Resurrecting the Ecological Underpinnings of Ocean Plankton Blooms

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Abstract

Nutrient and light conditions control phytoplankton division rates in the surface ocean and, it is commonly believed, dictate when and where high concentrations, or blooms, of plankton occur. Yet after a century of investigation, rates of phytoplankton biomass accumulation show no correlation with cell division rates. Consequently, factors controlling plankton blooms remain highly controversial. In this review, we endorse the view that blooms are not governed by abiotic factors controlling cell division, but rather reflect subtle ecosystem imbalances instigated by climate forcings or food-web shifts. The annual global procession of ocean plankton blooms thus represents a report on the recent history of predator-prey interactions modulated by physical processes that, almost coincidentally, also control surface nutrient inputs.

INTRODUCTION

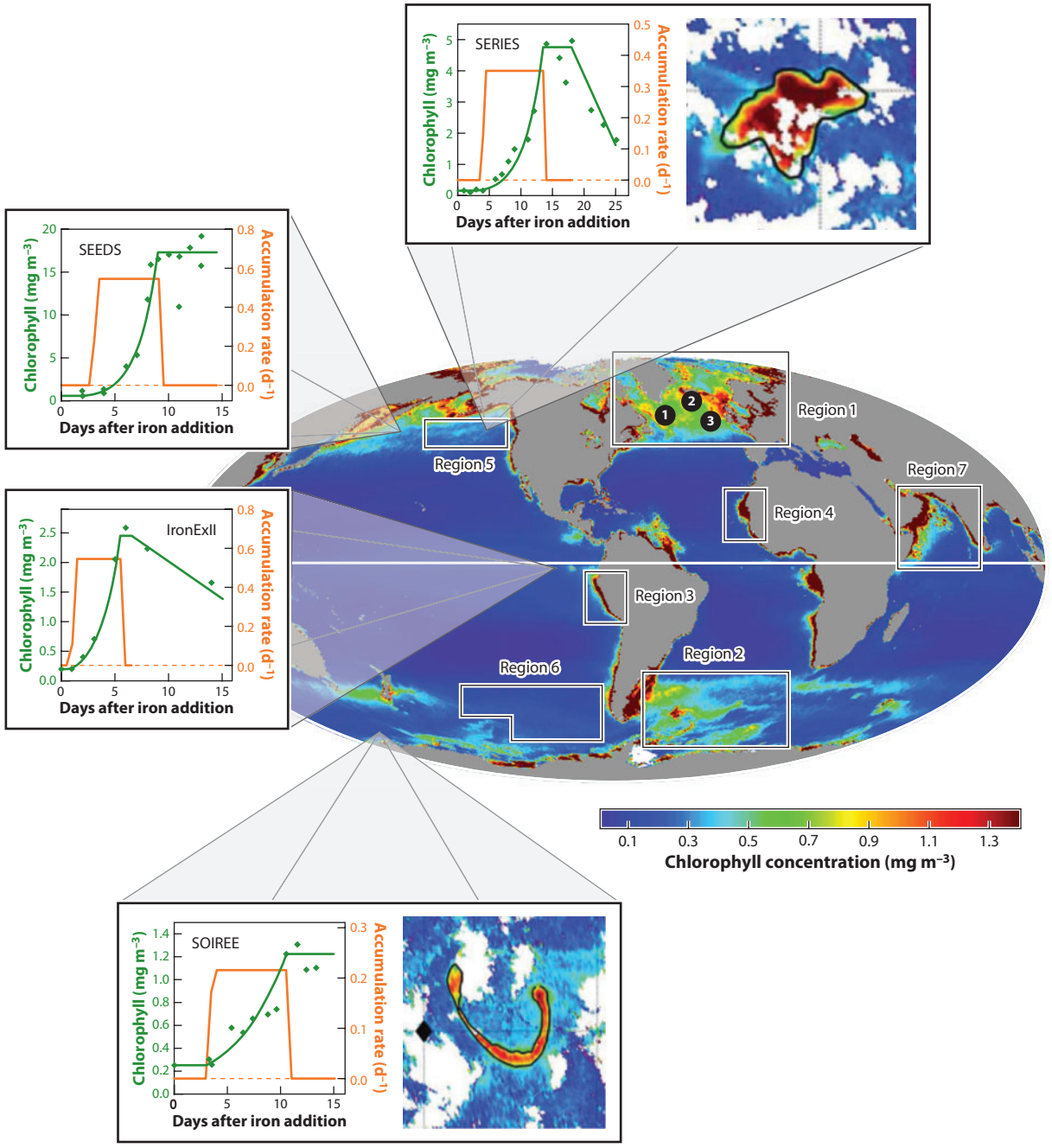
The ocean surface mixed layer between 40°N and 40°S latitude is largely oligotrophic (low nutrient, low biomass) and permanently stratified. Within this vast "blue ocean" region, phytoplankton populations generally exhibit only low-amplitude seasonal cycles in chlorophyll concentration that largely reflect physiological adjustments in intracellular chlorophyll in response to changing growth conditions, rather than changes in biomass (Behrenfeld et al. 2005, 2008; Siegel et al. 2013). Despite low dissolved nutrient concentrations, phytoplankton in these areas are often found not to be growing slowly. Indeed, the numerically dominant small prokaryotic and eukaryotic picoplankton typically divide every day or two (e.g., André et al. 1999, Liu et al. 1999). This division rate is considerably higher than that in some bloom-forming ocean regions, but populations in the oligotrophic seas are perpetually maintained at low concentrations by a community of herbivorous zooplankton grazing at a rate equivalent to that of phytoplankton cell division. Through the combined activities of the microbial food web, this tight coupling between division and death is accompanied by a rapid recycling of the vanishingly scarce nutrients that sustain phytoplankton growth. Thus, the "blue ocean" is an environment of low biomass, high turnover, and relatively stable ecosystems. Although the focus of this review is on phytoplankton blooms, the contrasting condition of permanent oligotrophy provides insights into the conditions necessary to create a bloom and thus will be revisited below.

On the basis of global areal extent, phytoplankton blooms are uncommon. However, these periodic bursts in biomass are regular features in lakes, polar and subpolar oceans (e.g., regions 1 and 2 in **Figure 1**), and coastal upwelling systems (e.g., regions 3 and 4 in **Figure 1**). Blooms are ecological hot spots (Ryther 1969, Hjort 1981, Chassot et al. 2010), and the life cycles and migration patterns of many grazers and carnivores are evolutionarily tuned to the timing and location of these major ocean events (Longhurst 2007). Accordingly, changes in bloom phenology may have catastrophic implications for higher trophic levels (Platt et al. 2003, Edwards & Richardson 2004, Mackas et al. 2007, Koeller et al. 2009, Kahru et al. 2011). Blooms are similarly important biogeochemically (Lochte et al. 1993, Arrigo et al. 2008, Takahashi et al. 2009, Martin et al. 2011, Alkire et al. 2012). Indeed, the production of plankton biomass during a bloom can be sufficient to reverse the annual cycle of surface-ocean CO_2 uptake from what would occur from physical-chemical changes in solubility alone (Körtzinger et al. 2008, Signorini et al. 2012), and the export flux of sinking biomass to depth contributes to these regions' net annual uptake of atmospheric

Figure 1

Phytoplankton blooms of the global ocean. The map shows satellite-based summer-average mixed-layer chlorophyll concentrations from the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS) record, with a horizontal white line separating data for boreal summer from those for austral summer. The concentrations are shown on a linear scale to highlight significant blooms (rather than on the typical log scale used to emphasize minor features in more oligotrophic waters). Bloom-forming regions, where chlorophyll concentrations average ~0.5 mg m^{-3} or higher (often much higher), are identified by warm colors. Numbered regions: region 1, high-latitude North Atlantic bloom; region 2, Southern Ocean blooms where surface iron levels are elevated; regions 3 and 4, coastal upwelling blooms; regions 5 and 6, low-iron subarctic Pacific and Southern Ocean areas, respectively; region 7, Arabian Sea monsoon-driven bloom. Numbered circles in region 1: ①, location of two-year autonomous profiling optical measurements (Boss & Behrenfeld 2010); ②, location of ship-based 2008 North Atlantic Bloom study (NAB-08) (Mahadevan et al. 2012); ③, location of ship-based Joint Global Ocean Flux Study (JGOFS) North Atlantic Bloom Experiment (NABE) (Ducklow & Harris 1993). The inset graphs show time series of chlorophyll concentrations (*green lines and diamonds*) and chlorophyll accumulation rates (*orange lines*) for four iron-stimulated experimental blooms: Subarctic Ecosystem Response to Iron Enrichment Study (SERIES) (Boyd et al. 2004), Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study (SEEDS) (Tsuda et al. 2003), Iron Enrichment Experiment II (IronExII) (Coale et al. 1996), and Southern Ocean Iron Release Experiment (SOIREE) (Boyd et al. 2000). Satellite images of the blooms are available only for SERIES (19 days after iron addition) and SOIREE (~46 days after iron addition).

CO_2 (Takahashi et al. 2009). Blooms are also ecological harbingers of environmental change. In extreme cases, blooms identify freshwater and coastal eutrophication, but they can also provide a sensitive index of climate variability through their dependence on physical processes that transport nutrients and control the exposure of phytoplankton to sunlight (Sommer & Lengfellner 2008, Henson et al. 2009). In general, climate-driven surface warming and reduced winter mixing



appear to allow blooms to occur earlier (Henson et al. 2009, Winder & Sommer 2012), may select for smaller warm-water phytoplankton and grazer species with lower carbon export and higher recycling efficiencies (Winder & Sommer 2012), and can alter the frequency of blooms over the annual cycle (e.g., both spring and fall blooms or only a spring bloom) (Martinez et al. 2011, Henson et al. 2013). However, no consensus exists on the relationship between climate warming and the maximum phytoplankton biomass achieved at bloom climax (Henson et al. 2009, Winder & Sommer 2012, Behrenfeld et al. 2013).

