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Physiological constrains on Sverdrup's Critical-Depth-Hypothesis: the influences of dark respiration and sinking

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Abstract:

Discussions on the controls initiating the onset of the phytoplankton spring bloom in particular in the North Atlantic have since Sverdrup been dominated by the role of physical and biological drivers. Undoubtedly, these drivers play an important role in phytoplankton dynamics and thus the onset of the spring bloom. However, they neglect the cells ability to modify vital rates in response to changes in the external environment. In this study, we use a non-hydrostatic convection model coupled to an Individual-Based-Model to simulate changes phytoplankton cells during the transition from winter conditions as driven by convective mixing, and the onset of thermal stratification resulting in the spring bloom. The comparison between a simulation using a standard fixed rate approach in line with the original Sverdrup hypothesis and a simulation parameterized to include variable respiration and sinking rates showed that the latter approach was able to capture the observed phytoplankton concentration during deep convective mixing, the timing and magnitude of the spring bloom as well as simulating realistic physiological rates. In contrast, the model employing fixed rate parameterizations could only replicate field observations when employing unrealistic parameter values. These results highlight the necessity to consider not only the physical and biological external controls determining phytoplankton dynamics but also the cells ability to modify critical physiological rates in response to external constraints. Understanding these adaptive qualities will be of increasing importance in the future as species assemblages and physical controls change with changing climate.

Keywords: cell sinking ; dark respiration ; deep convection ; phytoplankton spring bloom

Introduction

The onset of the North Atlantic phytoplankton spring bloom has received a significant amount of attention due in part to its influence on the dynamics of higher trophic levels (Houde, 2008) and role in the biological carbon pump (Sanders *et al.,* 2014). The 'Critical Depth Hypothesis' (Sverdrup, 1953) with its foundations in the works of Gran and Braarud (1935) and Riley (1946) has served as the starting point for predicting the onset of the spring bloom. It has however been widely discussed, criticized and extended based on increased understanding of the role of abiotic and biotic mechanisms. For example, Eilertsen *et al.* (1995) based on the role of light on phytoplankton proposed that photo-period control as a driving mechanism for the onset of the spring bloom. Moreover, the ’Critical Turbulence Hypothesis’ (Huisman *et al.,* 1999) predicts bloom conditions based on turbulent diffusivity, light-limited growth and mixed layer depth. Following this mechanism, low levels of turbulent diffusivity are not able to counteract cell sinking, while high levels of turbulence mix cells out of the euphotic zone, at an intermediate level sinking is balanced by turbulent mixing, retaining the cells in the euphotic zone where they receive sufficient light to generate a surface phytoplankton bloom. The ‘Convection-Shutdown-Hypothesis’ (Ferrari *et al.*, 2014) builds upon the earlier findings of Townsend *et al.* (1994) and Taylor and Ferrari (2011) and suggests that the shutdown of winter convective mixing could serve as a better indicator for the onset of the spring bloom than the mixed layer depth, the basis of the ‘Critical-Depth-Hypothesis’. This approach has subsequently been interpreted as an extension of Huisman's 'Critical Turbulence Hypothesis’ (Behrenfeld and Boss, 2014). Furthermore processes such as frontal systems (Taylor and Ferrari, 2011b) and vertical processes (Mahadevan *et al.*, 2012) can play an important role in creating stratification and thus providing sufficient light to initiate surface blooms without a change in net surface heat flux. All of these mechanisms infer physical controls as the primary cause of the rapid increase in surface chlorophyll observed in early spring. A more biologically based interpretation of the controls on the spring bloom has been presented by Behrenfeld (2010). This 'Disturbance-Recovery-Hypothesis' suggests that phytoplankton blooming is predominately the result of biological

interactions, namely the release of grazing pressure due to dilution of microzooplankton grazers (Landry and Hassett, 1982; Behrenfeld and Boss, 2014).

Given the multiple and interrelated mechanisms acting to influence the phytoplankton community, it is unlikely that one dominant mechanism, biological or physical in nature controls phytoplankton growth and the onset of the spring bloom. More likely these dynamics are controlled by an interplay between the aforementioned mechanisms with one or the other dominating spatially and or temporally and leading to the heterogeneous manifestation of the bloom as seen in satellite imagery (Lindemann and St. John, 2014).

An omission in the discussion to date has been the fundamental physiological ability of phytoplankton to modify their vital rates relative to their external conditions. The Critical-Depth-Hypothesis (Sverdrup, 1953) assumes a constant loss rate, encompassing grazing, sinking and cell respiration, independent of depth and the diurnal cycle. This does not reflect the cells ability to modify critical rates such as respiration and sinking, which potentially lead to a change in the critical depth (Smetacek and Passow, 1990).

Cell respiration is a highly variable internal process influenced by environmental conditions such as temperature (Verity, 1982), nutrients (Laws and Bannister, 1980) and light (Falkowski and Owens, 1980) and subsequently cellular growth. Light-limited low growth rates can induce a reduction of metabolic rates and thus dark respiration (Jochem, 1999). Based on laboratory studies Falkowski and Owens (1980) determined that for cells acclimatized to a specific light level, the ratio of maximum production and dark respiration remained the same over a wide variety of light intensities suggesting that the maximum growth and respiration rates can be equally affected by light. This observation was supported in subsequent studies e.g. Cosper (1982), Verity (1982), Langdon (1988), and Sakshaug *et al*. (1989).

However, in the North Atlantic during winter, within the deep convective layer, cells can be exposed to rapidly changing light levels, thus not conforming to the assumption of constant light or a steady state. Investigations of short-term dark respiration responses to changing light conditions have shown that dark respiration increases rapidly with photosynthesis as a result of increases in light (Weger *et al.*, 1989). As light declines, photosynthesis declines commensurate

with the reduction in light, however dark respiration does not react instantaneously but decreases gradually to a minimum (Weger *et al.*, 1989; Xue *et al.*, 1996). This decoupling of photosynthesis and respiration results in proportionally higher rates of respiration after light exposure (Falkowski *et al.*, 1985).

