

On Conditions for the Vernal Blooming of Phytoplankton.

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IN order that the vernal blooming of phytoplankton shall begin it is necessary that in the surface layer the production of organic matter by photosynthesis exceeds the destruction by respiration. The destruction of organic matter by respiration goes on continuously wherever there are plants or animals, but photosynthesis can take place only in the presence of light, carbon dioxide, and nutrient salt such as nitrates, phosphates, and other minor constituents. Gran and Braarud (1935) have pointed out that production cannot exceed destruction if there exists a deep mixed top layer. Their reasoning is that within a well mixed layer the plankton organisms are about evenly distributed, but a net production takes place only above the compensation depth, whereas below the compensation depth there is a net loss of organic matter. The total population cannot increase if this loss exceeds the net production.

The reasoning is illustrated in Figure 1, where the curves dp and dr show the increase of organic matter by photosynthesis and the decrease by respiration, respectively, as functions of depth. Both increase and decrease apply to unit volume and unit time. The production is supposed to decrease logarithmically with depth, corresponding to the logarithmic decrease of light intensity, but the destruction is supposed to be independent of depth in agreement with the assumption that the organisms are evenly distributed in the mixed layer. At the compensation depth, D_c (Fig. 1), gain and loss balance each other, $dp = dr$. The condition for an increase of the total population is that the total production P must exceed the total destruction by respiration, R , or in our representation, that on an average for 24 hours the area acd must be greater than the area $abcd$. This implies that there must exist a *critical depth* such that blooming can occur only if the depth of the mixed layer is *less* than the critical value.

Gran and Brarud concluded that the critical depth was 5 to 10 times the compensation depth. Riley (1942) has carried some of these ideas further and has shown that on Georges Bank there existed in the spring of 1941 a relation between plankton and stability. We will attempt a more precise description of the conditions that are shown in Figure 1 and, on certain assumptions, we will derive an analytical expression for the critical depth.

Our assumptions are:—

1. There exists a thoroughly mixed top layer of thickness D .
2. Within the top layer the turbulence is strong enough to distribute the plankton organisms evenly through the layer.
3. Within the top layer the production is not limited by lack of plant-nutrition salts.

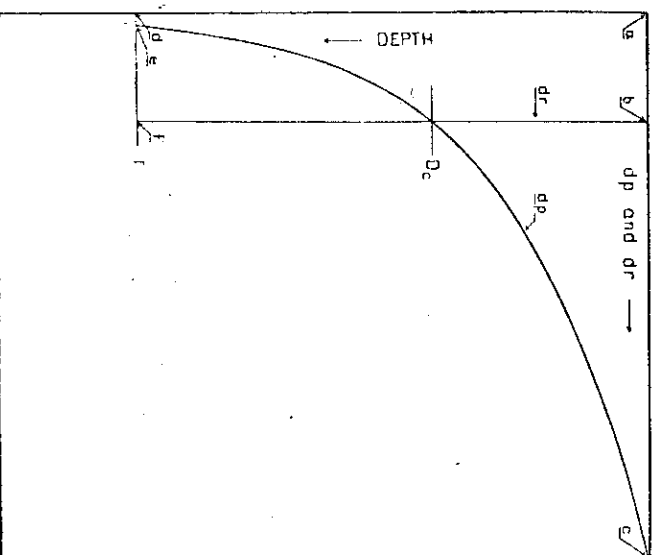


Figure 1. Schematic representation of the variation with depth of the increase of organic matter by photosynthesis, dp , and the decrease by respiration, dr . Increases and decrease apply to unit volume and unit time.

4. Within the top layer the extinction coefficient, k , of radiation energy is constant. This assumption is not quite correct even if the transparency of the water is independent of depth because, owing to selective absorption, the spectrum of the radiation changes with depth. The wave-lengths for which the extinction coefficient is smallest pertain to the greatest depths, for which reason the extinction coefficient for total energy decreases with depth (Sverdrup *et al.*, 1942, p. 107; Jerlov, 1951). However, below a depth of a few metres the decrease is so small that the introduction of a constant value of the coefficient does not lead to a serious error, provided that the transparency of the water does not change greatly with depth.

