




Sverdrup meets Lambert: analytical solution for Sverdrup's critical depth

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In his 1953 paper, Harald Sverdrup argued that the development of a spring bloom in the ocean depends on the juxtaposition of two depth horizons: the mixed-layer depth and the critical depth. Mixed-layer depth shallower than the critical depth favours phytoplankton growth in the layer and vice versa. However, mathematically, Sverdrup left the problem unsolved in the form of a transcendental equation. In spite of the high number of citations that this paper has garnered, the solution to this equation has not been found, until now. In this work, we present an analytical solution for the critical depth, as originally defined by Sverdrup. The paper opens with the definition of the critical depth and the description of the Lambert W function. The analytical solution for critical depth follows. Sverdrup's original model is extended to include the effect of light attenuation by phytoplankton and the analytical solution for steady-state biomass in the mixed layer is derived. The expression for mixed-layer production at steady state is also presented. Two novel variants of the critical depth are defined: the optically uncoupled critical depth and the optically coupled critical depth. It is demonstrated that at steady state the optically coupled critical depth equals the mixed-layer depth and that the irradiance at the base of the mixed layer equals the irradiance at the optically uncoupled critical depth. Competitive exclusion is demonstrated to hold and the optically uncoupled critical depth is linked to the critical light intensity in multi-species competition. Finally, a conservation principle for the critical depth is found.

Keywords: critical depth hypothesis, Harald Sverdrup, Lambert W function, primary production

Introduction

In 1953, 4 years before his death, Harald Sverdrup published a paper titled: “On Conditions for the Vernal Blooming of Phytoplankton”; in which he sought to explain spring bloom initiation in the ocean, by providing a mathematical backbone to the theory of [Gran and Braarud \(1935\)](#). The paper opens with the following sentence:

In order that the vernal blooming of phytoplankton shall begin it is necessary that in the surface layer the production of organic matter by photosynthesis exceeds the destruction by respiration.

With the opening sentence he defined phytoplankton growth as an imbalance resulting from two competing factors: photosynthesis and respiration. He closed the paper with the following sentence:

On certain assumptions a “critical depth” is defined. The depth of a mixed surface layer must be less than this critical depth if the phytoplankton population of the mixed layer shall increase.

With the closing sentence he translated an argument of growth versus loss into an argument of mixing depth versus critical

depth. These two sentences perhaps best summarize the key question asked by Sverdrup's paper: How does a phytoplankton bloom get initiated?

Modern variants of the concepts advanced by Sverdrup, aiming to explain the mechanism and ultimately predict the outbreak of phytoplankton blooms can be classified into three groups (Lindeman and St. John, 2014): the Critical Depth Hypothesis (Sverdrup, 1953; Bishop *et al.*, 1986), the Critical Turbulence Hypothesis (Huisman *et al.*, 1999, 2002), and the Disturbance Recovery Hypothesis (Behrenfeld, 2010; Behrenfeld *et al.*, 2013a). All three use the concept of the critical depth in one form or another, either to argue in its favour, to complement it, or to argue against it.

Although simple in its premise and consequences, the Critical Depth Hypothesis sparked much debate in recent years (Behrenfeld *et al.*, 2013a, b; Chiswell, 2013; Lindeman and St. John, 2014; Sathyendranath *et al.*, 2015), but tests of Sverdrup's hypothesis against *in situ* observations continue to demonstrate its relevance to the problems of the day (Rumyantseva *et al.*, 2019). Perhaps this debate can be aided by providing the analytical solution for the original Sverdrup's critical depth. In his paper, Sverdrup (1953) stated the critical depth implicitly in the form of a transcendental equation [Equation (6) in Sverdrup (1953)]. To this day, the solution to this equation has not been found even though the paper itself has been cited 1391 times according to Web of Science (at the time of writing). If it had not been so, and Sverdrup had provided an explicit expression for the critical depth, perhaps the ensuing debates would have been less fierce.

In fact, Sverdrup's transcendental equation can be solved explicitly for the critical depth. In 1779 Leonhard Euler solved the equation $xe^x = a$, by finding the inverse of xe^x (Euler, 1779). Today, this inverse is called the Lambert W function, named after Johann Heinrich Lambert (Gray and Tiling, 1978) who was the first to solve the trinomial equation, which laid the groundwork for Euler. The history behind the W in the name is somewhat debatable (Corless *et al.*, 1996; Hays, 2005). The procedure of applying the Lambert W function to a given problem is simple. Reduce the problem to a statement of the form $xe^x = a$ and simply invert it by using the Lambert W function. This procedure has been applied numerous times in several disciplines, so much so that Gouvea (2000) even pushed for the function to be included amongst the elementary functions.

A seminal paper by Corless *et al.* (1996) provides a survey of applications of the Lambert W function: those of interest to oceanographers include the inversion of the dispersion relation of surface gravity waves (Mező and Keady, 2016) and the exact expression for Wien's peak in the solar spectrum (Stewart, 2011). Here we provide another application of the Lambert W function in oceanography: We derive the first analytical solution for Sverdrup's critical depth (Sverdrup, 1953), an important principle in the ecology of the pelagic ecosystem related to the outbreak of phytoplankton blooms. The primary aim of the paper is to gain further insight into Sverdrup's original work by mathematical means.

Governing equations

Model

The model we employ to describe phytoplankton distribution in the vertical is a generic one-dimensional model of the advection-diffusion-reaction type, commonly used in oceanographic practice (Huisman *et al.*, 2002; Ryabov and Blasius, 2008; Du and Mei, 2011; Enriquez and Taylor, 2015; Dai *et al.*, 2015). For this

model setup, let the z axis be positive downwards. Let $B = B(z, t)$ mark the phytoplankton cell concentration (biomass), w the sinking velocity of phytoplankton cells and K_z the vertical eddy diffusivity. The governing equation for biomass reads:

$$\frac{\partial B}{\partial t} + w \frac{\partial B}{\partial z} = \frac{1}{\chi} (P(z, t) - L(z, t)) + K_z \frac{\partial^2 B}{\partial z^2}, \quad (1)$$

where χ is the carbon to chlorophyll ratio. The $P(z, t)$ term describes photosynthesis, which can be parametrized in numerous ways (Kovač *et al.*, 2017b) and the $L(z, t)$ term represents losses in the broadest sense (respiration, grazing), which can also be parameterized in numerous ways (Zhai *et al.*, 2010). A detailed list of notations and parameters used throughout the paper, along with corresponding units, is provided in the [Supplementary data](#).

Let us now consider a mixed layer of depth Z_m subject to no-flux boundary conditions at the ocean surface ($z=0$) and the base of the mixed layer ($z=Z_m$). The reader is referred to Huisman and Sommeijer (2002), Platt *et al.* (2003), and Kovač *et al.* (2020) for the study of mixed-layer phytoplankton dynamics with an open boundary condition at the base of the mixed layer. By integrating the previous equation from the surface to the base of the mixed layer and acknowledging boundary conditions we get:

$$\frac{\partial B}{\partial t} = \frac{1}{\chi Z_m} \int_0^{Z_m} (P(z, t) - L(z, t)) dz, \quad (2)$$

as the governing equation for the evolution of average mixed-layer biomass, where now $B = B(t)$ is the uniform phytoplankton biomass in the mixed layer and the right-hand side gives the average production and losses in the mixed layer. We see that growth or decline in phytoplankton biomass is determined by the overall balance between photosynthesis and losses in the mixed layer. As photosynthesis is light-driven, and light decreases with depth in the ocean (Figure 1), the stage is set for the following question: How deep can Z_m be for the right-hand side to remain positive? Numerous authors have attempted to answer this question recently, e.g. Chiswell *et al.* (2015); Levy (2015); Behrenfeld and Boss (2018), with the first quantitative attempt given by Sverdrup (1953). We now demonstrate how Sverdrup approached this problem in his seminal 1953 paper, but with a slightly altered formalism.