Phytoplankton cells have been observed to exhibit a wide range of sinking rates, from several meters per day (Smayda, 1970) to positive buoyancy (Acuña *et al.*, 2010). For cells of similar shape and density, the sinking speed can be estimated using Stokes law (Miklasz and Denny, 2010). However, density is influenced by the species-specific cell composition and growth phase. Cells can maintain density levels close to neutral buoyancy, or even achieve positive buoyancy (Acuna et al 2010) via active regulation of inorganic (Anderson and Sweeney, 1977) and organic material (Boyd and Gradmann, 2002). Buoyancy regulation and hence the sinking rate of phytoplankton cells has been related to growth (Brookes and Ganf, 2001, Waite *et al.*, 1992). Fast growing cells typically are found to show lower sinking rates than cells growing under conditions of limiting light (Waite *et al.*, 1992), nutrients (Bienfang *et al.*, 1982) or iron (Waite and Nodder, 2001), independent of cell size. These observations suggest that cell growth is more important in controlling sinking rate than cell size (Bienfang *et al.*, 1982; Peperzak and Colijn, 2003).

In order toTo assess the importance of a cells ability to modify dark respiration and sinking, we developed and employed a Lagrangian Individual-Based-Model (IBM) for phytoplankton cells. IBM models have proven to be a useful tool for understanding the growth dynamics of phytoplankton cells (Hellweger and Kianirad, 2007). One of the advantages of the Lagrangian approach relative to the Eulerian approach is that an individual cell can be followed through space and time. Thus the history of one particle can not only be stored for analysis, but particle properties can depend on the ‘life history’ as well as the abiotic and biotic constraints impacting on the individual. In this study using a non-hydrostatic convection model (CM) coupled to a Lagrangian IBM, we investigated the effect of a cells ability to adjust respiration and sinking in relation to changes in environmental conditions prior to and during the spring bloom.

Materials and methods

Non-hydrostatic convection model

The non-hydrostatic convection model utilized has been employed in several studies (Backhaus *et al.*, 1999; Kämpf and Backhaus, 1998; Wehde and Backhaus, 2000; Wehde *et al.*, 2001; Große *et al.*, 2014) and is set on an isotropic, equidistant grid. The model uses Boussinesq-equations for an incompressible fluid to describe a 2,5 dimensional ocean slice. The ocean slice itself is two dimensional (*x,z*), however fluxes are calculated for all three dimensions (*x,y,z*). The equations for conservation of movement are as follows:

$$\frac{\partial U}{\partial t}+U\frac{\partial U}{\partial x}+W\frac{\partial U}{\partial z}-fV+f^{\circ}W=-\frac{1}{\rho_0}\frac{\partial P}{\partial x}+\frac{\partial}{\partial x}\left(\nu_t\frac{\partial U}{\partial x}\right)+\frac{\partial}{\partial z}\left(\nu_t\frac{\partial U}{\partial z}\right) \tag{1}$$

$$\frac{\partial V}{\partial t}+U\frac{\partial V}{\partial x}+W\frac{\partial V}{\partial z}+fU=\frac{\partial}{\partial x}\left(\nu_t\frac{\partial V}{\partial x}\right)+\frac{\partial}{\partial z}\left(\nu_t\frac{\partial V}{\partial z}\right) \tag{2}$$

$$\frac{\partial W}{\partial t}+U\frac{\partial W}{\partial x}+W\frac{\partial W}{\partial z}-f^{\circ}U=-\frac{1}{\rho_0}\frac{\partial P}{\partial x}-\frac{\rho'}{\rho_0}g+\frac{\partial}{\partial x}\left(\nu_t\frac{\partial W}{\partial x}\right)+\frac{\partial}{\partial z}\left(\nu_t\frac{\partial W}{\partial z}\right) \tag{3}$$

with U, V and W being the velocity components for the three dimensions (*x,y,z*). P denotes the non-hydrostatic part of the pressure, g represents the gravity, ν_t the eddy viscosity, ρ' the reduced density and ρ_0 represents the reference density. f and $f°$ are the complete Coriolis parameters. The turbulent eddy viscosity (ν_t), is parameterized by the zero-order turbulence closure by Kochergin (1987). The numerical stability is ensured by the CFL stability criteria with a physical time steps for advection of temperature, salinity and momentum set to a maximum of one minute.

The equations of conservation for temperature (T), salinity (S) are:

$$\frac{\partial T}{\partial t}+U\frac{\partial T}{\partial x}+W\frac{\partial T}{\partial z}=\frac{\partial}{\partial x}\left(K_T\frac{\partial T}{\partial x}\right)+\frac{\partial}{\partial z}\left(K_T\frac{\partial T}{\partial z}\right)+\frac{\delta E_T}{\partial t} \tag{4}$$

$$\frac{\partial S}{\partial t} + U\,\frac{\partial S}{\partial x} + W\,\frac{\partial S}{\partial z} = \frac{\partial}{\partial x}\left(K_S\,\frac{\partial S}{\partial x}\right) + \frac{\partial}{\partial z}\left(K_S\,\frac{\partial S}{\partial z}\right) + \frac{\delta E_S}{\partial t} \tag{5}$$

with the terms $\frac{\delta E_T}{\partial t}$ and $\frac{\delta E_s}{\partial t}$ being the thermal and saline sea surface forcing respectively. K_T and K_S are the eddy diffusivities for heat and salt respectively and are set equal to the eddy viscosity (ν_t). The thermal surface forcing changes according to

$$\frac{\delta E_T}{\partial t} = \frac{-Q_{net}}{\rho c_{sw}} \tag{6}$$

with c_{sw} being the specific heat of seawater. Q_{net} denotes the net surface heat flux calculated by

$$Q_{net} = \Delta Q_{lw} + Q_{sw} + Q_{lat} + Q_{nses} \tag{7}$$

where ΔQ_{lw} is the difference between the atmospheric long-wave radiation and the long-wave radiation from the sea surface, Q_{sw} the incoming short wave radiation, Q_{lat} the latent heat flux and Q_{sens} the sensible heat flux.