5. When dealing with photosynthesis it is not necessary to consider the energy at wave-lengths shorter than 4200 or longer than 5600 Å. This assumption is justified because for the shorter and the longer wave-lengths the extinction coefficients are so large that the energy associated with these wave-lengths is absorbed in the upper one metre or less. The energy of the spectrum in the wave-length range 4200 to 5600 Å represents about 20 per cent. of the total energy of the incoming radiation, but of the latter a fraction, a , is reflected from the surface.

6. The production of organic matter by photosynthesis is proportional to the energy of the radiation at the level under consideration. According to Jenkins (1937) this assumption is correct if the energy flux is less than 1.8 g. cal. $\text{cm}^{-2} \text{hour}^{-1}$. In spring this condition may be expected to be fulfilled below a depth of a few metres.

7. The energy, I_0 , at the compensation depth is known. The compensation depth is defined as the depth at which the energy intensity is such that the production by photosynthesis balances destruction by respiration. This energy level may depend upon the temperature because photosynthesis and respiration may not stand in the same relation to temperature, and it must depend upon the composition of the plankton. It must, for instance, be higher for a mixed population of phyto- and zooplankton than for a pure phytoplankton population. For the latter it may depend on the species of which the population is composed. By experiments in the English Channel with the diatom *Coscinodiscus eccentricus* Jenkins (1937) found the energy at the compensation depth equal to 0.13 g. cal. $\text{cm}^{-2} \text{hour}^{-1}$. Pettersson *et al.* (1934) found a value of 400 luxes in Gullmar Fjord, Sweden, working with a mixed population. Using the same conversion factor as Jenkins this light intensity corresponds to an energy of 0.15 g. cal. $\text{cm}^{-2} \text{hour}^{-1}$.

On the basis of these assumptions we can derive an expression for the critical depth. It will be shown that the critical value depends upon the amount of incoming radiation, the transparency of the water as expressed by the extinction coefficient for total energy, and the energy level at the compensation depth.

Let the total incoming energy from the sun and the sky, expressed in g. cal. $\text{cm}^{-2} \text{hour}^{-1}$, be I_0 . Of this amount a fraction, a , is lost by reflection from the sea surface. The energy that passes through the sea surface, I_w , is then $I_w = (1-a)I_0$. With a clear sky the fraction a depends upon the altitude of the sun as follows:—

Altitude of sun ($^\circ$)	5	10	20	30	40	50 to 90
Fraction reflected	.40	.25	.12	.06	.04	.03

With a completely overcast sky the fraction is assumed to have the constant value $a = .08$.

Of the amount of energy that passes the sea surface only 20 per cent. need be considered when dealing with photosynthesis because the major part is absorbed in the upper one metre (assumption 5). The "effective" energy that passes the sea surface is, therefore, $I_e = 0.2I_w$. With a

constant coefficient of extinction, k , the energy that reaches a depth z is then, taking the z -axis position upwards:—

$$I_z = I_0 e^{-kz} = 0.2 (1-a) I_0 e^{-kz} \quad (1)$$

The production at the depth z is supposed to be proportional to the available energy. The production in the time interval dt is then $dp = m I_z dt$, whereas the destruction in the same time interval is simply $dI = n dt$. Here m and n are factors which are independent of z , but depend upon the character of the population and the temperature of the water. By definition $dp = dr$ at the compensation depth where $I_z = I$. Therefore, $n/m = I_c$.

