ICES Journal of Marine Science

ICES Journal of Marine Science (2015), 72(6), 2051–2060. doi:10.1093/icesjms/fsv032

Contribution to the Themed Section: '*Revisiting Sverdrup's Critical Depth Hypothesis*'

Original Article

An experimental demonstration of the critical depth principle

Sebastian Diehl[1,2]*, Stella A. Berger[1,3], Quentin Soissons[1], Darren P. Giling[3], and Herwig Stibor[1,4]

[1]*Department of Biology II, Ludwig-Maximilians-University Munich, Grosshaderner Str. 2, Planegg-Martinsried 82152, Germany*
[2]*Department of Ecology and Environmental Science, Umeå University, Umeå 90187, Sweden*
[3]*Department of Experimental Limnology, Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Alte Fischerhütte 2, Stechlin 16775, Germany*
[4]*European Institute for Marine Studies, LEMAR, Technopole Brest-Iroise, Place Nicolas Copernic, Plouzane 29280, France*

**Corresponding author: tel: +46 90 7865738; fax: +46 90 7866705; e-mail: sebastian.diehl@emg.umu.se*

Diehl, S., Berger, S. A., Soissons, Q., Giling, D. P., and Stibor, H. An experimental demonstration of the critical depth principle. – ICES Journal of Marine Science, 72: 2051–2060.

Received 4 August 2014; revised 28 January 2015; accepted 10 February 2015; advance access publication 2 March 2015.

Sverdrup's critical depth hypothesis, which has had an almost canonical status in biological oceanography, has recently been challenged as a universal explanation for the formation of oceanic spring blooms, and several alternative hypotheses have been proposed. Arguments pro and contra alternative explanations have so far relied on theoretical considerations and purely observational data. In this paper, we propose that mesocosm experiments with natural plankton communities could make important contributions to the resolution of the issue. We first briefly review the foundations of the critical depth concept and derive an approximate relationship that relates optically scaled critical depth (="critical optical depth", i.e. the product of the light attenuation coefficient and the critical depth) to light-dependent phytoplankton production in the mixed surface layer. We describe how this relationship can be used to scale experimental mesocosms such that they reproduce ambient light conditions of natural water columns from the surface down to the critical depth and beyond. We illustrate the power of the approach with a mesocosm study in which we experimentally controlled the onset of the spring bloom of a lake plankton community through the manipulation of optically scaled mixed-layer depth. This experiment may be the first experimental demonstration of the critical depth principle acting on a natural plankton community. Compensation light intensity (=minimum average mixed-layer light intensity required to trigger a bloom of the ambient plankton community) could be constrained to be somewhat above 3.2 moles PAR m^{-2} d^{-1}, corresponding to a critical optical depth of 10.5. We compare these numbers to estimates from marine systems and end with a discussion of how experiments could be designed to (i) more accurately determine the critical depth in a given system and (ii) resolve among competing hypotheses for vernal bloom onset.

Keywords: compensation light intensity, critical optical depth, dimensional analysis, mesocosm experiment, phytoplankton spring bloom, scaling.

Introduction

Phytoplankton blooms are regular and often spectacular phenomena in many lakes, estuaries, coastal seas, and oceanic regions. Most prominent is the spring bloom, which is an annual occurrence in most freshwater and many marine systems above 45° latitude. It is commonly believed that the spring bloom is triggered by a combination of biotic and abiotic factors creating an opportunity for phytoplankton to temporarily outgrow grazing losses. These factors include an extended period of declining phytoplankton and grazer densities during fall and winter, a nutrient pulse created by deep, convective mixing of the water column during fall overturn, and a subsequent increase in light availability in the mixed surface layer caused by seasonally increasing surface irradiation and concomitant thermal stratification and shallowing of the surface layer. The above components are widely agreed upon cornerstones of conceptual models such as the Plankton Ecology Group model of seasonal plankton succession in freshwater ecology and the critical depth concept in biological oceanography (Sverdrup, 1953; Sommer *et al.*, 1986, 2012a; Siegel *et al.*, 2002).

Phytoplankton spring blooms make large contributions to annual primary and secondary production and to biogeochemical processes such as the biological carbon pump (Körtzinger *et al.*, 2008; Chassot *et al.*, 2010; Martin *et al.*, 2011). Much effort has therefore been directed towards the study of spring blooms. In a recent review, Behrenfeld and Boss (2014) highlight three mechanisms that can trigger a spring bloom: (i) the critical depth hypothesis,

which proposes that vertical mixing of the surface layer must stay above a critical depth beyond which phytoplankton has negative growth because of light limitation (Sverdrup, 1953); (ii) the critical turbulence hypothesis, which proposes that surface blooms can be triggered in the absence of significant vertical density gradients when turbulent vertical transport is weak (Huisman *et al.*, 1999; Taylor and Ferrari, 2011), and (iii) the dilution-recoupling hypothesis, which proposes that winter mixing stays above the critical depth and that the bloom onset is triggered during autumn and winter mixing by a decrease in grazing pressure when phytoplankton become diluted in the deepening mixed layer (Behrenfeld, 2010). Although the critical depth hypothesis has had an almost canonical status in biological oceanography for decades, recent studies have cast doubt on its legitimacy as a universal explanation for the occurrence of oceanic spring blooms (Behrenfeld, 2010; Taylor and Ferrari, 2011). The latter has spurred controversy that needs to be resolved (Chiswell, 2011; Behrenfeld and Boss, 2014; Fischer *et al.*, 2014). In this paper, we propose that carefully designed experiments can make important contributions to the resolution of this issue.

Oceanography has a long history of studying vernal phytoplankton blooms based on observation. Over recent decades, the geographical and temporal coverage of observation has reached unprecedented levels with the advent of remote sensing from satellites (Behrenfeld *et al.*, 2006; Henson *et al.*, 2009; Boyce *et al.*, 2010). In combination with data-driven mathematical modelling of ocean physics and mixed-layer climatology, this wealth of data has been used to descriptively parameterize elements of the critical depth hypothesis and/or to find support for alternative bloom explanations (Siegel *et al.*, 2002; Behrenfeld, 2010; Taylor and Ferrari, 2011). Large-scale, high-resolution data and coupled biogeochemical-physical ocean models are clearly indispensable to the accurate description of blooms and to the validation of potential mechanisms explaining their occurrence (or absence!). Yet, when it comes to discriminating among competing ecological hypotheses, nothing is more compelling than evidence from carefully designed field experiments (Hairston, 1989). Although spring bloom formation has been studied experimentally at the community level in some marine systems (e.g. Sommer *et al.*, 2012b), to our knowledge, the critical depth concept has not yet been explicitly addressed with field experiments.

Irrespective of which hypothesis correctly describes the mechanisms underlying spring bloom formation, the "concept" of a critical depth is clearly relevant to the resolution of the issue. It would therefore be extremely useful if the critical depth in a given field situation could be experimentally determined. In this paper, we describe how appropriately designed mesocosm experiments with ambient plankton communities can be used to accomplish this goal. We first briefly review the foundations of the critical depth concept and derive an approximate relationship that relates optically scaled critical depth to light-dependent phytoplankton production in the mixed surface layer. We describe how this relationship can be used to scale experimental mesocosms such that they reproduce ambient light conditions of natural water columns from the surface down to the critical depth and beyond. We illustrate the power of the approach by briefly summarizing a decade of relevant experiments from our own lab and by describing in detail a mesocosm study in which we experimentally controlled the onset of the spring bloom through the manipulation of optically scaled mixed-layer depth. We end with a discussion of how experiments could be designed to most accurately measure the critical depth as well as to resolve among alternative hypotheses for vernal bloom onset.