Light intensity (I) in the water column at depth (z) is described by:

$$I(z) = I_0 * exp^{-(k_e + s)z} \tag{8}$$

Here I_0 is the incoming radiation at the sea surface, z is the depth, k_e is the extinction coefficient due to turbidity and s the self-shading of phytoplankton estimated by:

$$s = k_{phy}\,C \tag{9}$$

with k_{phy}, the extinction coefficient of phytoplankton, being 0.03 (Große *et al.*, 2014) and C the phytoplankton concentration in [mmol C m^{-3}].

For further details of the physical model reference is made to Kämpf and Backhaus (1998) and Wehde and Backhaus (2000). Deviating from the older versions of this model, this version uses the equation of state proposed by McDougall *et al.* (2003) which uses potential temperature instead of the situ temperature (UNESCO, 1981).

Biological Individual-Based-Model

The biological IBM consists of Lagrangian tracers depicting phytoplankton cells of indefinite biomass within the ocean slice with the biological time step set to five minutes.

Phytoplankton growth during winter and early spring in the North Atlantic is not believed to be nutrient limited, therefore the model does not account for nutrient limitation. Grazing is not accounted for explicitly, but is parameterized by a biomass dependent mortality rate (*m*). All biological parameter values are given in Table 1.

Cell growth

Net phytoplankton concentration is dependent on the cells growth rate μ, the cells sinking rate *v* and advection and diffusion in the three dimensions:

$$\frac{DC}{Dt} = \frac{\partial C}{\partial t} + U_t \frac{\partial C}{\partial t} \tag{10}$$

with U=(*U,V,W*). The growth-rate is estimated by

$$\mu = P^C - r - m \tag{11}$$

where P^C is the photosynthesis, r is the respiration and *m* is the mortality.

Photosynthesis is calculated according to:

$$P^C = P^C_{\max}\left[1 - \exp\left(-\frac{\alpha^{chl} I \theta^C}{P^C_{\max}}\right)\right] \tag{12}$$

with P^C_{max} being the maximum specific photosynthesis rate, α^{chl} the initial slope of the function and θ^C the chlorophyll to carbon ratio. Changes in chlorophyll are described following Geider *et al*., (1997):

$$\frac{dChl}{dt} = \rho^{chl} P^C C - rChl \tag{13}$$

where ρ^{chl} is the biosynthesis of chlorophyll according to

$$\rho^{chl} = \theta_m^C \left(\frac{P^C}{\alpha^{chl} I \theta^C} \right) \tag{14}$$

with θ_m^C being the maximum Chlorophyll to carbon ratio.

Cell respiration

In this model cell respiration rate consists of maintenance metabolism (r^0) and the cost of biosynthesis which, under the influence of light, is proportionally related to photosynthesis. However, when photosynthesis ceases, biosynthesis does not stop immediately, but decays over time (e.g. Walter *et al*., this issue). Weger *et al*. (1989) investigated short term acclimation of phytoplankton dark respiration to variable light conditions. While the shutdown of light led to a gradual decrease of respiratory loss, moving from dark to light conditions showed an almost instantaneous return of high respiration rates. Here the respiration rate is modeled accounting for these dynamics through:

$$r = \max \begin{pmatrix} \zeta P^C + r^0 \\ r * exp^{\alpha^r} \end{pmatrix} \tag{15}$$

where the upper term represents respiration in light with ζ being the cost of biosynthesis. The second expresses the decrease of respiration in the dark where α^r is the rate of decrease with time, which was extracted from Weger *et al*. (1989).

Cell sinking

The sinking rate of each cell is modelled based on the concept by Waite *et al*. (1992), who coupled the sinking rate to the overall metabolic state of the cell. They found that when cells

where transferred from light into darkness their sinking rate could be described as a negative function of their respiration rate.

The sinking rate can therefore be described by the maximum sinking velocity v_{max} and a scaling factor (α^v) of the relative respiration (r'), which was extracted from Waite *et al*. (1992):

$$v = v_{max}^{-\alpha^v r'} \tag{16}$$

with

$$r' = \frac{r}{\zeta P_{\max}^C + r^0} \tag{17}$$

Model setup and initial conditions

The model was set up to simulate conditions at Ocean Weather Station Mike (OWM) (66°N 02°E), the same station where the observations by Sverdrup (1953) were used to develop the Critical Depth Hypothesis. Three hourly meteorological forcing for the period was obtained from the Norwegian Meteorological Office (METNO) and was used for the simulation from the 06th of April to the – 11th of May 1997 (yearday 100-135) with the first 5 days considered as spin-up. The simulation was initialized with vertical profiles from Ocean Weather Ship Mike. This period was chosen since it encompassed the period from pre-bloom conditions with typical deep convective mixing to stratified conditions with shallow wind-driven mixing towards the end of the simulation. Here (and in the following) we refer to deep convection as convection that is not driven by nocturnal cooling, but extends over a longer period, hence leading to deeper convective mixing. The simulation was not continued throughout the full spring bloom as our assumptions (i.e. no nutrient limitation) would be invalid. Field observations of the further development of the spring bloom after our simulation period showed the maximum chlorophyll concentration occurred on 23rd May (yearday 147) with values of over 3 mg Chl m^{-3} (Niehoff *et al.*, 1999). In our study Lagrangian tracers (20,000 particles) were randomly distributed from 10 to 400 m depth at the beginning of the simulation. The model domain was set to 1000x1500 meters with a

grid size of five by five meters.

