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Critical Optical Depth Hypothesis for Phytoplankton Growth and Bloom. A New Graphical Approach to the Classic Sverdrup Critical Depth Model

Hipoteza o wzroście i zakwicie fitoplanktonu wykorzystująca optyczną głębokość krytyczną. Nowa graficzna prezentacja klasycznego modelu głębokości krytycznej Svedrupa

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Abstract: A modification to the classic Sverdrup Critical Depth Model relating phytoplankton light-limited net growth in a mixed water column to its depth is presented by introducing optical depth in place of the physical depth of the column, as well as by the inclusion of self-shading and competition among phytoplankton species for light. The concept of critical optical depth of a well-mixed column is used to establish criteria for phytoplankton growth and competitive exclusion. This model shows not only the direction of the growth for a given column, such as the classic Sverdrup model, but also the magnitude of that growth. The model relies on plots of the average specific (per unit biomass) rate of this growth in the column against the optical depth of that column. These graphs are invariant under changes of light absorbers in the column as well as the depth of the column. In particular, these graphs do not change in the presence of competing species or with changes in column biomass, thus facilitating the analysis of these processes. Also, for this purpose, the concept of opacity load is introduced to name the optical depth. Such an extended Sverdrup model provides a simple visual, qualitative way of obtaining results consistent with Huisman and Weissing's (1994) critical light theory. It is convenient for considering more complex phytoplankton growth scenarios.

Keywords: critical depth, critical light, Sverdrup model, phytoplankton, growth, competition, optical depth

Streszczenie: Przedstawiono modyfikacje klasycznego modelu głębokości krytycznej Sverdrupa wiążącego ograniczony światłem wzrost netto fitoplanktonu w wymieszanej kolumnie wody z jej głębokością, wprowadzając głębokość optyczną w miejsce fizycznej głębokości kolumny, a także uwzględniając samozacienianie i konkurencję między gatunkami fitoplanktonu o światło. Dla sformułowania kryteriów wzrostu fitoplanktonu i wykluczenia konkurencyjnego zastosowano koncepcję krytycznej głębokości optycznej wymieszanej kolumny wody. Model ten pokazuje nie tylko kierunek powyższego wzrostu dla danej kolumny, jak klasyczny model Sverdrupa, ale także wielkość tego wzrostu. Model opiera się na wykresach średniej specyficznej (na jednostkę biomasy) szybkości tego wzrostu w kolumnie względem głębokości optycznej tej kolumny. Wykresy te są niezmiennicze w przypadku zmian absorberów światła w kolumnie, jak również głębokości kolumny. W szczególności, wykresy te nie zmieniają się w obecności gatunków konkurujących i przy zmianach biomasy w kolumnie, co ułatwia analizę tych procesów. Również w tym celu dla nazwania głębokości optycznej wprowadza się pojęcie ładunku nieprzezroczystości. Taki rozszerzony model Sverdrupa zapewnia prosty wizualny, jakościowy sposób uzyskania wyników zgodnych z teorią światła krytycznego Huismana i Weissinga (1994). Jest dogodny do rozważania bardziej złożonych scenariuszy wzrostu fitoplanktonu.

Słowa kluczowe: głębokość krytyczna, krytyczne natężenie światła, model Sverdrupa, fitoplankton, wzrost, konkurencja, głębokość optyczna

Introduction

The public is often warned about toxic algal blooms in bodies of water, dangerous to humans, bringing losses to farming and tourism, as well as posing problems for drinking water treatment (Pinchin 2022, Kowal et al. 2022). However, these organisms classified as phytoplankton can present themselves not only in an unfavourable light. Phytoplankton – microscopic photoautotrophic cells passively suspended in water – play a key role in shaping the Earth's climate (e.g., Falkowski 2012), atmospheric oxygen and carbon dioxide concentrations, and are the base of the food chains of aquatic ecosystems (Wang et al. 2020, Chavez et al. 2011). Although, they represent less than 1% of the Earth's photosynthetic biomass, they are estimated to account for almost half of the annual net primary production (Field et al. 1998, Fox et al. 2020) and have a profound influence on pelagic ecosystems and on life on Earth in general. Understanding phytoplankton ecology and the factors responsible for phytoplankton growth and triggering blooms – "one of the most fundamental processes in biological oceanography" (Sathyendranath et al. 2015) – are among the major challenges in "global change biology" (Behrenfeld and Boss 2017). Nowadays, laboratory and field experiments, satellite observations and a variety of airborne, surface and underwater vehicles are used to investigate these issues (Kislik et al. 2018, Mignot et al. 2018, Rumyantseva et al. 2019, Fox et al. 2020, Wang et al. 2020, Yang 2020, Ferreira et al. 2021). However, a mathematical description is also sought to analyse and interpret these data, to enable predictions, and to show the factors controlling the driving mechanisms of these processes.

When studying phytoplankton growth and blooms, the literature focuses on the surface, a relatively well-mixed layer, as the main location where these processes occur (cf. Behrenfeld and Boss 2017). This is because, phytoplankton need light for photosynthesis and, therefore, accumulate close to the water surface. In turn, the occurrence of mixing of this part of water in oceans and inland reservoirs is an almost universal phenomenon. The extent and rate of this mixing affect many processes in this area, including availability of light for photosynthesis, nutrient supply to the euphotic zone and pelagic temperature.

Almost 70 years ago a Norwegian meteorologist and oceanographer, Harald Ulrik Sverdrup, presented a model of phytoplankton bloom formation in the North Atlantic (Sverdrup 1953), in which he referred to this layer and related light-limited phytoplankton growth to its depth. The model is now regarded as the canonical framework for the mechanism of this phenomenon, also said to be the "cornerstone" or "central concept" of biological oceanography (Fischer et al. 2014, Asknes 2015). The model is also widely used in limnology. It has also become a "landmark" for later alternative competing concepts, descriptions and modelling of this phenomenon (Platt et al. 1991, Behrenfeld and Boss 2014). In the following part, I will use both the term mixed layer and the term mixed water column. This column represents here that layer. The Sverdrup model is a mathematical formalization of earlier investigations concerning, among other, light availability as a determinant of phytoplankton growth in the water column (Gran and Braarud 1935, Riley 1942, 1946). The Sverdrup's model incorporates the concept of compensation depth used by these authors as well as their anticipated notion of critical depth Z_{cr} of this column (Sverdrup 1953, Tett and Edwards 1984, Smetacek and Passow 1990, Behrenfeld and Boss 2017). Then, according to the Sverdrup model, in the column of depth Z_{mix} light-limited phytoplankton growth takes place, i.e. its biomass increases if $Z_{mix}<Z_{cr}$, and if $Z_{mix}=Z_{cr}$ the biomass remains stationary, while if $Z_{mix}>Z_{cr}$ the biomass decreases. Perhaps the simplicity of the concept of this model is one of its strong points and an important reason for its popularity and longevity. However, the trouble with the practical application of this model is, among other, that its

basic parameter Z_{cr} does not have a constant value but depends on water turbidity (Huisman and Weissing 1994). As a result, it changes with phytoplankton biomass and other light absorbers, making the model more difficult to apply. Furthermore, Z_{cr} is difficult to assess in practice.

The issue of light-limited phytoplankton growth and blooms in a mixed column is also addressed in the critical light model (Huisman and Weissing 1994, Weissing and Huisman 1994) where the growth at a given constant light supply to the column I_{in} is expressed as a function of light at the bottom of the column I_{out}. The model takes into account shading by phytoplankton and competition for light among phytoplankton species. Shading by biomass inhibits growth, leading to a steady state. According to this model, phytoplankton biomass in a monoculture increases if I_{out} is higher than the so-called critical light I^*_{out}, while it decreases if I_{out} is lower than I^*_{out}. When phytoplankton biomass reaches equilibrium I_{out} reaches I^*_{out}. Furthermore, I^*_{out} is independent on water turbidity. This makes the value of I^*_{out} for a given phytoplankton species the same in a monoculture of that species as in the presence of other phytoplankton species as well as other light absorbers. When competing for light in a column, the winning species is the one with the lowest I^*_{out}. Furthermore, the I^*_{out} value does not depend on Z_{mix} (Huisman and Weissing 1994, Weissing and Huisman 1994, Huisman 1999). This makes it possible, in particular, to measure the value of I^*_{out} in microcosm experiments at different values of Z_{mix} (Huisman 1999).

The results of critical light theory can be interpreted in terms of critical depths (Szeligiewicz 1996, 1998, 1999, 2000, Huisman 1999). This extends the Sverdrup critical depth model by incorporating self-shading as a mechanism of regulation of phytoplankton biomass, and by including competition for light between phytoplankton species in the surface mixed water column (Szeligiewicz 1996, 1998). Albeit the results of the critical light theory were obtained by introducing the concepts such as "quantum yield" or "quantum return", which perhaps makes such an extended of Sverdrup model a bit far from the simplicity of its original version.

However, it was suggested that when the phytoplankton biomass in a mixed water column reaches equilibrium, at the same time the optical depth of this column reaches a constant value (Wofsy 1983, Szeligiewicz 2000). This would refer to situations where the light supply to the column is constant or subject to defined diurnal variations (Szeligiewicz 2000). This constant optical depth was called "critical optical depth" (Szeligiewicz 1999, 2000). Later on, Diehl et al. (2015) introduced analogous definition. The value of critical optical depth also does not depend on light absorbers and Z_{mix}[1].

This paper presents modifications to Sverdrup's model by introducing optical depth, as well as self-shading and competition between phytoplankton species for light. The essence of the implementation of optical depth was captured by Paul G. Falkowski and John A. Raven (1997) in their book "Aquatic Photosynthesis": "Optical depths are independent of physical depths. It is often convenient to relate vertical profiles of photosynthesis in aquatic systems to optical depth rather than physical depth. In doing so, vertical profiles are related to the rate of attenuation of light; such examination frequently reduces much of the variance between profiles (Morel 1988)". The analyses carried out in this work deal with these types of profiles.

The optical depth of the mixed layer was probably first used to describe phytoplankton growth in a mathematical model by Talling (1957). In order to express the depth integrated daily primary production as a formula, he introduced a parameterisation of the generally plotted photosynthesis profile in relation to the optical depth

1 In this regard, Szeligiewicz (2000) proposed theoretical systems for measuring critical optical depth experimentally. Diehl et al. (2015) made similar measurements.

of the column. This allowed him to derive an equation for calculating the optical depth of the column for which the "column compensation point" occurs (i.e., when the integrated column production equals the integrated column respiration). This corresponds to the criterion introduced by Sverdrup (1953) for the stationarity of phytoplankton biomass in a column. In the original form it did not take into account self-shading and competition for light.

Wofsy (1983), on the other hand, in his equation representing the mean rate of change of phytoplankton biomass in the mixed column, takes into account self-shading and, optionally, sinking of phytoplankton. In this formula, he uses a simplified description of the photosynthetic curve as a function of light, expressed as two connected straight-line sections, without taking photoinhibition into account. Perhaps the most important conclusions from Wofsy's model (his Eq.10, without sinking) that have been obtained through applying mathematical analysis are that in steady-state (1) the light absorption coefficient (denoted as ε in this paper) is inversely related to the depth of the water column, and consequently (2) that the optical depth of the mixed column is constant when the biomass reaches steady-state. It can therefore be noted that Szeligiewicz's (2000) results are consistent with those of Wofsy. However, Szeligiewicz (2000) obtained them through qualitative considerations.