What exactly is a phytoplankton bloom? In some cases, blooms have been described as periods of rapid [even "explosive" (Platt et al. 1991)] growth in phytoplankton biomass. However, this definition is unsatisfactory because, although some blooms happen quickly, others develop over long periods and have rates of biomass accumulation equivalent to only one or two doublings per month (Behrenfeld 2010). More generally, blooms are understood as a condition of elevated phytoplankton concentration, although there is no established quantitative threshold defining "elevated." The concentration of the photosynthetic pigment chlorophyll (Chl) is commonly used as an index of phytoplankton abundance, and has the benefit of being detectable from space (see **Figure 1**) (McClain 2009). From the satellite view of global ocean chlorophyll concentrations shown in **Figure 1**, it is clear that bloom-forming regions correspond to waters enriched in nutrients by convective and wind-driven mixing (e.g., regions 1–4), riverine input (e.g., the Amazon plume), or coastal upwelling (e.g., eastern boundary currents). Satellite data also illustrate both the prevalence of blooms at higher latitudes and the absence of such blooms where a lack of iron curtails significant phytoplankton accumulation (e.g., regions 5 and 6).

Although the concept of a bloom is at least qualitatively agreed upon as a condition of high phytoplankton biomass, consensus on what causes a bloom is altogether another matter. The appearance of blooms in nutrient-replete waters, particularly following a period of low light and deep mixing, has contributed to the widely held view that these events are consequences of rapid phytoplankton division rates.[1] Accordingly, bloom research has focused largely on processes impacting the abiotic factors governing cell division (light, nutrients, and temperature). However, recent purposeful iron enrichment experiments (de Baar et al. 2005, Boyd et al. 2007), global satellite data (Behrenfeld 2010), in situ autonomous profiling measurements (circle 1 in **Figure 1**) (Boss & Behrenfeld 2010), and modeling studies (Behrenfeld et al. 2013) have provided critical new insights on bloom regulation that challenge traditional concepts. Our review therefore begins with a summary of three contemporary schools of thought regarding bloom initiation, with particular emphasis on how recent observations align with these concepts. We then use field and model results to look at ecological underpinnings of blooms in greater detail and examine how these events contrast with conditions of permanent oligotrophy. The emergent view, reminiscent of Riley (1946) and Cushing (1959), portrays phytoplankton blooms as expressions of subtle imbalances in predator-prey relations rather than as reflections of rapid cell division. Recasting blooms as a fundamental problem in ecology demands a shift to a research strategy that emphasizes environmental controls on trophic interactions and mechanisms of succession in species dominance over the annual cycle.

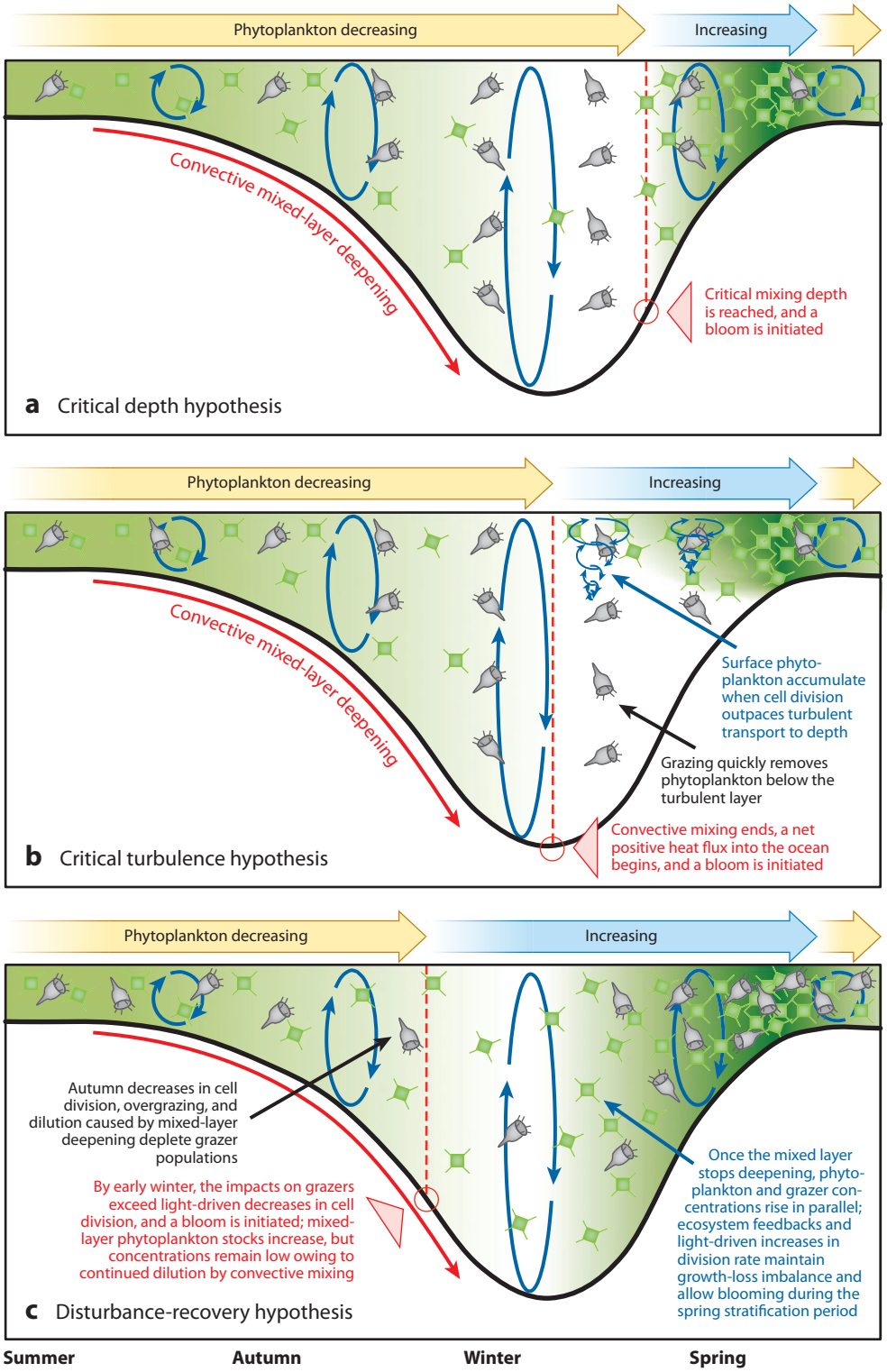
[1] Variability in phytoplankton division rate (μ), loss rate (l), and rate of biomass change (r) (often referred to as the accumulation rate) is a major theme throughout this review. When values for these rates are given, they are expressed as daily instantaneous rates, which are exponentials to the base e. To obtain daily changes, such as divisions or doublings per day, divide these reported specific rates by ln(e) = 0.693. The rate of biomass change (r) equals the difference between μ and l.

FIXATION ON DIVISION: DEBATE OF CAUSE AND EFFECT

The subarctic Atlantic spring phytoplankton bloom has captured the attention of oceanographers for well over a century because of its annual recurrence and ecological significance. It is the birthplace of the most popular explanation for bloom initiation (Gran & Braarud 1935, Sverdrup 1953) and continues to play a central role in guiding bloom theory development. The annual phytoplankton cycle of the subarctic Atlantic is well documented. In winter, the phytoplankton community is dominated by small (<3 μm) flagellated species, with annual minimum concentrations (on the order of 10^3 cells mL^{-1}) typically occurring during maximum surface mixing depths (around February) (Halldal 1953, Dale et al. 1999, Backhaus et al. 2003, Ward & Waniek 2007). These organisms continue to dominate the assemblage through much of the subsequent spring bloom, with abundances often exceeding 10^5 cells mL^{-1} (Parsons & Lalli 1988). In contrast, diatoms are exceedingly rare during the subarctic Atlantic winter (Halldal 1953, Dale et al. 1999, Backhaus et al. 2003), but a few species do reach concentrations later in the year of 10^5 cells mL^{-1} (Parsons & Lalli 1988), or sometimes much greater. Typically (but not always; Lohmann 1908, Murphy & Haugen 1985, Verity et al. 1993), these larger cells (>10 μm) briefly dominate the phytoplankton assemblage at the bloom climax (Halldal 1953, Robinson 1965, Colebrook 1982, Dale et al. 1999).

The springtime co-occurrence of rising phytoplankton concentration, increasing sunlight, and shoaling mixed-layer depths (MLDs) naturally led early investigators to assume that the subarctic Atlantic spring bloom is a consequence of rapid cell division triggered by increasing light. In particular, a critical mixing depth was envisioned (Gran & Braarud 1935) that determined bloom onset. Sverdrup (1953) formalized this concept into what is now referred to as the critical depth hypothesis (CDH). Descriptions of the CDH are included in most biological oceanography textbooks (e.g., Sarmiento & Gruber 2006, Miller & Wheeler 2012) and even emerge in the public media (e.g., the British Broadcasting Corporation's *The Blue Planet* series). According to this hypothesis, deep winter mixing and low light levels in temperate to polar seas cause phytoplankton division rates in the surface layer to be less than total loss rates from respiration, herbivore grazing, sinking, viral lysis, and other forms of mortality (**Figure 2*a***). As long as these losses exceed division, phytoplankton concentrations decline. However, as spring proceeds, decreasing MLDs and increasing sunlight allow more rapid phytoplankton division, such that the rate of biomass decline progressively slows (**Figure 2*a***). Eventually, improvements in mixed-layer light conditions allow division rates to equal loss rates (which are assumed to be constant over time), and conditions are set for bloom initiation. This tipping point marks the critical (mixing) depth, after which any further increase in light or decrease in MLD causes division to outpace losses, and a bloom commences (**Figure 2*a***).

