On the Oxygen and Chlorophyll Maxima Found in the Metalimnion of a Mesotrophic Lake

by Shun-ei ICHIMURA*, Sachiko NAGASAWA** and Toshie TANAKA*

Received September 8, 1967

Abstract

In Lake Haruna (mesotrophic lake) the oxygen and chlorophyll maxima were found in the metalimnion. Dominant species of phytoplankton in the low layer of the euphotic zone was Cryptomonas sp. and it showed a characteristic shade type in the photosynthesis-light curve. The photosynthetic activity of Cryptomonas sp. at low light intensities and low temperature was remarkably higher than that of other phytoplankters.

From the photosynthesis-light curve of Cryptomonas sp. obtained in the laboratory and depth-light profile observed in the lake, the depth-photosynthesis relation of the alga was calculated and it was found to be in good accordance with the relation measured in situ.

It was thus concluded that the oxygen maximum in the metalimnion of Lake Haruna is due to the special photosynthetic characteristics of Cryptomonas sp. living in that lake which is adapted to the environment of low light intensity and low temperature prevailing at the foot of the euphotic zone.

The lake was found to show the chlorophyll maximum in the deeper layer. This was attributed to the intensive growth of Cryptomonas and not to the accumulation of the deteriorated phytoplankton sedimented from the surface layer.

The majority of oligotrophic or mesotrophic lakes in Japan have a marked oxygen maximum in their middle layers. In some situations, especially in mesotrophic lakes, a supersaturation of oxygen appears occasionally in the upper layer of the metalimnion. These lakes are usually small and deep ones in the mountain districts and many of them are protected from the disturbance by strong wind. Yoshimura has propounded the opinion that the full development of metalimnetic oxygen maximum is due partly to warming of water in the epilimnion by solar radiation and partly to the photosynthetic activity of phytoplankton in the stable layer in question. Recently, a more detailed study was made by Eberly in plus heterograde lakes of northern Indiana. He measured the metalimnetic oxygen maximum greater than 12.7 ppm and also found an immense bloom of Oscillatoria agardhii in the metalimnion. The layer of oxygen maximum, however, did not always coincide with that of photosynthetic maximum found by the in situ experiments. Wetzel reported that in a lake of Indiana the major portion of the primary productivity occurred in the metalimnion where oxygen maximum developed and the dominant phytoplankton of the metalimnion were Ceratium hirundinella and Oscillatoria agardhii.

It has generally been said that in the stagnant layer of lakes the supersaturation
of oxygen is due mostly to the photosynthesis of phytoplankton. However, a large excess of oxygen near the compensation depth, can by no means be accounted for by the ordinary sunny type photosynthesis such as are performed by the surface phytoplankton. If the large excess of oxygen in the metalimnion is mainly of biological origin it may be assumed to be due to a special photosynthetic activity of the deeper phytoplankton dominating in that layer.

This paper attempts to ascertain this assumption by investigating the photosynthetic characteristics of deeper phytoplankton of a typical mesotrophic lake, Lake Haruna in Gunma Prefecture. The lake (altitude: 1048 m, total area: 8 km², maximum depth: 13.5 m) is one formed in the caldera of Mt. Haruna which is located about 100 km northwest of Tokyo. It has no inflows and water is derived directly from ground water and precipitation on and around the lake. Outflows are controlled with the gates at two places. Field observations were performed during 1963-1965. Diatoms such as Melosira italica, M. granulata, Cyclotella sp. and Asterionella formosa are dominant in phytoplankton community throughout the year. In the summer stagnant period, the water in the hypolimnion changes its color to beautiful deep pink owing to the profuse growth of purple sulfur bacteria.

Methods

With a Van Dorn type sampler made of plastic, the sample waters were taken from various depths at the center of the lake. Dissolved oxygen in the sample water was immediately measured by the Winkler method. One part of each sample water was filtered through a HA Millipore filter. The filters were kept in an ice-box and brought back to the laboratory for measuring chlorophyll. The water temperature was measured by means of a thermistor-thermometer and the light attenuation in water by a selenium underwater photometer with a neutral glass filter. Photosynthesis was measured by the tank and in situ methods using radioactive carbon. The amount of total carbon dioxide in the sample water was determined directly by means of a respirometer described by Yokohama and Ichimura (in press), and the rate of photosynthesis was determined by the radiocarbon technique. The density of phytoplankton in the sample water was determined by counting cells and by measuring chlorophyll content. Cell count, using a microscope, was made either with the Millipore filter after filtration of an aliquot of sample water or with the sample water concentrated from 100 ml to 10 ml. The concentration of chlorophyll was measured according to the method of Richards and Thompson.