Optical depth is also used in phytoplankton growth models in chemostats to determine the optimal growth conditions. In particular, Martinez et al. (2018a) derived a formula for the average growth rate in, among other things, a perfectly mixed vertical cylindrical photobioreactor which is a function of only the incident light and the optical depth of this reactor. They take into account self-shading and photoinhibition effect and introduce the notion of a critical optical depth at which this average growth is the greatest, thus taking a different approach than in the present work. Martinez et al. (2018b) additionally consider phytoplankton losses from the chemostat through dilution, mortality and respiration.

It is worth mentioning, in the context of the issue presented here, the work of Kovač et al. (2021), in which an analytical solution for Sverdrup's critical depth is given by using the Lambert *W* function. These authors also take into account self-shading and competition between species for light and diurnal changes in light intensity (as in Sverdrup's original model). They introduce the concept of "optically uncoupled" and "optically coupled critical depth", which would be, using the nomenclature from Szeligiewicz (2000), the critical depth, Z_{cr}, and the maximum critical depth, max_Z_{cr}, respectively. Both are calculated from "the optical depth corresponding to the critical depth" (in this paper called the optical critical depth, denoted as zo_{cr}) obtained by rearranging the equation expressing the condition for the steady state of phytoplankton biomass in the column using the Lambert *W* function. They show that Z_{cr} tends towards Z_{mix} due to self-shading, and that the competition is won by the species having the highest critical depth, as stated by Szeligiewicz (1998), which is also consistent with the considerations presented in this paper. They also show that the critical depth is related to the critical light intensity, which is also noted by Szeligiewicz (1998) and Huisman (1999), and which is also used in this study.

In this paper, I rely on graphs of the dependence of the average specific (per unit biomass) light-limited net growth rate of phytoplankton in a mixed column on the optical depth of the column. For the analyses of phytoplankton growth and competition for light, I benefit from the invariant properties of these graphs. I consider the advantages provided by this method over the Sverdrup critical depth model. I also compare obtained results with the results of the critical light intensity

model. The considerations presented below are theoretical and qualitative.

1. Models of phytoplankton growth

This section presents three models (i.e., g-based CD model, g-based COD model and g_{aver}-based COD model) which are the consecutive steps in the modification of Sverdrup's (1953) critical depth model by optical depth inclusion. The first model uses the depth distribution of phytoplankton local specific net growth rate within the column, similar to the classic Sverdrup's (1953) critical depth model. The second model replaces physical depth in the column of the first model by the optical depths within this column. The third one uses the graphs of the average of the above rate over the entire column as a function of the optical depth of the column. These three models refer to the same process – the balance of phytoplankton biomass in the whole well-mixed column. The critical parameters of these models indicate whether such a balance is achieved and, if not, in which direction the biomass in the column changes. In this way, these models express the ideas of Sverdrup's (1953) critical depth model. The three models complement each other. The first model will be a reference point for the other two models. All three models will also be compared with the critical light model of Huisman and Weissing (1994).

The basic assumptions for these models discussed here are taken from Sverdrup's critical depth model (named here as CD model) and the critical light model of Huisman and Weissing (1994) (referred to here as CL model), that is: (1) the change in phytoplankton biomass in a mixed water column extending from the reservoir surface to an assumed depth is estimated, (2) the phytoplankton is uniformly distributed throughout this column, (3) the phytoplankton growth is limited only by light, (4) light enters this column from above and decreases with depth. Furthermore, the assumption made in the CL model (and implicit in the CD model) is adopted here that (5) other possible ecological factors influencing phytoplankton growth e.g., nutrients, temperature, allelopathic interactions, incomplete mixing, zooplankton grazing, mixotrophy, viruses, spectrum of light, pigment composition, photoacclimation etc. are not explicitly taken into account.

1.1. g-based CD model

Let the column has a single unit cross-sectional area. According to the CD and CL models and in view of the above assumptions the rate of change in phytoplankton biomass W in the column results from integrated water-column net growth rate, i.e., from conservation of mass within it:

$$\frac{dW}{dt} = \int_0^{Z_{mix}} g\left(I\left(z\right)\right)\omega\, dz\,, \tag{1}$$

where t is the time, ω is the biomass density of phytoplankton in the column independent of position z in the column (assumption (2)), $I(z)$ is the light intensity at the depth z, within the column (z runs from zero (top of the column) to Z_{mix} (bottom)), and g is the specific (i.e. per unit biomass) light-limited (assumption (3)) phytoplankton net growth rate represented as a function of $I(z)$ and described for instance as a specific balance between carbon uptake and losses, like in the CL model. The specific loss rate includes all phytoplankton loss processes as in the CL model and presumably taken into account by the CD model.

In the CD model, the net growth is due to the difference between primary production as a linear function of light intensity and phytoplankton losses constant with depth. In contrast, the functional form describing function g is not specified. Instead, as in the CL model (Weissing and Huisman 1994), only a general assumption (6) is made, which is also met in the CD model, that g *is* species-specific and monotonically increases with light intensity:

$$\frac{dg}{dI} > 0. \tag{2}$$

Non-photoinhibited growth is considered as in the CD and the CL models. However, it is worth to note, that shapes of g expressing photoinhibition of growth with increasing light might also be incorporated into this approach, and it will be presented elsewhere. Function g is positive if light is sufficient to support the growth, it is negative otherwise, and is zero for an intermediate (compensation) light I_c.

Furthermore, in view of assumption (4) as in the CD and CL models framework, it is assumed (assumption (7)) that:

a. The light decreases exponentially with depth in the column according to Lambert-Beer's law

$$I(z) = I_{in}\, e^{-\varepsilon z}, \tag{3}$$

where I_{in} is the light intensity entering the column, and ε is the vertical attenuation coefficient for downwelling light in the water for the PAR range.

b. Within the column the coefficient ε is independent of depth as for the CL model (for comparison, the coefficient ε is constant in the CD model).

c. Moreover, shading by phytoplankton biomass is explicitly taken into account as in the CL model, that is

$$\varepsilon = \varepsilon_{bg} + \varepsilon_{\omega}, \tag{4}$$

where

$$\varepsilon_{\omega} = k_{\omega}\omega, \tag{5}$$

is the light attenuation coefficient by phytoplankton, where k_ω is the light attenuation coefficient of phytoplankton biomass, and

$$\varepsilon_{bg} = \sum_{i=1}^{n} k_{b,i} b_i, \tag{6}$$

is the light attenuation coefficient by background turbidity (Huisman et al. 2002) caused by non-phytoplankton absorbing substances, where $k_{b,i}$ is the specific light attenuation coefficient by i-th such substance, and b_i is the concentration of that substance, and n – is the number of these substances in the column. It is assumed that ε_{bg} is a constant.

d. I_{in} is constant as in the case of the CL model. Daily changes in I_{in} are included in the CD model. They may also be considered here as will be mentioned later.

Though the incoming light intensity, I_{in}, is constant by assumption (7d), the biomass of the phytoplankton in the column may change over time, so the light attenuation may also change (accounted for by the value of ε, Eqs.(4) and (5)). As a result, the profiles $I(z)$ and $g(I(z))$ may likewise change with ε. With this in mind, these profiles are denoted now as $I(z, \varepsilon)$ and $g(I(z, \varepsilon))$ and substituted in Eq.(1). Since $W = \omega Z_{mix}$ Eq. (1) can be rewritten as:

$$\frac{1}{\omega}\frac{d\omega}{dt} = \frac{1}{Z_{mix}} \int_0^{Z_{mix}} g\big(I(z,\varepsilon)\big)\, dz := g_{aver}\big(Z_{mix}, \varepsilon\big), \tag{7}$$

where $g_{aver}(Z_{mix}, \varepsilon)$ is the average g over the column depth of Z_{mix} for a given ε. For $g_{aver}(Z_{mix}, \varepsilon) > 0$ the biomass in the column increases, whereas for $g_{aver}(Z_{mix}, \varepsilon) < 0$ it decreases. The biomass does not change if $g_{aver}(Z_{mix}, \varepsilon) = 0$. In the latter case such a column depth, Zmix, is called the critical depth Zcr according to the CD model. Based on these relationships and on Fig.(1) one can derive the criteria for phytoplankton growth postulated by Sverdrup, i.e.

$$g_{aver}(Z_{mix}, \varepsilon) \begin{cases} < 0 & for \quad Z_{mix} > Z_{cr} \\ = 0 & for \quad Z_{mix} = Z_{cr} \\ > 0 & for \quad Z_{mix} < Z_{cr} \end{cases}. \tag{8}$$

However, as the functions $I(z, \varepsilon)$ and $g(I(z, \varepsilon))$ as well as the corresponding values of Z_c and Z_{cr} are ε-dependent, the above criteria (Eq.8) would therefore require an adjustment of the Z_{cr} value against the current ε value, which complicates the application of the critical depth theory, as already mentioned. The critical depth model, on the other hand, has the advantage of describing phytoplankton growth explicitely in the context of the Z_{mix} characterising

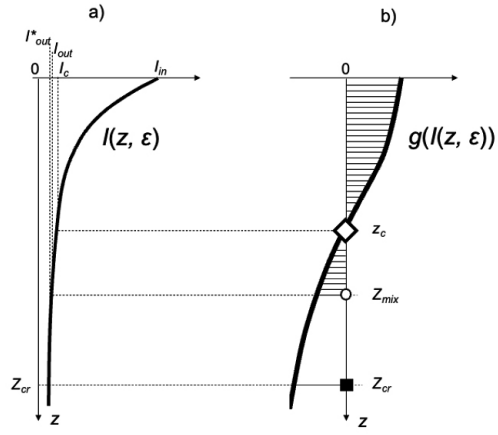

Figure 1. The idea of Sverdrup's critical depth model expressed in the g-based CD model. (a) graph of the light intensity $I(z, \varepsilon)$, where z is the depth extending from the water surface downwards, (b) graph of $g(I(z, \varepsilon))$ corresponding to the light shown in (a). The compensation depth Z_c, indicated by '◊', is the depth at which $g(I(z, \varepsilon))=0$, i.e. at which $I(z, \varepsilon)= I_c$. The critical depth Z_{cr} (marked by ■) is the depth of mixed column, where the net growth of phytoplankton (i.e. when $g > 0$) in the upper part of the column (up to the compensation depth Z_c) is balanced by losses (i.e. when $g < 0$) in the rest of the mixed column. This occurs when the right-hand side of Eq. (7), denoted also by g_{aver}, is equal to zero. Graphically, this condition means that the hatched areas above and below the depth Z_c are to be equal to each other. Z_{mix} is the mixing depth (for other symbols see text). If Z_{mix} (marked on the z-axis by symbol "o") is less than (as on the figure) or greater than Z_{cr}, then the two areas are not equal which means that there is a corresponding increase or decrease in the phytoplankton in the column. The proportions of the graph of g were taken to keep the graph compact. This is of little relevance to further considerations.

the physical structure of the vertical water column formed by mixing as well as stratification.