Optically scaled critical depth

In the context of this manuscript, we define a spring bloom as a vernal increase in the *volumetric* density of phytoplankton in the mixed surface layer, the depth z_{mix} of which may vary over time [note that this definition deviates from the *area-based* definition used in the dilution-recoupling hypothesis (Behrenfeld, 2010)]. Sverdrup's critical depth hypothesis for spring bloom initiation builds on three explicit assumptions: (i) turbulent mixing is strong enough to evenly distribute the plankton within the mixed surface layer; (ii) phytoplankton growth within the mixed surface layer is not limited by nutrients and is linearly dependent (with slope α) on the ambient photon flux density $I(z)$ of PAR at depth z; (iii) the light attenuation coefficient K is constant within the mixed surface layer. An obvious fourth, but implicit, assumption is that a bloom can only develop when specific growth exceeds specific losses R. Losses were not specified by Sverdrup but must reasonably encompass *all* loss processes including density and mixing depth-dependent processes such as grazing, sinking, and dilution in a deepening mixed layer. Under these assumptions, the specific rate of change of phytoplankton biomass density P in the mixed surface layer is described by

$$\frac{1}{P}\frac{\mathrm{d}P}{\mathrm{d}t} = \frac{\alpha}{z_{mix}}\int_0^{z_{mix}} I(z)\,\mathrm{d}z - R = \alpha I_{mix} - R, \qquad (1)$$

where $I_{mix} = \alpha I_0(1 - \mathrm{e}^{-Kz_{mix}})/(Kz_{mix})$ is average PAR in the mixed surface layer and I_0 is incident PAR at the water surface, averaged over a day–night cycle (see Table 1 for an overview of symbols, units, and descriptions) . Sverdrup hypothesized that the phytoplankton net rate of change is negative under conditions of winter mixing but would eventually turn positive (and initiate a bloom) when incident radiation I_0 increases and depth of the mixed surface layer z_{mix} becomes shallower as the season progresses. From Equation (1) follows that initiation of a bloom ($dP/\mathrm{d}t > 0$) requires that$z_{mix}/(1 - \mathrm{e}^{-Kz_{mix}}) < \alpha I_0/(KR)$, which during winter mixing (when Kz_{mix} is large and $\mathrm{e}^{-Kz_{mix}}$ approaches zero) is well approximated by

$$z_{mix} \approx z_{cr} < \frac{\alpha I_0}{KR}, \qquad (2)$$

Table 1. Definition of symbols used in model equations.

Symbol	Commonly used units	Description
α	m^2 (mol photons)$^{-1}$	Specific growth coefficient of phytoplankton
I	mol photons m^{-2} d^{-1}	Photosynthetically active radiation (PAR)
I_0	mol photons m^{-2} d^{-1}	Daily mean incident PAR at water surface
I_c	mol photons m^{-2} d^{-1}	Compensation irradiance
I_{mix}	mol photons m^{-2} d^{-1}	Daily mean PAR in mixed surface layer
K	m^{-1}	Light attenuation coefficient
P	g carbon m^{-3} or mg chl *a* m^{-3}	Phytoplankton biomass density
R	d^{-1}	Daily mean specific loss rate of phytoplankton
z	m	Depth below water surface
z_{cr}	m	Critical depth
z_{mix}	m	Depth of mixed surface layer

where z_{cr} is the critical depth, i.e. the maximum depth of the mixed surface layer that allows for positive phytoplankton growth. Inequality (2) can be rearranged and expressed in terms of an optically scaled, dimensionless critical depth Kz_{cr} as

$$Kz_{cr} < \frac{\alpha I_0}{R} = \frac{I_0}{I_c}, \quad (3)$$

where I_c is the compensation irradiance, i.e. the PAR intensity at which production equals losses defined by $\alpha I_c - R = 0$ (note that this differs from the physiological definition of a compensation irradiance which includes phytoplankton respiration as the only loss process). Equation (3) contains three physical variables (I_0, K, z_{mix}) that are relatively easy to measure (though different authors may use different operational definition of z_{mix}) and two biological variables (α and R, or their ratio $R/\alpha = I_c$) that are notoriously difficult to constrain. Consequently, empirical estimates of the compensation irradiance I_c differ by more than an order of magnitude (Smetacek and Passow, 1990; Townsend *et al.*, 1992), which likely reflects both real spatial and temporal variation in α and R but also an inability to accurately determine compensation depth from purely observational data.

The concept of an optical depth is well established in phytoplankton ecology (Reynolds, 1984; Kirk, 1994). We emphasize it here because extending it to the definition of a "critical optical depth" (Kz_{cr}, Equation 3) opens up for the possibility of determining critical depths experimentally by use of optically scaled mesocosms. In the following sections, we first describe such an experimental system that we have used for the manipulation of optical depth in several field experiments and briefly highlight a few relevant results from these studies.

An experimental system of optically deep mesocosms

For over a decade, our lab has performed field experiments in which we studied the influence of optically scaled mixed water column depth on phytoplankton and zooplankton dynamics in mesocosms. Common to most experiments were the following design features.

(i) The experiments were performed in Lake Brunnsee, a small, deep, oligotrophic clear-water lake close to the University of Munich's Limnological Research Station at Seeon 90 km east of Munich, Germany. Lake Brunnsee has a maximum depth of 19 m, total phosphorus concentrations are year-round <0.3 μM, while concentrations of dissolved inorganic nitrogen and silicon exceed 70 μM each, and Secchi depth ranges from 7 to 15 m.

(ii) Mesocosms consisted of cylindrical plastic bags made from transparent Tricoron (RKW Wasserburg, Germany). Mesocosms had an inner diameter of 0.95 m, were sealed at the bottom but open to the atmosphere (and thus exposed to direct sunlight), and were suspended from a wooden frame attached to a raft such that they extended 0.2 m above the lake surface (Figure 1). Mesocosms were made optically deep by surrounding them with light absorbing silage film. Depending on the pigmentation of the silage film the light attenuation coefficient inside a mesocosm could range from 0.77 [white, slightly translucent silage film, Diehl *et al.* (2002)] to 1.3 m^{-1} (black, opaque silage film, this study). For comparison, the attenuation coefficient in the lake typically ranges from 0.25 to 0.45 m^{-1}.

(iii) At the beginning of each experiment, all mesocosms were filled with 30–50 μm filtered lake water containing the natural community of phyto- and microzooplankton but excluding crustaceans. In some experiments, we deliberately excluded the latter group to keep grazing pressure on phytoplankton low. In other experiments, we subsequently re-stocked mesocosms with crustacean grazers. In most experiments, we fertilized mesocosms with an initial pulse of 0.25–1 μM inorganic phosphorus to mimic nutrient replete spring conditions and/or accentuate response patterns.

(iv) The total vertical extent of a mesocosm could range from 1 to 15 m depending on the experiment. Depth of the mixed water column inside a mesocosm was controlled by intermittently blowing compressed air to the desired depth using battery driven compressors. Depending on the question, we either mixed the entire water column inside a mesocosm or only its upper part (Figure 1, left panel).

(v) Mixing was highly effective but produced temperature differences between treatments differing in mixing depth (Diehl *et al.*, 2002), because more deeply mixed water columns extend deeper into colder parts of the thermally stratified lake. To manipulate mixed-layer depth independently of temperature, we surrounded mesocosms by a large, permanently mixed outer bag (Figure 1). Mesocosms suspended inside this destratified water bath have identical mixed-layer temperatures and exhibit negligible vertical temperature gradients in non-mixed parts of the water column (e.g. Jäger *et al.*, 2008a, b). Because the destratified water bath takes on the average, depth integrated temperature of the surrounding stratified lake, water temperatures in shallow mixed layers differ between mesocosms inside and outside the water bath. We exploited this in several experiments in which we manipulated temperature independently of mixing depth (Figure 1, Berger *et al.*, 2007, 2010, 2014, this study).