In the time, T , the total production by photosynthesis between the surface and the depth $z = -D$ is:—

$$P = m \int_0^T \int_{-D}^0 I_0 e^{-kz} dt dz = \frac{m}{k} (1 - e^{-kD}) \int_0^T I_0 dt \quad (2)$$

The total destruction is:—

$$R = n \int_0^T \int_{-D}^0 dz = nTD \quad (3)$$

The condition for an increase of the phytoplankton population is:—

$$P > R \quad (4)$$

Introducing the value for I_c from (2), putting

$$\bar{I}_c = \frac{0.2}{T} \int_0^T (1-a) I_0 dt \quad (5)$$

and remembering that $n/m = I_c$, we find that the critical depth, D_c , is defined by the equation

$$\frac{D_c}{1 - e^{-kD_c}} = \frac{1}{k} \frac{\bar{I}_c}{I_c} \quad (6)$$

So far we have been concerned only with the critical thickness of the mixed top layer, which must not be exceeded if the production in the layer shall be greater than the destruction. It is, however, possible to add a few observations. In the first place it may be pointed out that on the general assumptions made here the rapidity with which a given population may grow depends upon how much the thickness of the top layer deviates from the critical value. If it is only slightly smaller the increase of the total population must be slow, but if it is much smaller, the increase may be very rapid. These conclusions may be greatly modified if grazers are present (Fleming, 1939). In that case the phytoplankton population may remain small in spite of heavy production.

In the second place a phytoplankton population may increase independently of the thickness of the mixed layer if the turbulence is moderate. In this case the plankton may be unevenly distributed at the end of the daylight hours, with greater concentration above the

compensation depth where production has taken place. During the night hours mixing may not be complete and when daylight again makes photosynthesis possible, the concentration of plankton may still be greater near the surface. In these circumstances the production will be greater than according to our assumptions, and the population may increase as long as the conditions prevail. A similar development may take place even with strong turbulence if the phytoplankton displays a positive phototaxis.

Returning to our main topic we may interpret our results in terms of "stabilization". In middle and high latitudes there generally exists a deep mixed layer at the end of the winter, but as the season advances there develops a shallow mixed layer below which the density increases so rapidly with depth that turbulence is suppressed. By "stabilization" we understand the development of such a layer. This development may be caused by spring heating of the surface layer or by lowering of the salinity of the top layer, related to spring run-off.

Table 1. Thickness of top mixed layer according to observations at Weather Ship "M", 66°N., 66°E.Gr.

Date 1949	Thickness m.	Date 1949	Thickness m.	Date 1949	Thickness m.	Date Thickness 1949 m.	
3. March	150	4. April	300	28. April	100—300	16. May	25
7. "	100—150	6. "	50	29. "	100	18. "	100
10. "	100	8. "	100	2. May	100	19. "	100
17. "	100	11. "	50—100	4. "	>150	21. "	0
21. "	150	15. "	200—400	5. "	150	23. "	0
23. "	150	16. "	75—100	6. "	100	25. "	25
26. "	200	22. "	50	11. "	75	27. "	0
30. "	100	25. "	100	12. "	100	28. "	50
2. April	400	27. "	>100	14. "	75	31. "	0

Observations carried out in the spring of 1949 at Weather Ship "M" in the Norwegian Sea (66°N., 2°E.Gr.) make possible a test of our conclusions. The observations comprise measurements of the thickness of the upper mixed layer, counts of the number per litre of phytoplankton organisms at one or more depths near the surface, and counts of the copepods and nauplii as collected by vertical hauls from 100 m. to 50 m. and from 50 m. to the surface. We will deal only with the observations from the months of March, April, and May.

The observations of the thickness of the upper mixed layer were made several times a week. They are based on temperature and salinity observations at fixed depths and on continuous temperature records with the Mosby thermosonde. The latter has a very small scale, for which reason the thickness of the layer can be determined with an accuracy of only ± 25 m. The observed values as communicated by Mr. O. Sælen are entered in Table 1.

The counts of phytoplankton, copepods, and nauplii are entered in Tables 2 and 3. If observations were made at more than one depth the

Table 2. Phytoplankton organisms per litre in the surface layer according to observations at Weather Ship "M", 66°N., 20°E.Gr.