The CDH is appealing for multiple reasons. First, and not inconsequentially, it is consistent with our experiences of spring blooming in terrestrial systems. In seasonal forests, plants are dormant in winter, and the spring flush is incontrovertibly initiated by improved conditions for photosynthesis and growth (milder temperatures, increased light, and unfrozen water). The vernal bloom greatly outpaces all responses of the grazing community and thus creates vast standing stocks of leaves. However, this terrestrial scenario has no equivalent in the oceans. Mixed-layer temperatures in the ocean rarely fall below freezing, and there is no threat of desiccation (a major problem for terrestrial plants at subzero temperatures). Direct effects of low temperature on metabolism also do not appear to prevent biomass accumulation, as significant blooms can be observed in near-freezing water and under considerable surface ice (Smith & Nelson 1985, Vehmaa & Salonen 2009, Arrigo et al. 2012). Indeed, low temperatures may actually favor blooms by having a



greater impact on zooplankton grazing than on phytoplankton division rate (Allen et al. 2005, Rose & Caron 2007, López-Urrutia 2008, Taucher & Oschlies 2011). Unlike terrestrial plants, which have high respiratory:photosynthetic mass ratios, the single-celled phytoplankton can also achieve photosynthetic rates that exceed cell respiration (thus enabling net growth) at vanishingly low light levels, even in temperate species (Geider et al. 1986). Finally, grazing communities feeding on phytoplankton bear little resemblance to their terrestrial counterparts. Dominant zooplankton grazers have division rates that can even exceed those of the phytoplankton and have response times to changing phytoplankton abundance that can halt a developing bloom on timescales of just a week (see below). Thus, it is important to resist any temptation to draw parallels between terrestrial and oceanic systems when evaluating potential explanations for phytoplankton blooms.

Another appealing attribute of the CDH is that it apparently explains the empirical observation that the greatest absolute changes in phytoplankton biomass at high latitudes occur only after a period of significant mixed-layer shoaling and/or increasing sunlight. Furthermore, the CDH can account for the delay in the bloom climax commonly reported with increasing latitude (i.e., it takes longer for light and MLD changes to reach the threshold critical condition). The danger in these apparent successes lies in the age-old axiom that correlation does not necessarily imply causation.

Finally, the CDH also appeals to our intuition. Surely there is a depth of mixing that is sufficiently great and/or a light level that is sufficiently low (e.g., polar night) that phytoplankton photosynthesis is simply too low to allow biomass accumulation. The key question is, is this condition commonly experienced across high-latitude bloom-forming regions?

Like many scientific hypotheses, the CDH is easier to disprove than to prove. Far too often, confirmation of the CDH is proclaimed without adequately testing either potential alternative explanations or the hypothesis's fundamental tenet. In Sverdrup's (1953) landmark paper, bloom initiation was defined by the point in time when the rate of mixed-layer-integrated phytoplankton division first exceeds the rate of integrated loss, not when the absolute increment of change in biomass (r; see footnote 1) exceeds a threshold value. Thus, a key prediction is that growth conditions in the mixed layer are sufficiently poor prior to reaching the critical mixing depth that

Figure 2

Comparison of bloom hypotheses: (*a*) the critical depth hypothesis (CDH), (*b*) the critical turbulence hypothesis (CTH), and (*c*) the disturbance-recovery hypothesis (DRH). The seasonal cycle in each plot begins with summer on the left. Thick black lines indicate mixed-layer depth (MLD). Green phytoplankton cells and green shading above the MLD are proportional to phytoplankton concentration (in milligrams of carbon per cubic meter). Gray ciliates represent all phytoplankton grazers. Arrows above each panel indicate changes in phytoplankton abundance. In panel *c*, the blue arrows at the top correspond first to increasing water-column-integrated phytoplankton biomass (but not concentration) and then, once the mixed layer begins to shoal, to increasing phytoplankton concentration. Formulations of the CDH and CTH typically assume that volumetric phytoplankton loss rates (per unit time) are invariant; panels *a* and *b* therefore show constant concentrations of zooplankton over time (which consequently implies increased water-column-integrated zooplankton stocks in winter). In contrast, phytoplankton and zooplankton concentrations for the DRH are highly correlated in time. For the CDH, phytoplankton concentrations do not begin to rise in spring until a critical mixing threshold is reached; before this point, phytoplankton concentrations are decreasing. For the CTH, changes in plankton concentrations are identical to those of the CDH during the period of convective mixed-layer deepening. Once net heat flux to the ocean becomes positive, phytoplankton concentrations near the surface can begin increasing as long as near-surface division rates exceed the rate at which turbulence distributes these phytoplankton to greater depths (where they are consumed). For the DRH, autumn changes have a greater impact on grazers than phytoplankton division rates (μ), such that by early winter μ exceeds loss rates (l) and depth-integrated phytoplankton (but not concentration) begins increasing. This excess of μ over l is sustained during spring stratification because increasing grazing pressure is paralleled by increasing phytoplankton division rate.

phytoplankton biomass is decreasing. Testing this prediction requires evaluating rates of change in mixed-layer phytoplankton biomass throughout the annual cycle. Most field studies do not permit such an evaluation, because campaigns are typically too short and are biased toward the final climax period of high biomass. The few historical studies that have been conducted in winter suggest that biomass is increasing even during the period of deepest mixing (Halldal 1953, Brettum 1969, Dale et al. 1999, Backhaus et al. 2003, Boss & Behrenfeld 2010). Winter studies have also revealed significant nutrient drawdown by the phytoplankton prior to mixed-layer restratification (Garside & Garside 1993, Backhaus et al. 2003, Körtzinger et al. 2008). More recently, satellite and autonomous in situ measurements have shown that phytoplankton concentrations (in milligrams of carbon per cubic meter) in the subarctic Atlantic begin increasing as soon as convective deepening of the mixed layer stops, as long as at least some sunlight is available (i.e., not polar night) (Behrenfeld 2010, Boss & Behrenfeld 2010, Behrenfeld et al. 2013). In other words, the first signs of increasing phytoplankton concentration occur when growth conditions are near their worst (deepest mixing and lowest light). Thus, the fundamental tenet of the CDH is not upheld.

In his study of field data from Weather Station M in the subarctic Atlantic, Sverdrup (1953) initially evaluated critical depth values from changes in the seasonal thermocline. Insightfully, he noted that a bloom may still appear when the thermocline is deep if turbulence within this layer is low. Forty-five years later, this idea reappeared as the critical turbulence hypothesis (CTH) (Huisman et al. 1999, 2002). As in the CDH, the CTH presumes that phytoplankton loss rates are constant and that blooms do not occur during deep mixing because phytoplankton division is light limited (i.e., a "bottom-up" constraint). The difference between the CDH and the CTH is simply that the latter distinguishes between a density-defined mixed layer and the actively mixing layer. More specifically, the end of convective mixed-layer deepening generally corresponds to the beginning of net positive heat flux into the ocean. When this happens, the depth of active turbulent mixing can become shallow before any notable change in vertical density structure occurs. According to the CTH, bloom initiation is determined by the balance between two opposing processes: light-driven photosynthesis (which tends to create a near-surface layer of increasing biomass) and turbulence (which tends to erode this layer by distributing biomass over depth) (**Figure 2*b***). Under quiescent weather conditions, adequate surface sunlight, and minimal nighttime convection, the CTH predicts that near-surface phytoplankton growth can outpace the dissipatory effects of turbulence as soon as net heat flux into the ocean becomes positive. The appeal of the CTH, and thus its recent resurgence in the literature (Chiswell 2011; Taylor & Ferrari 2011a,b), is that it can potentially account for the satellite and autonomous sensor observations of phytoplankton concentrations increasing as soon as the mixed layer stops deepening (Behrenfeld 2010, Boss & Behrenfeld 2010).

The CTH predicts vertical gradients of decreasing chlorophyll with depth in water columns of deeply uniform density profiles (which is consistent with some observations but not others; Backhaus et al. 2003, Ward & Waniek 2007, Chiswell 2011). The CTH also predicts that bloom initiation coincides with a period of low turbulence and that integrated phytoplankton biomass is decreasing during convective mixed-layer deepening. During the 2008 North Atlantic Bloom study (NAB-08; circle 2 in **Figure 1**), direct measurements of active mixing using neutral-density floats demonstrated that transient periods of low turbulence are not essential for bloom development (Mahadevan et al. 2012). However, NAB-08 was conducted during the latter portion of the subarctic Atlantic spring bloom, and thus the study could not discount the potential importance of low-turbulence periods earlier in the year. Satellite and autonomous float data, in contrast, cover complete annual cycles in the subarctic Atlantic and demonstrate that mixed-layer phytoplankton division rates typically exceed loss rates (i.e., the depth-integrated phytoplankton population is increasing) while early-winter convection is still deepening the mixed layer. A basin-wide analysis of the subarctic Atlantic has further shown that the phytoplankton division:loss ratio actually

increases (rather than decreases) with increasing convective mixing depth (Behrenfeld et al. 2013). Thus, key predictions of the CTH are not upheld by observations.

The third school of thought regarding phytoplankton blooms focuses on physical and ecological processes influencing the balance between phytoplankton division and loss rates, in particular the losses to grazing (and viruses) (**Figure 2*c***). The key role of grazing in bloom control is illustrated by comparing subarctic Atlantic annual cycles of phytoplankton division rates and rates of biomass change (**Figure 3*a***; note that the *x* axis begins in July), where the division rate (μ) is calculated as mixed-layer net primary production divided by phytoplankton biomass, and the rate of biomass change (r) is observed as temporal changes in phytoplankton stocks (Behrenfeld 2010, Boss & Behrenfeld 2010, Behrenfeld et al. 2013). This comparison shows that the primary blooming period of increasing mixed-layer biomass can begin as early as December and coincides with decreasing division rates (**Figure 3*a***) (Behrenfeld 2010). The blooming period continues until around June and then abruptly ends while phytoplankton division rates are still increasing. Termination of the bloom is caused by overgrazing (i.e., the grazing rate exceeds even a high cell division rate), viral attack (Suttle et al. 1990, Vardi et al. 2009, Bidle & Vardi 2011), or biomass export (Briggs et al. 2011) and can be linked to decreases in division rates resulting from depletion of a macronutrient (e.g., nitrogen or silicon) or iron (Dale et al. 1999, Blain et al. 2004, Nielsdottir et al. 2009, Mahadevan et al. 2012). Importantly, **Figure 3*a*** shows that the rate of biomass accumulation is independent of the rate of division, which contrasts starkly with the CDH and CTH assumption that biomass accumulation rates covary linearly with division rates (**Figure 2*a*,*b***). More important, comparison of the left and right *y* axes in **Figure 3*a*** reveals that the rates of biomass change are an order of magnitude smaller than the division rates. In other words, the bloom is a consequence of residual differences between two much larger and opposing rates that are highly correlated in time: phytoplankton division and loss rates.