A glance on 10+ years of experimental manipulations of mixed water column depth

Early experiments performed in the described mesocosm facility focused on long-term (equilibrium) responses of late summer phytoplankton communities to mixed water column depth. Very generally, these experiments corroborate theoretical predictions about the influence of mixed-layer depth on light vs. nutrient limitation of phytoplankton (Diehl, 2002; Huisman and Sommeijer, 2002; Berger *et al.*, 2006; Jäger *et al.*, 2010) and support oceanographic theory on the influence of mixed layer deepening in different oceanic regions (Le Quéré *et al.*, 2003; Doney, 2006). Specifically, we found that steady state phytoplankton biomass has a maximum at an intermediate mixed-layer depth. Biomass decreases towards both deeper mixed layers where light limitation becomes increasingly severe (as in high-latitude oceans during winter) and towards shallower mixed layers where algal sinking losses and concurrent nutrient depletion become increasingly important (as in tropical oceans) (Diehl *et al.*, 2002, 2005; Ptacnik *et al.* 2003).

The above experiments support a body of process oriented theory that does not only explain equilibrium responses of phytoplankton to mixed-layer depth but is equally relevant to the formation of transient blooms. In subsequent experiments, we have therefore focused on seasonal plankton dynamics under spring conditions. Because water columns are nutrient replete at the onset of spring, phytoplankton concentrations during transient spring peaks are predicted to be the higher the shallower the mixed layer (i.e. at higher average mixed-layer PAR), except for extremely shallow layers where sinking losses are so high as to very rapidly deplete nutrients (Jäger *et al.*, 2008a). In accordance with these predictions, spring peak heights of both phytoplankton and zooplankton were found to decrease over realistic ranges of increasing mixed-layer depth (Berger *et al.*, 2007, 2010, 2014). Also in accordance with theory (Jäger *et al.*, 2008a; Peeters *et al.*, 2013),

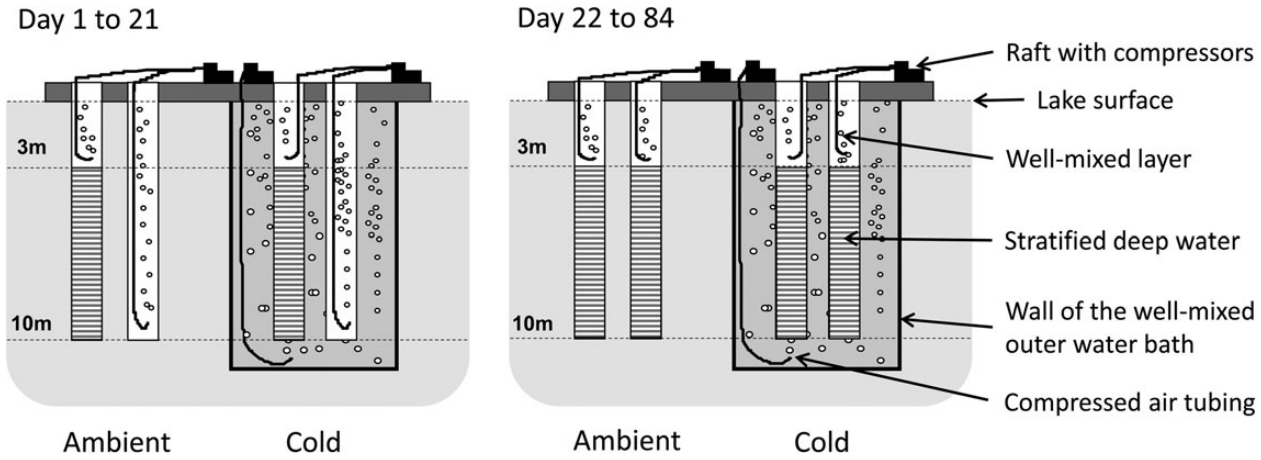

Figure 1. Schematic drawing of the experimental set-up. Shown is one mesocosm of each treatment and the compressed air system used to mix the mesocosms to the desired depths. The lake stratified thermally at 3–4-m depth. "Ambient" mesocosms were placed directly in the lake. "Cold" mesocosms were placed inside a well-mixed outer water bath with ~3°C colder water compared with the surface layer of the lake. "Early" stratification treatments were well mixed down to 3 m and stratified below from day 1 onward. "Late" stratification treatments were well mixed down to 10 m until day 21 and stratified at 3 m thereafter. Dots (symbolizing air bubbles) indicate the well-mixed water masses. Horizontal hatching indicates the stratified deepwater.

phytoplankton grew faster and reached the peak of the spring bloom earlier the shallower the mixed layer (Berger *et al.*, 2007, 2010, 2014).

An experimental demonstration of the critical depth principle

In this section, we describe a mesocosm study that explored the effects of water temperature and the timing of stratification on spring plankton dynamics by independently manipulating both factors. Specifically, we cross-classified (i) early and late water column stratification with (ii) ambient and reduced water temperature (Figures 1 and 2). Incidentally, this study provides an experimental demonstration of the critical depth principle and illustrates how the optically scaled critical depth can be estimated for a natural plankton community. Note, however, that estimation of the optically scaled critical depth was not the primary purpose of this experiment and that we would target the latter with a different experimental approach (described in the "Discussion" section). Below, we describe the experimental and analytical methods and the observed treatment effects, with special emphasis on the timing of the phytoplankton spring bloom and its quantitative relationship with mixed-layer light climate.

Methods

The experimental protocol followed the general recipe described above. Below, we emphasize additional details that are specific to this experiment. The mesocosm facility was set up in Lake Brunnsee in April 2006 soon after ice-out. At this time, the phytoplankton community was dominated by small centric diatoms (*Cyclotella* sp.) and cryptophytes (*Rhodomonas minuta*). On 16 April, when the lake had just started to thermally stratify, a total of 12 mesocosms (3 replicates per treatment) was filled with ambient, 30 μm filtered lake water containing the natural community of microplankton but excluding larger mesozooplankton. Mimicking natural recruitment from overwintering resting eggs,

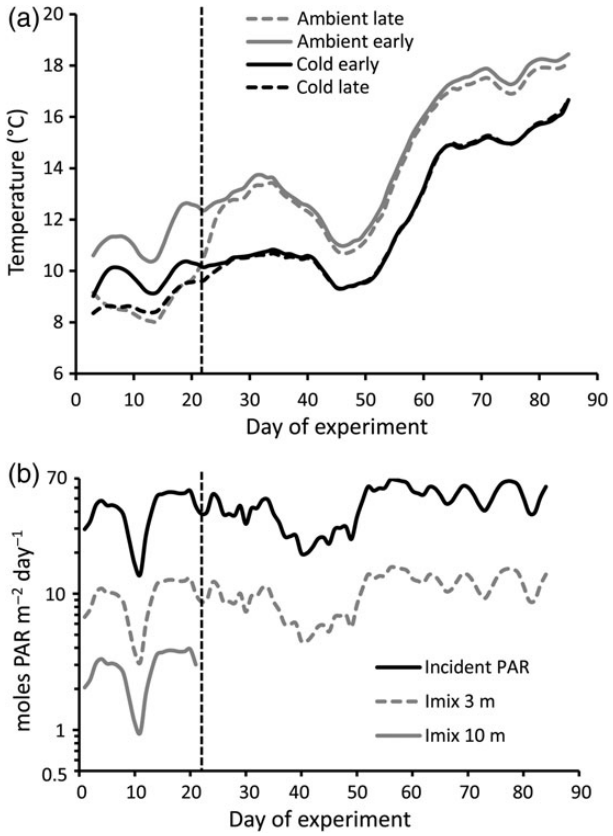

Figure 2. Temporal development of (a) daily mean water temperature in the mixed layers of the four different treatments and (b) of estimated daily PAR. Shown are 3-d running means of incident PAR at the water surface and of depth-averaged PAR [$=I_{mix}$ in Equation (5)] in mixed layers of 3- and 10-m depth, respectively. Dashed vertical lines indicate the onset of "late" stratification on day 22.

mesocosms were stocked on 18, 24, and 30 April with small, equal aliquots of *Daphnia hyalina* (in total 0.3 ind. l^{-1}) that had been isolated from the lake and pre-cultivated in the lab. Mesocosms extended 10 m below the water surface and were made optically deep by an outer layer of light absorbing, black, opaque silage film. To enhance the annual nutrient pulse following spring overturn, we fertilized all mesocosms once with KH_2PO_4 to a total phosphorus concentration of 0.8 μM P. Throughout the experiment, we logged water temperature in all mesocosms every 30 min at a depth of 15 cm.

