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Contribution to the Themed Section: 'Revisiting Sverdrup's Critical Depth Hypothesis'
Food for Thought

The importance of phytoplankton trait variability in spring bloom formation

Aleksandra M. Lewandowska[1,2]*, Maren Striebel[2], Ulrike Feudel[3], Helmut Hillebrand[2], and Ulrich Sommer[4]

[1]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, Leipzig 04103, Germany
[2]Institute for Chemistry and Biology of the Marine Environment (ICBM-Terramare), Carl-von-Ossietzky University Oldenburg, Schleusenstrasse 1, Wilhelmshaven 26382, Germany
[3]Institute for Chemistry and Biology of the Marine Environment (ICBM), Carl-von-Ossietzky University Oldenburg, Carl von Ossietzky Strasse 9-11, Oldenburg 26111, Germany
[4]Marine Ecology, GEOMAR Helmholtz Center for Ocean Research Kiel, Düsternbrooker Weg 20, Kiel 24105, Germany

*Corresponding author: tel: +49 44219448209; fax: +49 4421944299; e-mail: aleksandra.lewandowska@uni-oldenburg.de

About 60 years ago, the critical depth hypothesis was proposed to describe the occurrence of spring phytoplankton blooms and emphasized the role of stratification for the timing of onset. Since then, several alternative hypotheses appeared focusing on the role of grazing and mixing processes such as turbulent convection or wind activity. Surprisingly, the role of community composition—and thus the distribution of phytoplankton traits—for bloom formation has not been addressed. Here, we discuss how trait variability between competing species might influence phytoplankton growth during the onset of the spring bloom. We hypothesize that the bloom will only occur if there are species with a combination of traits fitting to the environmental conditions at the respective location and time. The basic traits for formation of the typical spring bloom are high growth rates and photoadaptation to low light conditions, but other traits such as nutrient kinetics and grazing resistance might also be important. We present concise ideas on how to test our theoretical considerations experimentally. Furthermore, we suggest that future models of phytoplankton blooms should include both water column dynamics and variability of phytoplankton traits to make realistic projections instead of treating the phytoplankton bloom as an aggregate community phenomenon.

Keywords: critical depth, light spectrum, phytoplankton, spring bloom, trait.

Introduction

The spring phytoplankton bloom is a ubiquitous phenomenon in temperate to boreal aquatic ecosystems, and the timing and magnitude of the spring bloom triggers much of the dynamics in these ecosystems throughout the year (Platt *et al.*, 2003; Edwards and Richardson, 2004). Consequently, it has been a major task of plankton ecology to explain the mechanisms driving the onset of the phytoplankton spring bloom and its dynamics. Since the 1920s, researchers have emphasized the role of light and mixing processes in bloom formation (Gran and Braarud, 1935; Atkins, 2009). In the early 1940s, Riley (1942) introduced the compensation depth concept—the depth at which photosynthesis exactly matches

respiration rate. By incorporating these concepts, Sverdrup (1953) proposed the first quantitative explanation of the occurrence of the spring phytoplankton bloom. In the following years, several theories were advanced to explain the spring bloom formation, highlighting the role of turbulence, grazing, and nutrients in phytoplankton blooms, but the critical depth hypothesis (Sverdrup, 1953) remains the most cited and widely accepted. A comprehensive review on the research following Sverdrup's critical depth hypothesis was recently published by Fischer *et al.* (2014).

According to Sverdrup (1953), there is a critical mixing depth for any given time and location at which light availability in the mixed water column is sufficient to allow photosynthetic production to

compensate for losses. This depth is estimated to be 5–10 times the compensation depth as defined by Riley (1942). The phytoplankton bloom can only occur if the actual mixing depth is less than the critical mixing depth, assuming that net photosynthesis and growth rates of phytoplankton are positive. Sverdrup argued that during spring warming, stratification compresses the mixing depth and the moment when the mixing depth becomes shallower than the critical mixing depth marks the onset of the phytoplankton bloom. The subsequent dynamics of the bloom are then governed by the stability and extent of the stratification.

Sverdrup's theory makes a number of simplifying assumptions, which might limit its application to natural systems. First, Sverdrup's hypothesis assumes that community respiration is constant with depth, whereas in reality respiration is species-specific and does not stay constant with depth (Smetacek and Passow, 1990; Williams, 1998; Robinson *et al.*, 2002). Second, the critical depth theory is based on light intensity alone, but the quality of the spectral availability of light changes as well with depth. These changes in available components (wavelengths) of solar radiation potentially create light niches for phytoplankton species, which are able to use different parts of the available light spectrum depending on the accessory pigments they contain (Polimene *et al.*, 2014). Third, Sverdrup's hypothesis assumes a thoroughly mixed water layer in which the phytoplankton cells are evenly distributed. In reality, mixing processes depend on wind activity and local hydrography which are not uniform (Taylor and Ferrari, 2011), leading to a rather patchy distribution of organisms (Chiswell, 2011). Furthermore, some species are able to actively migrate within the water column, also leading to an uneven distribution. Comparing phytoplankton blooms in the absence of vertical stratification in the Gulf of Maine (Townsend *et al.*, 1992) with the hypothesis proposed by Sverdrup (1953), Huisman *et al.* (1999a) formulated the critical turbulence hypothesis. Here, the focus is not on stratification but turbulence: if turbulence is below a species-specific threshold, phytoplankton can bloom in the euphotic upper water column before being transported deeper where light is insufficient.