Decoupling between phytoplankton division and biomass accumulation rates is not a new finding (e.g., Halldal 1953; Steemann Nielsen 1958; Pollingher & Berman 1977; Tilzer 1984; Strom & Welschmeyer 1991; Banse 1992, 2002), but it implies that any explanation of blooms focused only on abiotic factors regulating cell division will be (grossly) incomplete. The 1989 Joint Global Ocean Flux Study (JGOFS) North Atlantic Bloom Experiment (NABE; circle 3 in **Figure 1**) (Ducklow & Harris 1993) clearly showed that phytoplankton division and accumulation rates are independent because of rapidly responding changes in zooplankton grazing rates (Verity et al. 1993). The interrelation between these key rate terms is perhaps even better illustrated by a decade of satellite observations (**Figure 3*b*,*c***). Recognizing that the subarctic Atlantic bloom (one of the largest blooms in the global ocean) results from the minor deviations from the 1:1 line in **Figure 3*c***, it is clear that understanding blooms necessitates understanding the factors regulating the balance between phytoplankton division and loss rates.

The emergence of phytoplankton blooms in the global ocean has recently been discussed in the context of an ecological disturbance-recovery hypothesis (DRH)[2] (Behrenfeld et al. 2013). According to this view, blooms are initiated by physical processes that disrupt the balance between phytoplankton division and grazer consumption, such as deep winter mixing (**Figure 2*c***), freshwater input, upwelling, or polar night. Feedbacks between predator and prey populations subsequently lead to a recoupling of the ecosystem, but only after a period of significant phytoplankton accumulation (**Figure 2*c***). The DRH can account for (*a*) bloom initiation in the subarctic

[2]The bloom scenario illustrated in **Figure 2*c*** was originally termed the dilution-recoupling hypothesis, as it focused on the special conditions of the subarctic Atlantic bloom following deep winter mixing (Behrenfeld 2010). More recently, this view has been expanded into a more general framework for understanding blooms in other regions, and so it was renamed the disturbance-recovery hypothesis (Behrenfeld et al. 2013).

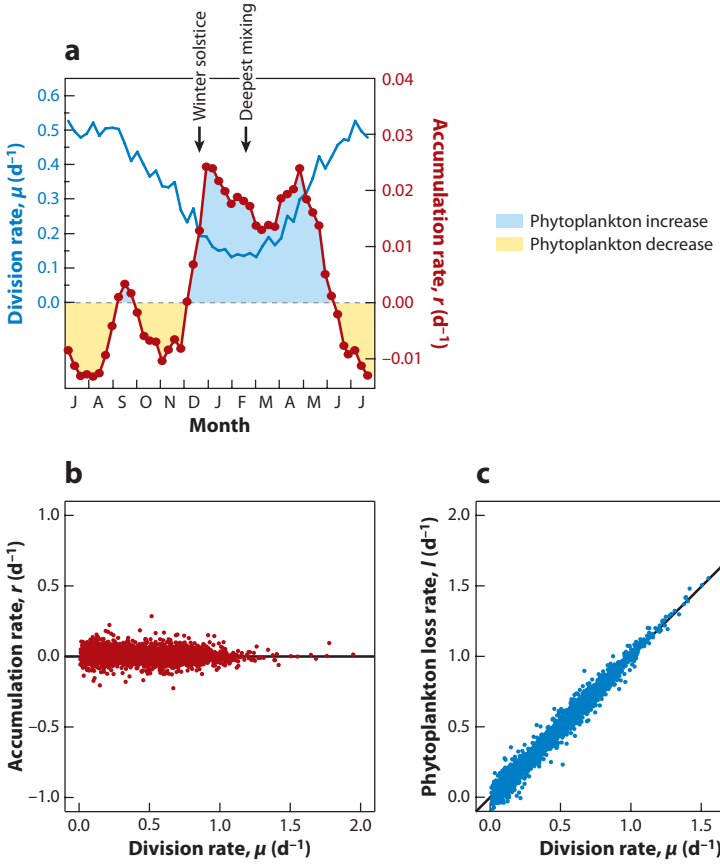


Figure 3

Satellite observations of the subarctic Atlantic bloom. (*a*) Annual cycles in phytoplankton division rate (μ) (*blue line*) and accumulation rate (r) (*red line with circles*) for a 5°-latitude-by-10°-longitude bin near the 1989 Joint Global Ocean Flux Study (JGOFS) North Atlantic Bloom Experiment (NABE) site. Annual cycles are based on 10 years of Sea-Viewing Wide Field-of-View Sensor (SeaWiFS) measurements (corresponding to bin B-05 in Behrenfeld 2010). Note that the annual cycle is split in July. Yellow shading denotes periods of decreasing phytoplankton abundance ($r < 0$); blue shading denotes periods of increasing phytoplankton abundance ($r > 0$). (*b*,*c*) SeaWiFS-based relationships between μ and r (panel *b*) and μ and phytoplankton-specific loss rate ($l = \mu - r$) (panel *c*). Data in panels *b* and *c* are for all subarctic Atlantic bins and all years analyzed by Behrenfeld (2010). Values of r are calculated from satellite-observed changes in phytoplankton biomass between 8-day-resolution time bins, μ is calculated as mixed-layer net primary production divided by mixed-layer phytoplankton biomass, and l is taken as the difference between μ and r (Behrenfeld 2010, Boss & Behrenfeld 2010, Behrenfeld et al. 2013). During mixed-layer shoaling, r is calculated from satellite-observed changes in phytoplankton carbon concentration (milligrams per cubic meter) rather than depth-integrated carbon (milligrams per square meter), to remove the purely physical effects of detrainment (Behrenfeld et al. 2013).

Atlantic during convective mixed-layer deepening, (*b*) increased predator-prey decoupling with deeper mixing, (*c*) the strong positive correlation between phytoplankton division and loss rates, and (*d*) the delay in bloom timing with increasing latitude (Behrenfeld et al. 2013).

The DRH, however, does raise important questions about pelagic ecosystem functioning. In the subarctic Atlantic, for example, only a subtle decoupling occurs between phytoplankton division

and losses during early winter convective mixing, yet the subsequent blooming period may last for many months. How can such a minor predator-prey disruption be sustained over such a long period? Is the early-winter perturbation even relevant to later stages of the bloom? Addressing these questions requires understanding the ecological response times between changing phytoplankton division rates and subsequent grazer control of phytoplankton biomass. In this regard, results from recent purposeful iron experiments provide useful new insights.

EXPERIMENTAL BLOOMS

The demonstration that iron is a primary limiting factor for phytoplankton division over large regions of the open ocean was one of the major accomplishments in biological oceanography during the latter half of the twentieth century. Although trace-metal clean bottle incubation experiments provided critical evidence of iron stress (Martin & Fitzwater 1988, Martin et al. 1989), the crowning achievements of this research were the in situ fertilization experiments that converted low-phytoplankton, high-macronutrient waters into blooms (de Baar et al. 2005, Boyd et al. 2007). These remarkable experiments represented the first large-scale (on the order of 50 km^2) purposeful manipulations of natural plankton assemblages and, although focused on iron limitation, yielded an unprecedented (and underappreciated) view of bloom dynamics. Reminiscent of the subarctic Atlantic bloom but occurring on much shorter timescales, these iron-stimulated experimental blooms typically begin with a phytoplankton community dominated by small prokaryotic and flagellated eukaryotic species dividing at moderate rates. Iron addition modestly increases division rates in these organisms, but their biomass generally changes little owing to tight grazer control (de Baar et al. 2005). Diatoms, in contrast, are typically rare in the initial populations, experience a significant increase in division rate upon iron addition, and rapidly dominate the phytoplankton biomass. This dominance usually reflects an accumulation of only a few moderately sized diatom species (de Baar et al. 2005).

Figure 1 shows changes in chlorophyll concentration during four in situ iron fertilization experiments: Subarctic Ecosystem Response to Iron Enrichment Study (SERIES) (Boyd et al. 2004), Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study (SEEDS) (Tsuda et al. 2003), Iron Enrichment Experiment II (IronExII) (Coale et al. 1996), and Southern Ocean Iron Release Experiment (SOIREE) (Boyd et al. 2000). These chlorophyll time courses are closely modeled by an initial delayed response of up to 5 days, followed by exponential growth at a constant rate to the bloom maximum, and then, for SERIES and IronExII, a subsequent linear decrease. In truth, the initial delay is misleading, because the originally rare species that eventually dominate the bloom are already increasing rapidly but simply have not yet accumulated enough biomass to be reflected in total chlorophyll concentration (Cavender-Bares et al. 1999). A particularly striking aspect of these experimental blooms is that the period of constant exponential growth of the emerging diatoms ends prior to macronutrient exhaustion (see de Baar et al. 2005, Boyd et al. 2007), being stopped by grazers after only a week or two (**Figure 1**). This rapid ecosystem reequilibration implies that the increase in food (phytoplankton) has a greater stimulating impact on the grazers than iron addition has on phytoplankton division rates (Landry et al. 2000, de Baar et al. 2005). Given that an iron fertilization experiment is a far more extreme perturbation to growth conditions than the slow seasonal changes occurring in the subarctic Atlantic, these findings appear to make the mere existence of blooms in the latter environment surprising. They also clarify why rates of biomass accumulation and phytoplankton division can be so uncorrelated (e.g., **Figure 3*b***).