A schematic drawing of the experimental set-up is given in Figure 1. Before the start of the experiment, mesocosms were fully mixed by intermittently blowing compressed air to their bottom (5 min every 35 min). "Early" stratification was accomplished by raising the outlet of compressed air from a depth of 10–3 m on 18 April (day 1). "Late" stratification treatments were completely mixed for another three weeks and stratified at 3 m on day 22 (Figure 1). On 3 May, we measured vertical profiles of PAR with a spherical quantum sensor (LICOR LI-139SA) in all mesocosms and calculated the light attenuation coefficient K as the slope of linear regressions of log-transformed PAR against depth. In mesocosms that were close to starting conditions (2.3 μg chl *a* l^{-1}) K was 1.3 m^{-1}, which yields values of optical mixed-layer depth Kz_{mix} of 13 before stratification and 3.9 thereafter. For comparison, these values correspond to physical depths of 260 and 78 m, respectively, in water columns with a light attenuation coefficient of 0.05 m^{-1}, which is a typical value for the North Atlantic before the onset of the spring bloom (Wroblewski, 1989; Henson, 2005).

The "ambient" temperature treatment consisted of mesocosms that were freely suspended and thus exposed to the lake's seasonal temperature regime (Figure 2a). In contrast, mesocosms with reduced temperature (hereafter "cold") were placed inside a 12 m deep, permanently mixed outer bag that served as a destratified water bath. The latter took on the vertically averaged temperature of the surrounding lake. Water temperatures in "cold" treatments thus followed the seasonal temperature trajectory in the lake, but once all mesocosms were stratified at 3 m, the mixed layers of the "cold" treatments remained ~3°C colder than "ambient" mixed layers throughout the rest of the experiment (Figure 2a).

The experiment was maintained for 84 d (until 10 July) to allow for the typical seasonal sequence of a phytoplankton spring bloom followed by a *Daphnia* peak and a clear-water phase with low phytoplankton biomass. We sampled phytoplankton and mesozooplankton twice weekly from the mixed surface layer and, where applicable, at mid-depth from the stratified water column below. Phytoplankton biomass was estimated as chlorophyll *a* concentration measured from *in vivo* fluorescence (TD 700, Turner Designs) of 250 μm filtered water immediately after sampling. The abundance of mesozooplankton (almost exclusively *D. hyalina*) was estimated from vertical hauls with a 55-μm plankton net. We also took vertical profiles of temperature, dissolved oxygen, and alkalinity from the surface to 10-m depth about once a week using a multiprobe LT1/T (WTW, Weilheim, Germany).

Knowledge of incident PAR is required to relate phytoplankton dynamics to depth-averaged PAR in the mixed layer. Continuous measurements of incident PAR are, however, not available for Lake Brunnsee. We therefore estimated incident PAR for each day of the experiment from daily sunshine hours recorded at Amerang 10 km to the west (www.dwd.de/WESTE) using the relationship

$$I_0 = [0.2468 + 1.1924o/c - 0.43791924(o/c)^2]Q \quad (4)$$

where I_0 is incident PAR at the water surface (mol PAR m^{-2} d^{-1}), o the observed sunshine hours, c the sunshine hours under a clear sky, and Q is incident PAR under a clear sky (Qin *et al.*, 2012). Values for c and Q for the latitude of Lake Brunnsee were obtained from solar radiation tables assuming that 50% of solar radiation is PAR and that PAR energy converts to photon flux density as 4.56 μmol photons s^{-1} W^{-1} (McCree, 1972). Monthly solar radiation sums calculated from Equation (4) consistently overestimated incident radiation by a factor of 1.26–1.29 compared with (spatially interpolated) monthly global radiation sums for the geographical location of Lake Brunnsee (available at www.dwd.de/WESTE). We therefore corrected our estimates of daily PAR by a factor 1/1.28. Incident PAR was converted to depth-averaged PAR in the mixed layer I_{mix} as

$$I_{mix} = I_0 \frac{1 - e^{-Kz_{mix}}}{Kz_{mix}}, \quad (5)$$

where optical mixed-layer depth Kz_{mix} was 14.5 and 4.35 before and after stratification, respectively. The time courses of incident PAR and mixed-layer PAR are shown in Figure 2b.

Data analyses

We estimated the timing of the onset, peak, and end of the phytoplankton spring bloom in each mesocosm by fitting a unimodal 6-parameter Weibull function to each chlorophyll *a* time-series using the "cardidates" package in R (Rolinski *et al.*, 2007; R Development Core Team, 2014). The function allows for non-zero baselines before the onset of the bloom and after its end as well as for lagged and different slopes in the increasing and decreasing sections (Figure 3). Neighbouring maxima were considered separate peaks only when the relative height of an intervening pit was <0.1 times the lower maximum. The beginning and end of a bloom were determined separately for the periods before and after the fitted peak (i.e. the left and right branch of the curve) as the date of the 10% quantile of the area under the curve before the maximum and the date of the 90% quantile of the area under the curve after the maximum, respectively (Rolinski *et al.*, 2007).

Effects of temperature ("ambient" and "cold") and stratification ("early" and "late") treatments on the timing of the onset and the peak of the bloom (as determined from the Weibull fits) were statistically analysed with two-factor analysis of variance (ANOVA) in R (R Development Core Team, 2014). We also attempted to delineate a bound to the compensation light intensity (I_c) by visually identifying periods of zero phytoplankton net growth in each replicate and comparing them with concomitant estimates of average mixed-layer PAR.

Results

Phytoplankton dynamics

Similar to other experiments with stratified water columns (Berger *et al.*, 2010, 2014), water chemistry and phytoplankton indicated that dynamics in the surface layer were unaffected by processes in deeper water. We therefore report phytoplankton data only from the mixed surface layer. The 6-parameter Weibull function gave a very good to excellent fit to the chlorophyll *a* time-series ($R^2 \geq 0.76$, Figure 3). In "early" stratification treatments, phytoplankton had a brief lag phase (likely caused by the initial disturbance of pumping lake water into the mesocosms) but grew exponentially within a week from the start of the experiment, reaching peak densities in weeks 3–4 (Figure 3, left panels). In contrast, chlorophyll