Date 1949	Numbers			Total
	Diatomaceae	Coccolithophoridae	Dinoflagellatae	
10. March	500	1,000	0	1,500
17. " *	120			120
28. " *	160	2,500	0	2,500
6. April	9,240	4,500	8,500	22,240
11. " *	4,300	9,500	1,020	14,820
22. " *	3,100	8,500	1,000	12,600
28. " *	6,100	10,000	1,000	17,100
5. May *	3,060	10,260	2,520	15,840
12. " *	8,500	28,000	40	36,540
19. " *	7,540	22,000	4,000	33,540

* An asterisk indicates observations from 0 m., otherwise the numbers pertain to depth of maximum concentration.

data apply to the depth of maximum population. In the case of the copepods and the nauplii the values from the two vertical hauls above 100 m. have been combined. The phytoplankton data have been placed at my disposal by cand. real. Per Haller-Nielsen, the zooplankton data by mag. sc. Ole J. Østvedt. I wish to express my thanks to these two and to Mr. Sælen for their kindness.

No observations of the incoming radiation were made at the Weather Ship, but approximate daily values have been computed by means of Møsbys' formula:—

$$\bar{I}_0 = 0.026 (1 - 0.075 \bar{C}) \bar{h} \quad (\text{g. cal. cm.}^{-2} \text{ min.}^{-1})$$

where \bar{C} is the average cloudiness on the scale 0 to 10 and \bar{h} is the average altitude of the sun. The latter can readily be computed for every day for the latitude of the Weather Ship, and the cloudiness is obtained from the meteorological observations. From the values of I_0 that have been determined in this manner daily values of D_{cr} have been found and have been smoothed by forming overlapping 5-day averages.

Measurements of transparency were not made, but at an oceanic

Table 3. Numbers of copepods and nauplii from vertical hauls between 100 m. and the surface at Weather Ship "M", 66°N., 20°E.Gr.

Date 1949	Numbers		Numbers		Total
	Copepods	Nauplii	Copepods	Nauplii	
2. March	1,319	0	1,319	11,220	21,415
9. " *	2,339	0	2,339	3,674	4,679
16. " *	2,758	0	2,758	2,313	5,043
7. April	1,644	85	1,729	39,131	49,681
14. " *	4,606	3,480	8,086	42,103	51,473

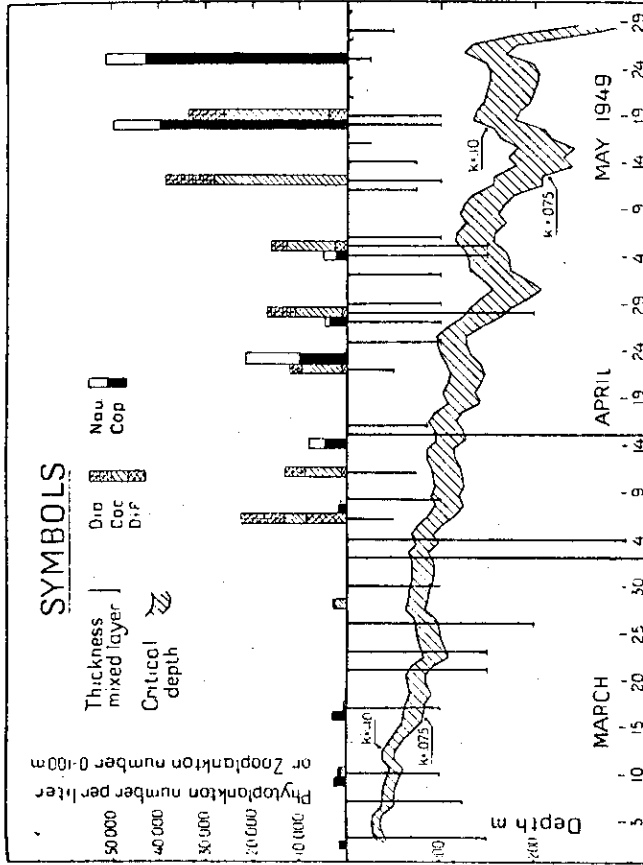


Figure 2. Results of observations at Weather Ship "M" (66°N., 20°E.Gr.). The symbols are explained in the graph, where the following abbreviations have been used:—Dia, Diatomaceae; Coc, Coccolithophoridae; Dif, Dinoflagellatae; Nau, Nauplii; and Cop, Copepods.

locality the coefficients of extinction of total energy may be assumed to lie between 0.075 and 0.10 (Jerlov, 1951; Sverdrup *et al.*, 1942, p. 107). According to Jerlov the value 0.075 is probably the more correct. It should, however, be borne in mind that the value may vary from day to day, and that it probably increases as the season advances.

