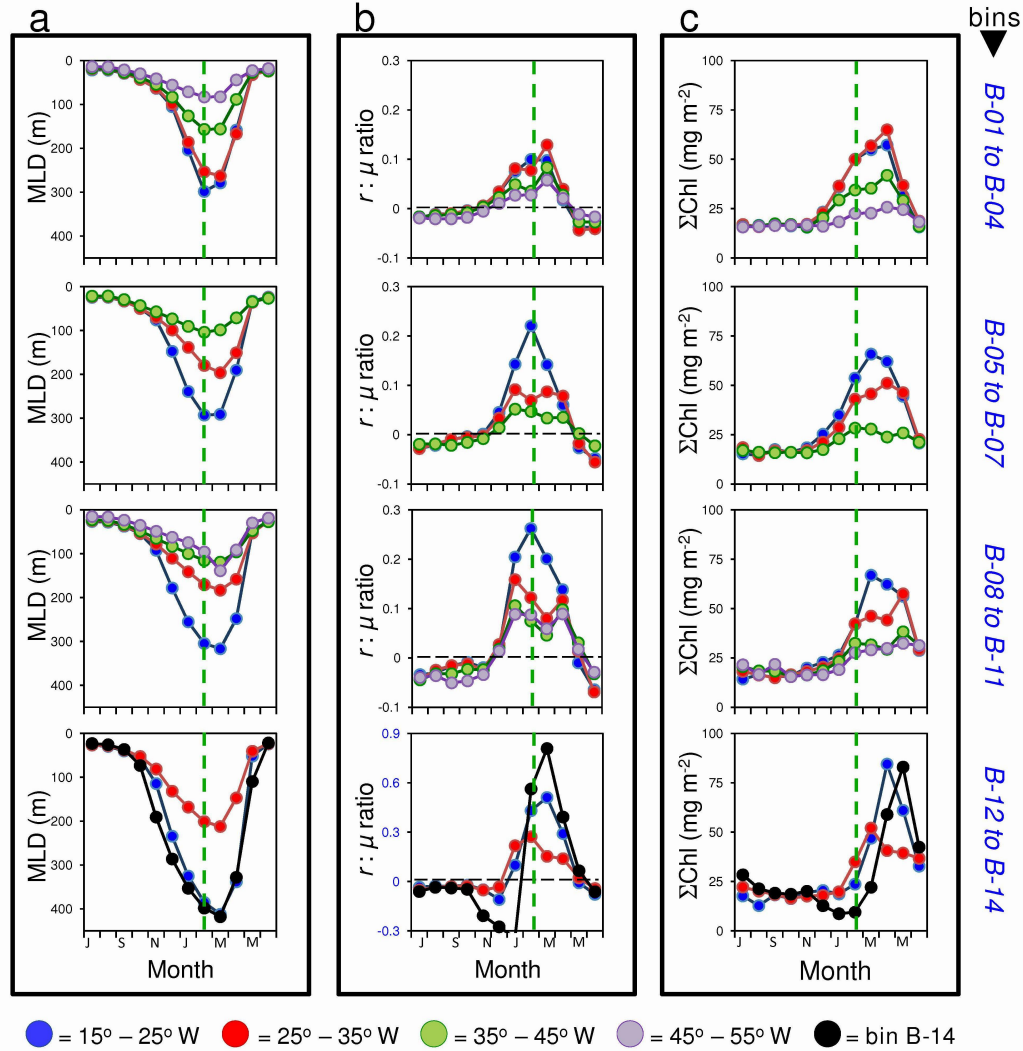


Figure 4. Key physical and ecosystems properties in all 14 subarctic Atlantic bins. (column a) Mixed layer depth (MLD). (column b) Ratio of net accumulation rate to division rate ($r:\mu$). (column c) Depth-integrated chlorophyll (ΣChl). Each row of panels corresponds to a latitudinal set of bins from figure 1a, increasing from south to north from the top of the figure to the bottom (bin numbers indicated in blue text on right of each row). Line and symbol colors correspond to specific longitudinal zones, as defined at bottom of figure. Black symbols in bottom panels correspond to bin B-14. y-axis ranges in each column are the same for all panels except the bottom panel of column b (emphasized by bold blue labels). Data in all plots are monthly mean values for the period 1997-2007 from the BEC-CCSM and are plotted beginning in July on the left to focus on the autumn-through-spring period critical to bloom development. Dashed vertical green line as in figure 1b.