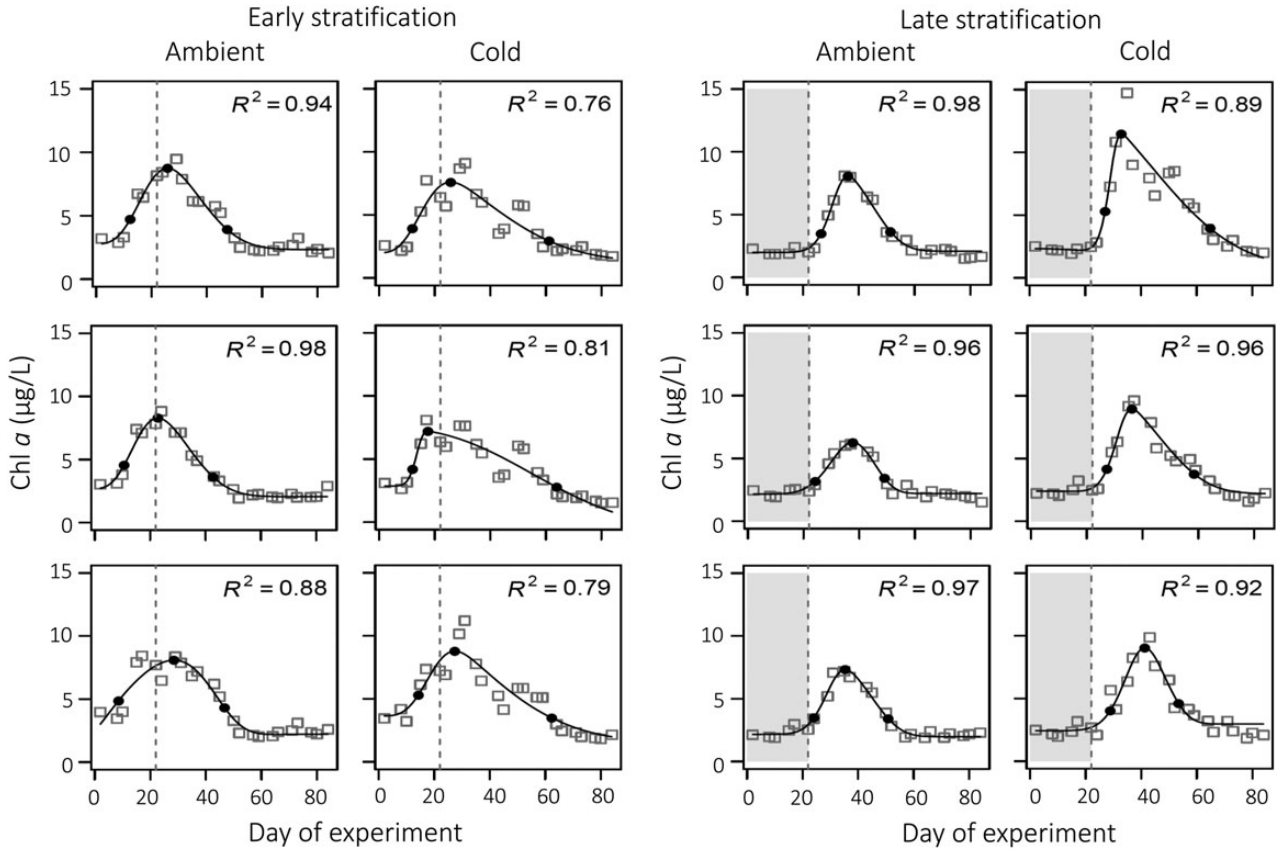

Figure 3. Time course of phytoplankton biomass (as chlorophyll *a* concentration) in the mixed layers of individual "ambient" and "cold" mesocosms that where stratified "early" (day 1, left panels) and "late" (day 22, right panels). Panels show data points (open squares), Weibull fits (solid lines), and R^2 values of the Weibull fits. Filled circles indicate the estimated beginning, peak, and end of the bloom in each mesocosm. For comparison, the date of late stratification is indicated in all panels (dashed vertical lines). The period of deep mixing of the "late" stratification treatments is highlighted in grey.

concentrations remained constant during the first 3 weeks in the "late" stratification treatments and did not start to increase until the mesocosms were stratified on day 22 (Figure 3, right panels). Chlorophyll concentrations in the "late" treatments peaked in weeks 5–6. On average, the onset of the phytoplankton bloom occurred 15 d earlier and the peak of the bloom occurred 12 d earlier in "early" than in "late" stratification treatments (Figure 4; ANOVA, effect of stratification timing, $p \leq 0.001$). In "cold" treatments, the onset, but not the peak, of the bloom was slightly delayed compared with "ambient" treatments (Figure 4; ANOVA, effect of temperature, $p = 0.007$ and $p > 0.7$, respectively).

At the time of the onset of the spring bloom, *Daphnia* densities were still very low (<1 ind. l^{-1}) in all mesocosms. Average *Daphnia* density before bloom onset was slightly higher in the treatment with the earliest bloom onset ("ambient-early", 0.55 ind. l^{-1}) than in the remaining treatments (0.33 ind. l^{-1}; ANOVA, $p = 0.02$). If grazing had been significant, it should rather have delayed phytoplankton development, suggesting that the influence of grazing on bloom initiation was weak. Once phytoplankton blooms peaked (weeks 3–6), *Daphnia* densities increased rapidly and subsequently reached own peak densities >80 ind. l^{-1} in weeks 7–10. The latter are likely responsible for the low chlorophyll levels during the second half of the experiment (Figure 3). After the onset of stratification, very few *Daphnia* were caught below the mixed surface layer. Further details of the zooplankton dynamics will be described elsewhere.

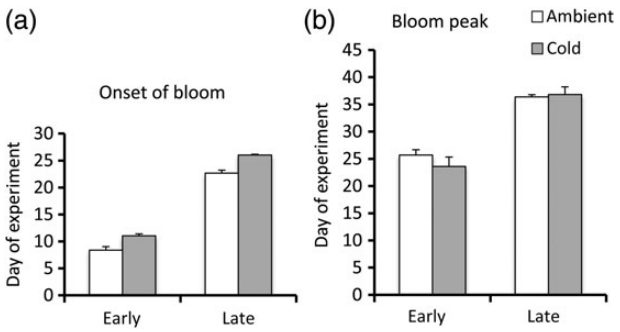

Figure 4. Timing of (a) the onset and (b) the peak of the phytoplankton spring bloom as estimated from the Weibull fits in Figure 3. Shown are means $\pm$ 1 SE.

Phytoplankton growth in relation to the light and temperature environment

Water temperature in the mixed surface layers of the "early" stratification treatments followed the temporal trends of incident PAR in a dampened and time-lagged manner (Figure 2), fluctuating from 10.5 to 14°C ("ambient early") and from 9 to 10.5°C ("cold early") during the period when the phytoplankton blooms occurred (up to day 50). Due to a miscalculation, the outer bag surrounding

the "cold" treatments was only mixed to a depth of 7 m (instead of 11 m). As a consequence, mixed layers in "cold early" treatments (3 m deep from day 1 on) were ~1–1.5°C warmer than in "cold late" treatments (10 m deep until day 21) during the first 3 weeks of the experiment, but quickly converged in temperature after the latter were stratified at 3 m on day 22 (Figure 2a).

Although these early differences in temperature slightly confound the interpretation of the phytoplankton growth data, it is obvious that the large differences in timing of the onset and peak of the spring bloom between "early" and "late" stratification treatments were primarily related to differences in light climate (Figures 2b and 4). In the "early" stratification treatments, estimated mean PAR in the mixed surface layer (I_{mix}) was 10.22 moles m^{-2} d^{-1} before the onset of the bloom (days 1–8) but dropped to an average value of 5.12 moles m^{-2} d^{-1} during a period of overcast (days 9–12, Figure 2b). Despite this temporary reduction in PAR, phytoplankton in "early" stratification treatments grew fast during this period and had doubled to tripled by day 15 (Figure 3). In contrast, phytoplankton did not show any net growth in "late" stratification treatments before stratification. Average PAR during this initial period of deep mixing was 3.2 moles m^{-2} d^{-1} (days 1–21) but shifted to a value of 9.67 moles m^{-2} d^{-1} on the day of stratification (day 22), triggering an almost instant net growth response (Figures 2b and 3).