Sverdrup himself was aware of some weaknesses of his hypothesis, especially emphasizing the role of community composition in bloom formation. He noted that the irradiance at the compensation depth must depend on plankton composition, including species composition within the phytoplankton as well as the interaction between phyto- and zooplankton (Sverdrup, 1953). As a replacement of the critical depth hypothesis, Behrenfeld (2010) proposed a dilution-recoupling hypothesis according to which physical processes like water column mixing affect the balance between phytoplankton growth and grazing by zooplankton. He defined the bloom as a combined effect of the decoupling between phytoplankton growth and losses due to the mixed layer deepening (Behrenfeld, 2010). According to Behrenfeld (2010), a deepening of the mixed layer 'dilutes' the grazing pressure on phytoplankton and allows a bloom to begin. This hypothesis does not necessarily require water column stratification to occur, but is rather based on changes in predator–prey interactions.

Alternative or amended theories to explain the bloom formation emphasized the role of grazers (Smetacek and Passow, 1990; Behrenfeld, 2010), stratification onset (Chiswell, 2011), and turbulent convection (Huisman *et al.*, 1999a; Taylor and Ferrari, 2011), but the role of phytoplankton trait composition has so far largely been omitted from the discussion of phytoplankton spring bloom formation. This is surprising, as phytoplankton succession can clearly be linked to interspecific variation in resource use.

Although the theory on species coexistence describes competition for resources at steady state (Tilman *et al.*, 1982), it might also be helpful in defining resource requirements for certain species. Tilman *et al.* (1982) showed that species can form a stable population only if they have enough limiting resource for their specific growth, such that mortality is balanced by reproduction. This minimal resource concentration was termed R⋆ and the best competitor should be the species with the lowest requirement for the limiting resource (lowest R⋆). For light, this theory has been modified, such that competitive interactions are mediated by self-shading whereby a species with the highest tolerance to self-shading (lowest critical light requirement I⋆) survives in competition for light (Huisman and Weissing, 1994). In Tilman's terminology, the onset of the spring phytoplankton bloom is triggered when light availability becomes larger than I⋆ for light during spring, when light is a limiting resource for most of the phytoplankton species, but mortality through grazing is low. Such conditions favour low light-adapted species with high chlorophyll concentration as shown in the modelling study by Polimene *et al.* (2014). These authors suggest that pigment-mediated photoadaptation plays a primary role in shaping phytoplankton communities during the winter–spring transition.

Based on this background, we propose that the onset of the spring phytoplankton bloom depends on both allogenic factors (water column mixing, temperature, grazing by zooplankton, etc.) and autogenic factors (species physiology and traits, life history, etc.). Both allogenic and autogenic factors affect the balance between reproduction and mortality, allogenic factors being additionally responsible for resource supply. We hypothesize that the match of environmental change at the winter–spring transition and an optimal trait combination of the phytoplankton community are required to allow rapid phytoplankton growth and bloom formation.

The role of hydrodynamics

Hydrodynamic flow patterns in the oceans play a pivotal role for the formation of plankton blooms. While horizontal flow patterns like eddies, fronts, and jets are responsible for the redistribution of nutrients and plankton on intermediate spatial scales (Abraham, 1998; Martin, 2003; Tél *et al.*, 2005), vertical flows often account for turbulent mixing on small spatial scales (Mann and Lazier, 1991; Kiørboe, 1993; Denman and Gargett, 1995; Prairie *et al.*, 2012). The vertical flow patterns are approximately one order of magnitude smaller in strength than the horizontal ones. The structure of hydrodynamic flows on all scales leads to an incomplete mixing of the water column which has a large impact on plankton communities.

Vertical flows

Depending on their density compared with the density of water, plankton cells rise or sink. Turbulent diffusion resolving small-scale turbulence interacts with the sinking motion and influences strongly the vertical distribution of phytoplankton. Sverdrup's critical depth hypothesis (Sverdrup, 1953) focuses on light-dependent growth and does not account for the implications of sinking and turbulent diffusion. In contrast, the critical turbulence hypothesis by Huisman et al. (1999a, b, 2002) takes the interplay between light-dependent growth and turbulent diffusion into account. They showed that the critical depth depends on the turbulence level. On the other hand, each species possesses a critical turbulence level at which growth rates exceed the vertical mixing rate, leading to a phytoplankton bloom independently of the critical depth. Since critical depth and critical turbulence are independent

phenomena, one can expect that different phytoplankton communities favour those different strategies leading to different species compositions depending on the strength of turbulent mixing. Whereas low turbulence conditions favour buoyant phytoplankton species, well-mixed waters benefit species with low light requirement. Huisman *et al.* (1999b) assumed a homogeneous turbulent diffusion across the whole water column, whereas more recent studies show how a depth-dependent turbulent diffusion would influence the location of the chlorophyll maximum (Jäger *et al.*, 2010; Ryabov *et al.*, 2010; Peeters *et al.*, 2013). To estimate the impact of turbulent mixing in more detail one has to take its depth dependence into account, instead of relying on simple two-layer models. Moreover, active movement of plankton organisms can also be important (Mellard *et al.*, 2012).

Horizontal flows

Looking at the horizontal mixing, the situation can be quite different with respect to the time-scales involved. Horizontal transport is much faster than the time needed for plankton growth. Therefore, redistribution of nutrients due to horizontal transport would not be able to have a visible effect in shaping plankton communities. However, there exist mesoscale hydrodynamic structures (Lagrangian coherent structures) of size of about 10–100 km in the ocean, which have a lifetime of several days to weeks. Such long-lived structures like eddies and fronts can have an important influence on the growth of plankton, since close to these structures biological time-scales of growth become comparable to the time-scale of the flow. As a result, stirring and mixing are essential determinants of plankton patterns occurring in the ocean (Abraham, 1998). Particularly, vortices in the flow can act as incubators for plankton growth giving rise to plankton blooms inside vortices. The emergence of the plankton blooms within mesoscale eddies can occur due to two different mechanisms. They can entrain nutrient-rich waters (i) from upwelling events close to the coast and transport them over long distances in the ocean or (ii) from deeper layers in the open ocean by rotation. In both cases, the transport barriers, which are formed around the eddies, decrease substantially the exchange of water masses between inside and outside. Owing to this confinement of the plankton, "hot spots" of their growth are maintained for a rather long time (Martin *et al.*, 2002; Sandulescu *et al.*, 2008; d'Ovidio *et al.*, 2013). Other structures like fronts and jets also play an important role in the formation of plankton blooms (López *et al.*, 2001; Hernández-García and López, 2004; Taylor and Ferrari, 2011; Levy *et al.*, 2012).