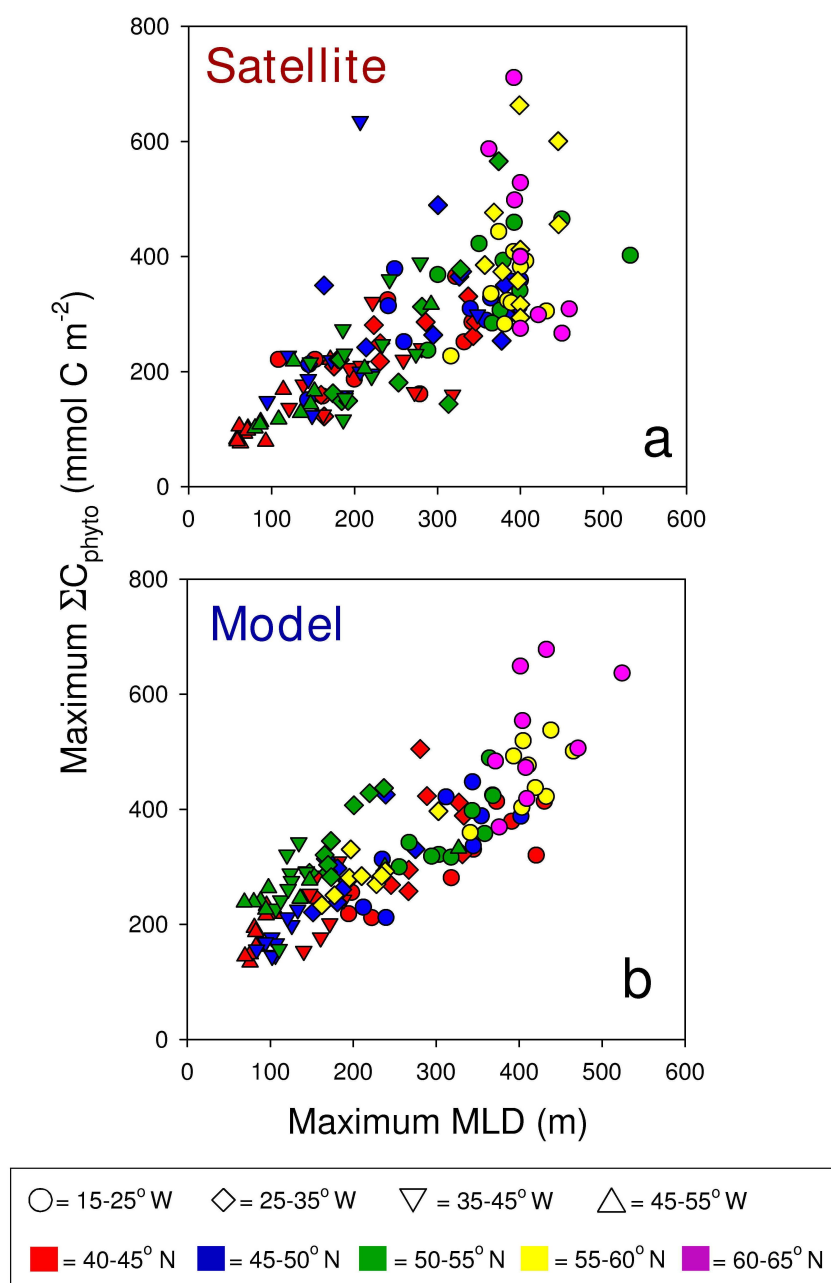


Figure 5. Relationship between maximum winter mixed layer depth (MLD) and maximum depth-integrated phytoplankton biomass (ΣC_{phyto}) for all bins and all years over the 1997-2007 period. (a) Satellite results ($R = 0.75$; $p < 0.001$; slope = $0.85 \text{ mmol C m}^{-2} \text{ m}^{-1}$). (b) BEC-CCSM results ($R = 0.84$; $p < 0.001$; slope = $0.81 \text{ mmol C m}^{-2} \text{ m}^{-1}$). Symbols and colors indicate bin longitudinal and latitudinal zone, respectively (see key at bottom of figure). For comparisons between maximum MLD and maximum ΣChl see figure S5 and between maximum MLD and bloom climax $[\text{Chl}]$ and $[\text{C}_{\text{phyto}}]$ see figure S10.