Results and Discussion

1. Oxygen and chlorophyll maxima in the metalimnion.

The vertical distribution of dissolved oxygen showed seasonal changes that were essentially the same throughout the study period from 1963 to 1965. A typical example obtained in 1964 is presented in Fig. 1. The dissolved oxygen at the spring overturn showed uniformity of the whole water layer. With the progress of thermal stratification in the lake, a rapid depletion of oxygen occurred in the hypolimnion. In the middle of May, a slight maximum of oxygen appeared in the thermocline. This maximum oxygen value further increased in succeeding weeks and an excess oxygen of 12 ppm was measured at the end of June. After the fall overturn oxygen was found equally distributed at all depths.
Fig. 1. Seasonal changes in the vertical distribution of dissolved oxygen in Lake Haruna, 1964.

Fig. 2. Seasonal changes in the vertical distribution of phytoplankton, expressed as chlorophyll-a per m³, in Lake Haruna, 1964.
The vertical distribution of phytoplankton was almost in parallel with that of dissolved oxygen. Fig. 2. shows the seasonal changes in the vertical distribution of phytoplankton measured on the chlorophyll basis. During the summer stagnation period a chlorophyll maximum was found in the lower layer of the thermocline. It was noticed that both the chlorophyll maximum and oxygen maximum were detected at nearly the same depth in the thermocline or somewhere below it, where the light intensity was lower than 5% of the surface illumination. We cannot, however, hastily conclude that the oxygen maximum in the thermocline depends primarily on the photosynthesis of phytoplankton which has caused the chlorophyll maximum in that layer, because phytoplankton in general hardly perform photosynthesis under low light conditions such as found at the foot of the euphotic zone.

In other lakes we have studied thus far we sometimes observed a high concentration of chlorophyll in the thermocline, which was, however, never accompanied by an oxygen maximum. Fig. 3 shows one of the data obtained in Lake Nakanuma, whose geomorphometric features are quite similar to those of Lake Haruna. During the summer stagnation period a large amount of chlorophyll was measured in the hypolimnion, whereas oxygen level decreased abruptly in this layer. Oxygen maximum appeared rather in the surface layer.

The relation between chlorophyll concentration and the level of dissolved oxygen in the metalimnion differs strikingly in the two lakes mentioned above. In order to make clear the causal relation between chlorophyll maximum and oxygen maximum in Lake Haruna, photosynthetic characteristics of phytoplankton in this lake should be examined in relation to light condition.

2. Characteristics of productivity-depth profiles in Lake Haruna observed by in situ experiments.

Under natural conditions, the photosynthetic activity and, therefore, oxygen out-
put of phytoplankton in a lake generally shows the maximum in the surface layer and decreases with the increase of depth. Fig. 4-A illustrates the in situ vertical profiles of the primary productivity and the amount of chlorophyll in Lake Fukami, whose geomorphometric features are also similar to those of Lake Haruna. During the summer stagnations, the largest amount of chlorophyll was found in the metalmnion or in the hypolimnion, whereas one maximum of productivity occurred in the surface layer. The dominant species of phytoplankton community were diatoms and green algae, the ratio of which appeared to be independent of the depth. Hence the high concentration of chlorophyll found in deeper layers is not due to intensive growth of phytoplankton in that depth but seems to have resulted from the sedimentation of phytoplankton which had propagated in the surface layer. Productivity-depth profile obtained in Lake Nakanuma also showed one photosynthetic maximum in the surface layer.

It is of interest that in Lake Haruna during the summer stagnation period two

![Graphs showing vertical changes in primary production rates and chlorophyll amount in Lake Fukami.](image)

*Fig. 4. A: Vertical changes in primary production rates and chlorophyll amount in Lake Fukami. B: Photosynthesis-light curves of phytoplankton.*
maxima were detected in the productivity-depth profiles as seen in Fig. 5. One maximum was found in a layer between the surface and 2 m depth, and the other was in a layer from 6 m to 8 m. The presence of two productivity maxima suggests the vertical changes in species or in physiological characteristics of phytoplankton.

To clarify the species composition of the community, the identification of species and cell count were made for the sample waters collected from various depths in August. The results are presented in Fig. 6. In the surface layer diatoms such as Melosira, Cyclotella were dominant, whereas Cryptomonas sp. was predominant in the upper layer of the thermocline, where chlorophyll showed a maximum value. This finding suggests that the photosynthetic maximum in the thermocline would probably be due to some special photosynthetic characteristics of Cryptomonas sp.