Model simulations

In order to demonstrate the effect of a cells ability to modify rates of both sinking and respiration, we compared model simulations, using the variable parameterizations for respiration and sinking as described above, to simulations using fixed values. Other than employing the variable parameterizations, both the fixed value simulations and the adaptive simulation are identical. The values used in the simulations with fixed parameter values were chosen to encompass the range of values found in the adaptive simulation. These fixed values were 0.02, 0.135, 0.25, 0.47 for the daily average carbon-specific respiration [day^{-1}] and 0, 2.25, 4.5 and 6.8 sinking [m day^{-1}] respectively. We compared the adaptive run to runs with each of the four by four combinations of these fixed respiration and sinking rates. The outputs of these fixed value simulations and the respective fixed parameter combinations are presented in Figure 5.

Table 1. Biological model parameters and scaling coefficients. The values for the specific respiration reduction in dark and the sinking rate scaling coefficient were extracted from Weger *et al*. (1989), and Waite *et al*. (1992) respectively.

Description	**Symbol**	**Value**	**Unit**	**Source**
maximum photosynthsis rate	P^c_{max}	3	day^{-1}	Geider *et al.* 1998
Chl-specific initial slope of PI curve	α^{chl}	0.5	10^{-5} gC m^{-2} (gChl mmol photons)$^{-1}$	Geider *et al.* 1997
maximum Chl to Carbon ratio	θ^{chl}_m	0.05	gChl (gC)$^{-1}$	Cloern *et al.*, 1995
cost of biosynthesis	ζ	0.23	gC (gC)$^{-1}$	Geider *et al.* 1998
Mortality rate	m	0.05	day^{-1}	Wehde *et al*. 2001
Specific respiration reduction in dark	α^r	0.0455	h^{-1}	Weger *et al*. 1989
Maintenance cost	r^0	0.02	gC (gC)$^{-1}$	Geider and Osbourne 1989
maximum sinking velocity	v^{max}	6.8	m day^{-1}	Smyada 1970*
Sinking rate scaling coefficient	α^v	4.15	-	Waite *et al*. 1992

*Only considering alive cells

Results

The beginning of the simulation is characterized by a negative net surface heat flux (Fig. 1a), with minimal values of circa -350 W m^{-2}. This led to strong convective mixing as indicated by the Turbulent Kinetic Energy (TKE) (Fig. 1b). The initial period of strong mixing was followed by a reduction in net surface heat loss (-100 to 70 W m^{-2}) causing a reduction in convective mixing, followed by a stabilization of the water column (~6th May, yearday 130) as indicated by the temperature profile (Fig. 1c). This resulted in changes in the mixed layer depth, defined here as the depth range over which the temperature deviates by less than 0.2°C from 10 m below the surface. This value is on the lower range of values commonly used to define the MLD (de Boyer Montégut *et al.*, 2004). The temperature within the surface layer (~6.3°C - 6.5°C) as predicted by the model compares well with observations and the onset of stratification was captured by the model both with regard to the timing (~6th May) and stratification depth (~50 m) (Irigoien *et al.*, 1998).

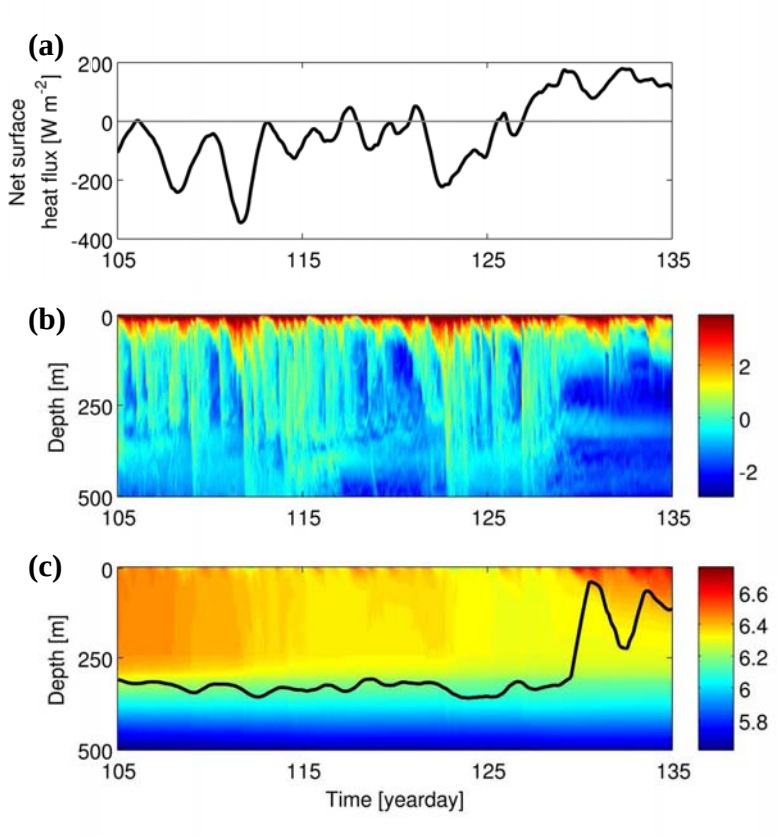

Figure 1. Physical water properties as predicted by the non-hydrostatic convection model over the course of the simulation at Ocean Weather Ship Mike. (a) Simulated Net Surface Heat Flux [W m^{-2}] (b) Hovmöller diagram showing simulated water column Turbulent Kinetic Energy (TKE) [cm^2 sec^{-1}] on a log scale. (c) Simulated temperature within the water column [°C]. The black line indicates the estimated mixed layer depth.