Using the profiles $g(I(z, \varepsilon))$ in this model, together with the depths Z_{mix}, Z_c, Z_{cr} identified therein, it is possible to indicate the corresponding light intensities I_{out}, I_c, and I^*_{out} in the light profile $I(z, \varepsilon)$ in the column, defined according to the CL model (Fig. 1). From Eq.(3) it follows that the compensation light, I_c, can be written as

$$I_c = I_{in}\, e^{-\varepsilon Z_c}, \tag{9}$$

when $z = Z_c$, where Z_c is the compensation depth. Since light at the base of the mixed column, I_{out}, i.e., when $z=Z_{mix}$, is given by:

$$I_{out} = I_{in}\, e^{-\varepsilon Z_{mix}}, \tag{10}$$

then, in the case of stationary biomass in this column, i.e., when $Z_{mix} = Z_{cr}$, it is equal to the critical light

$$I^*_{out} = I_{in}\, e^{-\varepsilon Z_{cr}}. \tag{11}$$

Based on the criteria expressed by Eq.(8) and Fig. 1, the respective relations between I_{out} and I^*_{out} can be established. Moreover, these relationships are consistent with the phytoplankton growth criteria postulated by the CL model. Inversely, the growth criteria derived from the CL model can be directly expressed in terms of Z_{mix} and Z_{cr} as growth criteria in line with the g-based CD model (as well as in the calssic Sverdrup model). Thus, it is possible to express Z_{cr} through the critical light intensity I^*_{out} (Szeligiewicz 1996, 1998, 1999, 2000, Huisman 1999), and vice versa, as also shown in Fig. 1. However, in addition, the CL model says that I^*_{out} does not depend on Z_{mix} and on ε. This property does not follow directly from the criteria expressed in Eq.(8) but will be shown in the g-based COD model described below.

1.2. g-based COD model

The rate of light-limited phytoplankton growth in a mixed water column can be expressed as a certain dependence on the optical depth of the column. Furthermore, a similar to Eq. (8) criterion for this growth can be formulated using the concept of critical optical depth (COD) (e.g. Szeligiewicz 1999, 2000). In fact, based on Eq. (3) and the assumptions (7b) and (7d) the specific net growth rate g may be viewed as

a function of the product εz itself for a given constant light supply to the water I_{in}. Then, the right-hand side of Eq. (7) reads:

$$g_{aver}(Z_{mix}, \varepsilon) = \frac{1}{Z_{mix}} \int_0^{Z_{mix}} g(\varepsilon z)\, dz\,. \quad (12)$$

The product (εz) is dimensionless parameter and according to definition is called optical depth (Kirk 1983), hereafter denoted as *zo*:

$$zo = \varepsilon z\,. \quad (13)$$

It is worthwhile mentioning that there is a fundamental and tacitly hidden assumption within this formula included also in most phytoplankton models that changing in ε and/or z do not influence on g unless the optical depth (εz), and at the same time light intensity, remain the same. It means that effects of photoadaptation, spectral distribution of light penetrating water, spatio-temporal scale (i.e., mixing time and depth of the column) are not considered in the description of phytoplankton growth. The value of g is therefore the same no matter what contributes to the value of *zo*, i.e., whether the *zo* results from turbidity of water in the column and/or from the depth within the column.

The right-hand side of Eq. (12), denoted now as a function $g_{aver}(zo_{mix})$, may be rewritten as[2]

$$g_{aver}(zo_{mix}) = \frac{1}{zo_{mix}} \int_0^{zo_{mix}} g(zo)\, d(zo)\,, \quad (14)$$

using a change the variable of integration from the depth z to the optical depth *zo*, where zo_{mix} is the optical depth of the mixed column

$$zo_{mix} = \varepsilon\, Z_{mix}\,. \quad (15)$$

An analogous equation to Eq. (12) and its transformation to Eq. (14) was used by Bernard and Lu (2022) for optimising the productivity of microalgal biomass in photobioreactors.

The integral $g_{aver}(zo_{mix})$ may be viewed as the average net specific growth rate over optical depth of the mixed column. The average net specific growth rate over physical depth of the column is therefore transformed into average net specific growth rate over optical depth of the column. The resulting identity $g_{aver}(Z_{mix},\varepsilon) = g_{aver}(zo_{mix})$ reads that the average specific net growth rate over depth of the mixed column depends on the optical depth of this column and is the same for given g and zo_{mix} for any values of Z_{mix} and ε if $\varepsilon Z_{mix} = zo_{mix}$. In other words, the average net specific growth rate over depth of the mixed column $g_{aver}(zo_{mix})$ may be represented as a function of one lumped variable zo_{mix} in the form $g_{aver}(zo_{mix})$. Consequently, the function $g_{aver}(zo_{mix})$ is visualized in the next section by a single curve for any combinations of the values of ε and Z_{mix} giving the same product $zo_{mix.}$ This is not possible for the function $g_{aver}(Z_{mix}, \varepsilon)$, which is function of Z_{mix} with ε as a parameter.

Eq. (7) can, therefore, take the following form:

$$\frac{1}{\omega}\frac{d\omega}{dt} = g_{aver}(zo_{mix})\,. \quad (16)$$

Hence, the phytoplankton biomass in the column does not change if the right-hand side of Eq. (16) satisfies the condition:

$$g_{aver}(zo_{mix}) = 0\,. \quad (17)$$

2 The results obtained from this equation after taking into account phytoplankton shading, competition for light, photoinhibition, sinking and flushing were included in grant applications (entitled *„Growth and competition of phytoplankton for light in a mixed water layer – theoretical analyses"*) to the Ministry of Science and Higher Education (in Poland) No N304 095 31/3419 of 31 January 2006, and No N304 098 32/3666 of 31 July 2006. The essential part of this article, along with this equation and comments on it, was written at that time.

When such a zo_{mix} exists it is called, as already mentioned, the critical optical depth (Szeligiewicz 1999, 2000) denoted here by zo_{cr}. Similar concept of critical optical depth was also later proposed by Diehl et al. (2015). Based on Eq.(17), the position of zo_{cr} on the zo axis in the graph of the function $g(zo)$ can be indicated (Fig. 2).

The graph of the relationship between g_{aver} and zo_{mix} , as an example, can be determined from the qualitative graph of the g *vs* zo function. The latter follows from generally assumed shape of the $g(I)$ function and from the dependence of light intensity I on zo. According to Eq. (3) and Eq. (13) the light at the optical depth zo in the column is given by:

$$I(zo) = I_{in}\, e^{-zo}. \qquad (18)$$

Therefore, light intensity I monotonically decreases with zo (Fig. 2a), then at a given I_{in} following the assumption (6) the specific growth rate g as a function of zo also monotonically decreases with zo ($dg/d(zo) < 0$) (Fig. 2b). If $g > 0$ at $zo = 0$ then $g < 0$ if zo is too large and resulting I too low to support phytoplankton growth, and $g = 0$ for an intermediate (compensation) optical depth zo_c at which light is said to be compensation light I_c, i.e. following Eq. (9) (Fig. 2a)

$$I_c = I_{in}\, e^{-zo_c}, \qquad (19)$$

where

$$zo_c = \varepsilon\, Z_c. \qquad (20)$$

Further considerations will be performed under assumption (8), that $I_{in}>I_c$, or:

$$zo_c > 0 \quad (\text{or } g\,(0)>0). \qquad (21)$$

For qualitative concordance of the curves with reality in case of lack of photoinhibition, an additional assumption (9) (yet not necessary for further considerations) resulting from physiological limits of the growth is adopted that function $g(I)$ reveals saturation (i.e., it is no greater than a species-specific positive limit constant value) for high light intensities.

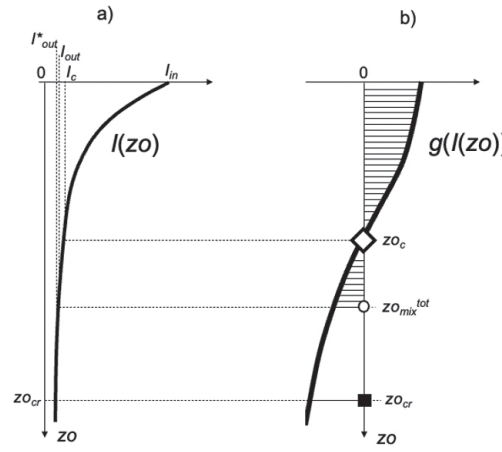

Figure 2. g**-based COD model. It presents the idea of Sverdrup's critical depth model included also in the** g**-based CD model of Fig.1, expressed now by optical depth. (a) Variation of light intensity** I **vs. optical depth (**zo**) within the mixed column for a particular value of** I_{in}**, with compensation light** I_c**, light at the bottom of the column,** I_{out}**, and critical light intensity** I^*_{out} **indicated. (b) The net specific growth rate** g **as a function of optical depth** zo **within this column. The meaning of the symbols used here is analogous to that in Fig.1, i.e., the optical compensation depth (**zo_c**) and the optical critical depth (**zo_{cr}**) are denoted by '◊' and '■' respectively, whereas "o" marks position of a given optical depth of the mixed column,** zo_{mix}^{tot}**. For further explanations, see text**

In what follows, hypothetical curves $g(I)$ that satisfy above assumptions will be used. In this context it is worth mentioning that the curves $g(zo)$ for a given ε are simply the curves $g(z)$ with respect to the z axis which is multiplied (rescaled) by the factor ε. Similarly, this applies to $I(zo)$ curves relative to $I(z)$ curves. In addition, the incorporation of assumption (9) causes the curves $g(I)$ and $g(zo)$ to assume more or less sigmoidal shape that was already tacitly included in Fig. 1, which in the extreme case also comprises mimicking the variation of $I(zo)$ or $I(z)$ as in the classical version of the CD model (Sverdrup 1953).

If the optical depth of a column is equal to zo_{cr}, then Eq.17 is satisfied. That is, the biomass produced in the column above zo_c (i.e., where $g(zo)>0$) is balanced by its net losses in the rest of the column (i.e., where $g(zo)< 0$). Graphically this means (Fig. 2) that the respective (hatched) areas between the plot of the $g(zo)$ curve and the zo axis are equal to each other, analogous to the g-based CD model, and to the model of Sverdrup (1953). Maintaining the convention of the Sverdrup (1953) model and analysing Fig.(2) the growth criteria are derived in this version of the model expressed through the relationship between a given optical depth of the mixed column, denoted now as $zo_{mix}{}^{tot}$ for further purposes (e.g. to discern this value on the zo_{mix} axis) and zo_{cr} (cf. Szeligiewicz 2000), i.e.,

$$g_{aver}(zo_{mix}^{tot}) \begin{cases} < 0 \quad for \quad zo_{mix}^{tot} > zo_{cr} \\ = 0 \quad for \quad zo_{mix}^{tot} = zo_{cr} \\ > 0 \quad for \quad zo_{mix}^{tot} < zo_{cr} \end{cases}. \tag{22}$$

The above results expressed by the critical optical depths can also be interpreted by the critical light intensity at the bottom of the column, thus obtaining the growth criteria established by the CL model (cf. Introductionto to this paper) (Fig. 2), and inversely. It should be noted that following Eqs (10) and (11) the light at the base of the column is equal to (Szeligiewicz 2000):

$$I_{out} = I_{in}\, e^{-zo_{mix}^{tot}}, \tag{23}$$

and at a stationary state

$$I_{out}^{*} = I_{in}\, e^{-zo_{cr}}, \tag{24}$$

where

$$zo_{cr} = \varepsilon Z_{cr}. \tag{25}$$

The main difference from Fig. (1) is the independence of the functions $I(zo)$ and $g(zo)$ used here from Z_{mix} and ε. Since the value of zo_c is determined by the intersection point of the function $g(zo)$ with the zo-axis, whereas the point of zo_{cr} is related to Eq. (17), that is both of them characterise the course of the function $g(zo)$ then both zo_c and zo_{cr} are also not affected by ε and Z_{mix}. Hence: result (1): zo_c and zo_{cr}, and consequently also I^{*}_{out} (Eq.24) do not depend on either Z_{mix} or ε. Moreover, also: result (2): the ratio zo_c/zo_{cr} does not depend on either Z_{mix} or ε.