Together, these data suggest that an average mixed-layer photon flux density of 3.2 moles m^{-2} d^{-1} was insufficient to trigger a phytoplankton bloom, whereas a photon flux density of 5.12 moles m^{-2} d^{-1} allowed for rapid growth. The compensation light intensity (I_c) of the plankton community of Lake Brunnsee in spring 2006 can thus be estimated to be somewhat above 3.2 moles PAR m^{-2} d^{-1}. Using an average incident PAR value of 33.5 moles m^{-2} d^{-1} (the mean for April 2006), this yields an estimate of the critical "optical" depth [Kz_{cr}, Equation (3)] of the Lake Brunnsee community of somewhat below 10.5 in 2006.

Discussion

Pelagic mesocosms provide a near natural environment in which complex plankton communities can be maintained and manipulated for many weeks, while simultaneously enabling detailed monitoring of the pools and fluxes of the components under study (Petersen *et al.*, 2003). If properly designed and scaled, pelagic mesocosm experiments therefore allow strong inference on underlying processes, scaling-up to larger ecosystems, and discrimination among competing hypotheses (Petersen *et al.*, 2009). Not surprisingly, the experimental study of plankton dynamics in mesocosms has a long history in marine science (McAllister *et al.*, 1961; Grice *et al.*, 1977; Davies *et al.*, 1979; Banse, 1982). Yet, the use of mesocosms has been largely restricted to estuarine and sheltered ecosystems and has only very recently been added to the toolbox of biological oceanography (Sommer *et al.*, 2007; Riebesell *et al.*, 2013).

Reasons for this absence are likely twofold. First, mesocosm experiments in the open ocean pose severe technical and logistical challenges. It is not until very recently that mesocosms have been developed that withstand the mechanical strain exerted by waves and currents in the open ocean (Riebesell *et al.*, 2013). Moreover, mesocosm experiments require continuous maintenance and frequent sampling and thus entail costly ship time if performed in remote oceanic regions. Second, ocean stratification, productivity, and biogeochemistry are all strongly affected by turbulent hydrodynamic forces acting at multiple spatial scales many times larger than the enclosed systems under study (Falkowski *et al.*, 1998; McGillicuddy *et al.*, 2007; Mahadevan *et al.*, 2010). It may therefore seem difficult to justify approaching large-scale phenomena such as the North Atlantic spring bloom with costly experimentation on enclosed, local communities. The latter is, however, in principle no different from the general scaling issues inherent to all kinds of mesocosm experiments, and methods such as dimensional analysis are available to accommodate many of these issues (Perez *et al.*, 1977; Petersen and Hastings, 2001; Petersen and Englund, 2005).

For example, despite the complex, three-dimensional nature of hydrodynamical forces in the ocean, the three hypotheses on mechanisms triggering vernal plankton blooms described in the introduction do only include physical and biological structure in the "vertical" dimension (Behrenfeld and Boss, 2014). This means that principles of vertical gradient compression (Petersen and Kemp, 2009) can be applied to scale mesocosms that are used in experimental hypothesis testing. We have already described how a deepwater light environment can be simulated in relatively shallow mesocosms and have developed the concept of a "critical optical depth" from this approach.

Our experimental estimate of the compensation light intensity I_c of closely above 3.2 moles PAR m^{-2} d^{-1} for the plankton community of Lake Brunnsee in spring 2006 is similar to Riley's (1957) classical estimate of 3.5 moles PAR m^{-2} d^{-1} for the Sargasso Sea [recalculated by Siegel *et al.* (2002)] and consistent with a mesocosm study in which an experimental doubling of the ambient mixed-layer light dose from 2 to 4 moles PAR m^{-2} d^{-1} triggered a bloom of a Baltic Sea plankton community (Sommer *et al.*, 2011). It is also within the range of local (1° by 1° grid cell) estimates of I_c for the North Atlantic spring bloom in 1998–2000 calculated from satellite data and oceanic climatologies (Figure 1d in Siegel *et al.*, 2002) but about a factor 2–3 higher than regionally averaged estimates (Siegel *et al.*, 2002).

We emphasize that, compared with the many assumptions that go into the estimation of local compensation light intensities from satellite data, our experimentally determined estimates are likely more reliable. In particular, the physical mixing depths and the dates of the onset of the phytoplankton bloom could be almost exactly determined in each experimental mesocosm. Yet, perhaps our method overestimates the true compensation light intensity. Incident radiation at the water surface was probably lower inside than outside the mesocosms, because the opaque, black walls extended 0.2 m above the water surface. Second, our vertical light measurements did not take into account horizontal light gradients inside the mesocosms. We attempted to measure PAR at a central location of the mesocosm cross section, where light levels are typically appreciably higher than close to walls. Although we did not gather data to quantify these biases, it would be easy to do so.

Although our mesocosm study may be the first experimental demonstration of the critical depth principle acting on a natural plankton community, a precise estimate of the critical optical depth (and thus I_c) was not the primary goal of the study. To that end, we would suggest a gradient design that covers a broad range of optical depth treatments. The reason is that near the critical optical depth phytoplankton biomass and net growth rate are very low and thus difficult to measure with precision. Instead, because the relationship between gross primary production and average PAR in the mixed surface layer I_{mix} is approximately linear at the onset of a spring bloom (Equation 1), the compensation light intensity can be estimated as the x-axis intercept of a regression of experimentally determined phytoplankton net growth rates vs. I_{mix}. We illustrate this with a hypothetical example of a mesocosm experiment performed under conditions similar to the onset of the North Atlantic spring bloom (Figure 5). In the example we

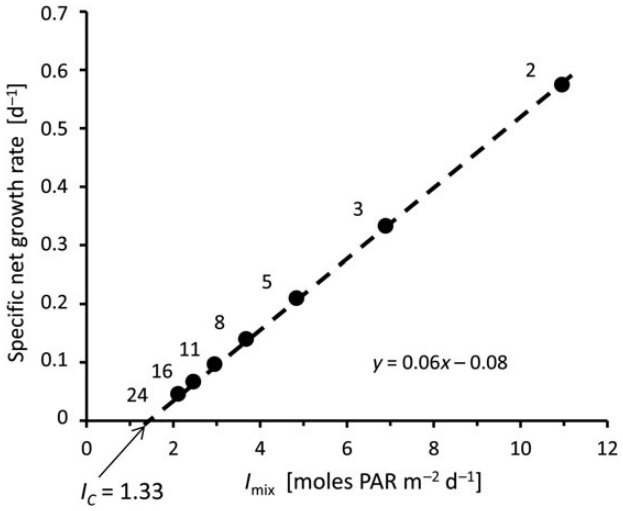

Figure 5. An experimental approach to the determination of the compensation irradiance. The (hypothetical) example assumes that seven optically scaled mesocosms, covering a range of physical mixed-layer depths from 1–7 m (regularly spaced at 1 m intervals), were filled with water containing the plankton community of a well-mixed oceanic water column near the onset of the spring bloom. Initial chlorophyll P_0 was 0.1 mg chl *a* m^{-3} and its net rate of change followed Equation (1), with $I_0 = 20$, $\alpha = 0.06$, $R = 0.08$, $z_{mix} =$ mesocosm depth, and $K = K_{bg} + k_P P$ with chlorophyll-specific attenuation coefficient $k_P = 0.05$. Light attenuation is dominated by the mesocosm walls (background attenuation coefficient $K_{bg} = 1.35$). The remaining parameter values are representative of the onset of the North Atlantic spring bloom (Bricaud *et al.*, 1995; Siegel *et al.*, 2002; Behrenfeld, 2010; see Table 1 for units). Specific net growth rate in each mesocosm was estimated as $(\ln P_0 - \ln P_t)/t$, where t is the time required for chlorophyll to increase to $P_t = 0.3$ mg chl *a* m^{-3} (assuming that an increase from 0.1 to 0.3 mg chl *a* m^{-3} is required for a precise measurement of the change in P). Feedback from self-shading is minimal under these conditions and growth is near exponential if R is constant over time t. Shown are specific net growth rates from the seven mesocosms plotted against average PAR in the mixed layer I_{mix}. The compensation irradiance I_c is equal to the x-axis intercept of a linear regression of the specific growth rate against average mixed layer PAR I_{mix} (broken line). Numbers next to data points indicate the time t required to reach 0.3 mg chl *a* m^{-3} (in days).

assume that an increase in chlorophyll *a* from an initial value of 0.1 mg m^{-3} to a concentration of 0.3 mg m^{-3} is required to yield sufficient measurement precision. Note that, since specific production and losses (and thus bloom timing, Figure 4a) depend on temperature, one must ensure that the experimental I_{mix} gradient does not co-vary with temperature.

