Critical depth concept: current state and prospects

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Abstract – The foundations of the classical critical depth model as well as problems and limitations related to its application are outlined. Recent modifications of the model resulting from reinterpretation of the critical light concept and from the inclusion the effect of temperature on phytoplankton growth are referred to. New possibilities of evaluation of the critical depth value – the key parameter of the model – without the necessity of explicit knowledge of the phytoplankton loss rate are also mentioned.

Key words: phytoplankton growth, critical depth, critical light, measurement concepts.

1. Introduction

Sverdrup (1953) critical depth model and its later versions have been frequently and successfully applied for nearly 50 years (see e.g. Platt et al. 1991) as an explanatory and prognostic tool for phytoplankton blooms. The model deals with a phytoplankton biomass change in the surface mixed layer of a water body that results from a change in light availability for the phytoplankton growth in the layer. The light availability is expressed by the ratio of Z_{mix}/Z_{cr}, where Z_{mix} is the mixed-layer depth, and Z_{cr} is critical depth corresponding to a given field of light in the water column and phytoplankton in question. The model represents a simple and rapid approach based on the relatively easy measurements in the examined aquatic system.

The aim of this review is to evaluate the current position of the critical depth model and to give some insight into its possible development.

2. Critical depth concept, current state, and new ideas

The critical depth model evaluates whether the phytoplankton biomass in the mixed surface layer increases, decreases, or remains unchanged. In order to show it, the phytoplankton biomass increment in this layer is assessed from phytoplankton biomass balance. The model is based on the assumptions that (1) gross primary production diminishes with depth (where the depth axis is positive downwards), whereas (2) phytoplankton losses are constant within the mixed layer. Hence, net primary production decreases with increasing depth of the mixed layer (Z_{mix}). At some depth therefore (if only the water column is sufficiently deep) called the

critical mixing depth (Z_{cr}), net primary production becomes equal to zero. This means that at $Z_{mix}=Z_{cr}$ there is no phytoplankton biomass change in this layer. However, as long as $Z_{mix}<Z_{cr}$ the biomass rises. This inequality also expresses a necessary but insufficient condition for the phytoplankton to bloom (Platt et al. 1991). Finally, $Z_{mix}>Z_{cr}$ implies that the biomass decreases. The latter inequality may be considered as a criterion for the bloom to stop (Platt et al. 1991, 1994).

There are several simplifying assumptions (see e.g. Szeligiewicz 1998) that (3) the phytoplankton growth is solely light-limited which, in turn, is stimulated by mixing depth, as was mentioned above, (4) the photosynthesis-light curve is linear, (5) the irradiance is averaged daily, and (6) the vertical attenuation coefficient is constant. More distantly, spectral effects on photosynthesis are most often suppressed. The mixing layer is homogeneous and the mixing pattern within this layer is not involved in the model. This assumption is retained also for simplicity of the model, since otherwise the growth would not be a simple function of Z_{mix} and the shape of the mixing pattern should be taken into account. For similar reasons, mixing intensity is not explicitly included. Instead, it is tacitly assumed that the mixing is full and occurs instantaneously. Finally, throughflow in a reservoir, plankton and other water constituents vertical active or passive transport, and entrainment of bottom layers are neglected in order to avoid introducing other forcing functions and variables.

The critical depth model was further developed by involving the selfshading effect and many phytoplankton species (Szeligiewicz 1996, 1997, 1998). The selfshading was considered as a feedback mechanism regulating phytoplankton growth. According to this modification, the growth of each species in the mixed layer depends on the relation between critical depth corresponding to that species and the mixing depth. In addition, the species with the greatest critical depth will tend to win the competition for light of all other species in this layer. As selfshading tends to drive Z_{cr} of the winning species to the Z_{mix} then the Z_{mix} may become the critical depth for that species. These are the conclusions of reinterpretation of the Huisman and Weissing (1994) critical light concept in terms of critical depth (Szeligiewicz 1996, 1997, 1998). Also Huisman (1999) recently published such a modification. These temporal tendencies may be valid for vast class of cases even when growth conditions and growth functions change with time (e.g. in case of internally or externally induced oscillations within the phytoplankton community) if only the momentary magnitudes of the critical values are known.

Wofsy (1983) proposed a concept that "systems may be so turbid, or have the mixed layer so deep, that the phytoplankton population cannot be self-sustaining". In view of the critical depth theory, such a maximum mixing depth may be accepted as the maximum critical depth (max Z_{cr}) that was formulated quantitatively for a specified phytoplankton species (Szeligiewicz 1996, 1998) in line with the modified critical depth theory. This value tells whether the species can appear or survive in the mixed layer (in the sense of maintaining its whatever positive biomass in the layer) in the face of a given Z_{mix} and given other conditions. Given species and light supply to the water surface, max Z_{cr} appears at the bottom of the layer at which critical light for that species and for that light supply is equal to the light at the background level at that depth (Szeligiewicz 1996, 1998). A similar suggestion has been made recently by Huisman (1999).

When net primary production is stimulated also by water temperature, i.e. the assumption (3) is removed, then momentary Z_{cr} as well as momentary max Z_{cr} for a specified species should decrease with increasing temperature (Szeligiewicz, in

prep.). This finding has a straightforward interpretation in terms of critical light or critical optical depth.