The heterogeneous distribution of nutrients mediated by mesoscale hydrodynamic structures can not only give rise to particular mechanisms of the formation of plankton blooms, but can also induce different species dominance patterns and hence different plankton communities across the ocean (Bastine and Feudel, 2010; d'Ovidio *et al.*, 2010). Eddies typically persist for weeks, but may in some instances persist for several months (Kang and Curchitser, 2013). Therefore, eddies may strongly influence the development of different communities. In fact, incomplete mixing can promote the coexistence of species (Bracco *et al.*, 2000; Scheuring *et al.*, 2000, 2003) and can be considered as one possible solution of the paradox of plankton (Hutchinson, 1961).

The role of solar irradiance

Besides temporal and spatial changes in mixing processes, during winter-spring transition phytoplankton experience rapid changes in solar irradiance (in intensity, as well as spectral characteristic) caused by changing solar angle and meteorological conditions (e.g. cloud cover). The light spectrum within the pelagic environment changes temporarily on a dial rhythm following the daily spectral shifts of light entering a water column and spatially by selective absorption of light (specific wavelength) with water depth. Phytoplankton responds to mixing processes and changing irradiance by varying the amounts and proportions of photosynthetic pigments, enzymatic activities, and cell volumes (Barlow *et al.*, 2013). These adjustments are species-specific. Some species are best adapted to high or low light intensities, while others are more competitive under well-mixed conditions (Strzepek and Harrison, 2004). Hickman *et al.* (2009) demonstrated that chromatic adaptations along with cell size markedly contribute to the balance of growth and loss rates for phytoplankton taxa and determine their distribution along light and nutrient gradients.

At high latitudes, daylight is considerable longer during summer than in winter (Kirk, 1994) and the lower solar angle in winter results in higher reflectance from the water surface (Runcie and Riddle, 2006). Low light conditions in winter strongly favour large diatoms which have high requirement for nutrients, especially silicate, but are good competitors for light (low I^* for light). Dramatically changing light conditions on the onset of stratification in spring favour fast-growing diatoms adapted to variable light, which can form the spring phytoplankton bloom (Widdicombe *et al.*, 2010; Polimene *et al.*, 2014). The low light-adapted species still significantly contribute to the bloom biomass because of their size and high chlorophyll content. At lower latitudes, changes in solar irradiance are less seasonal and the ecosystem is limited by nutrients and grazing rather than by light (Siegel *et al.*, 2002). High light availability allows phytoplankton to reach relatively high biomass even in winter (Moustaka-Gouni *et al.*, 2014). Thus, phytoplankton traits related to nutrient uptake (and nitrogen fixation) and grazing resistance (e.g. toxin production) might be more important in lower latitudes than in irradiance-related traits.

The role of phytoplankton traits

Recently, the trait-based approach has been successfully used in phytoplankton ecology, mainly to model community structure in response to global change (Litchman *et al.*, 2012). A characterization of functional traits (growth rate, cell size, and composition of photosynthetic pigments) can help in predicting what group of species is likely to dominate the bloom (Margalef, 1978). Using information on traits to parameterize population dynamic models, it is possible to predict which species can coexist under which environmental conditions (Litchman and Klausmeier, 2008; Edwards *et al.*, 2012; Litchman *et al.*, 2012). However, it should be kept in mind that most phytoplankton traits (growth rate, cell size, and nitrogen uptake kinetics) are plastic to some extent and depend on physical factors like temperature and irradiance (Eppley, 1972).

At any time and location, there will be a limited number of species with optimal traits (well adapted to low light–high turbulence conditions and characterized by a high growth rate) that can form the spring phytoplankton bloom. Here, to better understand the role of traits (in particular growth rates and photoadaptation), we use data on natural marine phytoplankton communities from an indoor mesocosm experiment which addressed the impact of warming and mixing depth on the spring phytoplankton bloom [for details, see Lewandowska and Sommer (2010)].

Selection for high growth rates

We assume that the spring phytoplankton bloom is a rapid event which selects for fast growing species. Slow growing species do not multiply fast enough to exceed losses (grazing and sinking) and therefore they cannot rapidly increase their biomass.

Figure 1a represents maximum observed growth rates of phytoplankton species from the Baltic Sea under light-limiting conditions ($\sim$6 mol photons m^{-2} d^{-1}) during winter–spring transition (16th February–6th April 2008). Phytoplankton biomass peaked around 4th March and was dominated by species having growth rates at least two times higher than the average community. Emphasizing the role of species-specific traits, community response depended on those species (Figure 1b).

If such fast growing species are absent, a spring bloom might not occur despite favourable hydrodynamic conditions. There already is ample evidence of this: warming and wind changes altered phytoplankton community composition and lead to disappearance of the typical spring diatom bloom in Narragansett Bay (Nixon and Fulweiler, 2009), Bahia Blanca Estuary (Guinder *et al.*, 2010), Mediterranean Sea (Goffart *et al.*, 2002), and coccolithophorid bloom in the Western English Channel (Garcia-Soto *et al.*, 2011). Always, the abundance of a usually dominant species dramatically decreased and the remaining species were not able to form a bloom.