Result (1) means, among other things, that zo_c , zo_{cr} and I^{*}_{out} at a given constant I_{in} are the same both in a phytoplankton monoculture and in a multispecies system, or in general, they are independent of the light absorbers in the column. They are g-specific (or species-specific) under assumptions adopted in the model. This result related to I^{*}_{out} is one of the key findings in the CL model, but it is obtained here as a straightforward consequence of the dependence of the g function exclusively on zo. These quantities, though, depend on the I_{in}. However, it can be assumed that the values of the g function do not refer to a constant value of I_{in}, but denotes the specific net growth rate on a time scale of one day at a fixed daily variation of I_{in}.

Result (2), in turn, says that a stationary state of phytoplankton occurs at a g-specific (or species-specific) constant value of the zo_c/zo_{cr} ratio. This means that this stationary state occurs when the quotient zo_c/zo_{mix} attains this ratio zo_c/zo_{cr}. This leads to another important statement that phytoplankton growth is related to the Z_c/Z_{mix} ratio which attains the critical value of Z_c/Z_{cr} when phytoplankton biomass approaches the stationary state. Although both Z_c and Z_{cr} depend on ε, given result (2) and putting $Z_{mix} = Z_{cr}$ it appears that the ratio Z_c/Z_{cr} is species-specific and does not depend either on ε or on Z_{mix} since within a mixed column

$$\frac{Z_c}{Z_{cr}} = \frac{\varepsilon Z_c}{\varepsilon Z_{cr}} = \frac{zo_c}{zo_{cr}}. \tag{26}$$

The constant value of the Z_c/Z_{cr} ratio also emerges from the critical light theory (Huisman 1999), as well as from the critical depth model, namely, as stated by Sverdrup (1953)

$$\frac{Z_{cr}}{Z_c} = \frac{e^{\varepsilon Z_c}}{\varepsilon Z_c}, \qquad (27)$$

using the notation of the present work. So, if zo_c (equal to εZ_c) is constant for a given function $g(zo)$ (result (1)) then it follows from the above equation that the value of Z_c/Z_{cr} is also constant. It is worth noting that the ratio Z_c/Z_{cr} (usually written as Z_{eu}/Z_{cr}, where Z_{eu} – the depth of the euphotic zone) is regarded by many researchers as the proportion between the time spend by phytoplankton cells in the light and the time in the dark, or as the amount of energy they receive, or as the extent to which phytoplankton production is limited by light (e.g. Reynolds 1987; Gameiro et al.2007; Huisman 1999; Várbíró et al. 2018). They report that certain "critical values" of this ratio determine phytoplankton growth.

1.3. g_{aver} -based COD model

The model uses a g_{aver} plot representing a function of the optical depth of the column (Eq.14) to determine the balance of biomass in the column and the critical optical depth (COD) of that column. According to Eq.(14) each point on the curve g_{aver} expresses average net specific growth rate *(g)* over optical depth $zo=zo_{mix}$ of the mixed column at a constant light supply to the column I_{in}. Each such point is obtained at a given value of ε and a given value of Z_{mix} following assumptions admitted to derivation of Eq.(1) and Eq.(14). However, any combination of these values is possible at this point, if their product is equal to zo_{mix} as g_{aver} is a function of zo_{mix}, and not of Z_{mix} or ε separately.

According to the general shape of *g vs zo* mentioned above the *zo*-average specific net growth rate over interval $[0, zo_{mix}]$, g_{aver}, is a monotonically decreasing function of zo_{mix} (when the effect of photoinhibition on *g,* and consequently on g_{aver}, is not taken into account following assumption (6)), reaches zero at $zo_{mix}=zo_{cr,}$ is positive for $zo_{mix}< zo_{cr}$ and negative for $zo_{mix}>zo_{cr}$ (Fig. 3). Moreover g_{aver} attains the value of $g(0)$ for $zo_{mix}=0$ because g_{aver} as the average of g over interval $[0, zo_{mix}]$ approaches $g(0)$ when zo_{mix} draws near 0.

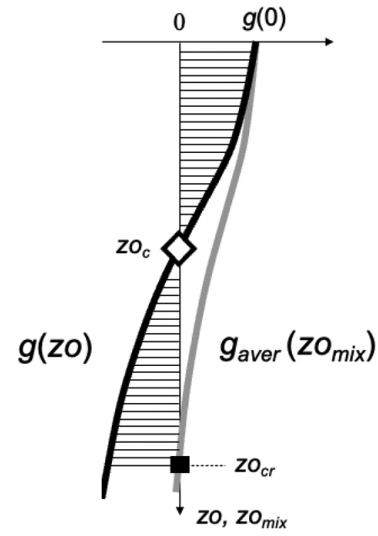

Figure 3. A hypothetical graph of the function $g(zo)$ (thick black line) and related graph of $g_{aver}(zo_{mix})$ (thick grey line). The optical critical depth zo_{cr}, is that of the optical depth of the mixed column, for wich the hatched areas above and below the zo_c are equal to each other (Eqs 14 and 17). At the zo_{cr} point, the g_{aver} line crosses the zo_{mix} axis. Other symbols as in the previous figures. Both the graph $g(zo)$ and g_{aver} do not depend on Z_{mix} and ε. In particular, they do not depend on the biomass or its density in the column.

Using similar reasoning as before for the function $g(zo)$, we can say that g_{aver} for a given I_{in}, is only function of zo_{mix} and in these considerations it does not depend on either ε or Z_{mix}. This means in particular that (result (3)): the g_{aver} function (like g) is not affected by light absorbers in the water column, including phytoplankton biomass.

Since the function g_{aver} does not depend on ε and Z_{mix}, then in particular the point where g_{aver} intersects the zo_{mix} axis (that is zo_{cr}, or zero point in Fig.(3)) also does not depend on ε and Z_{mix}, as result (1) says.

Results (1) – (3) are relevant to further considerations on phytoplankton growth

in the column and competition for light between different phytoplankton species. Both the $g(zo)$ and $g_{aver}(zo_{mix})$ functions can be used for this.

The CD and CL models, as well as the g-based COD model, only indicate the direction of biomass change in the column. But from the point of view of e.g., bloom formation, the rate of growth is also important. Svedrup (1953) suggests that a certain measure of the mixed column production is the magnitude of the deviation of the value of Z_{mix} from Z_{cr}. For g-based COD model, one can proceed similarly, i.e., compare the absolute magnitudes of zo_{mix} and zo_{cr} with each other and infer from this the level of growth rate (when there is no photoinhibition). However, the use of the function g_{aver} seems to be more convenient and allows not only to show the position of the critical point on the zo_{mix} axis, but also to demonstrate the value of g_{aver} ($zo_{mix}{}^{tot}$), or equivalently (Eq.16), the rate of relative change in phytoplankton density in the mixed column of the optical depth $zo_{mix}{}^{tot}$ (Fig. 4). Therefore, further considerations will mainly be based on g_{aver} function, where this information will be used.

A given optical depth of a mixed column labelled as $zo_{mix}{}^{tot}$ according to assumption (7c) and Eq. (15) can be expressed as the sum of the optical depth due to the presence of background and phytoplankton biomass light absorbers (Fig. 4):

$$zo_{mix}^{tot} = zo_{mix}^{bg} + zo_{mix}^{\omega}, \qquad (28)$$

where

$$zo_{mix}^{bg} = \varepsilon_{bg} Z_{mix}, \qquad (29)$$

$$zo_{mix}^{\omega} = \varepsilon_{\omega} Z_{mix}. \qquad (30)$$

Thus, $zo_{mix}{}^{bg}$ represents the smallest optical depth, $min\_zo_{mix}{}^{tot}$, of the water column at the given value of Z_{mix} and ε_{bg}

$$min\_zo_{mix}^{tot} = zo_{mix}^{bg}, \qquad (31)$$

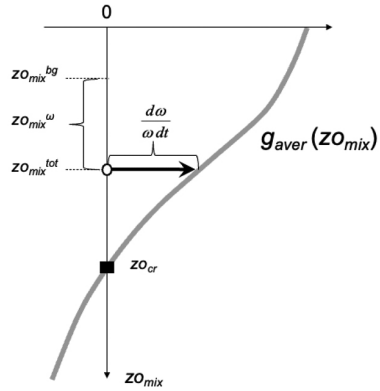

Figure 4. g_{aver} -based COD model. The idea of the critical optical depth model as expressed by the graph of g_{aver} (zo_{mix}). The zo_{cr} corresponds to the intersection of this curve with zo_{mix} axis. The components of a given optical depth of the water column $zo_{mix}{}^{tot}$ i.e., related to the attenuation of light by the biomass, $zo_{mix}{}^{\omega}$, and the background, $zo_{mix}{}^{bg}$, (Eqs 29 and 30) are shown. As in the previous case, depending on whether the $zo_{mix}{}^{tot}$ is equal to, greater than or less than the zo_{cr}, the phytoplankton increase, decrease, or are at stationary state accordingly. But now, in addition, the value of g_{aver} ($zo_{mix}{}^{tot}$) directly represents the magnitude of the rate of these changes corresponding to $zo_{mix}{}^{tot}$, which is shown by the length of the horizontal arrow fixed at point "o": it is directed to the right (if g_{aver} ($zo_{mix}{}^{tot}$)>0), or to the left (not shown) if g_{aver}($zo_{mix}{}^{tot}$)<0. With a given $zo_{mix}{}^{bg}$, the magnitude of the $zo_{mix}{}^{tot}$ and thus the magnitude and direction of this rate depend on the magnitude of the $zo_{mix}{}^{\omega}$, which is linearly dependent on the phytoplankton biomass (Eq.33). The presence of phytoplankton biomass in the column means that $zo_{mix}{}^{\omega}$ >0, while in the absence of the biomass $zo_{mix}{}^{tot}$=$zo_{mix}{}^{bg}$. In contrast, the values of $zo_{mix}{}^{tot}$< $zo_{mix}{}^{bg}$ do not occur in the column – they have no physical sense. This applies to all subsequent drawings containing g_{aver}(zo_{mix}) curves. For further explanations, see text

which occurs when there are no phytoplankton in this column, i.e., when $zo_{mix}{}^{\omega}$=0. Then, also, the column's light attenuation coefficient, ε, has a minimum value, min_ε, equal to

$$min\_\varepsilon = \varepsilon_{bg}. \qquad (32)$$

Moreover, Eqs (30) and (29) given Eqs (5) and (6,) can be written as (cf. Huisman and Weissing 1994)

$$zo_{mix}^{\omega} = k_{\omega}\,\omega\, Z_{mix} = k_{\omega} W, \qquad (33)$$

and

$$zo_{mix}^{bg} = Z_{mix} \sum_{i=1}^{n} k_{b,i} b_i = \sum_{i=1}^{n} k_{b,i} M_i := Q_{bg.} \qquad (34)$$

That is, the optical depth $zo_{mix}{}^{\omega}$ associated with a phytoplankton species is a measure of the biomass, W, of that species in the column with a proportionality factor k_{ω}. The optical depth of the background, denoted here by Q_{bg}, is, in turn, the sum of the optical depths of the background absorbers. Each of them is proportional to the mass, M_i, (cf. Eq. 34) of this absorber in the column. Hence

$$zo_{mix}^{tot} = k_{\omega} W + Q_{bg}. \qquad (35)$$

With this in mind, in the following, instead of the term "optical depth" I will also alternatively use the term "opacity load". The rationale is that loads are related here to the masses of the absorbers. In addition, the term "load" is more appropriate to the situation where the mass of absorbers is created or destructed in the column (in the case of phytoplankton), or is added to or removed from the column e.g., in the case of Z_{mix} changes. Furthermore, the term "opacity load" expresses the sense of its negative impact on light intensity and consequently on phytoplankton growth.