Critical depth

Photosynthesis is light-driven, therefore to model $P(z, t)$ light at depth has to be specified (Platt and Sathyendranath, 1991). Let irradiance at depth be given by the Beer–Lambert law (Kirk, 2011):

$$I(z, t) = I_0(t) \exp(-Kz), \quad (3)$$

where $I_0(t)$ is the surface irradiance and K is the attenuation coefficient (not to be confused with the vertical eddy diffusivity K_z). Following Sverdrup (1953), we use a linear dependence of production on available light:

$$P(z, t) = B \alpha^B I(z, t), \quad (4)$$

where B is the average phytoplankton biomass in the mixed layer and α^B the initial slope of the photosynthesis-irradiance function

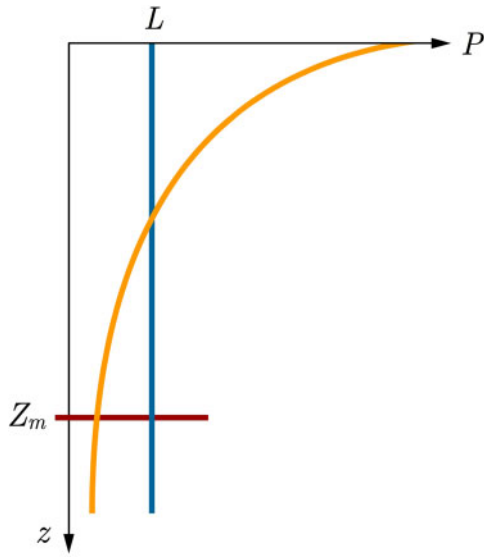


Figure 1. Depiction of the vertical dependence of photosynthesis P (orange curve) and losses L (blue line) in a water column with a mixed layer of depth Z_m (red line). Photosynthesis declines with depth due to the reduction in light intensity, whereas losses are assumed constant in the mixed layer. At a given depth, the integral of photosynthesis (the area prescribed by the orange curve and the z axis) and losses (area prescribed by the blue line and the z axis) will equal and this depth is referred to as the critical depth Z_c . Sverdrup (1953) argued that when Z_c exceeds Z_m phytoplankton in the mixed layer will be sustained and with Z_c shallower than Z_m it will not be sustained.

(Platt *et al.*, 1980). We also assume a depth-independent, biomass-specific, loss rate, such that the total loss $L(z, t)$ at each depth and time is given by:

$$L(z, t) = BL^B, \quad (5)$$

where L^B is the loss rate per unit biomass (Smetacek and Passow, 1990). In his work, Sverdrup (1953) subtracts losses from production and integrates their difference over time, obtaining a function of depth $f(z)$:

$$f(z) = \int_0^D \alpha^B I_0(t) \exp(-Kz) dt - \int_0^{24} L^B dt, \quad (6)$$

where D is daylength (time from sunrise till sunset). Note that α^B and L^B are rates per hour, and D is in hours in this equation, and that integration is carried out over the daylight hours for primary production (due to it being zero overnight) and over 24 h for the loss terms, such that $f(z)$ yields change in biomass per day. The first integral on the left is $\alpha^B I_T \exp(-Kz)$, with the total available light energy at the surface over 1 d designated as $I_T = \int_0^D I_0(t) dt$. Sverdrup then integrates over depth:

$$F(Z) = \alpha^B I_T \int_0^Z \exp(-Kz) dz - \int_0^Z L_T^B dz, \quad (7)$$

obtaining a function of the upper limit in the integrals, here

marked Z . The loss term, being constant, now incorporates the 24 h integration interval $L_T^B = 24 L^B$. Explicitly, for $F(Z)$ we have:

$$F(Z) = \frac{\alpha^B I_T}{K} (1 - e^{-KZ}) - L_T^B Z. \quad (8)$$

In this formulation, the critical depth Z_c is defined as the depth for which the following holds:

$$F(Z_c) = 0, \quad (9)$$

where $F(Z_c)$ refers to the integral over the layer $(0, Z_c)$. If there is to be a positive growth of the overall population the following condition has to be met:

$$Z_c > 0, \quad (10)$$

implying:

$$f(0) > 0. \quad (11)$$

The condition $f(0) > 0$ means that daily production (photosynthesis) at the surface has to be greater than losses. This translates into the following condition:

$$\frac{\alpha^B I_T}{L_T^B} > 1. \quad (12)$$

To solve (9), we employ the Lambert W function. Before doing so, we provide a short description of it.

Lambert W function

Consider the transcendental equation:

$$xe^x = a, \quad (13)$$

where both x and a are real numbers. The Lambert W function is the inverse of the left-hand side function xe^x and is denoted W . It is defined as (Corless *et al.*, 1996):

$$W(x)e^{W(x)} = x, \quad (14)$$

where in general x can be a complex number. By using $W(x)$, the solution of (13) follows:

$$x = W(a). \quad (15)$$

There are two real branches of the Lambert W function (Figure 2). By convention, the branch satisfying $W(x) \geq -1$ is taken to be the principal branch and is denoted $W_0(x)$ (blue curve in Figure 1). The branch satisfying $W(x) \leq -1$ is denoted $W_{-1}(x)$ (dashed blue curve in Figure 1). More details on the Lambert W function can be found in Corless *et al.* (1996), Gautschi (2011), and Golnicnik (2012). We now proceed to use the Lambert W function to solve for Sverdrup's critical depth explicitly.

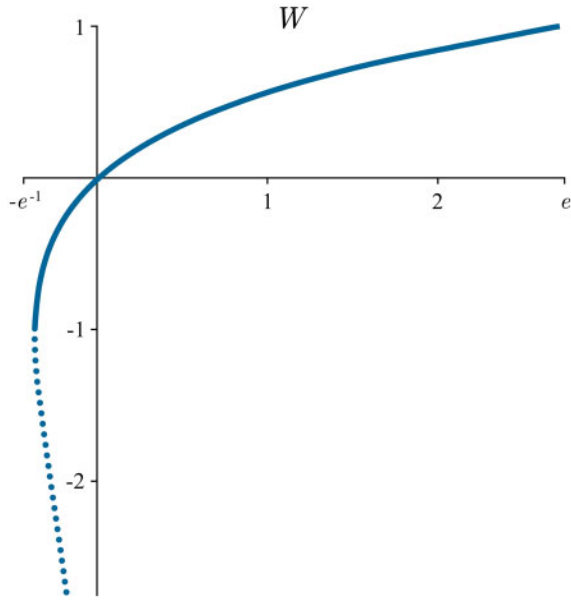


Figure 2. Real branches of the Lambert W function. The thick blue curve is the principal branch W_0 and satisfies $W(x) \geq -1$. The dotted blue curve is the W_{-1} branch and satisfies $W(x) \leq -1$.