Adaptive Simulations:

The simulated biomass and dynamics of the winter phytoplankton community using our adaptive parameterizations compares well with the published 100 m integrated values of Irigoien *et al.* (1998) and Niehoff *et al.* (1999), showing an increase in biomass of around 200 % (Fig. 2) over the period of the simulation.

Until the onset of stratification, the integrated chlorophyll over the mixed layer showed a decreasing trend (Fig. 2). The onset of stratification was marked by a short lived drop in mixed-layer integrated phytoplankton biomass after which the mixed-layer integrated phytoplankton biomass started to increase similar to that of the 100m integrated chlorophyll. This drop can be attributed to some cells being 'left behind' below the now stratifying mixed layer, thus reducing the integrated biomass due to a decrease in the water column depth now defining as the mixed layer.

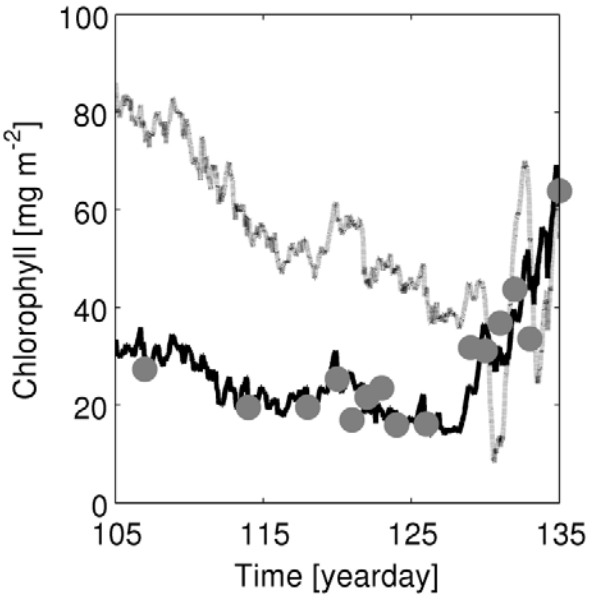

Figure 2. Integrated chlorophyll at Ocean Weather Ship Mike over the course of the simulation. The solid lines shows chlorophyll integrated over the upper 100 meters. Gray dots are observations of 100 meter integrated chlorophyll. The dashed line shows chlorophyll integrated over the mixed layer depth and hence over the varying convective layer depth.

Depending upon their position within the water column, the phytoplankton ‘particles’ were either retained within the mixed layer or where 'detrained' (Behrenfeld and Boss, 2014) into deeper waters as has been suggested earlier by Evans and Parslow (1985). Our simulations illustrate that during deep convective mixing all tracers are generally homogeneously distributed throughout the mixed layer (Fig. 3c). However, occasionally increased production occurred in agreement with the critical turbulence hypothesis (Huisman *et al.*, 1999) leading to an increased phytoplankton biomass near the surface. This biomass was however subsequently quickly mixed throughout the convective mixed layer as result of an increase in turbulent mixing.

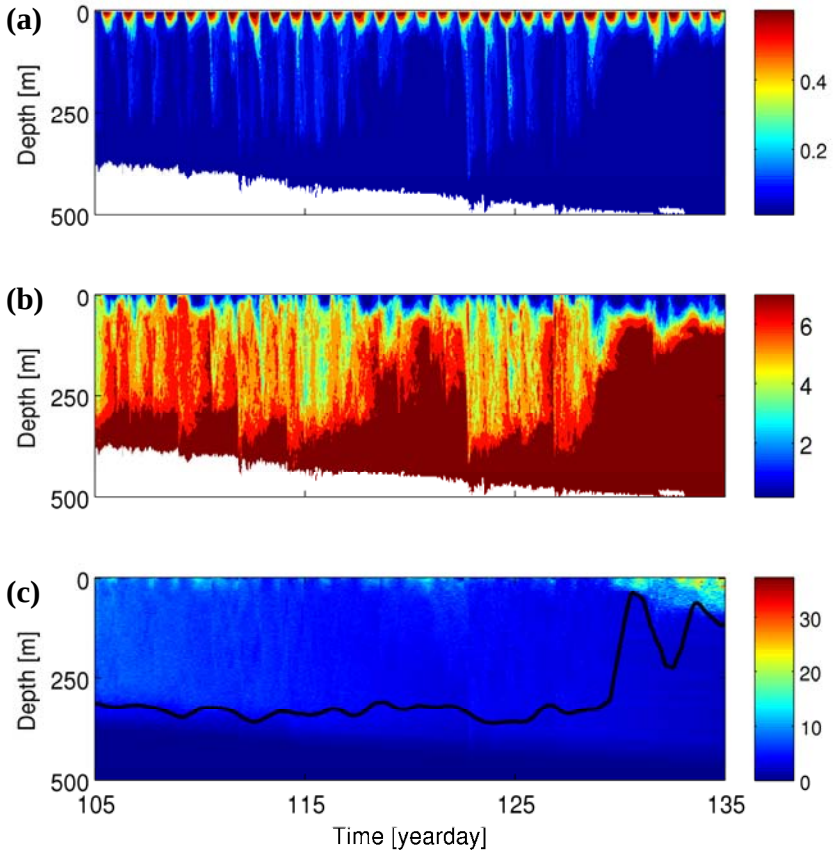

Figure 3. Phytoplankton properties simulated by the non-hydrostatic convection model over the course of the simulation at Ocean Weather Ship Mike. Hovmöller diagrams show the (a) carbon-specific respiration rate [day^{-1}], (b) sinking rate [$m\ day^{-1}$], and (c) phytoplankton biomass [$mg\ C\ m^{-3}$].