The approach described in Figure 5 is exact only if phytoplankton net growth is exponential over the measurement period. This requires two things. First, the measurement period should be short enough that specific losses R remain approximately constant. Perhaps counter-intuitively, measurements of net growth taken at I_{mix} much higher than I_c are therefore likely to be more reliable than ones taken near I_c (because it takes very much longer to reach measurable phytoplankton biomass changes at low light levels, Figure 5). Second, negative feedback from self-shading should be minimal over the measurement period. The latter condition is well met in experimentally compressed light gradients, where background light attenuation can be easily tuned to be 1–2 orders of magnitude higher than the contribution of phytoplankton self-shading. Note, however, that self-shading is significant in clear oceanic waters. In other circumstances, the absence of feedback from self-shading may therefore be a limitation of experimentally compressed light gradients. For example, if the longer-term balance of phytoplankton production vs. grazing losses is a study focus (as would be relevant to the dilution-recoupling hypothesis), insignificant self-shading may artificially allow phytoplankton to outgrow more slowly changing grazing losses.

Looking forward, we suggest that mesocosm experiments should be performed that can simultaneously address two or more of the competing hypotheses for vernal spring blooms proposed by Behrenfeld and Boss (2014). For example, it should be feasible to test the principal working of the dilution-recoupling hypothesis with experiments in (optically scaled) mesocosms in which autumnal deepening of a mixed surface layer into a deepwater mass is simulated, followed by simulated vernal re-stratification. Observed plankton dynamics could be related to the critical depth hypothesis by using control treatments without re-stratification or a gradient of re-stratification depth treatments. Similarly, it should be feasible to assess the relative influences of critical depth and critical turbulence mechanisms on plankton dynamics by using appropriately scaled optical depth and turbulence treatments. For example, a finely tunable mixing mechanism can in principle be scaled to any compressed light gradient such as to realistically mimic natural PAR fluctuations experienced by phytoplankters in different turbulence regimes (Sanford, 1997; Petersen and Kemp, 2009).

To be quantitatively most relevant to plankton blooms in the open ocean, mesocosm experiments could be conducted in coastal regions that harbour near oceanic water and plankton communities [see Stibor *et al.* (2004) and Thingstad *et al.* (2008) for examples from western Norway and Svalbard]. It is, however, also conceivable to design ship borne systems. Although the construction of on-board plankton towers may appear daunting (and likely pose challenges to the simulation of low turbulence regimes), vertical ocean gradients can be approximated on board with sets of linked, discrete compartments representing different depth strata (Petersen and Kemp, 2009). The latter could be seeded with water and plankton from relevant depths and exposed to depth-specific light and temperature regimes, while exchange rates between neighbouring compartments could be tuned to simulate different turbulence regimes. Clearly, there is much room for creative, hypothesis-driven experimentation in mesocosms in biological oceanography, and we expect that such experimentation will yield crucial insights into the causes and consequences of oceanic plankton dynamics.

Acknowledgements

We thank Angelika Wild, Achim Weigert, Miriam Ruhenstroth, Gabriele Trommer, Florian Hantzsche, and Tanja Weibulat for laboratory analyses and/or help with fieldwork, Margit Feissel, Maria Stockenreiter, and Michaela Baumgartner for culturing *Daphnia* and/or help during the preparation of the experiment, and three anonymous reviewers for very helpful comments. The work was financially supported by the German Science Foundation (DFG) within the priority program AQUASHIFT through grant DI 745/5-1.

References

Banse, K. 1982. Experimental marine ecosystem enclosures in a historical perspective. *In* Marine Mesocosms, pp. 11–24. Ed. by G. D. Grice, and M. R. Reeve. Springer-Verlag, New York.

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

Behrenfeld, M. J., and Boss, E. S. 2014. Resurrecting the ecological underpinnings of ocean plankton blooms. Annual Review of Marine Science, 6: 167–194.

Behrenfeld, M. J., O'Malley, R. T., Siegel, D. A., McClain, C. R., Sarmiento, J. L., Feldman, G. C., Milligan, A. J., *et al.* 2006. Climate-driven trends in contemporary ocean productivity. Nature, 444: 752–755.

Berger, S. A., Diehl, S., Kunz, T. J., Albrecht, D., Oucible, A. M., and Ritzer, S. 2006. Light supply, plankton biomass and seston stoichiometry in a gradient of lake mixing depths. Limnology and Oceanography, 51: 1898–1905.

Berger, S. A., Diehl, S., Stibor, H., Sebastian, P., and Scherz, A. 2014. Separating effects of climatic drivers and biotic feedbacks on seasonal plankton dynamics: no sign of trophic mismatch. Freshwater Biology, 59: 2204–2220.

Berger, S. A., Diehl, S., Stibor, H., Trommer, G., and Ruhenstroth, M. 2010. Water temperature and stratification depth independently shift cardinal events during plankton spring succession. Global Change Biology, 16: 1954–1965.

Berger, S. A., Diehl, S., Stibor, H., Trommer, G., Ruhenstroth, M., Wild, A., Weigert, A., *et al.* 2007. Water temperature and mixing depth affect timing and intensity of events during spring succession of the plankton. Oecologia, 150: 643–654.

Boyce, D. G., Lewis, M. R., and Worm, B. 2010. Global phytoplankton decline over the past century. Nature, 466: 591–596.

Bricaud, A., Babin, M., Morel, A., and Claustre, H. 1995. Variability in chlorophyll-specific absorption coefficients of natural phytoplankton: analysis and parameterization. Journal of Geophysical Research, 100: 13321–13332.

Chassot, E., Bonhommeau, S., Dulvy, N. K., Mélin, F., Watson, R., Gascuel, D., and Le Pape, O. 2010. Global marine primary production constrains fisheries catches. Ecology Letters, 13: 495–505.

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

Davies, J. M., Gamble, J. C., Morris, R. J., and Wilson, J. G. 1979. Experiments with large enclosed ecosystems. Philosophical Transactions of the Royal Society London, Series B, 286: 523–544.

Diehl, S. 2002. Phytoplankton, light, and nutrients in a gradient of mixing depths: theory. Ecology, 83: 386–398.

Diehl, S., Berger, S., Ptacnik, R., and Wild, A. 2002. Phytoplankton, light, and nutrients in a gradient of mixing depths: field experiments. Ecology, 83: 399–411.

Diehl, S., Berger, S. A., and Wöhrl, R. 2005. Flexible nutrient stoichiometry mediates environmental influences on phytoplankton and its abiotic resources. Ecology, 86: 2931–2945.

Doney, S. C. 2006. Oceanography: plankton in a warmer world. Nature, 444: 695–696.

Falkowski, P. G., Barber, R. T., and Smetacek, V. 1998. Biogeochemical controls and feedbacks on ocean primary production. Science, 281: 200–206.

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

Grice, G. D., Reeve, M. R., Koeller, P., and Menzel, D. W. 1977. The use of large volume, transparent, enclosed sea-surface water columns in the study of stress on plankton ecosystems. Helgoländer Wissenschaftliche Meeresuntersuchungen, 30: 118–133.

Hairston, N. G. 1989. Ecological experiments: purpose, design and execution. Cambridge University Press, New York.