All variables are presented graphically in Figure 2. In the lower part of the figure the critical depth is shown, which is supposed to lie between the curves marked $k = 0.10$ and $k = 0.075$. These curves are based on 5-day means of D_{cr} . It is seen that the critical depth increases more or less regularly from about 30 to 40 m. at the beginning of March to nearly 300 m. at the end of May. The observed values of the depth of the mixed layer are also entered. It is seen that stabilization leading to the development of a very shallow mixed layer does not take place before the middle of May.

The graphs bring out two striking features. (1) Until the final week of April the depth of the mixed layer is greater than the critical depth, and (2) after the middle of May the depth of the mixed layer is very much smaller than the critical depth. This implies, if our reasoning is correct, (1) that until the beginning of April the phytoplankton population must remain very small, (2) that it should be expected to increase

during April and the first half of May, and (3) to increase rapidly during the last half of May, provided that the increase is not checked by the presence of grazers.

The observed amounts of phyto- and zooplankton that are shown in the upper part of the graph fully confirm these conclusions. Through March the amounts of plankton remained insignificant. On 4 April the depth of the mixed layer was for the first time smaller than the critical depth, and on the following day an appreciable phytoplankton population was recorded, but only a small number of copepods should be observed that the change in the depth of the mixed layer from more than 300 m. on 2 April to 50 m. on 4 April probably indicates advection of another water mass and not local stabilization. The plankton count suggests that for some time conditions for growth have been favourable in this water mass.

During the remaining part of April and the first half of May, when the depth of the mixed layer was only moderately smaller than the critical depth, the phytoplankton population remained moderately large, and did not increase systematically. At the same time copepods appeared in greater numbers, indicating that considerable grazing took place.

In the latter half of May when conditions for phytoplankton growth should be very favourable, the counts show larger numbers of phytoplankton organisms and very much larger numbers of copepods. The latter feature suggests that the development of the phytoplankton is effectively suppressed by a heavy grazing. Thus, the entire sequence of the development of the plankton of the surface layer appears to be consistent with our conclusions.

It may be pointed out that in the spring of 1949 the first increase in phytoplankton was not associated with stabilization, but with the seasonal increase of the compensation depth. Stabilization led to a second increase in population after the middle of May.

In the introduction it was mentioned that Gran and Braarud estimated the critical depth to be about 5 to 10 times the compensation depth. Since $D_c = \bar{I}/k$ (Equation 6) and $I_c = I_e - kD_c$, we obtain

$$\frac{D_c}{D_c} = \frac{I_e D_c}{k D_c} \quad (7)$$

Applying this equation to the data that are shown in Figure 2 we find that the ratio D_c/D_c increases as the season advances and exceeds the value 5 after the beginning of May. A curve showing the values of the ratio could have been entered on the graph but would have complicated the presentation. It is sufficient to state that on 15 March, 15 April, and 15 May the values of D_c/D_c were 2.9, 4.0, and 5.5 respectively, meaning that the results arrived at here appear to confirm the conclusions by Gran and Braarud.

The data shown in Figure 2 represent the only available series of fairly complete records which make possible an analysis of certain features of the productivity of the surface layer as related to available

light and thickness of mixed layer. It is, therefore, not advisable to place too great emphasis on the agreement between theory and observations. It is hoped, though, that the results presented here may encourage further systematic observations and collections, not only at Weather Ship "M", but at other Weather Ships as well.

Summary.

On certain assumptions a "critical depth" is defined. The depth of a mixed surface layer must be less than this critical depth if the phytoplankton population of the mixed layer shall increase. The results are applied to observations made at Weather Ship "M" (66°N., 2°E. Gr.) in March, April, and May 1949. A striking agreement is found between the hydrographic conditions and the development of the plankton communities.

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