1.4. g_{aver}-based COD model with feed-back between growth and self-shading

So far, the feedback loop between growth and self-shading was not included in the above considerations. That case corresponded to the growth conditions specified in the CD model. That is, no account was taken of the biomass currently produced and its contribution to ε. As in the case of CD model, the feedback loop was therefore not closed. In other words, that case described a momentary trend or snapshot of the situation occurring in the column. In the case of the g-based CD model, it was pointed out that a change in ε as a result of, for example, changes in column biomass would affect the Z_c and Z_{cr} values, as it could reshape the $I(z, \varepsilon)$ and $g(I(z, \varepsilon)$ profiles. In the g-based COD and the g_{aver}-based COD models, the biomass did not affect $I(zo)$ and $g(zo)$ (as well as $g_{aver}(zo_{mix})$) profiles. Thus, the value of zo_c and zo_{cr} did not change either. However, it has not yet been said how the optical depth of the column changes as the phytoplankton grows. In contrast, Fig. 5 shows when such a feed-back, as in the CL model, occurs, and Fig. 6 presents the effects it imposes.

In the situation shown in Fig. 5, the biomass is growing, so $zo_{mix}{}^{\omega}$ increases and reaches an equilibrium maximum value (Fig. 6) labelled as $zo^{*}{}_{mix}{}^{\omega}$, corresponding to the equilibrium biomass when $zo_{mix}{}^{tot}$ equals zo_{cr}. The length of the section $zo_{mix}{}^{bg}$ does not change during this time, because in this case neither the Z_{mix} changes nor the concentration of the background absorbers. So, Eq.(28) can be rewritten as

$$zo_{cr} = zo_{mix}^{*\,\omega} + zo_{mix}^{bg}. \qquad (36)$$

Once the biomass has reached equilibrium W^*, Eq.(35) can take the form (cf. Huisman and Weissing 1994)

$$zo_{cr} = k_{\omega} W^{*} + Q_{bg}. \qquad (37)$$

The zo_{cr} can be interpreted in view of Eqs (36) and (37) together with Figs (5) and (6) as the total critical opacity load in the column, which suppresses the net growth in that column to zero (Eq.22). The components of the total load are the opacity load associated with the phytoplankton biomass $k_{\omega}W$ and opacity load associated with background absorber masses Q_{bg}. The magnitude of the total critical opacity load is determined by the function g_{aver} (as the zero point of this function, cf. result (1)) and not on the relative proportions of its components.

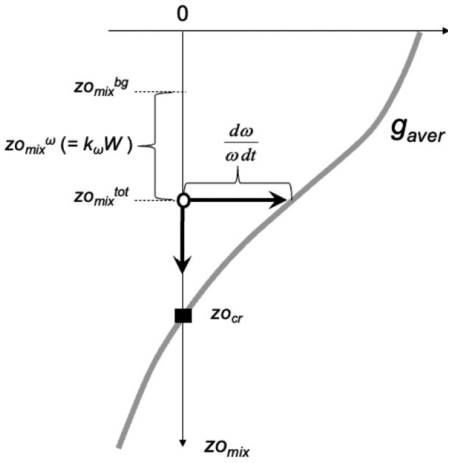

Figure 5. g_{aver}-based COD model taking into account the feedback between zo_{mix}^{ω}, and indirectly between zo_{mix}^{tot}, and $g_{aver}(zo_{mix}^{tot})$. The figure shows the case when initially $zo_{mix}^{tot} < zo_{cr}$ and consequently $g_{aver}(zo_{mix}^{tot})>0$. There is therefore an increase in the phytoplankton density in the column and thus an increase in zo_{mix}^{ω} (as well as in biomass, W), and consequent an increase in the zo_{mix}^{tot} (symbolised by an arrow pointing downwards on the zo_{mix} axis). The rate of these changes slows down as the zo_{mix}^{tot} increases and consequently the value of the $g_{aver}(zo_{mix}^{tot})$ decreases. The change stops at $zo_{mix}^{tot} = zo_{cr}$, when $g_{aver}(zo_{mix}^{tot})=0$. Similar reasoning can be performed when initially $zo_{mix}^{tot} > zo_{cr}$. The g_{aver} curve for $zo_{mix}^{tot}<zo_{mix}^{bg}$ has no physical sense, cf. Fig. 4)

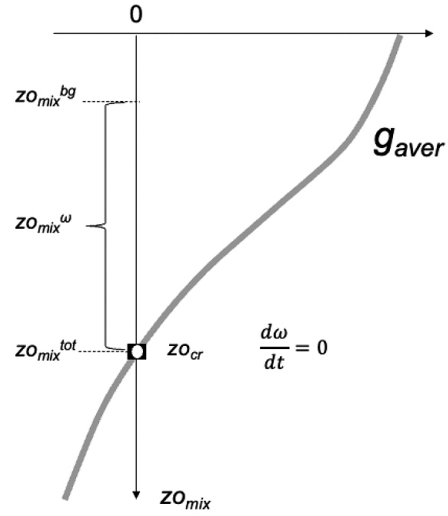

Figure 6. The final result of the approaching of equilibrium by the biomass. The position of the zo_{mix}^{tot} (marked with an "o") due to growth regulation by self-shading then overlaps with the critical optical depth . The biomass in this situation no longer changes. In such a case zo_{mix}^{ω} can be denoted as $zo^{*}_{mix}{}^{\omega}$ and Z_{mix} as Z_{cr}. Meaning of the other symbols as in the previous figures

The optical depth of the mixed column, zo_{mix}^{tot} , tends to the critical optical depth, zo_{cr}, and at the same time the phytoplankton biomass in this column, W, tends to the equilibrium biomass W*>0, if (Fig. 6)

$$zo_{mix}^{bg} < zo_{cr}\,. \tag{38}$$

This figure shows that the opacity load, $k_\omega W$, related to phytoplankton attains its maximum value when the biomass reaches equilibrium, i.e. when $zo_{mix}^{tot} = zo_{cr}$, provided that initially $zo_{mix}^{tot} < zo_{cr}$. The size of the equilibrium zo_{mix}^{ω} and thus the equilibrium biomass, W^{*}, is larger the smaller is the zo_{mix}^{bg} (Fig. 6). In particular, there will be a theoretical maximum W^{*} in the column and thus a maximum $zo^{*}_{mix}{}^{\omega}$ (equal to zo_{cr}) when $zo_{mix}^{bg} = 0$. This would occur if, for example, a) water was perfectly transparent (ε_{bg}=0) when at the same time Z_{mix} had any finite positive value, b) Z_{mix}=0, in this case, however, the phytoplankton density ω would have to reach infinitely high values (Szeligiewicz 1997), as $W^{*} = \omega Z_{mix}$. If the water was perfectly transparent, biomass growth would initially occur throughout the whole column, regardless of its depth. But regardless of the value of Z_{mix}, the same equilibrium biomass would be achieved, and the same optical load would be attained equal to zo_{cr} (cf. Eq.37). The value of the zo_c/zo_{cr} quotient would, according to result (2), be the same as in the presence of background absorbers.

If there is a larger component of zo_{cr} associated with the background Q_{bg} (equal to zo_{mix}^{bg}), there will be a correspondingly smaller component associated with equilibrium biomass to maintain the total critical load (Eq.(36) and Eq.(37)). In the extreme case, there is:

$$zo_{mix}^{bg} = zo_{cr}, \tag{39}$$

then $zo^{*}_{mix}{}^{\omega} = 0$, and consequently $W^{*} = 0$. If at the same time one assumes that the larger Q_{bg} and the larger zo_{mix}^{bg} are due to the larger Z_{mix}, i.e. that the deeper column contains more background absorbers, then Eq.(39) together with Eq.(29) imposes a limit for such the largest Z_{cr}, that I call the maximum critical depth, max_Z_{cr} (Szeligiewicz 1998), i.e.

$$\varepsilon_{bg}\, max\_Z_{cr} = zo_{cr}, \tag{40}$$

hence

$$\max\_Z_{cr} = \frac{zo_{cr}}{\varepsilon_{bg}}, \tag{41}$$

in other words, in view of Eq. (32)

$$\max\_Z_{cr} = \frac{zo_{cr}}{\min\_\varepsilon}. \tag{42}$$

Therefore, if

$$Z_{mix} < \max\_Z_{cr}, \tag{43}$$

then an equilibrium biomass ($W^{*} > 0$) in such a mixed column may arise (Szeligiewicz 1998). Eq. (38) is then satisfied. Fig. 7, on the other hand, shows an example where the condition expressed by Eq. (38) is not fulfilled. This figure refers to the column initially containing biomass ($W > 0$) because $zo_{mix}^{tot} > zo_{mix}^{bg}$, and zo_{mix}^{tot} diminishes as a result of $g_{aver}(zo_{mix}^{tot}) < 0$. However, it doesn't reach the zo_{cr} value, but the zo_{mix}^{bg}, which is the lowest possible value of zo_{mix}^{tot} (Eq.31). This means that the biomass disappears not having achieved an equilibrium $W^{*} > 0$. It is worth noting that if $zo_{mix}^{tot} < zo_{cr}$, the condition for reaching such equilibrium biomass (Eq.38) is ensured. Fig. 7, on the other hand, shows that this is not necessarily the case if initially $zo_{mix}^{tot} > zo_{cr}$.

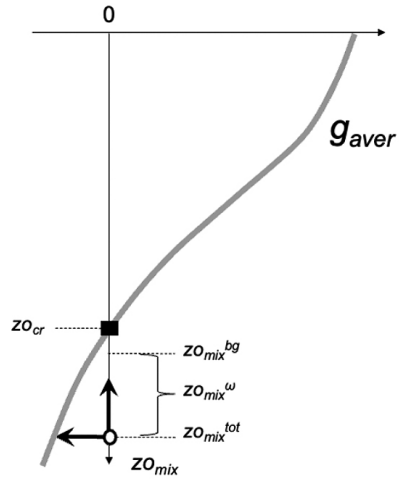

Figure 7. Example of the situation when the equilibrium positive biomass ($W^{*} > 0$) is not formed. In this case the condition set out in Eq. (38) or Eq. (43) does not hold

Eq. (38) can be expressed in terms of light intensity at the bottom of the column. Fig. 8 allows for cross-reference analyses between the results obtained here and the critical light intensity theory (CL model). For example, Fig. 8 shows that if zo_{mix}^{tot} follows, e.g. due to self-shading, to zo_{cr} (cf. Fig. 5), then at that time I_{out} goes to I^{*}_{out}, according to the CL model theory. It is possible to derive these conclusions similar as from Fig. 2, but now it is apparent not only whether the biomass is increasing (i.e., when $g_{aver}(zo_{mix}^{tot}) > 0$) or decreasing (when $g_{aver}(zo_{mix}^{tot}) < 0$), but also what is the rate of these changes depending on the value of zo_{mix}^{tot} as the course of the $g_{aver}(zo_{mix}^{tot})$ function is shown. Moreover, in particular, it can be shown from this figure that the condition expressed by Eq. (38) can be given as:

$$I_{out\ bg} > I^{*}_{out}. \tag{44}$$

i.e., as a necessary condition for growth also given by Huisman and Weissing (1994). At the same time, the considerations so far and Fig. 8 itself make it clear where this condition arises from.