Solutions

Explicit solution for the critical depth

Our strategy in solving Equation (9) is to reduce it to the form (13) and simply apply the Lambert W function. From (9), we have:

$$1 - e^{-KZ_c} = \frac{L_T^B}{\alpha^B I_T} KZ_c, \quad (16)$$

[Equation 6 in Sverdrup (1953)]. We define ζ_c as the optical depth corresponding to the critical depth:

$$\zeta_c = KZ_c, \quad (17)$$

and we also define A as the ratio of surface production to losses (uniform over depth):

$$A = \frac{\alpha^B I_T}{L_T^B}. \quad (18)$$

With these definitions, the starting Equation (16) becomes simply:

$$1 - e^{-\zeta_c} = \frac{\zeta_c}{A}. \quad (19)$$

We rewrite this equation as:

$$(\zeta_c - A)e^{(\zeta_c - A)} = -Ae^{-A}, \quad (20)$$

which is now in the form of (13) and we can use the Lambert W function. The equation has the trivial solution $\zeta_c = 0$ and the non-trivial solution (Stewart, 2011; Houari, 2013):

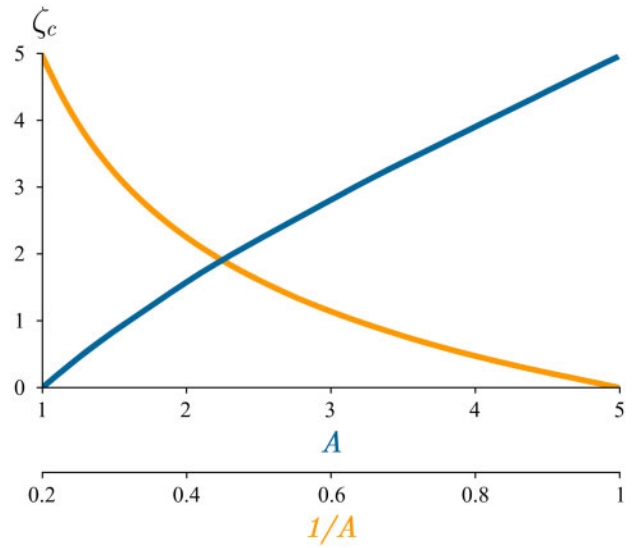


Figure 3. Critical depth (expressed as optical depth) ζ_c as a function of: (i) the ratio of surface production to losses A (blue curve) and (ii) the ratio of losses to surface production $1/A$ (orange curve). Both plots are given by (21). To calculate the critical depth in metres, simply apply Equation (22).

$$\zeta_c = W_0(-Ae^{-A}) + A, \quad (21)$$

from which we get the explicit expression for the critical depth:

$$Z_c = \frac{1}{K} \left(W_0(-Ae^{-A}) + A \right). \quad (22)$$

From (12) and the definition (18), we have $A > 1$. Therefore, the minimum value the argument $-Ae^{-A}$ could take is $-1/e$ so that $W_0(-Ae^{-A}) \geq -1$, making $Z_c \geq 0$. Plot of (21) is given in Figure (3) both as a function of A and $1/A$ to highlight the non-linearity. Fully expanded expression (22) reads:

$$Z_c = \frac{1}{K} \left[W \left(-\frac{\alpha^B I_T}{L_T^B} \exp \left(\frac{-\alpha^B I_T}{L_T^B} \right) \right) + \frac{\alpha^B I_T}{L_T^B} \right]. \quad (23)$$

Critical Depth Hypothesis

Let us now reconsider a mixed layer of depth Z_m . Having selected a model for $P(z, t)$, the equation for the temporal evolution of the mixed-layer biomass (2) becomes (Kovač et al., 2017a):

$$\frac{dB}{dt} = \frac{1}{24\chi} \frac{F(Z_m)}{Z_m} B, \quad (24)$$

where $B = B(t)$, with 24 in the denominator as the scaling factor. The scaling factor is easily removed by opting to use instantaneous production and losses. In this case, daily irradiance I_T has to be replaced with $I_0(t)$ and daily losses L_T^B with instantaneous losses L^B . The resulting equations with these changes would still hold. We chose to use the 24 h time scale to be in line with the original work of Sverdrup (1953).

Since $F(Z_m)$ is a function of only Z_m , the equation is linear with respect to biomass. The solution is simply:

$$B = B_0 \exp\left(\frac{1}{24\chi} \frac{F(Z_m)}{Z_m} t\right), \quad (25)$$

where B_0 is the initial condition. Equation (25) has the form of an exponential growth equation, with the growth rate given by $F(Z_m)/(24\chi Z_m)$. From this solution, we can determine whether biomass will grow or decline based on the relation between Z_c and Z_m . It is clear that the exponent dictates the behaviour of B with time. We have three cases:

$$\begin{aligned} F(Z_m) > 0 & \quad B/B_0 > 1; \\ F(Z_m) = 0 & \quad B/B_0 = 1; \\ F(Z_m) < 0 & \quad B/B_0 < 1. \end{aligned} \quad (26)$$

Now, the critical depth Z_c from Equation (22) gives the depth for which $F(Z) = 0$. Therefore, if Z_m happens to equal Z_c we have a steady state $B^* = B_0$, the only steady state possible for this model, aside from the trivial steady state $B^* = 0$ (the asterisk indicates steady state). That this is the only possible steady state is a consequence of not considering light attenuation by phytoplankton, as we now proceed to demonstrate.

Explicit solution for steady-state biomass

To be more realistic, we set the attenuation coefficient to be biomass dependent, which represents the physical process of absorbing and scattering of light by phytoplankton (Sathyendranath and Platt, 1988; Platt *et al.*, 1990):

$$K = K_w + k_B B, \quad (27)$$

where K_w is the attenuation coefficient of sea water, including non-varying vertical attenuation by any substance present in the water, such that we can consider K_w as representing a constant background attenuation independent of phytoplankton; and k_B is the specific attenuation coefficient of phytoplankton. Note that Equation (27) assumes that the effect of other substances that covary with phytoplankton is accounted for, through k_B . Equation (24) now becomes non-linear in B :

$$\frac{dB}{dt} = \frac{1}{24\chi} \frac{F(Z_m, B)}{Z_m} B, \quad (28)$$

where $F(Z, B)$ is now:

$$F(Z, B) = \frac{\alpha^B I_T}{K_w + k_B B} [1 - \exp(-(K_w + k_B B)Z)] - L_T^B Z. \quad (29)$$

The steady state B^* satisfies $F(Z, B) = 0$, or:

$$1 - \exp(-(K_w + k_B B)Z_m) = \frac{(K_w + k_B B)Z_m}{A}, \quad (30)$$

and we wish to solve it for B . Following the same procedure as in Explicit solution for the critical depth section, we obtain the solution for the steady-state biomass B^* :

$$B^* = \frac{1}{k_B Z_m} \left(W_0(-Ae^{-A}) + A \right) - \frac{K_w}{k_B}. \quad (31)$$

Noticing that the expression in the brackets is given by (22) and setting $K = K_w$ in that equation, and after some algebra we have:

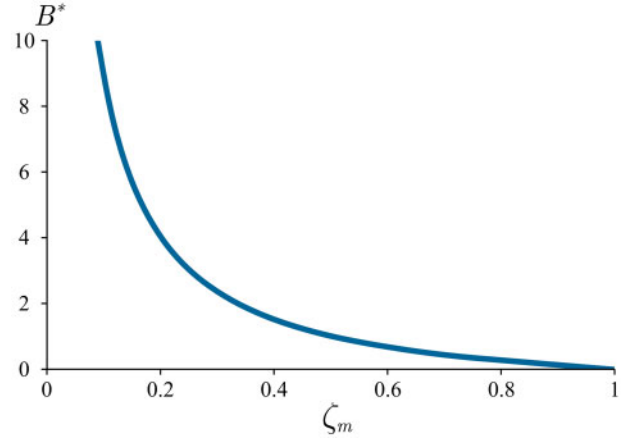


Figure 4. Steady-state biomass as a function of $\zeta_m = K_w Z_m$ for $K_w/k_B = 1$ and $\zeta_c = 1$. After ζ_m becomes larger than 1, the critical depth criterion is violated and biomass can no longer be sustained.

$$B^* = \frac{K_w}{k_B} \left(\frac{Z_c}{Z_m} - 1 \right), \quad (32)$$

where Z_c is the critical depth for the case in which the diffuse attenuation coefficient is not optically coupled to phytoplankton biomass ($K = K_w$). Plot of (32), with Z_c and Z_m expressed as optical depths for generality, is given in Figure (4). For the biomass in the mixed layer of depth Z_m to be sustained, we require $B^* > 0$, translating (32) into:

$$Z_c > Z_m, \quad (33)$$

which is recognized as the critical depth criterion. The system also admits the trivial steady state $B^* = 0$, which is reached when the previous condition is not met.