The in situ enrichment experiments also give the apparently contradictory result that the maximum chlorophyll concentrations achieved during an experiment are proportional to division rates. For the four experiments shown in **Figure 1**, SOIREE had the greatest MLDs (~200 m) and

presumably the slowest division rates (owing to low median mixed-layer light levels), and it achieved the lowest peak chlorophyll concentration (~1.2 mg Chl m^{-3}). In contrast, SEEDS had shallow mixing (~10 m) that could support rapid cell division, and it yielded a truly spectacular bloom (~18 mg Chl m^{-3}). Interestingly, this apparent relationship between division rate and climax chlorophyll concentration (de Baar et al. 2005) contrasts with the peak mixed-layer-integrated chlorophyll produced during an experiment. Specifically, the SOIREE bloom of ~240 mg Chl m^{-2} (i.e., 1.2 mg Chl m^{-3} × 200 m) exceeds that of the ~180 mg Chl m^{-2} bloom achieved during SEEDS (i.e., 18 mg Chl m^{-3} × 10 m). To illuminate mechanisms underlying these dynamics of experimental (as well as natural) blooms, it is necessary to turn to plankton models.

HISTORICAL BIFURCATION

The foundation for quantitative modeling of planktonic ecosystems was established in the 1940s (Riley 1946, Riley & Bumpus 1946, Riley et al. 1949). The CDH was a major simplification of this framework that targeted a specific problem (high-latitude blooms) and ignored ecosystem interactions (i.e., by assuming that phytoplankton loss rates are invariant). Its formalization marked a bifurcation point in biological oceanography. Although many field-oriented researchers embraced the CDH, it was not explicitly adopted by the modeling community. Nevertheless, contemporary ocean ecosystem models reliably reproduce the global locations and timing of observed phytoplankton blooms. This success implies that these models capture fundamental principles governing blooms.

Ecosystem models are continually increasing in complexity, but many basic relationships are conserved. Here, we focus on these basic relationships to investigate why models successfully reproduce blooms. Phytoplankton division rate (μ) in ecosystem models is described as a function of light, nutrients, and cellular respiration (e.g., Evans & Parslow 1985). Phytoplankton (P) concentration changes (dP/dt) can then be expressed as a function of population division (μP) minus consumption by herbivores (H), decreases due to dilution when the mixed layer deepens (w^+P/MLD, where w^+ is the rate of change in MLD and the superscript indicates that dilution occurs only when MLD is deepening; e.g., Evans & Parslow 1985), and eddy diffusion across the bottom of the mixed layer (mP/MLD):

$$\frac{dP}{dt} = \mu p - \left(c_1 \frac{P^2}{P^2 + c_2}\right) H - \frac{(m + w^+)\, P}{MLD}. \quad (1)$$

In Equation 1, mortality due to viruses (Suttle et al. 1990, Vardi et al. 2009, Bidle & Vardi 2011) and sinking losses out of the mixed layer are not included, and the description of herbivore grazing as a saturating function of P (middle term on the right side of Equation 1) follows a formulation by Moore et al. (2002). Note that when included, sinking is modeled as a linear term in P and mortality to viruses is a nonlinear term in P (proportional to P^2); hence, we would not expect the addition of such terms to critically change the qualitative behavior of Equation 1.

For herbivores, concentration changes (dH/dt) are similarly described as a function of reproduction (first term on the right side of Equation 2) minus nonpredatory mortality (second term), density-dependent losses representing predation by carnivores (third term), and effects of MLD changes (last term):

$$\frac{dH}{dt} = \left(c_1 c_3 \frac{P^2}{P^2 + c_2}\right) H - c_4 H - c_5 H^2 - \frac{wH}{MLD}. \quad (2)$$

Similarly to Equation 1, MLD deepening results in dilution of the herbivore population in Equation 2. In contrast to Equation 1, MLD shoaling concentrates herbivores within the mixed

layer in recognition of their ability to swim (thus, the superscript + is not used, and at all times $w = dMLD/dt$; Evans & Parslow 1985). For clarity, advective fluxes have been omitted in Equations 1 and 2, so these representations are best thought of as either parcel-tracking (Lagrangian) or representative of properties integrated over a sufficiently large horizontal area that contributions from advection are negligible. Using published values for parameters c_1–c_5 (Evans & Parslow 1985, Moore et al. 2002), these two equations provide a simple system for interrogating why ecosystem models re-create global blooms (see **Supplemental Methods**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**).

As an initial simplification, we can ignore the effects of MLD changes (w^+P/MLD in Equation 1 and wH/MLD in Equation 2) and the term representing carnivore predation (c_5H^2 in Equation 2), and can describe the phytoplankton division rate (μ) as ranging from 0.05 to 0.55 d^{-1} (representative of some subarctic Atlantic regions) and having an annual cycle that first increases and then decreases in evenly spaced increments of 0.1 d^{-1}. This scenario yields four pertinent results (**Figure 4*a***). First, each increasing step in μ results in a one- to two-week transient increase in phytoplankton concentration before herbivory stops the bloom and begins to reestablish predator-prey equilibrium. This response timescale is similar to that observed during the iron enrichment bloom experiments (see above). Second, a decreasing increment in μ initially results in overgrazing of the phytoplankton. This decrease in food consequently decreases herbivore abundance, which allows phytoplankton concentrations to subsequently rise again, which is then followed by an increase in grazers until equilibrium is reestablished. In other words, strong ecosystem feedbacks exist in the model. Third, the transient changes in phytoplankton have a magnitude proportional to the relative (not absolute) change in μ (Evans & Parslow 1985), which is qualitatively similar to responses during the purposeful iron enrichment blooms. Finally, the order-of-magnitude range in μ has no impact on equilibrium phytoplankton concentrations and instead is expressed, perhaps ironically, through changes in the herbivore population (**Figure 4*a***).

The above scenario clearly does not reproduce natural blooms. However, if we repeat the incremental steps of μ in the model and now reintroduce the carnivore predation term (c_5H^2 in Equation 2), an annual cycle in phytoplankton concentration appears (**Figure 4*b***). Furthermore, the same cycle is achieved if μ is allowed to change smoothly over the year (**Figure 4*b***), indicating that the system is perpetually functioning near equilibrium. The resultant minor phytoplankton bloom in **Figure 4*b*** is not a direct consequence of higher μ (i.e., no bloom is seen in **Figure 4*a*** for the same μ cycle) but rather arises because the added density-dependent loss term representing carnivory dampens the herbivore response to phytoplankton division rate (compare the herbivore lines in **Figure 4*a*,*b***) (Calbet & Landry 1999). This phenomenon is referred to as a trophic cascade (Verity & Smetacek 1996, Pace et al. 1999, Verity et al. 2002). Although it yields an annual cycle in phytoplankton, the amplitude of this cycle is small (factor of three change) because the ecosystem feedbacks described above allow only minor disequilibria between phytoplankton division and loss rates. The model can be further modified to include an annual cycle in μ with a range representative of regions in the subarctic Atlantic, but again the resultant phytoplankton bloom (**Figure 4*c***) is relatively minor (factor of eight change). The primary conclusion from these results is that, without additional forcing, a model plankton system with equilibrium response times consistent with iron enrichment bloom experiments cannot replicate the magnitude of natural blooms, which may reach biomass concentrations two or more orders of magnitude greater than annual minima.

A strikingly different result emerges when the physical consequences of MLD changes are included: The model yields a major bloom (factor of >500 change) (**Figure 4*d***). This bloom is caused by autumn–winter MLD deepening having a greater impact on herbivore populations than on phytoplankton. Specifically, autumn decreases in division rate (owing to decreasing sunlight and deeper mixing) are paralleled by reductions in phytoplankton concentration because of