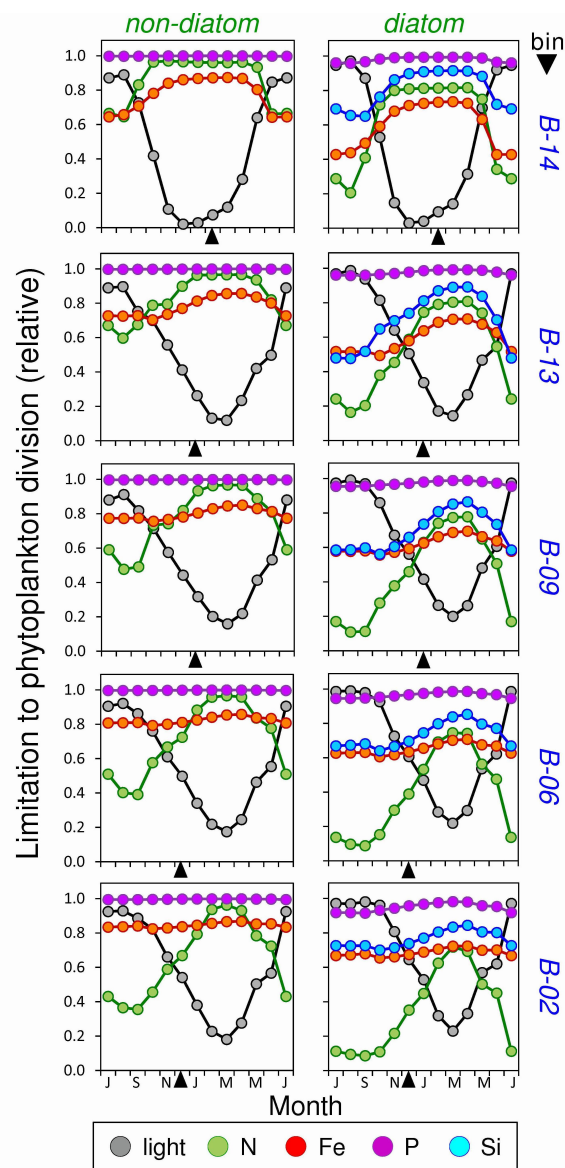


Figure 6. Relative importance of different environmental factors limiting phytoplankton division rates over the annual cycle. Left and right columns are for the ‘non-diatom’ and ‘diatom’ phytoplankton groups in the BEC-CCSM, respectively. Symbol and line colors in each panel distinguish division-limiting factor (defined at bottom of figure). Severity of limitation (y-axes) refers to achieved division rate relative to maximum potential division rate and thus ranges from 0 = complete limitation to 1 = no limitation. Panels in each column are for the 25°W to 35°W longitudinal band in figure 1a and are arranged top-to-bottom from 65°N to 40°N latitude (bin numbers shown in blue text on right). Black triangle along each x-axis identifies onset of blooming phase. Data in all plots are monthly mean values for the period 1997–2007 and are plotted beginning in July on the left to focus on the autumn-through-spring period critical to bloom development.

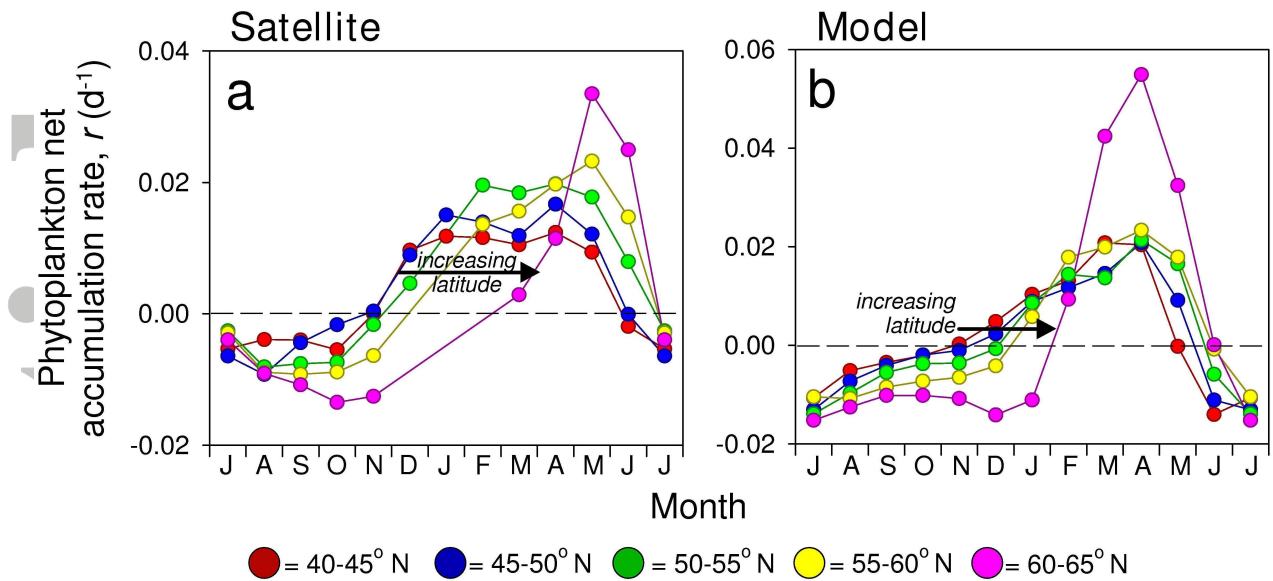


Figure 7. Latitudinal differences in annual cycles of phytoplankton net accumulation rates (r) for bins B-02, B-06, B-09, B-13, and B-14 (Figure 1a). (a) Satellite data. (b) BEC-CCSM data. Colors designate bin locations, as indicated at the bottom of the figure. Missing months in panel a are due to lack satellite coverage during the middle of winter at higher latitudes.