Critical depth properties

Considering that Z_c in Equation (32) is not optically coupled to the phytoplankton biomass, such that Z_c in Equation (22) is determined by K_w and not by K as given in (27), theoretically we are led to distinguish two critical depths. The first one, we re-label as the optically uncoupled critical depth C and the second one, as the optically coupled critical depth S . We give the following definitions:

Optically uncoupled critical depth C is the critical depth associated with $k_B = 0$ and is defined as:

$$C = \frac{1}{K_w} \left(W_0(-Ae^{-A}) + A \right). \quad (34)$$

The optically uncoupled critical depth is independent of time $C \neq C(t)$.

Optically coupled critical depth S is the critical depth associated with $k_B \neq 0$ and is defined as:

$$S = \frac{1}{K_w + k_B B} \left(W_0(-Ae^{-A}) + A \right). \quad (35)$$

Optically coupled critical depth is time-dependent $S = S(t)$, as explored in more detail in the next section.

With the previous definitions, the steady-state biomass (32) simply becomes:

$$B^* = \frac{K_w}{k_B} \left(\frac{C}{Z_m} - 1 \right). \quad (36)$$

For $C < Z_m$, this equation yields negative biomass, which is physically unrealistic. However, $C < Z_m$ corresponds to the condition in which biomass losses exceed production, and this result suggests that in this instance, losses would continue until biomass drops to zero. Hence, the solution is only valid for C/Z_m larger than one, which is in accordance with the Critical Depth Hypothesis.

Having B^* , we are now in a position to calculate daily mixed-layer production $P_{Z_m, T}$ at steady state. We first recognize that daily mixed-layer production is given by the first term on the right-hand side of expression (29) multiplied by B :

$$P_{Z_m, T} = \frac{B\alpha^B I_T}{K_w + k_B B} [1 - \exp(-(K_w + k_B B)Z_m)]. \quad (37)$$

Inserting (32) into (37) we get:

$$P_{Z_m, T} = \frac{\alpha^B I_T}{k_B} [1 - \exp(-K_w C)] \frac{C - Z_m}{C}, \quad (38)$$

as the daily mixed-layer production at steady state, which is seen to be linearly dependent on mixed-layer depth Z_m . Only when $C > Z_m$ is this expression positive in accordance with the Critical Depth Hypothesis. In other words, we have to bear in mind that C is the critical depth in case of no shading by phytoplankton, given by (34).

Having defined the two critical depths and knowing B^* , we can now calculate the light intensity at the base of the mixed layer at steady state and compare it with the light intensities at C and S . By inserting (27) and (36) into (3), the irradiance at the base of the mixed layer can be shown to be equal to the irradiance at the optically uncoupled critical depth:

$$I(Z_m) = I_0 \exp(-K_w C) = I(C), \quad (39)$$

although the two depths Z_m and C need not be equal (Figure 5). Therefore, at steady state the light intensity at the base of the mixed layer equals the light intensity at the optically uncoupled critical depth. Although the mixed-layer depth does not equal the optically uncoupled critical depth, their light levels are equal, due to shading by phytoplankton. It is important to stress that $I(C)$ is biomass independent and this result is therefore a more general result than (32). We can now rewrite (38) as:

$$P_{Z_m, T} = \frac{\alpha^B}{k_B C} (I_T - I_T(C))(C - Z_m). \quad (40)$$

We can also calculate S at steady state. Inserting (36) into (35) gives:

$$S^* = Z_m, \quad (41)$$

where we have labelled the optically coupled critical depth at steady state as S^* . Therefore, at steady state the optically coupled

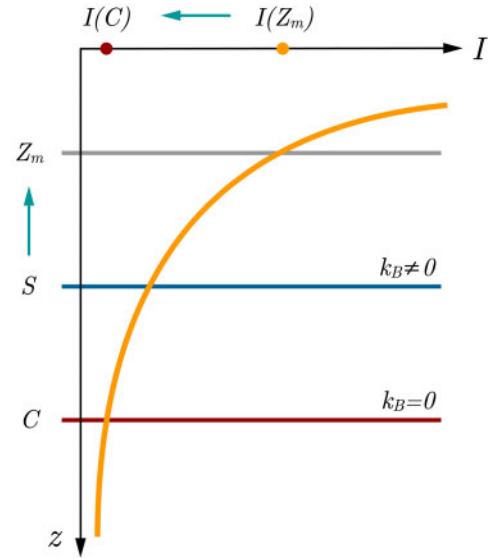


Figure 5. Sketch of the relation between mixed-layer depth Z_m , optically uncoupled critical depth C and optically coupled critical depth S . With time S converges to Z_m while C remains constant. Simultaneously, irradiance at the mixed-layer base $I(Z_m)$ converges to irradiance at the optically uncoupled critical depth $I(C)$. Finally, at steady state, we have $S^* = Z_m$ and $I(Z_m) = I(C)$.

critical depth equals the mixed-layer depth, but the optically uncoupled critical depth does not (Figure 5).

Time evolution of the optically coupled critical depth

Having defined the optically coupled critical depth (35) and knowing its value at steady state (41) enables us to calculate it at any time instance, given information on B . It also enables us to derive an equation describing the time evolution of S . This equation is obtained by taking the time derivative of (35):

$$\frac{dS}{dt} = - \left(\frac{k_B}{K_w + k_B B} \frac{dB}{dt} \right) S, \quad (42)$$

which translates to:

$$\frac{dS}{dB} = - \frac{k_B S}{K_w + k_B B}. \quad (43)$$

Integration by separation of variables from $S(0) = S_0$ to $S(t) = S$ and $B(0) = B_0$ to $B(t) = B$ gives:

$$S = S_0 \left(\frac{K_w + k_B B_0}{K_w + k_B B} \right), \quad (44)$$

whereas integration from $S(t) = S$ to $S(\infty) = S^*$, while acknowledging (41), gives:

$$S = Z_m \left(\frac{K_w + k_B B^*}{K_w + k_B B} \right). \quad (45)$$

This result was first derived by Platt *et al.* (2003) [their Equation (4.5)] for a non-linear production model with discrete

time steps. It is now shown that the linear model of Sverdrup (1953) also leads to the same equation. The fact that both, the linear and non-linear, production models have the same solution adds to the generality of the result.