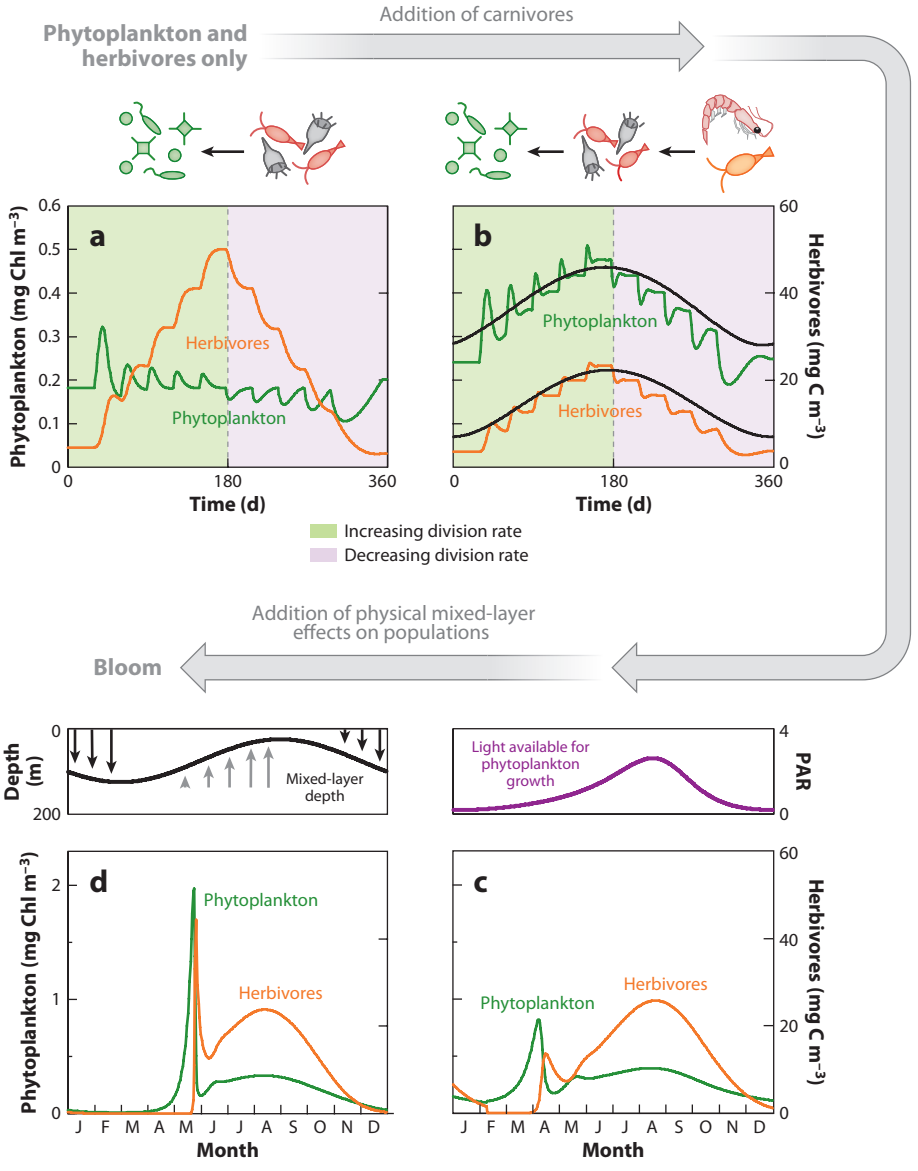


Figure 4

Modeled annual cycles in the concentrations of phytoplankton (*green lines*) and herbivores (*orange lines*). (*a*) Model results with no carnivores (i.e., no density-dependent herbivore-specific mortality term) and incremental changes in phytoplankton division rate (μ). (*b*) Model results after the addition of carnivore predation on herbivores. Here, the green and orange lines are phytoplankton and herbivore concentrations, respectively, for incremental changes in μ; the black lines are phytoplankton (*top*) and herbivore (*bottom*) concentrations when μ changes smoothly over the annual cycle. (*c*) The same as panel *b* except that μ is calculated from an annual cycle in mixed-layer light levels (*upper subpanel*) corresponding to an annual range in mixed-layer depth (MLD) that is representative of areas in the subarctic Atlantic. (*d*) The same as panel *c* but additionally accounting for the physical effects of MLD changes (*upper subpanel*) on phytoplankton and herbivore concentrations and interactions. Abbreviation: PAR, photosynthetically active radiation (mol photons m^{-2} h^{-1}).

overgrazing, as in the two previous scenarios (**Figure 4*b*,*c***). Herbivore concentrations consequently begin to decline. However, although this reduction in herbivores again reduces grazing losses and initiates an accumulation of phytoplankton, the continued deepening of the mixed layer causes phytoplankton concentrations (per cubic meter) to further decrease (rather than increase) because the slowly accumulating population is being distributed over an increasing volume of water (i.e., being diluted) (**Figure 2*c***) (Banse 1992, Backhaus et al. 2003, Ward & Waniek 2007, Behrenfeld 2010). This decrease in food concentration results in further herbivore losses, because it causes herbivore reproduction rates to be slower than mortality rates (this mortality predominantly reflects the linear herbivore loss term, c_4H, in Equation 2) (Evans & Parslow 1985). Consequently, the decoupling between phytoplankton division and loss rates increases for as long as the mixed layer continues to deepen. By the time this deepening period ends (around February in the subarctic Atlantic), herbivore populations are heavily depleted, and phytoplankton concentrations are at a minimum. In contrast, water-column-integrated phytoplankton stocks (per square meter) are actually approaching their annual maximum at this time (Dale et al. 1999, Backhaus et al. 2003, Körtzinger et al. 2008, Behrenfeld 2010) and are greatest in areas with deepest winter mixing (Behrenfeld et al. 2013). From this point on, phytoplankton concentrations (per cubic meter) begin to increase because the accumulating biomass is no longer diluted (**Figure 2*c***). The increase in concentration stimulates grazing and initiates a subsequent increase in herbivores, but this process of recoupling is slow because net accumulation rates are small (**Figure 3*a***). Ultimately, the winter decimation of the herbivore population and rising phytoplankton division rates repress ecosystem reequilibration enough that a bloom eventually emerges (**Figure 4*d***) (Behrenfeld et al. 2013). If polar night is included in this scenario, the bloom is delayed, the herbivore population declines further, and the subsequent bloom can potentially achieve a greater climax concentration (Behrenfeld et al. 2013).

This simple modeling exercise illustrates an important point. Ecosystem models reproduce global phytoplankton blooms at appropriate places and times because they encapsulate the physical processes disrupting the ecosystem feedbacks that tend to maintain quasi equilibria between predators and prey. Perhaps surprisingly, seasonal changes in μ play only a secondary role in blooms and fail to produce major blooms in the absence of a preliminary (physical) disturbance to ecosystem balances (e.g., compare the phytoplankton lines in **Figure 4*c*,*d***).

OVERDUE PARADIGM SHIFT

Despite its simplicity, the model employed in **Figure 4** identifies key requirements for phytoplankton blooms and yields both a strong correlation between phytoplankton division rates and loss rates ($R^2 = 0.7$) and an independent behavior of phytoplankton division rates and accumulation rates ($R^2 < 0.01$). These latter properties are consistent with field and satellite-based results (**Figure 3*b*,*c***) (Pollingher & Berman 1977, Tilzer 1984, Strom & Welschmeyer 1991, Verity et al. 1993, Longhurst 2007, Behrenfeld 2010). Our finding is that phytoplankton blooms require a physically forced preconditioning of ecosystems that significantly disrupts phytoplankton-herbivore relationships. In a sense, the ability of phytoplankton to become uncommonly abundant (i.e., bloom) relies on them first being uncommonly rare.

The notion that rarity can be an important precursor to abundance may have particular relevance to species succession during blooms. For example, small flagellated phytoplankton maintain a significant presence throughout the winter in the subarctic Atlantic, despite dilution by mixed-layer deepening. These winter concentrations accordingly foster only a modest predator-prey decoupling, which allows the herbivore population to later constrain spring blooming of these small species (Irigoien et al. 2005). In contrast, larger diatoms are eaten, or encyst, or sink out of

the mixed layer during winter and become exceedingly rare, with dire consequences for their grazers. Indeed, many diatom grazers (e.g., copepods) hibernate at great depth over winter (Longhurst & Williams 1979, Longhurst 2007, Miller & Wheeler 2012). Winter predator-prey decoupling for diatoms and their grazers is therefore far more severe, which is likely essential for their late-bloom dominance (Kiørboe 1997).

A similar scenario applies to experimental blooms (de Baar et al. 2005, Fujii & Chai 2007). These purposeful iron enrichment studies are conducted where grazers of large phytoplankton are initially rare, thus providing a brief window of opportunity for the equally rare diatoms to flourish once iron limitation is relieved. All of these natural and experimental bloom conditions contrast strongly with the vast open-ocean regions where biomass is temporally stable and phytoplankton division and loss rates are tightly coupled throughout the year (see below).

An important attribute of blooms is that a limited number of diatom species often dominate the climax phytoplankton assemblage. These dominant species represent only a small fraction of the diatom diversity extant before a bloom. Many of these species presumably have comparable division capacities and experience similar stimulation from purposeful iron additions or natural seasonal improvements in environmental conditions (e.g., mixed-layer shoaling and increasing light in spring). The failure of most species to reach high concentrations at bloom climax implies that physical disruption of predator-prey interactions is only part of the story. The other factor now emerging as critical to phytoplankton succession during blooms is that zooplankton are selective feeders (Landry 1981, Crumpton & Wetzel 1982, Cowles et al. 1988, Tiselius & Jonsson 1990, Kiørboe 1997, Verity et al. 2002, Mariani et al. 2013). Selective feeding involves switching between preferred phytoplankton species and, in the case of larger zooplankton, between herbivory and carnivory. Focused consumption of a dominant phytoplankton group allows the abundance of secondary species to increase (Kiørboe et al. 1996), but ecosystem interactions during a bloom are complex. Relationships between adjacent trophic levels are influenced by phytoplankton, herbivore, and carnivore morphologies; chemical and physical deterrents on predation; changes in food quality; and life histories (Grover 1989, Verity & Smetacek 1996, Miralto et al. 1999, Verity et al. 2002, Irigoien et al. 2005). Indeed, the dynamics of plankton ecosystems have been referred to as an arms race, where significant resources are invested in minimizing casualties (Verity & Smetacek 1996). Thus, bloom succession reflects a cascade of ecosystem interactions that open loopholes for the brief dominance of a few particular species (Bakun & Broad 2003, Irigoien et al. 2005), where the winners (i.e., the most abundant species) at the end of a bloom are not necessarily the best competitors for resources or the fastest dividers, but are perhaps simply the least "tasty" (Irigoien et al. 2005). Added to this interplay between phytoplankton and zooplankton is a potential major role for viruses, which can impact phytoplankton species in a density-dependent manner and thus contribute significantly to temporal succession in phytoplankton dominance.

Satellites, autonomous floats and gliders (e.g., Boss et al. 2008, Fennel et al. 2011), in situ enrichment experiments (de Baar et al. 2005, Boyd et al. 2007), models (e.g., Anderson et al. 2010, Prowe et al. 2012), and advanced field sensors (e.g., Olson & Sosik 2007, Picheral et al. 2010) are providing a wealth of new information on phytoplankton blooms. Traditional division-centric, or bottom-up-only, views are clearly inadequate, and a paradigm shift focused on ecosystem interactions is overdue (Verity & Smetacek 1996). Recasting blooms as primarily an issue of phytoplankton-herbivore (and virus) interactions necessitates not a complete upheaval of ecological theory but merely a resurrection of earlier concepts (e.g., Steemann Nielsen 1958, Cushing 1959, Tilzer 1984, Banse 2002). Indeed, Nathansohn (1910) had already called attention to the importance of grazers in controlling phytoplankton stocks in the early twentieth century. By the 1940s, blooms were recognized as a consequence of subtle

imbalances between phytoplankton division rates and loss rates, with near equilibrium maintained between predators (grazers) and prey (phytoplankton) on a timescale of only a few days (Riley 1946, Riley & Bumpus 1946). At first, these conclusions were problematic, because early plankton research was strongly biased toward larger mesozooplankton species (e.g., copepods) with complicated life histories that seemed incompatible with rapid response times (e.g., Steemann Nielsen 1958, Cushing 1959). Today, however, we understand that the tight predator-prey coupling predominantly involves a diverse community of microzooplankton grazers (<200 μm) (Calbet & Landry 2004) that feed on small species up to modest-sized diatoms (Verity et al. 1993, Strom et al. 2001, Sommer & Lengfellner 2008) and have rapid potential growth rates (Banse 1982, 2002).