Selection for low light adaptations

We propose that the occurrence of the spring phytoplankton bloom depends not only on stratification onset and mixed layer depth, but also on the balance of available resources in concert with phytoplankton community composition. The initiation of the bloom is determined by the light dose which has to be sufficient for the fast-growing species with the lowest I* for light. A bloom cannot start without good competitors for light and species with high growth rates. These conclusions place a major emphasis on the role of overwintering for the spring phytoplankton bloom as well as the match between stratification- and mixing-mediated resource supply and phytoplankton community structure. In winter, when light is a limiting factor for most of the phytoplankton species, low light-adapted species with high cellular chlorophyll concentrations become dominant, followed by fast-growing species adapted to variable light conditions (Widdicombe *et al.*, 2010). Experiments on phytoplankton monocultures converge on the conclusion that cellular chlorophyll concentrations increase with low irradiances (maximizing photon capture), but decrease with increasing light availability (Falkowski and Owens, 1980; Iriarte and Purdie, 1993; Dubinsky and Stambler, 2009)—a pattern also reflected in our sample dataset on natural phytoplankton community (Lewandowska and Sommer, 2010; Figure 2). The bloom of these species is possible, because mortality (mainly via grazing) is still low in relation to reproduction rates, whereas with the seasonal increase of zooplankton biomass, traits such as the resistance to grazing become more important.

Diatoms typically have high cellular chlorophyll concentrations and often dominate spring phytoplankton blooms at temperate latitudes. In our example datasets, diatoms dominating the bloom (*Skeletonema*, *Thalassiosira*, and *Chaetoceros*) had high growth rates under low light conditions (Figure 3a). In contrast, picoplankton with low tolerance to limiting light increased growth rates with increased light (Figure 3a). Since they possibly also suffered from high losses to heterotrophic protists, they did not achieve high abundances during the spring bloom (cf. Figure 1b). Similar examples of growth-irradiance relationships were presented for bloom forming haptophyte species isolated from the Bay of Biscay (Seoane *et al.*, 2009; Figure 3b), which in contrast to diatoms form blooms under high light conditions.

Efficient use of light spectrum

Rapid changes in solar irradiance, mixing depth, and turbidity during the winter–spring transition affect spectral attenuation coefficients of seawater. Increasing self-shading by growing phytoplankton further alters the underwater light spectrum, because available light is partitioned by phytoplankton with different pigment compositions. Consequently, the underwater light spectrum substantially changes selecting for different phytoplankton groups. Therefore, besides general light requirement and specific growth rate, the pigment composition can be a basic trait shaping the phytoplankton community during the spring bloom (Polimene *et al.*, 2014). Pigment composition determines not only adaptation to low or high light conditions, but also the light use efficiency across the wavelength spectrum and thereby the "spectral niche" used. Besides chlorophyll, xanthophyll pigments play a pivotal role in phytoplankton physiology, especially with respect to photoacclimation. They are involved in both light harvesting (acting as antenna pigments) and photoprotection mechanisms being an indicator of photoadaptation (Meyer *et al.*, 2000; Polimene *et al.*, 2014). Some phytoplankton species can regulate which parts of the spectrum they utilize by adjusting their pigment composition, depending on the availability of different wavelengths of light (Ting *et al.*, 2002; Stomp *et al.*, 2004). Therefore, phytoplankton community structure during winter–spring transition might not only depend on species-specific growth rates, but also on phytoplankton traits related to pigment composition. Specific light absorption by phytoplankton species should shift the competitive advantage towards species being able to use the remaining part of the light spectrum, which however has rarely been assessed during spring phytoplankton blooms. Wall and Briand (1979) showed in a field experiment that long wavelength radiation increased the relative proportion of cyanobacteria and diatoms and reduced the proportion of dinoflagellates. Thus, cyanobacteria and diatoms might have an advantage in the upper part of the water column, where the red wavelengths are mostly confined, in contrast to dinoflagellates, which should prefer lower parts of the water column.