3. Main problems and prospects

The general theory of the model relies on the (bio)mass conservation principle, thus it is always true. Limitations of the model stem from simplifications facilitating calculations as well as from unclear definition of the working area. Therefore, a problem may arise as to how to define a well-mixed layer (i.e. how to approximate the value of Z_{mix}) and whether well mixed conditions may appear at all. A vertically uniform layer, for example, may not exactly correspond to an actively mixed layer (Platt et al. 1994). Moreover, some errors in primary production evaluation may be caused by neglecting departure from homogeneities of phytoplankton concentration through the water column (e.g. Walsby 1997). It is also known that the mixing intensity may affect phytoplankton growth, in particular, if the dynamic effects of photosynthesis and respiration are included (e.g. Pahl-Wost and Imboden 1990, Szeligiewicz 1999) and it may affect the removal rate from the mixed layer (Steel 1995). Furthermore, specific loss rate is commonly implicitly assumed to be independent of Z_{mix} although Visser et al. (1996) showed that sedimentation losses may be in relation to mixing depth. Moreover, spatial (expressed here by Z_{mix}) and temporal scales of the mixing may probably modify the mortality rate of phytoplankton cells since they affect, inter alia, the time range at which the cells remain below compensation depth. The scales may have an additional impact on the growth of a selected species when the selfshading effect is taken into account (Huisman et al. 1999b). Besides, other than autotrophic forms of phytoplankton may affect real primary production that is not included in the model. Finally, if $Z_{mix} < Z_{cr}$ then critical depth models might have not much to say about the absolute localization of Z_{cr}, because model assumptions (1), (2), and (6) may not be held outside the mixed layer.

However, the main problems arise while estimating the critical mixing depth (Z_{cr}) or phytoplankton biomass losses (L) in the mixed layer that are necessary to assess Z_{cr} (Platt et al. 1991, Capblancq 1995, Falkowski and Raven 1997). The direct evaluation of L has frequently been avoided in these models by relating L with compensation light intensity (I_c). Besides, the commonly held practice is to approximate the value of I_c as 1% of subsurface light (e.g. Smetacek and Passow 1990), which is often too crude an approximation and may induce considerable errors in Z_{cr} (e.g. Marra 1978). Having I_c, light intensity reaching the water surface and coefficient of light attenuation in the water one may infer Z_{cr} *a priori*. However, L would represent phytoplankton dark respiration in such a case instead of all phytoplankton losses needed for proper Z_{cr} evaluation (Smetacek and Passow 1990). Platt et al. (1991) presented calculations of Z_{cr} when the assumptions (4) and (5) were removed and L was estimated by summing up all possible estimated phytoplankton losses. Nevertheless, the approximation of the phytoplankton losses in the model required rather good personal intuition and experience, hence implementation of the model to given conditions seems to be somewhat difficult.

Critical depth could be determined from critical light intensity (I^*) (Szeligiewicz 1996, 1997, 1998), i.e. assuming Lambert-Beer's law for light attenuation in the water:

$$Z_{cr} = (1/\varepsilon) \ln(I_{in}/I^*)$$

where: ε – light attenuation coefficient in the water, I_{in} – light supply to the water, I^* – critical light (the light at the bottom of the mixed layer when phytoplankton biomass is in equilibrium in this layer). However, this method seems to be of little practical importance because the critical light concept was developed rather for idealized laboratory than for field conditions. Although it would potentially enable estimation of Z_{cr} to some degree independently from the examined water column, it could be implemented for a unique case only. The value of I^* for a given phytoplankton species measured under constant (laboratory) conditions in a monoculture of that species (Huisman and Weissing 1994, Weissing and Huisman 1994, Huisman 1999, Huisman et al. 1999a) may not correspond to field conditions. This would hold only if the growth conditions were the same and constant in the examined water column and laboratory. Besides, phytoplankton specific growth rate in the systems must be functionally identical, i.e. the growth has to be the same for the two systems for any light intensity experienced there by phytoplankton cells. It is known, however, that the specific growth may be affected by many agents more or less difficult to assess and control that, in addition, may continuously change with time (see e.g. Harris 1980, Wallen 1991). The external field conditions also vary. Thus, the value of I^* is not species-specific except in particular situations. Therefore, the value of Zcr evaluated in the field may at most momentarily correspond to the value assessed from a single value of I^* (Szeligiewicz 1998).

In conclusion, the problem of Z_{cr} estimation has not yet been satisfactorily resolved. Some progress in this matter seems to have been made recently when certain theoretical foundations of simple methods of measurement Z_{cr} and max Z_{cr} *in situ* and potentially in the laboratory, without the necessity of L being estimated separately, was proposed for given variable with time external conditions (Szeligiewicz, in prep.). The methods rely, inter alia, on the finding that the biomass equilibrium state of a given phytoplankton community (or a single species) appears in the mixed layer if the optical depth of this layer reaches a given constant value (called "critical optical depth"), even under conditions of daily change in the light supply to the water (Szeligiewicz, in prep.). This is the same conclusion as that published by Han et al. (1999) but found independently (where critical optical depth corresponds to their "critical light extinction").

Finally, Platt et al. (1991, 1994) pointed out that the same information necessary for the estimation of critical depth are sufficient to determine the rate of increase in phytoplankton biomass in the mixed layer, thus directly providing a criterion for phytoplankton bloom. However, the formula for the rate given by Platt et al. (1991, 1994) contains the value of phytoplankton losses which are difficult to assess The problem could probably be addressed by evaluating the phytoplankton growth normalized to phytoplankton losses in the mixed layer which is approximately related only with the current optical depth of the mixed layer and the critical optical depth (Szeligiewicz, in prep.). The estimation of the critical optical depth, in turn, is inherent in the methods for the critical depth evaluation mentioned above.

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