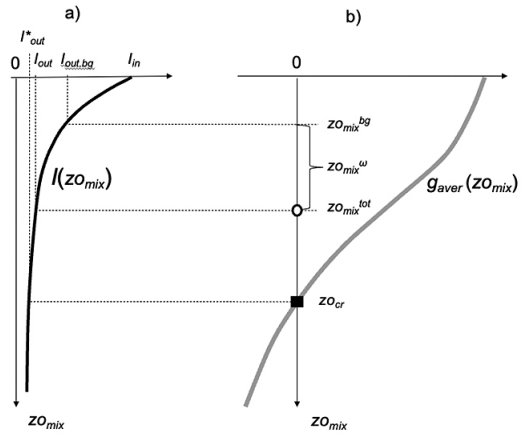

Figure 8. A juxtaposition of the light intensities at the base of the mixed column (a), as used in the CL model, with optical depths (or opacity loads) in that column (b), as referred to in the work discussed here, i.e. $I^*_{out}=I_{in}\exp(-zo_{cr})$, $I_{out}=I_{in}\exp(-zo_{mix}^{tot})$, $I_{out,bg}=I_{in}\exp(-zo_{mix}^{bg})$. **Note that the graph of the** I **vs.** zo_{mix} **relationship is actually the graph of** I **vs.** zo

In the CD model, the condition expressed by Eq.(43) in this case, is not needed, as the model only indicates whether net growth is increasing or decreasing, not whether an equilibrium state can be reached. If, on the other hand, the CD model is extended to include a self-shading regulation by which the biomass tends towards equilibrium, then any Z_{mix} satisfying the condition expressed by Eq.(43) becomes over time a critical depth once the biomass has reached equilibrium (Szeligiewicz 1998). It can also be said in another way that it is the Z_{cr} that goes to a given Z_{mix} due to self-shading (Szeligiewicz 1998, Platt et al. 2003, Kovač et al. 2021) when the biomass reaches an equilibrium. Indeed, if the column of depth Z_{mix} has an optical depth zo_{mix}^{tot}, then the light attenuation coefficient ε in this column is

$$\varepsilon = \frac{zo_{mix}^{tot}}{Z_{mix}} . \qquad (45)$$

If it is further assumed that the above ε is independent of the depth of the water column, then deepening the column leads to an increase in the opacity load in the column and shallowing the column results in a decrease in this load. It is therefore possible, if necessary, to adjust this depth in such a way that the opacity load in this column to be equal to zo_{cr}. Then such a column depth would be equal to Z_{cr}:

$$Z_{cr} = \frac{zo_{cr}}{\varepsilon} = \frac{zo_{cr}}{zo_{mix}^{tot}} Z_{mix} . \qquad (46)$$

If $zo_{mix}^{tot} < zo_{cr}$, there is a deficiency in the optical load zo_{mix}^{tot} in the column of depth Z_{mix} relative to the critical load zo_{cr}. From Eq.(46), the value of Z_{cr} can be found, but instead the qualitative essence of this result will be expressed, that then

$$Z_{cr} > Z_{mix} , \qquad (47)$$

i.e., the load must be completed by deepening this column to a depth of Z_{cr}. In contrast, when $zo_{mix}^{tot} > zo_{cr}$, the opacity load in the column of depth Z_{mix} is in excess of the critical optical load zo_{cr}. Then one states that

$$Z_{cr} < Z_{mix} . \qquad (48)$$

That is, this load should be reduced to the zo_{cr} value by shallowing this column to the depth Z_{cr}. Since, however, with the passage of time the zo_{mix}^{tot} load tends towards the zo_{cr} load as a result of self-shading, the aforementioned excesses or deficits in load become progressively smaller. Hence, the Z_{cr} calculated in the above manner – as shown from Eq.46 – tends towards the depth Z_{mix}.

The above reasoning assumes that the coefficient ε does not change with changes in Z_{mix}. This is satisfied when the column is shallowed, i.e., when $Z_{cr} < Z_{mix}$, as the column is well-mixed. However, ε may change when the column is deepened, as it also includes the water hitherto beneath the column, in

which the concentrations of light absorbers may be different from those in this column. However, this should not affect the above qualitative conclusion. Nevertheless, this reasoning can be repeated by considering directly the opacity loads of these absorbers in the following way (Fig. 9).

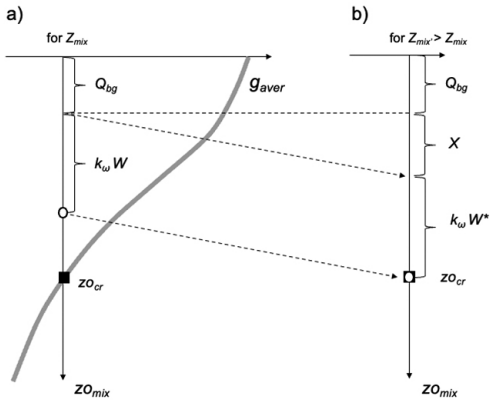

Figure 9. The effect of deepening Z_{mix} to Z_{mix}' which incorporates the opacity load X coming from under this column into that column, so that $Q_{bg} + X + k_w W = zo_{cr}$. Then the existing biomass (and possibly also the biomass added to the column as a result of its deepening) W in the column becomes the equilibrium biomass W^*. This procedure can be seen as a demonstration that, in the case of opacity load deficiency relative to the total critical opacity load (i.e., zo_{cr}) in the column, the critical depth ($Z_{cr} = Z_{mix}$') would lie deeper than Z_{mix}. The order in which the opacity loads appear on the zo_{mix} axis does not matter, but it is assumed that the load subject to change as a result of phytoplankton growth, i.e., $k_w W$ (equal to zo_{mix}^{ω}), lies beneath the other loads

Let a column of depth Z_{mix} contain a certain (opacity) load of background absorbers Q_{bg} and a certain (opacity) load of biomass $k_\omega W$, but the zo_{mix}^{tot} is too small for the biomass to remain in equilibrium, i.e. $zo_{mix}^{to} = Q_{bg} + k_\omega W < zo_{cr}$ (Fig. 9). Let there be, at the same time, water under the column in question containing some load of absorbers distributed continuously with depth. Furthermore, let the g_{aver} function describe the relative biomass rate of change in the column. The missing load X to balance the total load could, however, theoretically be supplemented as a result of an increase in the mixing range, i.e., by a corresponding increase in Z_{mix} to the value of Z_{mix}'. This X load can include the load of phytoplankton biomass as well as the load of other absorbers – it does not need to be specified. What is important, however, is that owing to X the $zo_{mix}^{tot} = zo_{cr}$, in which case the contained biomass in the column becomes equilibrium, both the biomass already present and potentially added. I will call such Z_{mix}' as calculated Z_{cr}, denoted hereafter as Z_{cr}^{calc}. An analogous reasoning can be carried out with an overload of zo_{mix}^{tot}, i.e., when $zo_{mix}^{tot} > zo_{cr}$. Z_{mix} would then need to be reduced to the appropriate Z_{cr}^{calc}. However, in view of the change in W due to self-shading towards equilibrium biomass in the existing column of depth Z_{mix}, the attached or detached load X to obtain equilibrium biomass would be progressively smaller. In fact, the Z_{cr}^{calc} tends towards the Z_{mix} value over time.

This example also demonstrates that changes in Z_{mix} and the attachment or detachment of an opacity load to or from the column in question can be included in the presented model. To my knowledge, in general, these effects in the CD type models have not yet been fully considered. This example further shows that simply deepening the Z_{mix} without attaching an opacity load (leading only to dilution of the absorbers), does not affect the growth of phytoplankton in the column. Furthermore, the effect of this deepening may depend on what optical load is added. This can probably be a useful remark when trying to apply the Sverdrup model to the case considering Z_{mix} changes, since phytoplankton growth is driven in this model by Z_{mix}. Therefore, the result 4 can be stated as: the use of opacity loads (or optical depths) is more appropriate than the use of depth of the column to express the idea of the Sverdrup critical depth model especially when the effects of Z_{mix} changes are considered.

1.5. g_{aver}-based COD model of competition among phytoplankton species for light

So far, the case of a single phytoplankton species in the water column has been considered, or a given assemblage of species taken as a whole (similar, it seems, to the CD model, as that model was applied to naturally occurring phytoplankton communities), characterized by a single function g, and consequently by the single function g_{aver} determined here for a given I_{in}. It is now assumed that N phytoplankton species are present in the column. Each i-th species among them is assigned a function g_i and the resulting function $g_{aver,i}$, built as already described (Eq. 14), i.e.

$$g_{aver,i}\left(zo_{mix}\right)=\frac{1}{zo_{mix}}\int_0^{zo_{mix}} g_i\left(zo\right)d\left(zo\right) . \quad (49)$$

The increase in biomass density of the i-th species, ω_i, in a mixed column of optical depth zo_{mix} will be described by an equation analogous to Eq.(16), i.e.,

$$\frac{1}{\omega_i}\frac{d\,\omega_i}{dt}=g_{aver,i}\left(zo_{mix}\right) . \quad (50)$$

The co-occurrence of species in the column does not affect the g_i and $g_{aver,i}$ as these functions do not depend on ε (light attenuation coefficient dependent on light absorbers in the column), and other impacts on growth than mutual shading of species are not considered. Therefore, these species do not affect the values of the critical optical depth, $zo_{cr,i}$, and the compensation optical depth, $zo_{c,i}$, of each of these species. Interactions through mutual shading, on the other hand, occur, as in the CL model, through the influence of each species on the value of the ε. In turn, ε influences the value of zo_{mix}^{tot}. Let the light attenuation coefficient be expressed analogously to Eqs (4), (5) and (6), i.e.,

$$\varepsilon = \varepsilon_{bg} + \varepsilon_{\omega} , \quad (51)$$

where now, in particular

$$\varepsilon_{\omega} = \sum_i \varepsilon_{\omega_i} \quad (52)$$

$$\varepsilon_{\omega_i} = k_{\omega_i}\omega_i , \quad (53)$$

i.e. ε_{ω}, the attenuation of light due to phytoplankton is represented here by the sum of products of the $k_{\omega i}\,\omega_i$ where $k_{\omega i}$ is the specific light attenuation coefficient of phytoplankton biomass and ω_i is the biomass density of the i-th phytoplankton species contained in the column. The summation runs from i =1 to N. Whereas ε_{bg} is the constant background light attenuation coefficient related to water and other non-phytoplankton absorbers given by Eq. (6).

In view of the above and Eqs (28) and (30), the optical depth of the mixed column will be equal to

$$zo_{mix}^{tot}=zo_{mix}^{bg}+\sum_i zo_{mix}^{\omega_i} , \quad (54)$$

where

$$zo_{mix}^{\omega_i}=\varepsilon_{\omega_i} Z_{mix} , \quad (55)$$

is the opacity load (or optical depth) contributed to the total opacity load in the column by biomass of the i-th species.