Perhaps ironically, the most significant role of the omnivorous mesozooplankton, which captured the attention of researchers for decades, may be their predatory impacts on microzooplankton (Verity et al. 1993, Kiørboe 1997, Verity et al. 2002). For the phytoplankton, therefore, the arms race is focused on deterring microzooplankton (more than mesozooplankton) grazing, and even a minor advantage over other phytoplankton species can differentiate between static and blooming populations (Verity & Smetacek 1996, Irigoien et al. 2005).

FIXATION ON BLOOMS: THE CASE OF PERMANENT OLIGOTROPHY

Seasonal phytoplankton blooms continue to hold the attention of planktologists and biogeochemists, but the prominence of temporally stable, low-biomass regions worldwide deserves attention. In these vast low-nutrient regions (blue colors in the **Figure 1** satellite image), phytoplankton concentrations are held at perpetually low levels by a daily mortality that is overwhelmingly dominated by grazing (as opposed to viral lysis, sinking, or vertical mixing losses) (Banse 1992, 2013). Surprisingly, the magnitude of this mortality rate is still not as widely recognized as it should be, despite nearly three decades of shipboard grazing rate measurements, where the technique of choice is the dilution method (see Selph et al. 2011). According to the global review of open-ocean measurements by Calbet & Landry (2004), three-fifths to three-quarters of phytoplankton production is consumed the same day by microzooplankton (<0.2 mm in length, with most being <0.1 mm), to which another one-tenth to two-tenths can be added for consumption by larger suspension feeders. The remaining fraction of daily phytoplankton production is divided into biomass accumulation, export from the euphotic zone, and other losses.

In contrast to the bloom-forming condition, phytoplankton biomass is stable over most of the permanently stratified lower-latitude oceans (Landry et al. 1997), where seasonal surface temperature changes are insufficient for significant convective vertical mixing and associated nutrient injection. This lid on nutrient supply, however, can be broken by vertical displacement of isopycnals within eddy interiors or equatorial upwelling, resulting in a temporary local bloom (e.g., Falkowski et al. 1991; McGillicuddy et al. 1998, 2007; Rii et al. 2008). Natural blooms may also be observed in response to iron enrichment by dust-fall events [e.g., the threefold chlorophyll increase in the Gulf of Alaska reported by Hamme et al. (2010)] and downstream from the sea beds of oceanic archipelago [e.g., the Kerguelen Islands in the Southern Ocean (Blain et al. 2008) and the Galápagos Islands (Gordon et al. 1998)]. However, as in the purposeful iron enrichment blooms discussed above, grazing pressure essentially covaries with phytoplankton division, ensuring that much of the organic carbon formed through photosynthesis is recycled within the mixed layer and rereleased as inorganic carbon rather than exported to depth. This carbon recycling is highlighted during the experimental blooms in which decreases in dissolved inorganic carbon were only 51% ± 26% of the production implied by ^{14}C uptake measurements and in which concurrent CO_2 influx from the atmosphere averaged 8% of the drawdown (de Baar et al. 2005).

Although permanent oligotrophy with quasi-steady-state aspects may appear to be the simpler case for ecological modeling, challenges remain. For example, why do these systems yield an equilibrium solution of low biomass and high division rate rather than, say, higher biomass and lower division rate? Mortality is an emergent property of populations, and in planktonic systems it is finely tuned to cell division rates. These rates act at the level of individuals through their impact on resources, yet they fail to result in Lotka-Volterra-type oscillations of the protists. Mathematical modeling, in principle, characterizes the balance between phytoplankton abundance and ingestion by grazers, but we cannot yet specify precisely why the globally observed quasi-steady-state chlorophyll concentrations are not, say, one-third or three times what they are. Are they determined by the inability of grazers to extract particles to a lower level at the very low Reynolds numbers, or do their predators keep them accurately in check such that, in effect, there is a feeding threshold for the grazers? Addressing these issues for conditions of permanent oligotrophy will likely also inform understanding of bloom-forming regions, particularly regarding processes during the low-biomass season that precedes and is apparently essential to bloom development.

HINDSIGHT

Phytoplankton blooms are ecologically complex events, with characteristics differing between regions and from year to year. Mechanisms driving this variability will continue to be debated, but as we move forward, it would be advantageous to avoid certain practices from the past. First, and in keeping with Sverdrup's early work, it is essential to evaluate bloom dynamics in the context of rates of biomass change rather than absolute concentrations. For example, one can envision two mixed layers where conditions permit a doubling of biomass every week but where, say, one has an initial biomass of 1 mg C m^{-3} and the other has an initial biomass of 10 mg C m^{-3}. After a week, biomass in the latter system will have increased by an order of magnitude more than the former (increasing by 10 mg m^{-3} rather than by only 1 mg m^{-3}), but in both systems the rate of change is the same because mixed-layer conditions are equally favorable for blooming.

A recent analysis of NAB-08 data provides a specific example of this problem. For this study, bloom initiation was taken as occurring in late April based on the appearance of high chlorophyll concentrations (Mahadevan et al. 2012). However, reevaluation of the chlorophyll time series indicates that rates of chlorophyll increase were comparable early in the study when concentrations were low and later in the study when the bloom was near climax (**Supplemental Figure 1**). This result implies that threshold conditions for bloom initiation were not encountered during the study. Furthermore, satellite data suggest that phytoplankton concentrations in the NAB-08 region may actually begin increasing as soon as the mixed layer stops deepening in February (Behrenfeld 2010, Behrenfeld et al. 2013). Thus, absolute changes in biomass can be misleading in terms of understanding bloom dynamics.

A similar problem arises with the practice of assessing bloom initiation based on phytoplankton concentration exceeding a specific threshold, commonly 5% above the annual median concentration (Siegel et al. 2002, Henson et al. 2009). Once again, mixed-layer growth conditions may be favorable for biomass accumulation for months before a chosen concentration threshold is crossed. In the laboratory, a concentration threshold is never used to assess when a culture begins exponential growth (**Supplemental Figure 2**). Instead, phytoplankton cultures are monitored in terms of population growth rates.

Analyzing rates of biomass change can also have its pitfalls. For example, Behrenfeld (2010) showed that satellite-derived phytoplankton concentrations (in milligrams of carbon per cubic meter) often begin increasing in the subarctic Atlantic as soon as the mixed layer stops

Supplemental Material

PHYTOPLANKTON ACCUMULATION DURING CHANGING MIXED-LAYER DEPTHS

Evaluating whether mixed-layer abiotic conditions controlling division rates are preventing phytoplankton populations from increasing requires considering how mixed-layer depth (MLD) changes impact phytoplankton concentrations. **Figure 5** shows three scenarios where the balance (r) between phytoplankton division and loss is assumed to be constant and to allow for the equivalent of one cell division to survive from the initial state (left side of the figure) to the final state (right side of the figure) over an increment of time (i.e., $r = 0.69\ \text{time}^{-1}$). The initial condition in this example is MLD = 100 m, chlorophyll concentration ([Chl]) = 0.2 mg m^{-3}, mixed-layer-integrated chlorophyll inventory (ΣChl) = 20 mg m^{-2}, and euphotic depth (Z_{eu}) = 65 m.

Assuming no change in MLD (middle scenario in **Figure 5**), the final [Chl] after a unit of time is 0.4 mg m^{-3}, the final ΣChl is 40 mg m^{-2}, and Z_{eu} decreases to 50 m. In this case, the specific rate of biomass change (r) can be correctly calculated from either the change in [Chl] or the change in ΣChl [i.e., $r = \ln(0.4/0.2) = \ln(40/20) = 0.69\ \text{time}^{-1}$]. A 50% decrease in MLD (top scenario in **Figure 5**), in contrast, results in the same final [Chl] of 0.4 mg m^{-3}, but ΣChl remains at 20 mg m^{-2} (i.e., 0.2 mg m^{-3} × 100 m = 0.4 mg m^{-3} × 50 m). In this case, the value of r can only be calculated from the change in [Chl] [$r = \ln(0.4/0.2) = 0.69\ \text{time}^{-1}$] and not from the change in ΣChl [$r = \ln(20/20) = 0\ \text{time}^{-1}$]. The opposite is true for a deepening mixed layer: Doubling the MLD (bottom scenario in **Figure 5**) dilutes the accumulating phytoplankton population such that the final concentration remains at 0.2 mg Chl m^{-3} while ΣChl increases to 40 mg m^{-2}. Now, the value of r must be calculated from the change in ΣChl [$r = \ln(40/20) = 0.69\ \text{time}^{-1}$] rather than from the change in [Chl] [$r = \ln(0.2/0.2) = 0\ \text{time}^{-1}$]. Understanding bloom dynamics requires consideration of these purely physical impacts on plankton concentrations and inventories.

deepening. But what does this observation imply in terms of the balance between phytoplankton division and loss? Addressing this question requires considering the impacts of deepwater entrainment on phytoplankton concentrations (see sidebar, Phytoplankton Accumulation During Changing Mixed-Layer Depths, along with **Figure 5**). Accounting for this dilution effect reveals that mixed-layer phytoplankton biomass (in milligrams of carbon per square meter) is often increasing during early-winter convective mixed-layer deepening, and thus that light limitation of division is not the proximate factor preventing a bloom (Behrenfeld 2010, Behrenfeld et al. 2013). If depth-integrated biomass were instead decreasing during convective mixing, it would imply that bloom initiation requires a change in net heat flux, or more specifically a decrease in turbulence (Huisman et al. 1999, 2002; Taylor & Ferrari 2011a,b; Chiswell 2011). Thus, considering changes in phytoplankton concentrations (in milligrams of carbon per cubic meter) alone and ignoring the effects of dilution during mixed-layer deepening can lead to incorrect conclusions.