Critical light intensity

The analysis thus far is valid for a single phytoplankton type, with its traits aggregated in the model through A (18). In case multiple phytoplankton species were present in the mixed layer, their traits could be represented for each phytoplankton functional type (Anderson, 2005). With multiple functional types the system dynamics gets altered and competitive exclusion has to be considered. Huisman and Weissing (1994) and Weissing and Huisman (1994) explored the role light plays in relation to the competitive exclusion principle in multi-species phytoplankton populations. They first analysed the monoculture case and defined the critical light intensity for a monoculture population: the light intensity at the bottom of the water column at steady state. They further demonstrated that in a multi-species population the species with the lowest critical light intensity competitively excludes all other species. We now explore whether the competitive exclusion principle holds for the Sverdrup (1953) model and demonstrate that the critical light intensity is in fact the light intensity at the optically uncoupled critical depth.

Let us divide the biomass into N phytoplankton functional types, each with biomass B_i , and let us group all functional types into a vector \mathbf{B} (size $N \times 1$) whose elements are B_i . In this notation, total biomass is given as a scalar product of \mathbf{B} and a unit vector \mathbf{u} of the same size as \mathbf{B} (see Supplementary data). Therefore, the total biomass B is now:

$$B = \mathbf{u} \cdot \mathbf{B}. \quad (46)$$

Likewise, the attenuation coefficient is now given as:

$$K = K_w + \mathbf{k}_B \cdot \mathbf{B}, \quad (47)$$

where \mathbf{k}_B is a vector (size $N \times 1$) with elements $k_{B,i}$, the specific attenuation coefficient of each phytoplankton functional type. Irradiance at depth is now calculated as:

$$I(z, t) = I_0(t) \exp(-(K_w + \mathbf{k}_B \cdot \mathbf{B})z). \quad (48)$$

In this formalism, the equation for the time evolution of total biomass reads:

$$\frac{dB}{dt} = \frac{1}{Z_m} \frac{\alpha^B \cdot \mathbf{B} I_T}{K_w + \mathbf{k} \cdot \mathbf{B}} [1 - \exp(-(K_w + \mathbf{k} \cdot \mathbf{B})Z_m)] - \mathbf{L}_T^B \cdot \mathbf{B}, \quad (49)$$

where α^B and \mathbf{L}_T^B are vectors of size $N \times 1$ (see Supplementary data).

For each individual phytoplankton functional type B_i , we can define the optically uncoupled critical depth C_i :

$$C_i = \frac{1}{K_w} \left(W_0(-A_i e^{-A_i}) + A_i \right), \quad (50)$$

and the optically coupled critical depth S_i :

$$S_i = \frac{1}{K_w + \mathbf{k}_B \cdot \mathbf{B}} \left(W_0(-A_i e^{-A_i}) + A_i \right), \quad (51)$$

where A_i is the ratio of surface production to losses (18) of each functional type. For each B_i , we can also calculate the monoculture steady-state biomass B_i^* by using (36):

$$B_i^* = \frac{K_w}{k_i} \left(\frac{C_i}{Z_m} - 1 \right). \quad (52)$$

As demonstrated in the previous section, this steady-state biomass is reached when only B_i is present in the mixed layer. We are now interested to explore what steady state is reached when multiple phytoplankton functional types are present in the mixed layer and how it is related to the critical depth.

Let us assume that at $t=0$, we have $B_i(0) > 0$ and $C_i > Z_m$ for all i , so that $dB_i/dt > 0$ at $t=0$. Let us also assume that $A_i \neq A_j$, $C_i \neq C_j$ and $S_i(0) \neq S_j(0)$ for all $i \neq j$. Taking the time derivative of (51) we have:

$$\frac{dS_i}{dt} = -\frac{1}{K_w + \mathbf{k}_B \cdot \mathbf{B}} \left(\mathbf{k}_B \cdot \frac{d\mathbf{B}}{dt} \right) S_i, \quad (53)$$

which integrated over time from $t=0$ to t , yields:

$$S_i(t) = S_i(0) \frac{K_w + \mathbf{k}_B \cdot \mathbf{B}_0}{K_w + \mathbf{k}_B \cdot \mathbf{B}(t)}. \quad (54)$$

The expressions obtained are multi-species analogues of (42) and (44), respectively, describing the time evolution of each optically coupled critical depth S_i .

Starting from $t=0$ as biomass grows so does the product $\mathbf{k}_B \cdot \mathbf{B}$, reducing mixed-layer irradiance and consequently primary production. The optically uncoupled critical depths C_i remain constant, but the optically coupled critical depths S_i become shallower as the product $\mathbf{k}_B \cdot \mathbf{B}$ increases. At a certain instance of time one S_i will become shallower than Z_m , at which point a reversal of its growth rate will occur, making $dB_i/dt < 0$. Subsequently, the same will occur for another functional type and the process will continue until only one functional type is left. For this functional type, we will have $S_i = Z_m$ and it will reach its monoculture steady-state biomass (52). At this point, the particular functional type has won the competition. Detailed equations for simulating this process along with the code for running the simulations are provided in the Supplementary data.

According to (39) when a single phytoplankton type is present in the mixed layer, at steady state, we have $I(Z_m) = I(C)$. The same condition can be written for C_i :

$$I(Z_m) = I(C_i). \quad (55)$$

By acknowledging (48) and (52), this expression becomes:

$$\mathbf{k} \cdot \mathbf{B} = k_i B_i^*, \quad (56)$$

implying that all phytoplankton functional types have zero biomass except B_i which has won the competition and reached B_i^* , so that at steady state $B = B_i^*$, given by (52). At this point, irradiance at the mixed layer base equals the irradiance at the optically uncoupled critical depth of the winning functional type.

This solution, cast in the form of a critical light argument, was first obtained by [Huisman and Weissing \(1994\)](#) and [Weissing and Huisman \(1994\)](#) as the outcome of multi-species competition in a light gradient. According to these authors, the species with the lowest monoculture light intensity at the base of the water column (critical light intensity) wins the multi-species competition. In our work, the critical light intensity corresponds to the light intensity at the bottom of the mixed layer, which at steady state was shown to equal the light intensity at the optically uncoupled critical depth (39). Therefore, the argument of [Huisman and Weissing \(1994\)](#) and [Weissing and Huisman \(1994\)](#) is translated back to a critical depth argument. The species with the deepest optically uncoupled critical depth wins the competition.

However, in these considerations, the physiological parameters of each phytoplankton functional type are constant. In the real ocean, this assumption may be questionable. One way to include the effect of changing environmental conditions on the phytoplankton physiology is to allow the physiological parameters to change with respect to average light conditions in the mixed layer ([Jackson et al., 2017](#); [Sathyendranath et al., 2020](#)). Since average light conditions are determined by surface irradiance, mixed-layer depth, and the phytoplankton biomass itself, having the phytoplankton adopt to average light conditions could affect the outcome of competition and consequently bloom initiation ([Lindemann et al., 2015](#)).

Discussion

In 1779, Leonhard Euler solved the equation $xe^x = a$, by finding the inverse of xe^x , today called the Lambert W function, named after Johann Heinrich Lambert, who laid the groundwork for Euler by solving the trinomial equation. Lambert W function laid dormant for quite some time since its discovery, until its re-emergence in the second half of the twentieth century. The re-emergence occurred in the field of computations ([Corless et al., 1996](#)) and since has been spreading over to other fields steadily. Today the function is easily accessible in many mathematical programmes.