Henson, S. A. 2005. Physical controls on spring bloom dynamics in the Irminger basin, North Atlantic. PhD thesis, University of Southampton.

Henson, S. A., Dunne, J. P., and Sarmiento, J. L. 2009. Decadal variability in North Atlantic phytoplankton blooms. Journal of Geophysical Research, 114: C04013.

Huisman, J., and Sommeijer, B. 2002. Maximal sustainable sinking velocity of phytoplankton. Marine Ecology Progress Series, 244: 39–48.

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

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.

Jäger, C. G., Diehl, S., Matauschek, C., Klausmeier, C. A., and Stibor, H. 2008a. Transient dynamics of pelagic producer-grazer systems in a gradient of nutrients and mixing depths. Ecology, 89: 1272–1286.

Jäger, C. G., Diehl, S., and Schmidt, G. 2008b. Influence of water column depth and mixing on phytoplankton biomass, community composition, and nutrients. Limnology and Oceanography, 53: 2361–2373.

Kirk, J. T. O. 1994. Light and photosythesis in aquatic ecosystems, 2nd edn. Cambridge University Press, Cambridge, UK.

Körtzinger, A., Send, U., Lampitt, R. S., Hartman, S., Wallace, D. W. R., Karstensen, J., Villagarcia, M. G., *et al.* 2008. The seasonal *p*CO2 cycle at 49°N/16.5°W in the northeastern Atlantic Ocean and what it tells us about biological productivity. Journal of Geophysical Research, 113: C04020.

Le Quéré, C., Aumont, O., Monfray, P., and Orr, J. 2003. Propagation of climatic events on ocean stratification, marine biology, and CO2: case studies over the 1979–1999 period. Journal of Geophysical Research, 108: 3375–3389.

Mahadevan, A., Tandon, A., and Ferrari, R. 2010. Rapid changes in mixed layer stratification driven by submesoscale instabilities and winds. Journal of Geophysical Research—Oceans, 115: C03017.

Martin, P., Lampitt, R. S., Perry, M. J., Sanders, R., Lee, C., and D'Asaro, E. 2011. Export and mesopelagic particle flux during a North Atlantic spring diatom bloom. Deep Sea Research I, 58: 338–349.

McAllister, C. D., Parsons, T. R., Stephens, K., and Strickland, J. D. H. 1961. Measurements of primary production in coastal sea water using a large-volume plastic sphere. Limnology and Oceanography, 6: 237–258.

McCree, K. J. 1972. Test of current definitions of photosynthetically active radiation against leaf photosynthesis data. Agricultural and Forest Meteorology, 10: 443–453.

McGillicuddy, D. J., Jr, Anderson, L. A., Bates, N. R., Bibby, T., Buesseler, K. O., Carlson, C. A., Davis, C. S., *et al.* 2007. Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms. Science, 316:1021–1026.

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

Perez, K. T., Morrison, G. M., Lackie, N. F., Oviatt, C. A., Nixon, S. W., Buckley, B. A., and Heltsche, J. F. 1977. The importance of physical and biotic scaling to the experimental simulation of a coastal marine ecosystem. Helgoländer Wissenschaftliche Meeresuntersuchungen, 30: 144–162.

Petersen, J. E., and Englund, G. 2005. Dimensional approaches to designing better experimental ecosystems: a practitioner's guide with examples. Oecologia, 145: 216–224.

Petersen, J. E., and Hastings, A. 2001. Dimensional approaches to scaling experimental ecosystems: designing mousetraps to catch elephants. American Naturalist, 157: 324–333.

Petersen, J. E., and Kemp, W. M. 2009. Dimensional analysis. *In* Enclosed Experimental Ecosystems and Scale: Tools for Understanding and Managing Coastal Ecosystems, pp. 145–160. Ed. by J. E. Petersen, V. S. Kennedy, W. C. Dennison, and W. M. Kemp. Springer, New York.

Petersen, J. E., Kemp, W. M., Bartleson, R., Boynton, W. R., Chen, C.-C., Cornwell, J. C., Gardner, R. H., *et al.* 2003. Multiscale experiments in

coastal ecology: improving realism and advancing theory. BioScience, 53: 1181–1197.

Petersen, J. E., Kennedy, V. S., Dennison, W. C., and Kemp, W. M. (eds.). 2009. Enclosed Experimental Ecosystems and Scale: Tools for Understanding and Managing Coastal Ecosystems. Springer, New York.

Ptacnik, R., Diehl, S., and Berger, S. A. 2003. Patterns of abundance of phytoplankton species along an experimental mixing depth gradient. Limnology and Oceanography, 48: 1903–1912.

Qin, J., Yang, K., Liang, S., and Tang, W. 2012. Estimation of daily mean photosynthetically active radiation under all-sky conditions based on relative sunshine data. Journal of Applied Meteorology and Climatology, 51: 150–160.

R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org.

Reynolds, C. S. 1984. The Ecology of Freshwater Phytoplankton. Cambridge University Press, Cambridge, UK.

Riebesell, U., Czerny, J., von Bröckel, K., Boxhammer, T., Büdenbender, J., Deckelnick, M., Fischer, M., *et al.* 2013. Technical note: a mobile sea-going mesocosm system—new opportunities for ocean change research. Biogeosciences, 10: 1835–1847.

Riley, G. A. 1957. Phytoplankton of the North Central Sargasso Sea. Limnology and Oceanography, 2: 252–270.

Rolinski, S., Horn, H., Petzoldt, T., and Paul, L. 2007. Identifying cardinal dates in phytoplankton time series to enable the analysis of long-term trends. Oecologia, 153: 997–1008.

Sanford, L. P. 1997. Turbulent mixing in experimental ecosystem studies. Marine Ecology-Progress Series, 161: 265–293.

Siegel, D. A., Doney, S. C., and Yoder, J. A. 2002. The North Atlantic spring bloom and Sverdrup's critical depth hypothesis. Science, 296: 730–733.

Smetacek, V., and Passow, U. 1990. Spring bloom initiation and Sverdrup's critical depth model. Limnology and Oceanography, 35: 228–233.

Sommer, U., Aberle, N., Engel, A., Hansen, T., Lengfellner, K., Sandow, M., Wohlers, J., *et al.* 2007. An indoor mesocosm system to study the effect of climate change on the late winter and spring succession of Baltic Sea phyto- and zooplankton. Oecologia, 150: 655–667.

Sommer, U., Aberle, N., Lengfellner, K., and Lewandowska, A. M. 2012b. The Baltic Sea spring phytoplankton bloom in a changing climate: an experimental approach. Marine Biology, 159: 2479–2490.

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

Sommer, U., Gliwicz, Z. M., Lampert, W., and Duncan, A. 1986. The peg-model of seasonal succession of planktonic events in fresh waters. Archiv für Hydrobiologie, 106: 433–471.

Sommer, U., Lengfellner, K., and Lewandowska, A. M. 2011. Experimental induction of a coastal spring bloom early in the year by intermittent high-light episodes. Marine Ecology Progress Series, 446: 61–71.

Stibor, H., Vadstein, O., Diehl, S., Gelzleichter, A., Hantzsche, F., Katechakis, A., Lippert, B., *et al.* 2004. Copepods act as a switch between alternative trophic cascades in marine food webs. Ecology Letters, 7: 321–328.

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.

Thingstad, T. F., Bellerby, R. G. J., Bratbak, G., Børsheim, K. Y., Egge, J. K., Heldal, M., Larsen, A., *et al.* 2008. Counterintuitive carbon-to-nutrient coupling in an Arctic pelagic ecosystem. Nature, 455: 387–390.

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, 260: 59–62.

Wroblewski, J. S. 1989. A model of the spring bloom in the North Atlantic and its impact on ocean optics. Limnology and Oceanography, 34: 1563–1571.

Handling editor: Rubao Ji