A reduction in net surface heat flux after the 29th April (yearday 123) (Fig 1.a) led to reduced cooling of surface water and a subsequent a reduction in convective depth (Fig 1b). Thereafter, primary production in the upper ~50 meters increased with reduced mixing to the end of the simulation (Fig 2). The simulated chlorophyll to carbon ratio varied during the simulation between 0.05 and 0.018 with surface values being the lowest, in particular toward the end of the simulation. These values are at the higher end of the range of values reported in the literature (Cloern *et al.*, 1995; Geider *et al.*, 1997), which is however not surprising given the overall low light levels. Dark respiration generally followed the same pattern as primary production. However, because the increase in primary production did not occur instantaneously, it showed a wider spread over time and space (Fig. 3a). Within the euphotic zone, defined as 1% of surface light level, the ratio of integrated daily carbon-specific gross production and integrated daily carbon-specific respiration rate varied in between ~28 and 33.5% (Fig. 4), which compares well to value reported in literature. Geider (1992) summarized several earlier measurements on phytoplankton respiration finding a range of 26 to 65 % of carbon being respired over 24 hours. Laws and Bannister (1980) found night losses in between 10 to 20 % of daytime production. A more theoretical approach (Marra and Barber, 2004) yielded values of around 35 to 40 % of daily respiratory losses. Sinking rates were lowest at the surface during this period with rates as low as 0.13 [meter day^{-1}]. Generally sinking rates increased with depth and were highest below the mixed layer reaching v^{max} of 6.8 [m day^{-1}] (Fig. 3b).

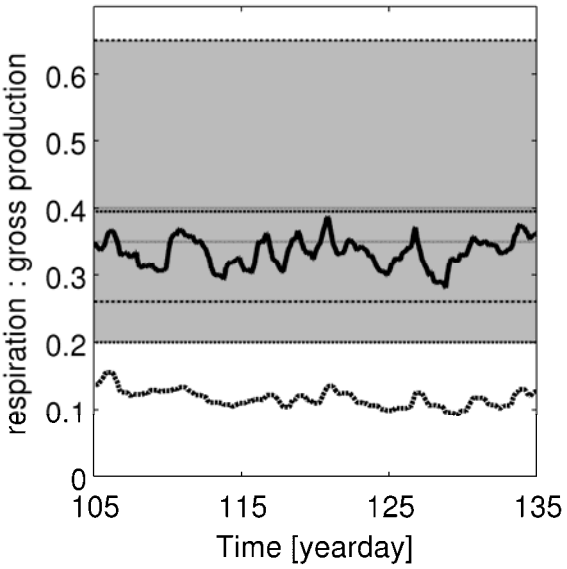

Figure 4. Simulated ratio of daily average respiration rate to daily gross production rate. The thick line indicates the result as simulated by the adaptive model. The thick dashed line indicates the result as simulated using a fixed specific respiration rate of 0.135 [day-1] and a sinking rate of 4.5 [m day^{-1}]. The shaded area indicates the range of values reported in literature. Vertical lines indicate limits of range reported by Geider (1992) (dashed), Laws and Bannister (1980) (dash-dotted) and Marra and Barber (2004) (dotted).

Adaptive vs Fixed Parameterizations

We compared the adaptive run to runs with different combinations of fixed respiration and sinking rates (Fig. 5). In general changes in respiration rates had a bigger influence on phytoplankton biomass than sinking rates. Runs with respiration set to the minimum value (r^0=0.02 [day^{-1}]), systematically overestimated phytoplankton biomass regardless of the sinking rate applied. Runs using respiration rates of 0.25 [day^{-1}] and 0.47 [day^{-1}] always underestimated phytoplankton concentrations. In the runs using a fixed respiration rate of 0.135 [day^{-1}] the simulated phytoplankton concentration showed a much better fit with observations (Fig. 5).

The impact of the sinking rate on phytoplankton biomass was more pronounced towards the end of the simulations, despite remaining less important than the respiration rate. In the simulations using fixed rates the ratio of daily carbon-specific gross production to respiration within the euphotic zone varied in between 0.08 and 0.105 [day^{-1}] (Fig. 4) which is lower than the lowest values than the values reported in literature.