In this paper, we have successfully used the Lambert W function to find the analytical solution for the critical depth (22), as formulated by [Sverdrup \(1953\)](#), in what is perhaps the first usage of Lambert W function in optical oceanography. In the field of optical oceanography, Lambert is most known for the extensive application of the Beer–Lambert Law to model the underwater light field ([Kirk, 2011](#)). Interestingly, the same law was used by [Sverdrup \(1953\)](#) in formulating his model (3). Therefore, it is fitting that the analytical solution for Sverdrup’s critical depth was found using the Lambert W function.

Lambert W function enabled the expression of the critical depth in terms of surface light intensity, attenuation coefficient, initial slope of the photosynthesis-irradiance function, and the loss rate (23). It further led to the analytical solution for steady-state biomass (32). The expression for the steady-state biomass was found to be in accord with the critical depth criterion: If the critical depth is larger than the mixed-layer depth ($Z_c > Z_m$), a positive steady-state biomass is attainable. Further analysis led us to distinguish between the optically uncoupled critical depth C (34) and the optically coupled critical depth S (35). To the best of our knowledge, this distinction had not been made in the literature prior to this work. We have demonstrated that at steady state the optically coupled critical depth matches the mixed-layer

depth (41) with the light intensity at the bottom of the mixed layer equal to the light intensity at the optically uncoupled critical depth (39). This demonstration would not have been possible if the distinction between the optically uncoupled critical depth and the optically coupled critical depth had not been made.

That the critical depth converges to the mixed-layer depth was already known, as was first demonstrated by [Platt et al. \(2003\)](#) for a dynamically evolving model. Recently, it was found by [Kovač et al. \(2020\)](#) that the convergence occurs due to phytoplankton shading. In the context of this work, we can now say the optically coupled critical depth converges to the mixed-layer depth, whereas the optically uncoupled critical depth remains constant. We can therefore look at the optically uncoupled critical depth as the maximum attainable critical depth when the biomass goes to zero and attenuation of light by phytoplankton in the mixed layer is negligible.

Another important perspective on the two new versions of the critical depth must be highlighted. Optically uncoupled critical depth being deeper than the mixed-layer depth is a prerequisite for a positive biomass in the mixed layer. In this context, the optically coupled critical depth determines the sign of the growth rate. Optically coupled critical depth deeper than the mixed layer yields a positive growth rate, whereas optically coupled critical depth shallower than the mixed-layer depth yields a negative growth rate. Note that optical coupling introduces a level of dynamic stability to phytoplankton: when mixed-layer deepens below the optically coupled critical depth, phytoplankton decrease towards a lower steady-state value, rather than towards zero, as in the optically uncoupled case. This highlights the importance of knowing the optical properties of phytoplankton, and the background optical properties, to understand phytoplankton dynamics.

It is also important to highlight that the light intensity at the optically uncoupled critical depth is independent of mixed-layer biomass and equal to the light intensity at the bottom of the mixed layer at steady state (39). In a dynamical context, this implies that biomass evolves over time until the two light levels equal. The fact that the light intensity at the optically uncoupled critical depth is independent of biomass also implies that all steady states have the same light intensity at the base of the mixed layer, despite having different steady-state biomass and different mixed-layer depths. We conclude that the optically uncoupled critical depth determines the light intensity that can be reached at the base of the mixed layer and how high a biomass will be present in the mixed layer further depends on the depth of the mixed layer according to (32). Mixed-layer production is determined in a similar fashion according to (40). It is important to stress that these expressions hold for a linear dependence of production on light, as used by [Sverdrup \(1953\)](#). These results also indicate the importance of water clarity in determining the steady-state biomass.

Non-linear formulations of the production–light relationship are well known ([Platt and Jassby, 1976](#)) and are modelled with photosynthesis irradiance functions ([Jassby and Platt, 1976](#)). Having a non-linear production–light dependence modifies production with depth, yielding a different production profile for each photosynthesis irradiance function ([Kovač et al., 2017b](#)). A distinction between a linear production profile, such as the one [Sverdrup \(1953\)](#) used, and a non-linear one is in production saturation, which typically occurs near the surface ([Kovač et al., 2016b](#)). Quantifying the total effect of production saturation on

mixed-layer production can easily be done by using the analytical solution for a non-linear model for mixed-layer production (Platt *et al.*, 1990). In the context of critical depth this changes the $F(Z)$ function (7), making it harder to solve (9) analytically and obtain the critical depth for this case.

However, validity of Sverdrup's argument does not lie in the linearity of the photosynthesis–light relation, nor in taking the loss term as constant. Production and losses can both be homogenized by turbulent mixing, irrespective of the mathematical formulation of these terms (Platt *et al.*, 1991). In other words, with respect to photosynthesis, it is not the exact form of the photosynthesis–light relation that is relevant, just the magnitude of production in the mixed layer. Although Sverdrup used a linear model of the photosynthesis–light relation (4), which for some time now is known to be non-linear (Jassby and Platt, 1976; Platt and Jassby, 1976), it does not change the argument. The reason is that all the commonly used photosynthesis–light functions give a monotonically decreasing rate of photosynthesis in a declining light field (Kovač *et al.*, 2016a, b). This implies that the integral of production over the mixed layer will be bounded. Therefore, how we calculate mixed-layer production does not reflect on the critical depth argument qualitatively, simply quantitatively. An argument in favour of this reasoning is that the expression for the convergence of the critical depth to the mixed-layer depth (45) is the same for a linear production–light model used by Sverdrup (1953) and a non-linear one used by Platt *et al.* (2003).

In fact, Equation (45) can be generalized easily by observing that it is a statement of a conservation principle. Rearranging (42), recognizing (27), and applying the chain rule, yields:

$$\frac{d(KS)}{dt} = 0, \quad (57)$$

demonstrating that the product of the attenuation coefficient and the optically coupled critical depth remains constant over time. Given initial conditions (K_0, S_0) , when the critical depth criterion is met the system ends in a steady state characterized by $S = Z_m$ and $B = B^*$. When the critical depth criterion is not met the system ends in the trivial steady state characterized by $S = C$ and $B = 0$. On the approach to these states, the system moves along a trajectory, which keeps the KS product constant (Figure 6).

Following the definition (35) and acknowledging (21), we observe that the quantity, which is conserved is in fact the critical depth expressed as an optical depth ζ_c (21) and therefore we can restate the previous expression simply as:

$$\frac{d\zeta_c}{dt} = 0. \quad (58)$$

We term this the Critical Depth Conservation Principle (Figure 6). Working backwards from it leads to Equation (45). The fact that both a linear model used in this paper and a non-linear production model of Platt *et al.* (2003) yield the same solution (45) points in the direction of generality of the Critical Depth Conservation Principle. Exploring this in more detail is a potential direction for future research.