Phytoplankton seasonal succession

A trait-based approach might not only help explaining the occurrence of the spring bloom, but inform our understanding of phytoplankton seasonal succession in general. Later in the season, increased zooplankton grazing rates select for different sets of traits, including grazing resistance, competition for limiting mineral nutrients, and efficient utilization of nutrient pulses induced by storms, upwelling, and turbulent mixing. It has been argued that much of the variation in aggregated phytoplankton biomass and cell size structure can be organized along turbulence and nutrient supply axes (Cullen *et al.*, 2002). Recently, Lewandowska *et al.* (2014) related seasonal differences in plankton community composition to nutrient supply, with cell size and grazing resistance as emerging important traits. More general, a trait-based approach can also serve as a mechanistic underpinning of the—recently revised—PEG-model on plankton succession (Sommer *et al.*, 2012).
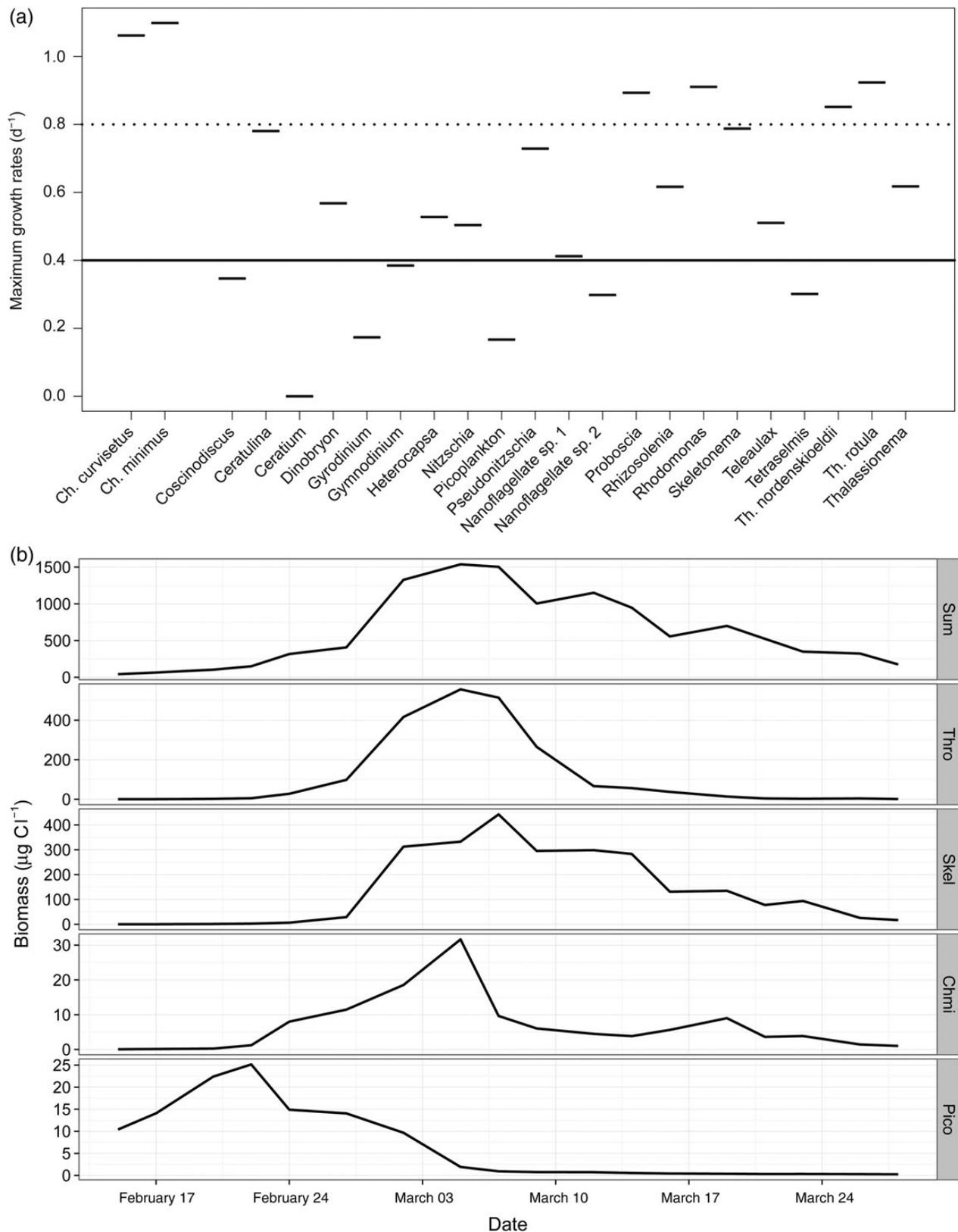
Figure 1. (a) Maximum growth rates of phytoplankton species under limited light conditions during winter – spring transition. The maximum growth rate of the whole community is represented by the solid line, and dashed line represents a threshold line: two times the maximum community growth rate. Species above or close to the threshold line are able to form the bloom. (b) Time course of phytoplankton species. Good competitors show high synchrony with the total community biomass (data source: Lewandowska and Sommer 2010). Sum, total phytoplankton biomass; Thro, *Thalassiosira rotula*; Skel, *Skeletonema costatum*; Chmi, *Chaetoceros minimum*; Pico, picoplankton.
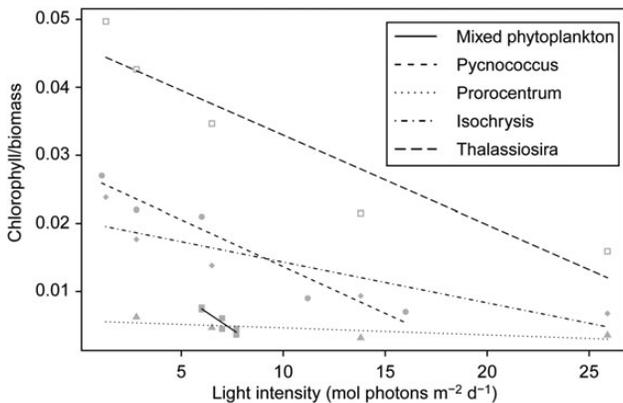
Figure 2. Impact of light intensity on cellular chlorophyll content. Data from Iriarte and Purdie (1993), Dubinsky and Stambler (2009), and Lewandowska and Sommer (2010).
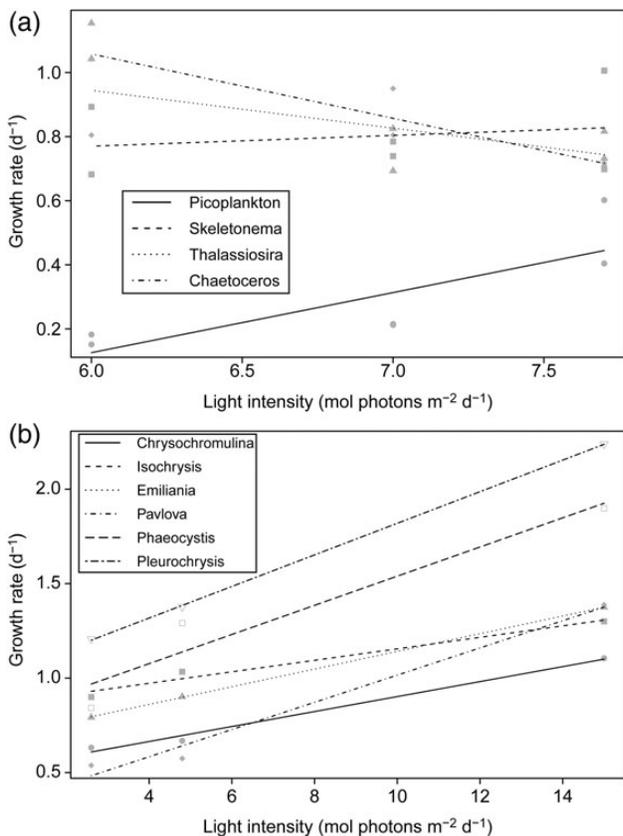

Figure 3. Impact of light intensity on maximum growth rates of selected key species in the natural Baltic Sea community (a) and bloom forming haptophyte species isolated from the Bay of Biscay (b). The less steep (or more negative) the slope, the better competitor for light. Data from Seoane *et al.* (2009), and Lewandowska and Sommer (2010).