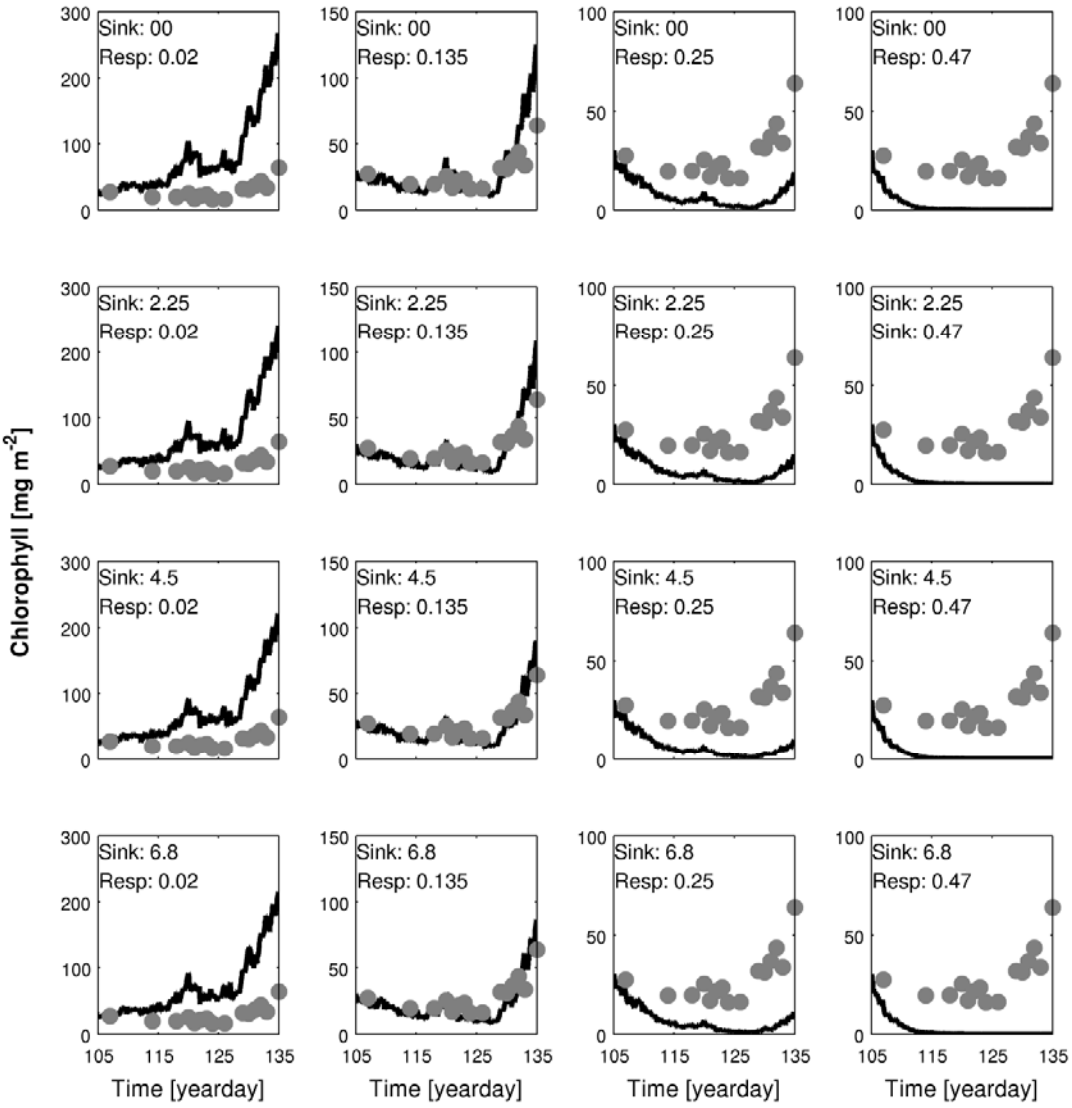

Figure 5. Simulated 100m integrated chlorophyll at Ocean Weather Ship Mike using different combinations of fixed values for carbon-specific respiration rate (0.02, 0.135, 0.35, 0.47 [day^{-1}]) and fixed sinking rates (0.0, 2.25, 4.5, 6.8 [m day^{-1}]). The gray dots indicated measured values.

Discussion

Phytoplankton Biomass

Traditionally it has been assumed that the peak integrated phytoplankton biomass is associated with the spring bloom. During this period, cells experience sufficient light for growth due to a reduced mixing depth while not under the influence of nutrient limitation i.e. the classical critical depth model (Sverdrup, 1953). However, the concept of 'Phyto-convection' (Backhaus *et al.*, 1999) suggests that deep convective mixing can sustain a homogeneously distributed viable phytoplankton biomass within the deep winter mixing zone. In our simulations phytoplankton cells were generally homogeneously distributed during deep convection which was closely followed by the onset of stratification and an increase in surface phytoplankton biomass (Fig. 3c). However, prior to the onset of stratification around the 26th of April (yearday 120), a reduction in surface cooling resulted in a net surface heat flux of around zero (Fig.1a). During this period no change in mixed layer depth was observed and a minor increase in phytoplankton surface concentration occurred (Fig. 3c). This result is similar to observations by Townsend *et al.*, (1992) and supports the hypothesis that the shutdown of deep convective mixing is a better indicator for growth conditions than the hydrostatic vertical water column profile (Taylor and Ferrari, 2011a; Townsend *et al*., 1994). This pulse of production also indicates that phytoplankton cells contained in an actively convective mixed layer represent a photosynthetic active phytoplankton community. Phytoplankton biomass within the deep convective mixed layer was observed by Backhaus *et al.* (2003) to be similar to estimates of biomass occurring during the spring bloom. Our model shows similar dynamics with the total standing stock over the convective mixed layer estimated to be of the same order of magnitude as that observed after the onset of stratification (Fig. 2). Hence, the upper one hundred meters, a traditional approach for estimating integrated biomass, has the potential to underestimate the standing stock during winter.

Given these observations the question then arises as to the mechanisms allowing phytoplankton cells to survive and maintain a viable phytoplankton stock in a deep mixed layer where they spend a large period of time below the euphotic zone. Over the course of the winter the release

from micro-zooplankton grazing pressure, has been suggested to compensate for the reduction in light exposure as the mixed layer deepens (Behrenfeld and Boss, 2014). Our model does not include an explicit representation of zooplankton grazing pressure hence we were not able to address this question. However, our adaptive simulation shows a good fit with field observations without a detailed representation of grazing suggesting that physiological acclimation could play an equally important role.

Individual physiology of phytoplankton growth

The ability of a phytoplankton cell to react to changing environmental conditions, although a key determinant of biomass production and community structure has received little attention in relation to the onset of the spring bloom. For an individual cell the internally determined growth rate is dependent upon nutrients, photosynthetically active radiation (PAR) for growth and loss terms such as sinking and respiration, which become proportionally more important under conditions of low growth (Sakshaug *et al.,* 1991).