The theory presented is valid for a mixed layer, which by definition is a region of uniform properties in the vertical (Chiswell, 2011). As Franks (2015) pointed out we are led to distinguish the mixed layer from the turbulent layer, in that a turbulent layer is a layer of active mixing, and the mixed layer is a layer of uniform

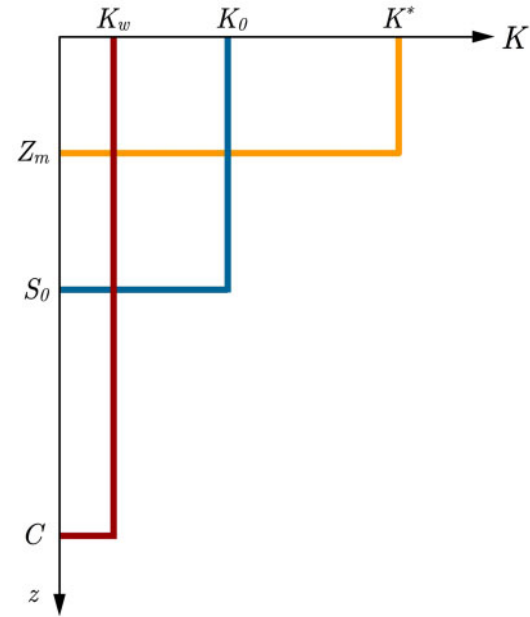


Figure 6. Illustration of the Critical Depth Conservation Principle. According to (57), the product of the attenuation coefficient K and the optically coupled critical depth S remains constant over time. Starting from the initial state with K_0 and S_0 , the system moves either to the steady state B^* (32) (critical depth criterion met $C > Z_m$), or to the trivial steady state $B^* = 0$ (critical depth criterion not met $C < Z_m$). The product KS remains constant, therefore the surfaces enclosed by the axes and the red/blue/orange lines are all equal. When $S_0 > Z_m$ (as in the figure), the biomass grows over time until it reaches steady state $S^* = Z_m$. When $S_0 < Z_m$ (not shown), the biomass declines over time until it also reaches steady state $S^* = Z_m$. In both cases, the condition $C > Z_m$ has to be met in order for biomass to reach a non-trivial steady state (32).

properties in the vertical. The second definition is an operational one, as the depth of the mixed layer can be easily determined from say the temperature profile. The depth of the turbulent layer is harder to determine operationally. In this work, the wording mixed layer was used in the context of a layer in which active mixing is occurring so that homogenization of biomass and losses is taking place within it, therefore every phytoplankton experiences the same light conditions (Franks, 2015). This is in line with Sverdrup (1953) who also referred to the turbulent layer as the mixed layer. Distinct usage of the mixed-layer term in modern literature should not be used to argue against Sverdrup, as he clearly stated:

... a phytoplankton population may increase independently of the thickness of the mixed layer if the turbulence is moderate. In this case the plankton may be unevenly distributed. . .

This paragraph demonstrates that Sverdrup (1953) was in fact referring to a turbulent layer, phrased in the modern terminology of Franks (2015), when using the wording “mixed-layer”.

In the real ocean, the mixed-layer depth is seldom constant over time. During winter, the mixed-layer depth tends to be deep and phytoplankton concentration low, implying the effect of shading on the attenuation of light may be negligible. In these conditions, it is the optically uncoupled critical depth that determines the onset of positive growth. As the season progresses,

mixed layer typically shallows, biomass rises, and the effect of phytoplankton absorption and back-scattering on light attenuation becomes more prominent and may become non-negligible. Under these conditions, it is the optically coupled critical depth that determines the sign of the growth rate. Therefore, as the mixed-layer depth varies over the season so too does the strength of the bio-optical coupling and with it the very magnitude of the critical depth. This should be noted when discussing different hypotheses of bloom onset. As demonstrated, the condition $C > Z_m$ (optically uncoupled critical depth deeper than the mixed-layer depth) tells us nothing on whether $S \gtrless Z_m$ (optically coupled critical depth deeper/equal/shallower than the mixed-layer depth). If one is to judge positive growth from the condition $C > Z_m$ alone erroneous conclusion may result, because the sign of the growth rate will be set by the relation of S and Z_m (Figure 6). However, when $C < Z_m$ (optically uncoupled critical depth shallower than the mixed-layer depth) the sign of the growth rate is always negative. This realization will perhaps aid the discussion on the Critical Depth Hypothesis.

Conclusions

In 1935, Graan and Braarud (1935) raised a vivid question:

Thus, the question, whether violent turbulence may make the phytoplankton increase or decrease, must to a large extent depend on the thickness of the productive layer and thus on the light conditions.

In 1953, Sverdrup attempted to answer this question in his seminal paper. To what extent the assumptions of Sverdrup (1953) are satisfied in the real world and the mathematical elegance and richness of the Sverdrup formalism applicable are still areas of active research (Sathyendranath *et al.*, 2015; Behrenfeld and Boss, 2018). The significance of Sverdrup (1953) paper, in a historical context, is that Sverdrup presented the first mathematical model for the growth of phytoplankton in the mixed layer, as a balance between photosynthesis and losses in the mixed-layer depth. This opened the way for quantitative tests, refinements, and modelling based on first principles to come to prominence in this scientific field, which at the time was quite revolutionary (Sathyendranath *et al.*, 2015). Sverdrup gave mathematical elegance to an already elegant concept of Gran and Braarud (1935), by providing a neat mathematical formulation for the critical depth (Sverdrup, 1953). Hopefully, the analytical solution presented here provides a fitting closure to the original work, in mathematical terms, with an exact solution to Sverdrup's original equations.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Data availability

No new data were generated or analysed in support of this research.

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References

- Anderson, T. R. 2005. Plankton functional type modelling: running before we can walk? *Journal of Plankton Research*, 27: 1073–1081.
- Behrenfeld, M. 2010. Abandoning Sverdrups critical depth hypothesis on phytoplankton blooms. *Ecology*, 91: 977–989.
- Behrenfeld, M., Doney, S., Lima, I., Boss, E., and Siegel, D. 2013a. Annual cycles of ecological disturbance and recovery underlying the subarctic Atlantic spring plankton bloom. *Global Biogeochemical Cycles*, 27: 526–540.
- Behrenfeld, M., Doney, S., Lima, I., Boss, E., and Siegel, D. 2013b. Reply to a comment by Stephen m. Chiswell on: annual cycles of ecological disturbance and recovery underlying the subarctic Atlantic spring plankton bloom by M. J. Behrenfeld et al. (2013). *Global Biogeochemical Cycles*, 27: 12941296.
- Behrenfeld, M. J., and Boss, E. S. 2018. Students tutorial on bloom hypotheses in the context of phytoplankton annual cycles. *Global Change Biology*, 24: 55–77.
- Bishop, J. K., Conte, M. H., Wiebe, P. H., Roman, M. R., and Langdon, C. 1986. Particulate matter production and consumption in deep mixed layers: observations in a warm-core ring. *Deep-Sea Research A*, 33: 1813–1841.
- Bouman, H. A., Platt, T., Doblin, M., Figueiras, F. G., Gudmundsson, K., Gudfinnsson, H. G., Huang, B. *et al.* 2018. Photosynthesis–irradiance parameters of marine phytoplankton: synthesis of a global data set. *Earth System Science Data*, 10: 251–266.
- Chiswell, S. 2011. Annual cycles and spring blooms in phytoplankton: dont abandon Sverdrup completely. *Marine Ecology Progress Series*, 443: 39–50.
- Chiswell, S. M. 2013. Comment on annual cycles of ecological disturbance and recovery underlying the subarctic Atlantic spring plankton bloom. *Global Biogeochemical Cycles*, 27: 1291–1293.
- Chiswell, S. M., Calil, P. H. R., and Boyd, P. W. 2015. Spring blooms and annual cycles of phytoplankton: a unified perspective. *Journal of Plankton Research*, 37: 500–508.
- Corless, R. M., Gonnet, G. H., Hare, D. E. G., Jeffrey, D. J., and Knuth, D. E. 1996. On the Lambert w function. *Advances in Computational Mathematics*, 5: 329–359.
- Dai, C., Zhao, M., Yu, H., and Wang, Y. 2015. Delay-induced instability in a nutrient-phytoplankton system with flow. *Physical Review E*, 91: 032929.
- Du, Y., and Mei, L. 2011. On a nonlocal reaction-diffusion-advection equation modelling phytoplankton dynamics. *Nonlinearity*, 24: 319–349.
- Enriquez, R. M., and Taylor, J. R. 2015. Numerical simulations of the competition between wind-driven mixing and surface heating in triggering spring phytoplankton blooms. *ICES Journal of Marine Science*, 72: 1926–1941.
- Euler, L. 1779. De serie lambertina plurimisque eius insignibus proprietatibus (reprinted 1992). *In Opera Omnia.*, pp. 350–369. Ed. by B. G. Teubner. Springer, Leipzig and Berlin.
- Franks, P. J. S. 2015. Has Sverdrups critical depth hypothesis been tested? Mixed layers vs. turbulent layers. *ICES Journal of Marine Science*, 72: 1897–1907.
- Gautschi, W. 2011. The Lambert w-functions and some of their integrals: a case study of high-precision computation. *Numerical Algorithms*, 57: 27–34.