Reasoning solely with the notion of optical depth and operating with the individual runs of the $g_{aver,i}$ function of each species, the process of mutual displacement of species in competition for light can be briefly described in a similar way to what Huisman and Weissing (1994) did with the light intensity at the base of a mixed column of water. As the biomass of each species increases or decreases, the zo_{mix}^{tot} value changes correspondingly. Thus, if only $zo_{mix}^{tot} > zo_{cr,i}$, the i-th species decreases, if $zo_{mix}^{tot} < zo_{cr,i}$, it increases, and when $zo_{mix}^{tot} = zo_{cr,i}$, it does not change, according to similar rule, as for a single species (Eq.22). Let the largest value among these $zo_{cr,i}$ values be denoted as max_zo_{cr}. If zo_{mix}^{tot} is less than the max_zo_{cr} (this is $zo_{cr,3}$ in the case shown in Fig. 10), then zo_{mix}^{tot} will reach max_zo_{cr} regardless of the

remaining $zo_{cr,i}$ values, because the biomass of the species corresponding to max_zo_{cr} is constantly increasing eventually making zo_{mix}^{tot} bigger until the latter equals max_zo_{cr}. At the same time, the biomass of each of the remaining species with smaller zo_{cr} will disappear, as it will start to decrease as soon as $zo_{mix}^{tot} > zo_{cr}$ for this species respectively. When $zo_{mix}^{tot} > max\_zo_{cr}$ initially, the biomasses of all species decrease as $g_{aver}(zo_{mix}^{tot}) < 0$ for each of these species. Consequently, zo_{mix}^{tot} is also decreasing. However, when zo_{mix}^{tot} approaches the value of max_zo_{cr}, the biomass of the species that is associated with this max_zo_{cr} stops decreasing, in contrast to the biomass of the other species, which decrease until they disappear (Fig. 10). It can be seen from these considerations and from Fig. 10 that the result of this competition does not depend on the initial value of zo_{mix}^{tot}, and that at the same time the biomass of the winning species reaches a positive equilibrium value in the column, as long as

$$zo_{mix}^{bg} < \max\_zo_{cr}\,, \qquad (56)$$

which is the equivalent of the condition expressed by Eq.(38) and now applies to a multispecies system. If $zo_{mix}^{tot} < max\_zo_{cr}$, then automatically the condition $zo_{mix}^{bg} < \max\_zo_{cr}$ holds, because zo_{mix}^{bg} is a non-negative component of zo_{mix}^{tot} (cf. the discussion on Eq.(38)). If $zo_{mix}^{bg} > max\_zo_{cr}$ then an equilibrium positive biomass is not achieved. In contrast, the biomasses of all competing species disappear if they were initially present in the column (cf. Fig. 7 for one species case in the column).

Fig. 10 shows that the competition for light is won by the species that is the most shade tolerant, i.e., that the value of the opacity load in the column still allows the winning species to grow or maintain positive equilibrium biomass but is too high for the other competing species to maintain itself. As a result, this species contributes to the highest opacity load (zo_{mix}^{tot}) in this column. If the coefficients $k_{\omega j}$ have all the same value, this competition leads to maximisation of the phytoplankton biomass in the column: the competition will be won by the species which produces the largest biomass in the column under the existing conditions. Hence, the result (5) can be formulated as follows: the winning species in the competition for light in the mixed water column is the species with the highest zo_{cr}. In other words, the winning species most of all the other species maximises the opacity load of the column. Huisman and Weissing (1994) also state that light absorption is maximised via this competition.

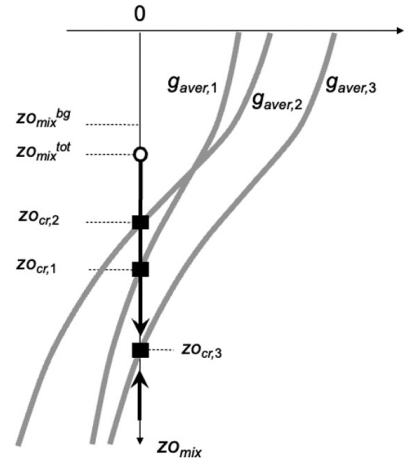

Figure 10. The mechanism of competition for light in the g_{aver}-based COD model using an example of three phytoplankton species (which are assigned the number 1, 2 and 3 correspondingly), whose average column specific net growth rates are described by the hypothetical functions $g_{aver,1}(zo_{mix})$, $g_{aver,2}(zo_{mix})$ and $g_{aver,3}(zo_{mix})$, determining the critical optical depths $zo_{cr,1}$, $zo_{cr,2}$ and $zo_{cr,3}$, respectively, where $zo_{cr,3} > zo_{cr,1} > zo_{cr,2}$. The initial value of zo_{mix}^{tot} is marked by the symbol "*o*" on the zo_{mix} axis (only its upper arbitrary position is shown). The values of $zo_{mix}^{tot} = zo_{cr1}$ and $zo_{mix}^{tot} = zo_{cr2}$ are related to a momentary biomass equilibrium for the species 1 and the species 2 accordingly, since biomass in the column, and consequently zo_{mix}^{tot}, tends to a stable equilibrium reached only at $zo_{mix}^{tot} = zo_{cr3}$. The $g_{aver,1}$, $g_{aver,2}$ and $g_{aver,3}$ curves for $zo_{mix}^{tot} < zo_{mix}^{bg}$ have no physical sense (cf. Fig. 4 and Eq. (31)). For further explanations, see text and previous figures

Result (5) can be directly told by the critical light intensity I^*_{out}, since taking into account Eq.(24), it follows that the winning species will be the one with the lowest I^*_{out}, in line with the CL model. Also conversely, based on the CL model one can formulate the result (5). Result (5) can also be expressed in terms of critical depths by applying, e.g., Eq.(46) separately to each of the optical depths of competing species, i.e.

$$Z_{cr,i} = \frac{zo_{cr,i}}{\varepsilon} = \frac{zo_{cr,i}}{zo^{tot}_{mix}} Z_{mix}. \qquad (57)$$

It follows that the winning species is the one with the highest Z_{cr} (Szeligiewicz 1998).

2. Discussion

The phytoplankton biomass balance in a surface-mixed water column formulated with Eq.14, once the critical optical depth has been determined, can be considered as a form of the critical depth model proposed by Sverdrup. To my knowledge, such a form of this model has not yet been discussed in literature. The considerations presented here focus on qualitative results and their relationship to the assumed profiles of $g(zo)$ or g_{aver} (zo_{mix}), rather than on approximations and formulae to obtain specific values of zo_{cr} or Z_{cr}. The method presented here makes it possible to look at the Sverdrup model from a more general perspective and directly relate the obtained qualitative results to the critical light intensity theory (CL model) and to the critical depth, Z_{cr}.

In order to show the differences in such a modified Sverdrup model with its primary version (CD model) based on the depth of the water column, the presentation of the former model was divided into three stages, which were named as the g-based CD model, g-based COD model and g_{aver}-based COD model, where each subsequent stage is related to the following modification introduced. Thus, each refers to the same balance of phytoplankton biomass in this column. The assumptions on which the CL and CD models are based were adopted. In particular, it was assumed that light reaches this column from above. Then, the light decreases with distance from the water surface (i.e., with depth in the column) as a result of its attenuation by the water and other absorbers in it, including phytoplankton.

The g-based CD model is an analogue of the Sverdrup model in the sense that the average specific net growth rate of phytoplankton across the column is related to the depth of that column (Eq.7). Diurnal variations in light were not considered. Attention was focused on light changes caused by depth. For the classical Sverdrup model, the local (at a given depth) specific net phytoplankton growth rate $g(I)$ is represented as a linear function of light intensity. Furthermore, the Sverdrup model assumes that the absorption of light in the column remains constant. However, in the g-based CD model, to emphasise potential variability of light absorption with time, and therefore also the variability of the $I(z)$ profile, it is assumed explicitly that this absorption depends on the amount of phytoplankton in the column. Furthermore, no specific form of the function $g(I)$ is introduced here, but instead it is considered that the function is subject to certain generally formulated assumptions. In addition, it is implicitly assumed that the function $g(I)$ (as in the CD and CL models) does not depend on time, so that it characterises a phytoplankton species in question, or the set of species in the column taken as a whole, depending on what is considered.

The second model (g-based COD model) involves changing the coordinate axis, i.e., replacing the depth z in the column of water with a light extinction coefficient equal to ε by the optical depth, zo, in that column. Thus, the column of depth Z_{mix} corresponds to the optical depth of this column, zo_{mix}. To make more intuitive sense of this substitution, I suggest that it is convenient to interpret the optical depth, zo, using the concept proposed in this work of a dimensionless

opacity or turbidity load along the light path from the water surface to the point in the column defined by the *zo*. The rationale for this is that, by definition, *zo* is the product of the masses of the absorbers in the path of that light and the "*k*" coefficients that assign these masses a capacity of attenuation of the light (Eqs 33 and 34). Moreover, for the sake of clarity, when I indicate a given value for the optical depth of a column on the zo_{mix} axis in the drawings, then to focus attention, I label it as zo_{mix}^{tot}. Then, the *zo* varies from zero (which corresponds to the water surface) to the zo_{mix}^{tot} value (related to the base of the column).

In view of the assumed constant light supply to the column the load *zo* determines the light intensity $I(zo)$ according to the Lambert-Beer law used in these considerations (Eq.18). Then the intensity of light at the point of the column determined by this load does not change, even if the load in the whole column were to change, as long as the intensity of light reaching the water remains the same. As a result, the value of $g(\mathrm{I}(zo))$, abbreviated in the paper as $g(zo)$, also does not change at this point in the column. This applies to any *zo* in the column. In other words, the course of these functions does not depend on the opacity load of the column. But the optical depth, zo_{mix}^{tot}, of this column, or in other words the opacity load in this column, changes, as opposed to the Z_{mix} depth, which is independent of this load. The optical depth of the column therefore only determines the upper range of variation of the optical depths within the column. However, the graphs $I(zo)$, $g(zo)$ and $g_{aver}(zo_{mix})$ themselves do not change. In the graphs in this paper this is shown as a shifting of the zo_{mix}^{tot} value along the zo_{mix} axis against unchanged graphs of the above relationships.

Thanks to the above properties, the $g(zo)$ functions established for each of the phytoplankton species in the column also do not depend on the biomasses of these species. They characterise each of these species in this column at a given light supply to it. For each of them, a compensation optical depth zo_c and a critical optical depth zo_{cr} can be determined, which will therefore also characterise the species under these conditions. As a result, the zo_{cr}/zo_c ratio is constant for a given species and is also characteristic of that species. This also applies to the Z_{cr}/Z_c ratio, which is also one of the important conclusions of the Sverdrup (1953) and CL models (Huisman 1999). It is worth noting that the independence of zo_{cr} for a species from ε and Z_{mix} is a direct consequence of the fact that the function $g(zo)$ is independent of ε and Z_{mix}. This finding is equivalent to one of the key results of the critical light model obtained by Huisman and Weissing (1994) through mathematical analyses, that the critical light intensity I^*_{out} for a given species is independent of ε and Z_{mix}. This is indeed the case, as there is a relationship between zo_{cr} and I^*_{out} expressed by Eq.(24). However, there is an important difference between the COD models (i.e., *g*-based COD and g_{aver}-based COD) and the CL-model. While in the CL model, invariability has been attributed only to the I^*_{out}, then in the case of the COD models, as already stated, the entire curves $g(zo)$ and $g_{aver}(zo_{mix})$ are invariant. This is particularly relevant in more complex growth scenarios (Szeligiewicz, in preparation).

Each $g(zo)$ profile can be assigned certain characteristic features from which, for example, the degree of relative shading tolerance to other species, determining the zo_{cr} value, can be inferred. So, it is possible to attribute some characteristics to $g(zo)$ profiles that confer a relative competitive advantage over other species. An analysis of the order of competitive exclusion of these species competing for light can be made in this context.