Sinking

Phytoplankton sinking rates are highly variable and depend upon species, cell shape, life stage, growth condition and particle aggregation (Smayda, 1970, Miklasz and Denny, 2010). Sinking velocities of phytoplankton cells rarely exceed a few tens of meters per day, while actively growing cells have been shown to have much lower sinking velocities and can even achieve positive buoyancy (Moore and Villareal, 1996; Acuña *et al.*, 2010). In a convective regime vertical velocities can be on the order of several hundred meters per day (Marshall and Schott, 1999; D'Asaro, 2008) thus greatly exceeding sinking rates. Nevertheless, sinking can remain an important aspect, since cells may still sink out at the bottom of the mixed layer, especially during periods of reduced winter deep convection which is of varying depth and temporal duration (Marshall and Schott, 1999). This is captured in our simulation (Figure 1b). Hence, cells can experience periods without convective mixing, causing increased sinking and increased

detrainment of cells at the base of the convective layer. Convective layer deepening, due to stronger winds and cooling, can lead to an entrainment of previous "lost" cells back into the convective mixed layer (CML) depending on the interaction between sinking rate and convective mixing. For example, D'Asaro (2008) found that the maximum sinking velocity for cells to be successfully re-incorporated into the CML to be 7 [m day^{-1}]. In our simulations, lower sinking rates (0.13 to 3.7 [m day^{-1}]) were recorded near the surface, generally below 2 [m day^{-1}]. Towards the end of the simulation when environmental conditions became more favorable for growth and stratification had commenced, sinking rates in the upper 50 meters ranged between 0.13 and 1.1 [m day^{-1}] (Fig. 3b). Sinking rates below the mixed layer depth remained relatively constant at the maximum of 6.8 [m day^{-1}]. These estimates cover the wide range of sinking rates reported for different taxa and environmental conditions (Smayda, 1970) incorporating the assumption of lower sinking rates for growing cells (Waite *et al.*, 1992). Our adaptive model was not able to reproduce positive buoyancy as reported for large fast growing diatoms (Moore and Villareal, 1996; Acuña *et al.*, 2010). However in field samples taken during the simulated period diatoms represented only a minor fraction of the phytoplankton composition (Irigoien *et al.*, 1998). Given the observed and simulated values of convective velocities, it is suggested that phytoplankton sinking rates play only minor role in the loss terms during periods of deep convection. However, sinking may be of significance for cells during periods of weakening convection. Here phytoplankton cells can be detrained below the convective mixing depth thus having the potential to be lost from the system and sequestered at depth.

Dark respiration

Dark respiration can be highly variable, and is known to change with growth and physiological condition of the cell (Waite *et al.*, 1992; Jochem, 1999). In the classical critical depth model (Sverdrup, 1953), as in most models, respiration is treated as a constant, potentially leading to significant errors (Smetacek and Passow, 1990).

As growth during winter is normally limited by light due to shorter photoperiod and deeper mixing, dark respiration holds the potential to be an important physiology component, impacting

on the onset of the spring bloom as well as the winter stock. Using variable respiration rates the model estimated higher values of respiration closer to the surface (Fig. 3a), where cells exhibit positive growth rates. This is in agreement with our mechanistic understanding of dark respiration (Falkowski and Owens, 1980; Jochem, 1999) and with the reported ratios of respiration to gross growth (Laws and Bannister, 1980; Geider, 1992; Marra and Barber, 2004).

A reduction of the respiratory losses with depth could allow cells to prolong the availability of energetic reserves thus survival in the dark. During winter in a deep convective layer this could be an important mechanism for survival (McMinn and Martin, 2013), potentially playing an important role in determining the seed population for the spring bloom (Backhaus *et al.*, 1999).

Fixed vs. flexible parameterizations

In this study we contrasted simulations with variable respiration and sinking rates with those using fixed values in order to highlight the potential importance of the cells response to environmental conditions. In most cases in our simulations, comparisons of fixed respiration and sinking rates over the range of values encompassed by our flexible parameterizations were unable to reproduce the observed concentrations (Fig. 5). Applying a specific respiration rate of of 0.135 [day^{-1}] showed a similarly good fit to observations. However, this fixed specific respiration rate, when expressed as respiration rate in percentage loss per gross growth (Fig. 4) is below the value reported for growing cells (Laws and Bannister, 1980; Geider, 1992; Marra and Barber, 2004). Conversely, the adaptive model and was able to simulate a realistic gross growth to respiration ratio (Fig. 4). This resulted in higher respiration rates near the surface, which needed to be compensated by lower respiration rates at depth (Fig. 3a) to achieve similar biomass to the observations (Fig. 2). Thus, in order to reproduce the observed concentrations the model required a variable respiration rate or employing fixed parameter values of respiration which are not substantiated in the literature. This indicates that during the winter and the spring transition period acclimation of physiological rates can be an important process to sustain the phytoplankton community.

Conclusion

In this study, we showed, using a Lagrangian phytoplankton IBM which allowed cells to modify physiological rates, that plasticity in physiological rates has the potential to play in important role in the persistence and composition of the North Atlantic phytoplankton community.

When using variable respiration and sinking rates, the model was able capture the observed phytoplankton concentration during deep convective mixing and the timing and magnitude of the onset of the spring bloom (Fig. 2), while simulating realistic physiological rates. In contrast, the model with fixed rates was only able to produce the observations when employing unrealistic parameter values. These results highlight the importance of considering flexible parameterizations in modelling approaches and suggest that a cells ability to adjust physiological rates to environmental conditions may play an important role in the onset of classical phytoplankton spring bloom. The adaptive model was able to maintain a viable phytoplankton biomass over the convective layer during the winter similar to that observed for the period by Backhaus *et al.* (2003), with potentially important implications for the carbon budget. Furthermore, minor phytoplankton surface blooms during the winter occurred in the absence of stratification due to a reduction in deep convective mixing. Similar features have been observed in the North Atlantic (Townsend *et al*., 1992) supporting the hypothesis that active mixing can be more important in controlling growth (Taylor and Ferrari, 2011a), than the hydrostatic conditions employed in the classical critical depth model (Sverdrup, 1953).

Clearly the biophysical environment sets the boundaries on phytoplankton dynamics and thereby plays a central role in phytoplankton community dynamics. However an organism's ability to acclimatize to these constraints cannot be neglected, as it allows the organism to find loopholes to escape these controls (Chisholm, 1992). In order to gain a more realistic understanding of phytoplankton bloom dynamics, the interplay between physical and biological controls needs to be merged with advances in our understanding of the physiologically determined adaptive capacities of phytoplankton cells.

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