Summary

The critical depth hypothesis has been used to explain the occurrence of the spring phytoplankton bloom for decades and is still widely accepted despite ongoing criticisms and alterations. Extending ideas presented by Sverdrup (1953), Huisman *et al.*

(1999a), and Behrenfeld (2010), we propose a hypothesis that each phytoplankton species has its own specific critical depth (SCD) which depends on its set of traits. A species with the most favoured traits and the highest SCD in given location and time will growth first and can form a bloom. The bloom will not occur if there is no species with set of traits matching environmental requirements as it happens in the high nutrients–low chlorophyll ocean regions which are lacking iron. The basic traits for detrainment blooms such as classical spring bloom in temperate latitudes are high growth rates and photoadaptation to low irradiance level in the red light spectrum. For other bloom types (e.g. upwelling blooms), other traits such as nutrient kinetics and grazing resistance might be more important.

Future directions

We do not abandon Sverdrup's hypothesis, but rather suggest that it can be made more robust by including information on hydrodynamic and functional traits of phytoplankton. Observational studies provide one way forward assessing the variation in phytoplankton bloom phenology in response to changing environment, but they do not necessarily address the effect of species identity in bloom formation. We need a new generation of experiments that target how community composition influences the dynamics of phytoplankton blooms. To better understand the role of phytoplankton traits in bloom formation, it will be useful to combine laboratory experiments investigating species-specific traits under controlled conditions with large field experiments using natural phytoplankton communities and manipulating temperature, light availability (intensity and spectral composition), or grazing. One possible approach is to use mesocosms that differ in their hydrodynamic and optical properties and contain natural plankton in combination with laboratory experiments that assess species-specific traits. Such multiscale experimental approaches provide the information needed to include phytoplankton traits and interspecific interactions between species into models predicting phytoplankton blooms. These experiments should also help in understanding mechanisms of species coexistence in fluctuating environment. Including both variability in resource supply and competition mechanisms, it should be possible to predict not only the start and magnitude of the phytoplankton bloom, but also which group of species will dominate the bloom. Such an approach, linking dynamic ecosystem models and experiments is urgently needed if we are to accurately understand and predict changes in marine phytoplankton.

Acknowledgements

References

Abraham, E. R. 1998. The generation of plankton patchiness by turbulent stirring. Nature, 391: 577–580.

Atkins, W. R. G. 2009. The phosphate content of Sea Water in relation to the growth of the Algal Plankton. Part III. Journal of the Marine Biological Association of the United Kingdom, 14: 447.

Barlow, R., Lamont, T., Britz, K., and Sessions, H. 2013. Mechanisms of phytoplankton adaptation to environmental variability in a shelf ecosystem. Estuarine, Coastal and Shelf Science, 133: 45–57.

Bastine, D., and Feudel, U. 2010. Inhomogeneous dominance patterns of competing phytoplankton groups in the wake of an island. Nonlinear Processes in Geophysics, 17: 715–731.

Behrenfeld, M. J. 2010. Abandoning Sverdrup's critical depth hypothesis on phytoplankton blooms. Ecology, 91: 977–989.

Bracco, A., Provenzale, A., and Scheuring, I. 2000. Mesoscale vortices and the paradox of the plankton. Proceedings of the Royal Society of London, Series B: Biological Sciences, 267: 1795–1800.

Chiswell, S. 2011. Annual cycles and spring blooms in phytoplankton: don't abandon Sverdrup completely. Marine Ecology Progress Series, 443: 39–50.

Cullen, J. J., Franks, P. S., Karl, D. M., and Longhusrt, A. 2002. Physical influences on marine ecosystem dynamics. *In* The Sea, pp. 297–336. Ed. by A. Robinson, J. McCarthy, and B. J. Rothschild. John Wiley & Sons, New York.

d'Ovidio, F., De Monte, S., Alvain, S., Dandonneau, Y., and Lévy, M. 2010. Fluid dynamical niches of phytoplankton types. Proceedings of the National Academy of Sciences of the United States of America, 107: 18366–18370.

d'Ovidio, F., De Monte, S., Penna, A. D., Cotté, C., and Guinet, C. 2013. Ecological implications of eddy retention in the open ocean: a Lagrangian approach. Journal of Physics A: Mathematical and Theoretical, 46: 254023.

Denman, K. L., and Gargett, A. E. 1995. Biological-physical interactions in the upper ocean: the role of vertical and small scale transport processes. Annual Review of Fluid Mechanics, 27: 225–256.

Dubinsky, Z., and Stambler, N. 2009. Photoacclimation processes in phytoplankton: mechanisms, consequences, and applications. Aquatic Microbial Ecology, 56: 163–176.

Edwards, K. F., Thomas, M. K., Klausmeier, C. A., and Litchman, E. 2012. Allometric scaling and taxonomic variation in nutrient utilization traits and maximum growth rate of phytoplankton. Limnology and Oceanography, 57: 554–566.

Edwards, M., and Richardson, A. J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature, 430: 881–884.

Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. Fishery Bulletin, 4: 1063–1085.

Falkowski, P., and Owens, T. 1980. Light—shade adaptation. Two strategies in marine phytoplankton. Plant Physiology, 66: 592–595.

Fischer, A., Moberg, E., Alexander, E., Brownlee, K., Hunter-Cevera, K., Pitz, K., Rosengard, S., *et al.* 2014. Sixty years of Sverdrup: A retrospective of progress in the study of phytoplankton blooms. Oceanography, 27: 222–235.

Garcia-Soto, C., Ferndndez, E., Pingree, R. D., and Harbour, D. S. 2011. Evolution and structure of a shelf coccolithophore bloom in the Western English Channel. Journal of Plankton Research, 17: 2011–2036.

Goffart, A., Hecq, J., and Legendre, L. 2002. Changes in the development of the winter-spring phytoplankton bloom in the Bay of Calvi (NW Mediterranean) over the last two decades: a response to changing climate? Marine Ecology Progress Series, 236: 45–60.

Gran, H., and Braarud, T. 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine (including Observations on Hydrography, Chemistr5r and Turbiditfi). Journal of the Biological Board of Canada, 1: 279–467.

Guinder, V., Popovich, C., Molinero, J., and Perillo, G. 2010. Long-term changes in phytoplankton phenology and community structure in the Bahía Blanca Estuary, Argentina. Marine Biology, 157: 2703–2716.

Hernández-García, E., and López, C. 2004. Sustained plankton blooms under open chaotic flows. Ecological Complexity, 1: 253–259.

Hickman, A. E., Holligan, P. M., Moore, C. M., Sharples, J., Krivtsov, V., and Palmer, M. R. 2009. Distribution and chromatic adaptation of phytoplankton within a shelf sea thermocline. Limnology and Oceanography, 54: 525–536.

Huisman, J., Arrayas, M., Ebert, U., and Sommeijer, B. 2002. How do sinking phytoplankton species manage to persist? American Naturalist, 159: 245–254.

Huisman, J., van Oostveen, P., and Weissing, F. 1999a. Critical depth and critical turbulence: two different mechanisms for the development of phytoplankton blooms. Limnology and Oceanography, 44: 1781–1787.

Huisman, J., van Oostveen, P., and Weissing, F. 1999b. Species dynamics in phytoplankton blooms: incomplete mixing and competition for light. American Naturalist, 154: 46–68.

Huisman, J., and Weissing, F. 1994. Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. Ecology, 75: 507–520.

Hutchinson, G. E. 1961. The paradox of the plankton. American Naturalist, 95: 137–145.

Iriarte, A., and Purdie, D. A. 1993. Photosynthesis and growth response of the oceanic picoplankter *Pycnococcus provasoli* Guillard (clone Ω48–23) (Chlorophyta) to variations in irradiance, photoperiod and temperature. Journal of Experimental Marine Biology and Ecology, 168: 239–257.

Jäger, C. G., Diehl, S., and Emans, M. 2010. Physical determinants of phytoplankton production, algal stoichiometry, and vertical nutrient fluxes. American Naturalist, 175: E91–E104.

Kang, D., and Curchitser, E. N. 2013. Gulf Stream eddy characteristics in a high-resolution ocean model. Journal of Geophysical Research: Oceans, 118: 4474–4487.

Kiørboe, T. 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. Advances in Marine Biology, 29:1–72.

Kirk, J. T. O. 1994. Light and photosynthesis in aquatic ecosystems. Cambridge university press, Cambridge.

Levy, M., Ferrari, R., Franks, P. J., Martin, A. P., and Riviere, P. 2012. Bringing physics to life at the submesoscale. Geophysical Research Letters, 39, L14602.

Lewandowska, A., and Sommer, U. 2010. Climate change and the spring bloom: a mesocosm study on the influence of light and temperature on phytoplankton and mesozooplankton. Marine Ecology Progress Series, 405: 101–111.

Lewandowska, A. M., Boyce, D. G., Hofmann, M., Matthiessen, B., Sommer, U., and Worm, B. 2014. Effects of sea surface warming on marine plankton. Ecology Letters, 17: 614–623.

Litchman, E., Edwards, K., Klausmeier, C., and Thomas, M. 2012. Phytoplankton niches, traits and eco-evolutionary responses to global environmental change. Marine Ecology Progress Series, 470: 235–248.

Litchman, E., and Klausmeier, C. A. 2008. Trait-based community ecology of phytoplankton. Annual Review of Ecology, Evolution, and Systematics, 39: 615–639.

López, C., Neufeld, Z., Hernández-García, E., and Haynes, P. H. 2001. Chaotic advection of reacting substances: Plankton dynamics on a meandering jet. Physics and Chemistry of the Earth, Part B: Hydrology, Oceans and Atmosphere, 26: 313–317.

Mann, K., and Lazier, J. 1991. Dynamics of marine ecosystems: biological-physical interactions in the oceans. Blackwell Scientific Publications, Boston.

Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta, 1: 493–509.

Martin, A. P. 2003. Phytoplankton patchiness: the role of lateral stirring and mixing. Progress in Oceanography, 57: 125–174.

Martin, A. P., Richards, K. J., Bracco, A., and Provenzal, A. 2002. Patchy productivity in the open ocean. Global Biogeochemical Cycles, 16: 9-1–9-9.

Mellard, J., Yoshiyama, K., Klausmeier, C. A., and Litchman, E. 2012. Experimental test of phytoplankton competition for nutrients and light in poorly mixed water columns. Ecological Monographs, 82: 239–256.

Meyer, A., Tackx, M., and Daro, N. 2000. Xanthophyll cycling in *Phaeocystis globosa* and *Thalassiosira* sp.: a possible mechanism for species succession. Journal of Sea Research, 43: 373–384.