Another problematic practice is the treatment of losses as a function of phytoplankton concentration times a constant loss rate (beginning with Sverdrup 1953). By default, this approach relegates changes in phytoplankton biomass to variability in division rates alone (i.e., bottom-up control), because the rate of change is proportional to the difference between division and (constant) loss rates. However, a constant loss rate is clearly not supported by observations (**Figure 3*c***) (Pollingher & Berman 1977, Tilzer 1984, Strom & Welschmeyer 1991, Verity et al. 1993, Longhurst 2007). Instead, phytoplankton losses are closely coupled to division rates in both time and space, because grazing is proportional to phytoplankton concentration, grazing efficiency, and grazer concentration (which tend to change in parallel with phytoplankton abundance). In modeling studies, a symptom of the inappropriate assignment of constant loss rates is that phytoplankton stocks tend to crash before the assumed bottom-up release of growth limitation, thereby

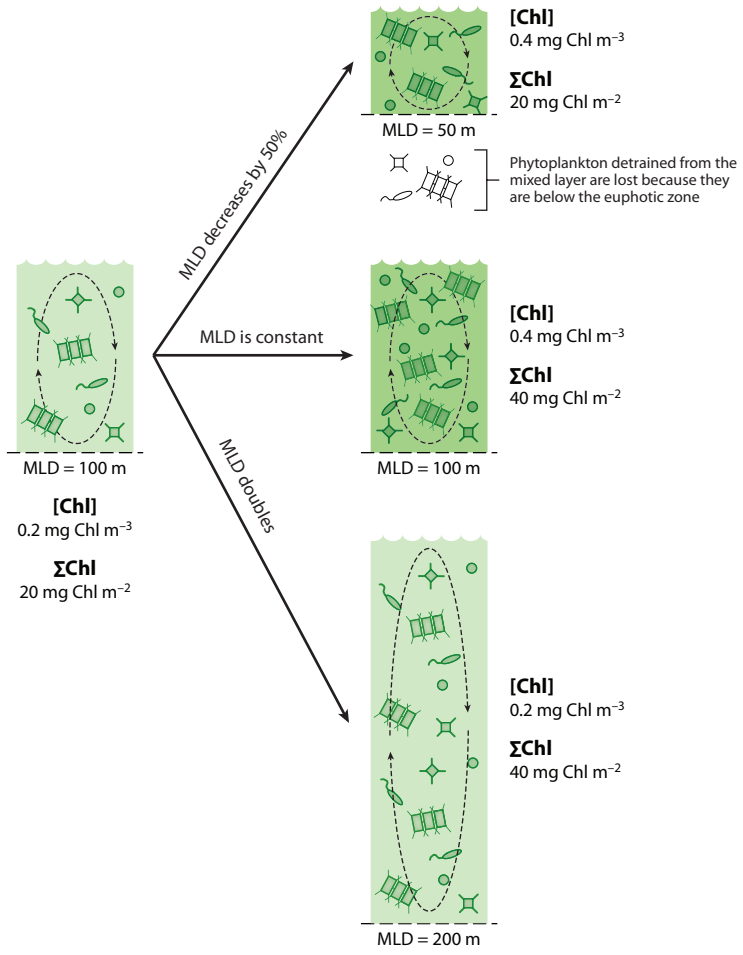


Figure 5

Three scenarios illustrating how changes in mixed-layer depth (MLD) affect phytoplankton concentrations, phytoplankton inventories, and assessments of the rate of biomass change (r) within the mixed layer. When the MLD does not change (*middle*), r can be correctly calculated from either the change in chlorophyll concentration ([Chl]) or the change in mixed-layer-integrated chlorophyll inventory (ΣChl). Because of detrainment of phytoplankton at depth, r can only be calculated from the change in [Chl] when the MLD decreases (*top*). Because the phytoplankton population is diluted over an increasing water volume, r can only be calculated from the change in ΣChl when the MLD increases (*bottom*).

requiring population recovery procedures in the model when growth conditions drive division rates below a presumed threshold level (e.g., Mahadevan et al. 2012).

Finally, the difficulty of constraining many ecological interactions in the field can make it tempting to limit bloom interpretations to readily observed (largely abiotic) properties. The dominance of diatoms during the climax of the subarctic Atlantic spring bloom provides an example. Does their late arrival as major constituents of the bloom indicate that, unlike the smaller species dominating earlier in the year, diatoms require mixed-layer light conditions to surpass a critical threshold? Certainly a correlation exists between their dominance and increased mixed-layer light conditions, but does this correlation indicate causation? A potential alternative explanation is that

diatom numbers are so greatly depleted during winter that a long delay is required before their recovery appears as dominance. Alternatively, or in addition, might their rise to dominance reflect an impact of mesozooplankton returning to the mixed layer after winter hibernation and switching in late spring from phytoplankton herbivory to microzooplankton carnivory, thereby opening a window of opportunity for a few opportunistic diatom species? Clearly, a deeper understanding of ecosystem interactions is required before a more comprehensive description of bloom dynamics can be achieved.

LOOKING FORWARD

Here, as in many previous accounts, the subarctic Atlantic has served as a focal region for examining bloom mechanisms. Our modeling results promote a view that this region's bloom is, in part, a consequence of early-winter physical processes that disrupt reequilibrating phytoplankton-herbivore feedbacks and have a persistent impact throughout the subsequent spring (Behrenfeld 2010). However, we also advocate the importance of selective feeding and density-dependent viral attack on bloom development, particularly in regard to species succession (Mariani et al. 2013). Our discussion of blooms has employed an extremely simplistic model compared with contemporary global ecosystem models. Although still evolving, these more sophisticated approaches typically track multiple phytoplankton groups that are differentially influenced by multiple nutrients (Moore et al. 2002, Follows et al. 2007, Doney et al. 2009). They can also accommodate different temperature sensitivities between trophic levels (Rose & Caron 2007, López-Urrutia 2008, Taucher & Oschlies 2011) and may even include multiple herbivore populations with selective feeding behavior (Prowe et al. 2012). Not surprisingly, such models can accurately reproduce the subarctic Atlantic annual cycle in net biomass accumulation rates observed from space (e.g., **Figure 3*a***) (Behrenfeld et al. 2013) and can re-create realistic annual plankton successions consistent with field observations (Evans 1988, Prowe et al. 2012, Signorini et al. 2012). Nevertheless, their fundamentals are consistent with our simple model, and they similarly generate blooms because of subtle predator-prey imbalances tethered to physical forcings.

With respect to characterizing grazing mortality under natural conditions, we have not yet surmounted the problem of appropriately parameterizing model equations that are themselves still debated. We are further still from consensus on model parameters suitable for mixtures of phytoplankton and communities of grazers that may differ in size, behavior, and tendency to switch between food preferences. Experimental field data addressing these deficiencies are difficult to obtain, especially in regions of low plankton concentrations. We do not know how to select some functions for the field, let alone measure the coefficients at a particular station. The significance of these issues to model outcomes was exemplified by the impact of differing grazing formulations in studies by Anderson et al. (2010) and Prowe et al. (2012). Their examples convincingly illustrate how far we have to go before global phytoplankton biomass, production, and vertical export of organic particles from the euphotic zone can be confidently forecast. These challenges not only are relevant to temporally stable plankton ecosystems, but also pertain to understanding seasonal blooms in the open ocean.

A major goal in biological oceanography is to mechanistically predict current and future phytoplankton distributions and rates of change. This aim implies a need for a general bloom theory that not only accounts for high-latitude blooms, such as those of the subarctic Atlantic, but also encompasses coastal blooms, blooms in high-light environments (e.g., the Arabian Sea; region 7 in **Figure 1**), and experimental blooms. Although specific bloom characteristics may differ between regions, these events are generally preceded by an ecologically disruptive process. In the

case of experimental blooms, this process is obviously the purposeful addition of a limiting nutrient (iron). In the Arabian Sea, it appears to be the dilution of phytoplankton and grazers by monsoon-driven mixing (Marra & Barber 2005, Marra & Moore 2009). Along coasts, upwelling of relatively plankton-free water (Cushing 1959) or riverine input of freshwater can provide the necessary disruption. This commonality suggests the general disturbance-recovery phenomenon encapsulated by the DRH, in which mechanisms of ecosystem disruption may vary from system to system but the subsequent processes of predator-prey recoupling have the consistent outcome of yielding a bloom (Behrenfeld et al. 2013).

Sverdrup (1955) noted that the spatial distribution of chlorophyll observed in the field largely reflects broad-scale patterns in wind-driven vertical nutrient transport. This observation is commonly interpreted as implying a relationship between nutrient-driven division rates and phytoplankton biomass. Perhaps this view requires revision. We instead propose that the global phytoplankton distribution (e.g., **Figure 1**) reflects, to first order, the recent history of ecological balances or imbalances between phytoplankton division and herbivore grazing, where the physical processes underlying imbalances are also, in a sense, coincidentally associated with surface nutrient inputs. This view echoes a sentiment voiced by Cushing (1959) that "the presence of large quantities of nutrients in such [bloom-forming] areas is, if not quite irrelevant, perhaps merely fortuitous." Although significant nutrient input to the surface layer is clearly required to support an accumulation of high biomass, these statements emphasize the unavoidable conclusion that phytoplankton blooms are first and foremost expressions of ecological processes.

Understanding the details of bloom development processes will require rethinking field phytoplankton investigation strategies (Giovannoni & Vergin 2012). Greater emphasis is needed on quantifying higher-trophic-level dynamics (Verity et al. 1993, Kiørboe 1997, Verity et al. 2002) and sustaining observations over complete annual cycles (Backhaus et al. 2003, Evans & Parslow 1985) in order to resolve the preconditioning events that ultimately enable blooms. Advanced satellite sensors [e.g., NASA's upcoming Pre-Aerosol, Clouds, and Ocean Ecosystem (PACE) mission] and novel in situ sensors [e.g., the Imaging FlowCytobot (Olson & Sosik 2007) and Underwater Vision Profiler (Picheral et al. 2010)] will certainly accelerate future understanding of blooms and species succession. The greatest hurdle may be the prerequisite renaissance in community thinking (Verity & Smetacek 1996, Verity et al. 2002), where research attention is focused more on physical-ecological interactions and less on the abiotic factors controlling division rates. A century has passed since Nathansohn's early insight on the major role of grazers in controlling phytoplankton stocks. Today, understanding the ecological underpinnings of blooms is essential in order to reliably forecast future change and quantify contemporary ocean carbon fluxes (Giovannoni & Vergin 2012).

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Errata

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