The concept of opacity load, introduced in this work, also appears to be useful in the intuitive interpretation of the phytoplankton growth criterion described by Eq.(22). It can then be formulated as follows. The phytoplankton biomass in the column increases ($g_{aver}(zo_{mix}^{tot})>0$) and thus

the opacity load of the column (zo_{mix}^{tot}) also increases, when this load is less than a critical load (zo_{cr}). The biomass does not change ($g_{aver}(zo_{mix}^{tot})=0$) and, as a result, the opacity load does not change when this load is equal to the critical load, while the biomass decreases ($g_{aver}(zo_{mix}^{tot})<0$) and the opacity load in the column decreases when it is greater than the critical load.

Hence, it can be seen that if this load is coupled to phytoplankton growth, i.e., it is increased or decreased as a result of the net phytoplankton growth, the opacity load will follow to the critical load (cf. Szeligiewicz 2000), and thus the biomass will tend towards the equilibrium biomass. Consequently, I_{out} follows to I^*_{out}, according to the CL model. At the same time – as shown in this paper (see also Szeligiewicz 1998, 2000) Z_{mix} will become Z_{cr}, or Z_{cr} will reach Z_{mix}. The model can thus also take into account the feedback between growth and self-shading.

This criterion (Eq.22), in contrast to Sverdrup's criterion based on Z_{mix}, is independent of Z_{mix} and light attenuation coefficient ε. The growth depends on the opacity load in the column, and therefore on the product of εZ_{mix}, which also indirectly encompasses the effects of changes in Z_{mix} as well as the effects of changes in ε. For example, it can show the obvious fact that the direction of phytoplankton growth in a column may be altered by adding or removing some opacity load from the column, and this need not be associated with a change in the Z_{mix} value. In particular, the direction of phytoplankton growth in a column even of constant depth Z_{mix} can be changed by flushing the column. It is also possible to take into account loads being added to or removed from the column as a result of entrainment or detrainment. This makes it possible to consider situations involving the effects of changing the Z_{mix} depth of this column. In my opinion the CD and CL models have so far not undertaken such issues.

It is worth noting that the Sverdrup criterion based on Z_{mix} (Eq.8) can also be derived from the criterion expressed by Eq.(22). In fact, if both sides of the relationship between zo_{mix}^{tot} and zo_{cr} in Eq.(22) are divided by a given value $\varepsilon>0$, then according to Eq. (15) and Eq.(25) the relationships between Z_{mix} and Z_{cr} results. In particular, it follows from Eq.(25) that the Z_{cr} thus obtained is related by this equation to ε, thus referring to the column where ε has the value resulting from this equation. Then in that column if Z_{mix} is equal to such Z_{cr}, then according to Eq.(25) $zo_{mix}=zo_{cr}$, which means that the biomass is stationary. With Z_{mix} deviations from Z_{cr}, the biomass will increase or decrease accordingly. In contrast, as mentioned earlier, with regard to the criterion expressed by Eq.(22), there is no such restriction on either ε or Z_{mix}.

It is also noteworthy that, despite the change in vertical coordinate, the form of the column phytoplankton biomass balance equation (Eq.16) remains unchanged with respect to Eq.7 representing the Sverdrup model. In both cases, the right-hand side of these equations expresses the same physical meaning – i.e., the average specific net growth rate in the column, regardless of whether the depth of the column is measured by depth Z_{mix} or depth zo_{mix}. Furthermore, the two averages are equal. Thus, the structure and consequently the simplicity of the Sverdrup model is retained, while the above-mentioned properties (i.e., invariance of $I(zo)$ and $g(zo)$ with respect to ε and Z_{mix}, or with respect to the opacity load in the column) are achieved.

The third model (g_{aver}-based COD model) analyses the plot of the right-hand side of the equation underlying the second model, g_{aver}, as a function of the optical depth (or opacity load) of the column. The graph of this function shows a simple relationship with the graph of the function $g(zo)$ (Fig. 3), which can also be seen as an advantage of the third model, facilitating intuitive interpretation of the results. Such a function can be formed for each species in the column. The intersection of the function with the zo_{mix} axis (or opacity load axis)

corresponds to the critical optical depth, or critical opacity load, for the growth of this species. However, instead of using the growth criterion based on critical values, which shows direction of the growth (Eq.8 and Eq.22), now one obtains direct information about the magnitude of the rate of the growth (equal to the value of $g_{aver,i}(zo_{mix}{}^{tot})$) for each species in question depending on the opacity load ($zo_{mix}{}^{tot}$) in the column. In spite of this, the critical optical depths (critical opacity loads) are still important information in these considerations. This is because, for a single species in the column, while taking self-shading into account, the opacity load of the column tends towards the critical opacity load for that species when, at that time, the biomass of that species reaches a stable equilibrium. When considering multiple species in a column, the winning species is the one which – unlike the other species – stops growing only at the highest critical opacity load. Thus, incorporating the self-shading mechanism leads to maximisation of the opacity load in the column. The outcome of the competition for light is thus obtained like in the CL model. These are results that, when expressed in terms of light intensity I_{out}, are the same as in the CL model. Anyway, in all three models ((i.e., g-based CD, g-based COD and g_{aver}-based COD) it was possible to express the results either by depths, or by optical depths, or by light intensities in the column. However, the terms such as "quantum yield" or "quantum return" used in the CL model were not currently needed for these considerations.

The approach proposed in the g_{aver}-based COD model for describing light-limited phytoplankton growth in a mixed water column provides a convenient tool for studying this growth in more complex scenarios (Szeligiewicz , in preparation). When competing species are considered, the graphical image to track this competition (e.g., Fig. 10) shows an array of g_{aver} curves corresponding to these species, independent of each other, and also independent of Z_{mix} and ε, placed in a common coordinate system. The only thing that changes in this graph e.g., during competition is the total opacity in the column, $zo_{mix}{}^{tot}$. This gives an easily accessible, intuitive insight into the process. This way of graphical presentation of competing species to my knowledge has not been shown in the literature. A consequence of the invariance of the functions $g(zo)$ and $g_{aver}(zo_{mix})$ with respect to the column opacity load is that these functions are also invariant when additional sources (S) affecting this load are included (Eq.58), which facilitates the consideration of more complex situations.

$$\frac{1}{\omega}\frac{d\omega}{dt} = g_{aver}\left(zo_{mix}\right) + S. \qquad (58)$$

For example, if phytoplankton sinking is explicitly taken into account in biomass growth, then Eq.(58) can be written as

$$\frac{1}{\omega}\frac{d\omega}{dt} = g_{aver}\left(zo_{mix}\right) - \frac{V}{Z_{mix}}, \qquad (59)$$

where V is the sinking speed of phytoplankton biomass. In that case the sinking reduces the produced phytoplankton biomass in the column and consequently influences the opacity load, $zo_{mix}{}^{tot}$, of the column, thus affecting the value $g_{aver}(zo_{mix}{}^{tot})$. However, the sinking does not impact on the course of the $g_{aver}(zo_{mix})$ function itself.

For theoretical experiments, any shape of the $g(zo)$ and $g_{aver}(zo_{mix})$ functions can be taken, including shapes that reflect photoinhibition, leading, for example, to alternative stable states of biomass in the column (Szeligiewicz[3], unpublished material). Such behaviour has been demonstrated by mathematical analysis and numerical experiments by Gerla et al. 2011, Hsu et al. 2013, and Martínez et al. (2018b). It is also worth noting that the $g_{aver}(zo_{mix})$ function does not have to be obtained by averaging of the function $g(zo)$ (Eq.14). It is postulated that thanks

3 In the already mentioned grant applications in 2006, the existence of such alternative equilibria was postulated in this context based on the method presented here.

to the direct biological interpretation of this quantity, it may come directly from measurements. In addition, it can be assumed that the functions $g(zo)$ and $g_{aver}(zo_{mix})$ refer to the daily net growth rate, taking into account diurnal fixed changes in the intensity of light reaching the column. This does not affect the reasoning presented here. The values of zo_c and zo_{cr} will then relate to the functions so understood.

In the presented COD models, it is possible to distinguish the components of the opacity load – the load originating from the background and the load originating from the phytoplankton biomass – and to visually study the effects of the size of these loads on growth and competitive exclusion of species. In addition, the opacity load associated with the biomass (zo_{mix}^{ω}) can be taken as a measure of that biomass, providing additional insight into the situation described (see, e.g., Fig. 9). Despite operating with opacity loads rather than Z_{mix} depth, the models presented in this paper allow for relating phytoplankton growth to Z_{mix} and its changes, in particular through the influence of Z_{mix} on the background loads (cf. Fig. 9, and Szeligiewicz, in preparation). The Sverdrup model concerns the evaluation of the direction of phytoplankton growth in a column of a given depth Z_{mix}. However, it does not consider the effect of changing the Z_{mix} combined with the entrainment of loads from under the column in question. The handling of opacity loads in the work presented here allows to take this phenomenon into account (cf. Fig. 9). However, it can be noticed that neither the Sverdrup model nor the CL model nor the COD models presented here take direct account of the dilution of phytoplankton when deepening the mixed layer (which is the basis of the dilution-recoupling hypothesis postulated by Behrenfeld (2010)). In the case of the COD models shown here, space has been eliminated – these models operate with dimensionless opacity loads. The COD models presented here only "perceive" Z_{mix} changes if these changes result in a change of opacity load in the column (cf. discussion to Fig. 9). It is also worth bearing in mind that changes in Z_{mix} can also lead, for example, to an influx of nutrients into the mixed column, or temperature changing in the column, which are also not included by these models.

The above considerations are based on assumptions taken from the CD and CL models, which impose constraints also on the models presented here. There is extensive discussion in literature (e.g., Sverdrup 1953, Platt et al. 1991, Smetacek and Passow 1990, Huisman and Weissing 1994, Weissing and Huisman 1994, Behrenfeld 2010, Fischer et al. 2014, Behrenfeld and Boss 2017, Paparella and Vichi 2019) on the implications of the assumptions made, as well as on the adequacy of the phytoplankton growth mechanism used to describe changes in phytoplankton biomass and blooms observed in the real reservoirs. These criticisms also apply to the considerations presented in this paper.

In summary, the modified Sverdrup models presented here (i.e. g-based COD and g_{aver}-based COD models) operate on invariant profiles of $g(zo)$ and $g_{aver}(zo_{mix})$ relative to opacity loads in the water column. In particular, these profiles depend neither on the column depth, nor on the presence of other phytoplankton species, nor on the phytoplankton biomass, nor do they change under the influence sinking or of entrainment or detrainment of biomass and other light absorbers, nor do they change upon the presence of other possible sources of these absorbers in the column. The phytoplankton growth criteria formulated from these models seem to be more universal. Furthermore, the result of competitive exclusion due to competition for light can be related to the individual, invariant (in the above sense) characteristics of these profiles that describe the species considered in the column. The g_{aver} profiles are related to the $g(zo)$ profiles by Eq. 14 (Fig. 3), i.e., by simple averaging, which also facilitates the intuitive interpretation

of the results of the COD models. In addition, the implemented $g_{aver}(zo_{mix})$ profiles directly provide the values of the growth rate corresponding to any optical depth of the mixed column, giving an insight into the whole picture of these relationships, which also widens the analysis of the above results. The COD models represent a more general form of the original Sverdrup model, retain its simplicity and become a convenient stage for further modifications and extensions, which to my knowledge, despite many studies published in the literature on the Sverdrup model, have not been fully exploited.

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