Moustaka-Gouni, M., Michaloudi, E., and Sommer, U. 2014. Modifying the PEG model for Mediterranean lakes–no biological winter and strong fish predation. Freshwater Biology, 59: 1136–1144.

Nixon, S., and Fulweiler, R. 2009. The impact of changing climate on phenology, productivity, and benthic–pelagic coupling in Narragansett Bay. Estuarine, Coastal and Shelf Science, 82: 1–18.

Peeters, F., Kerimoglu, O., and Straile, D. 2013. Implications of seasonal mixing for phytoplankton production and bloom development. Theoretical Ecology, 6: 115–129.

Platt, T., Fuentes-Yaco, C., and Frank, K. T. 2003. Spring algal bloom and larval fish survival. Nature, 423: 398–399.

Polimene, L., Brunet, C., Butenschon, M., Martinez-Vicente, V., Widdicombe, C., Torres, R., and Allen, J. I. 2014. Modelling a light-driven phytoplankton succession. Journal of Plankton Research, 36: 214–229.

Prairie, J. C., Sutherland, K. R., Nickols, K. J., and Kaltenberg, A. M. 2012. Biophysical interactions in the plankton: A cross-scale review. Limnology and Oceanography: Fluids and Environments, 2: 121–145.

Riley, G. 1942. The relationship of vertical turbulence and spring diatom flowerings. Journal of Marine Research, 5: 67–87.

Robinson, C., Serret, P., Tilstone, G., Teira, E., Zubkov, M. V., Rees, A. P., and Woodward, E. M. S. 2002. Plankton respiration in the Eastern Atlantic Ocean. Deep Sea Research Part I: Oceanographic Research Papers, 49: 787–813.

Runcie, J. W., and Riddle, M. J. 2006. Photosynthesis of marine macro-algae in ice-covered and ice-free environments in East Antarctica. European Journal of Phycology, 41: 223–233.

Ryabov, A. B., Rudolf, L., and Blasius, B. 2010. Vertical distribution and composition of phytoplankton under the influence of an upper mixed layer. Journal of Theoretical Biology, 263: 120–133.

Sandulescu, M., Lopez, C., Hernandez-Garcia, E., and Feudel, U. 2008. Plankton blooms in vortices: The role of biological and hydrodynamic time scales. Nonlinear Processes in Geophysics, 14: 443–454.

Scheuring, I., Károlyi, G., Pentek, A., Tél, T., and Toroczkai, Z. 2000. A model for resolving the plankton paradox: coexistence in open flows. Freshwater Biology, 45: 123–132.

Scheuring, I., Károlyi, G., Toroczkai, Z., Tél, T., and Péntek, Á. 2003. Competing populations in flows with chaotic mixing. Theoretical Population Biology, 63: 77–90.

Seoane, S., Zapata, M., and Orive, E. 2009. Growth rates and pigment patterns of haptophytes isolated from estuarine waters. Journal of Sea Research, 62: 286–294.

Siegel, D. A., Maritorena, S., Nelson, N. B., Hansell, D. A., and Lorenzi-Kayser, M. 2002. Global distribution and dynamics of colored dissolved and detrital organic materials. Journal of Geophysical Research: Oceans, 107: 21-1–21-14.

Smetacek, V., and Passow, U. 1990. Spring bloom initiation and Sverdrup's critical-depth model. Limnology and Oceanography, 35: 228–234.

Sommer, U., Adrian, R., De Senerpont Domis, L., Elser, J. J., Gaedke, U., Ibelings, B., Jeppesen, E., *et al.* 2012. Beyond the Plankton Ecology Group (PEG) model: Mechanisms driving plankton succession. Annual Review of Ecology, Evolution, and Systematics, 43: 429–448.

Stomp, M., Huisman, J., De Jongh, F., Veraart, A. J., Gerla, D., Rijkeboer, M., Ibelings, B. W., *et al.* 2004. Adaptive divergence in pigment composition promotes phytoplankton biodiversity. Nature, 432: 104–107.

Strzepek, R. F., and Harrison, P. J. 2004. Photosynthetic architecture differs in coastal and oceanic diatoms. Nature, 403: 689–692.

Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. Journal du Conseil International pour l'Exploration de la Mer, 18: 287–295.

Taylor, J. R., and Ferrari, R. 2011. Shutdown of turbulent convection as a new criterion for the onset of spring phytoplankton blooms. Limnology and Oceanography, 56: 2293–2307.

Tél, T., de Moura, A., Grebogi, C., and Károlyi, G. 2005. Chemical and biological activity in open flows: a dynamical system approach. Physics Reports, 413: 91–196.

Tilman, D., Kilham, S. S., and Kilham, P. 1982. Phytoplankton community ecology: The role of limiting nutrients. Annual Review of Ecology and Systematics, 13: 349–372.

Ting, C., Rocap, G., King, J., and Chisholm, S. 2002. Cyanobacterial photosynthesis in the oceans: the origins and significance of divergent light-harvesting strategies. Trends in Microbiology, 10: 134–142.

Townsend, D. W., Keller, M. D., Sieracki, M. E., and Ackleson, S. G. 1992. Spring phytoplankton blooms in the absence of vertical water column stratification. Nature, 360: 59–62.

Wall, D., and Briand, F. 1979. Response of lake phytoplankton communities to in situ manipulations of light intensity and colour. Journal of Plankton Research, 1: 103–112.

Widdicombe, C. E., Eloire, D., Harbour, D., Harris, R. P., and Somerfield, P. J. 2010. Long-term phytoplankton community dynamics in the Western English Channel. Journal of Plankton Research, 32: 643–655.

Williams, P. J. 1998. The balance of plankton respiration and photosynthesis in the open oceans. Nature, 394: 55–57.

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