- Goličnik, M. 2012. On the Lambert w function and its utility in biochemical kinetics. *Biochemical Engineering Journal*, 63: 116–123.
- Gouvea, F. 2000. Time for a new elementary function. *FOCUS (Newsletter of Mathematics Association of America)*, 20: 2.
- Gran, H. H., and Braarud, T. 1935. A quantitative study on the phytoplankton of the Bay of Fundy and the Gulf of Maine (including observations on hydrography, chemistry and morbidity). *Journal of the Biological Board of Canada*, 1: 279–467.
- Gray, J. J., and Tiling, L. 1978. Johann Heinrich Lambert, mathematician and scientist, 1725. *Historia Mathematica*, 5: 13–41.
- Hays, B. 2005. Why W . *American Scientist*, 93: 104–108.
- Houari, A. 2013. Additional application of the Lambert W function in physics. *European Journal of Physics*, 34: 695–702.
- Huisman, J., Arrayas, M., Ebert, U., and Sommeijer, B. 2002. How do sinking phytoplankton species manage to persist? *The American Naturalist*, 159: 245–254.
- 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.
- Huisman, J., and Weissing, F. J. 1994. Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. *Ecology*, 75: 507–520.
- Jackson, T., Sathyendranath, S., and Platt, T. 2017. An exact solution for modeling photoacclimation of the carbon-to-chlorophyll ratio in phytoplankton. *Frontiers in Marine Science*, 4: 283.
- Jassby, A. D., and Platt, T. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnology and Oceanography*, 21: 540–547.
- Kirk, J. T. O. 2011. *Light and Photosynthesis in Aquatic Ecosystems*, 3rd edn. Cambridge University Press, Cambridge. doi:10.1017/CBO9780511623370.
- Kovač, Ž., Platt, T., Antunović, S., Sathyendranath, S., Morović, M., and Gallegos, C. 2017a. Extended formulations and analytic solutions for watercolumn production integrals. *Frontiers in Marine Science*, 4: 163.
- Kovač, Ž., Platt, T., Sathyendranath, S., and Antunović, S. 2017b. Models for estimating photosynthesis parameters from *in situ* production profiles. *Progress in Oceanography*, 159: 255–266.
- Kovač, Ž., Platt, T., and Sathyendranath, S. 2020. Stability and resilience in a nutrient-phytoplankton marine ecosystem model. *ICES Journal of Marine Science*, 77: 1556–1572.
- Kovač, Ž., Platt, T., Sathyendranath, S., and Morović, M. 2016a. Analytical solution for the vertical profile of daily production in the ocean. *Journal of Geophysical Research: Oceans*, 121: 3532–3548.
- Kovač, Ž., Platt, T., Sathyendranath, S., Morović, M., and Jackson, T. 2016b. Recovery of photosynthesis parameters from *in situ* profiles of phytoplankton production. *ICES Journal of Marine Science*, 73: 275–285.
- Levy, M. 2015. Exploration of the critical depth hypothesis with a simple NPZ model. *ICES Journal of Marine Science*, 72: 1916–1925.
- Lindeman, C., and St. John, M. A. 2014. A seasonal diary of phytoplankton in the north Atlantic. *Frontiers in Marine Science*, 1: 1–6.
- Lindemann, C., Backhaus, J. O., and St. John, M. A. 2015. Physiological constraints on Sverdrup's critical-depth-hypothesis: the influences of dark respiration and sinking. *ICES Journal of Marine Science*, 72: 1942–1951.
- Mező, I., and Keady, G. 2016. Some physical applications of generalized Lambert functions. *European Journal of Physics*, 37: 065802.
- Platt, T., Bird, D. F., and Sathyendranath, S. 1991. Critical depth and marine primary production. *Proceeding of the Royal Society B*, 246: 205–217.
- Platt, T., Broomhead, D. S., Sathyendranath, S., Edwards, A. M., and Murphy, E. J. 2003. Phytoplankton biomass and residual nitrate in the pelagic ecosystem. *Proceeding of the Royal Society A*, 459: 1063–1073.
- Platt, T., Gallegos, C. L., and Harrison, W. G. 1980. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *Journal of Marine Research*, 38: 687–701.
- Platt, T., and Jassby, A. 1976. The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. *Journal of Phycology*, 12: 421–430.
- Platt, T., and Sathyendranath, S. 1991. Biological production models as elements of coupled, atmosphere-ocean models for climate research. *Journal of Geophysical Research*, 96: 2585–2592.
- Platt, T., Sathyendranath, S., and Ravindran, P. 1990. Primary production by phytoplankton: analytic solutions for daily rates per unit area of water surface. *Proceeding of the Royal Society B*, 241: 101–111.
- Rumyantseva, A., Henson, S., Martin, A., Thompson, A. F., Gillian, M. D., Kaiser, J., and Heywood, K. J. 2019. Phytoplankton spring bloom initiation: the impact of atmospheric forcing and light in the temperate North Atlantic Ocean. *Progress in Oceanography*, 178: 102202.
- Ryabov, A. B., and Blasius, B. 2008. Population growth and persistence in a heterogeneous environment: the role of diffusion and advection. *Mathematical Modelling of Natural Phenomena*, 3: 42–86.
- Sathyendranath, S., Ji, R., and Browman, H. I. 2015. Revisiting Sverdrup's critical depth hypothesis. *ICES Journal of Marine Science*, 72: 1892–1896.
- Sathyendranath, S., and Platt, T. 1988. The spectral irradiance field at the surface and in the interior of the ocean: a model for applications in oceanography and remote sensing. *Journal of Geophysical Research*, 93: 9270–9280.
- Sathyendranath, S., Platt, T., Kovač, Z., Dingle, J., Jackson, T., Brewin, R. J. W., Franks, P. *et al.* 2020. Reconciling models of primary production and photoacclimation. *Applied Optics*, 59: C100–C114.
- Smetacek, V., and Passow, U. 1990. Spring bloom initiation and Sverdrup's critical-depth model. *Limnology and Oceanography*, 35: 228–234.
- Stewart, S. M. 2011. Wien peaks and the Lambert w function. *Revista Brasileira de Ensino de Física*, 33: 3308–1–3308-6.
- 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.
- Weissing, F. J., and Huisman, J. 1994. Growth and competition in a light gradient. *Journal of Theoretical Biology*, 168: 323–336.
- Zhai, L., Platt, T., Tang, C., Sathyendranath, S., Fuentes-Yaco, C., Devred, E., and Wu, Y. 2010. Seasonal and geographic variations in phytoplankton losses from the mixed layer on the northwest Atlantic Shelf. *Journal of Marine Systems*, 80: 36–46.

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