3. Photosynthetic characteristics of deeper phytoplankton.

As reported in previous papers\(^\text{5-6}\) natural phytoplankton can be divided into two forms—sunny and shady—in respect to their photosynthetic characteristics. The sunny form of photosynthesis is usually found in the surface phytoplankton and the shady form is mostly observed in the deep phytoplankton. In Fig. 4-B are presented the typical photosynthesis-

![Fig. 5. Productivity-depth profiles of Lake Haruna, 1963.](image)

![Fig. 6. Vertical changes in cell number and chlorophyll amount in Lake Haruna, August 1965.](image)
light curves of phytoplankton sampled from the depths of 0, 4 and 6 m of Lake Fukami. The rate of photosynthesis was expressed in terms of O₂ mg per hour per mg of chlorophyll. As may be seen, the three curves coincided with each other at low light intensities but showed different level at higher light intensities. A similar phenomenon has been observed by Steemann Nielsen in his extensive works on photosynthesis of phytoplankton.

Corresponding curves obtained with the sample waters of Lake Haruna are shown in Fig. 7. The samples were those collected from the depths of 2 m and 6 m in August. Attention should be given to the fact that the photosynthesis-light curve shown by the deeper phytoplankton was markedly different from that presented in Fig. 4-B. Whereas the photosynthesis of the sample taken from 2 m depth was of the normal sunny form, the curve obtained with the deeper phytoplankton showed, at lower light intensities, an enormously steeper rise as compared with that of surface phytoplankton. Thus the photosynthetic characteristics of deeper phytoplankton in Lake Haruna differs from those of deeper phytoplankton of other lakes. The planktonic species in the 2 m sample, which had displayed a normal sunny form photosynthesis, were no doubt diatoms, whereas the organisms in the 6 m sample showing an abnormal shade-type photosynthesis are considered to be Cryptomonas sp.

Cryptomonas has been known to be a cold stenothermal phytoplankton. Using the samples from 2 m and 6 m depths we examined the effect of temperature upon the rate of photosynthesis. Photosynthesis was measured separately at 7000 lux in an incubator filled with water of 5°, 10°, 20° and 25°. In Fig. 8 are presented some of the data obtained in July 1965, when the water temperature was 22.6° and 12.8°, respectively, at 2 m and 6 m depths of sampling. It was revealed that the rate of photosynthesis of the two samples were affected by temperature in different manners. The temperature at which the maximum rate of photosynthesis was observed was 25° for the 2 m sample and 15° for the 6 m sample, and these values were 2-3° higher than those measured at the habitat. Aruga reported that the optimal temperature for photosynthesis of natural phytoplankton is usually 2° or 3° higher than the

![Fig. Photosynthesis-light curves of phytoplankton collected from the depths of 2 m and 6 m of Lake Haruna in August. Temperature 20°.](image-url)
temperature at the habitat of the phytoplankton. It is noteworthy that the deeper phytoplankton (Cryptomonas sp.) of Lake Haruna can perform photosynthesis actively in the environment of low light intensity and low temperature.

4. Some considerations on metalimnetic oxygen and chlorophyll maxima in relation to photosynthetic characteristics.

Assuming the homogeneous vertical distribution of phytoplankton in the lake, the rate of their photosynthesis as a function of depth was estimated based on the photosynthesis-light curve and the light-depth curve obtained in situ. The photosynthesis-light curve (Fig. 7) used were those obtained with the samples taken from 2 m and 6 m depths. The results obtained in August are presented in Fig. 9. Concerning the depth-dependency of photosynthetic rate, the 2 m sample showed the maximum in the sub-surface layer, while the 6 m sample gave the maximum in the thermocline. The compensation depth was 8 m for the former and 11 m for the latter.
Fig. 10 shows the vertical changes in the photosynthesis of phytoplankton under natural conditions of Lake Haruna. The data were obtained by submerging the bottles, each filled with the sample water from 2 m depth or that from 6 m depth, to various depths for three hours in daytime (10:00-13:00). The vertical changes in the photosynthesis of 2 m and 6 m samples both resembled fairly well those estimated by the respective photosynthesis-light curves. It would, therefore, be reasonable to consider that the phytoplankton in the natural habitat is responding to light conditions in a way similar to that reproduced in the laboratory. This has already been confirmed by Talling with marine phytoplankton by more elaborate experiments. Thus it has been made clear that the characteristic oxygen maximum observed in the metalimnion of Lake Haruna was due to the special photosynthetic characteristics of Cryptomonas sp. (the 6 m sample) thriving in an environment of low light intensity and low temperature.

As seen in Fig. 7 and 10, the photosynthetic activity under lower light intensities is considerably higher in the 6 m sample than in the 2 m sample. This may be another conceivable reason for the oxygen maximum in the deeper layer. According to the results obtained by Ohle in his studies on primary production in four lakes of northern Germany, a vertical zonation in the intensity of primary production is maintained with a maximum in the lower epilimnion during the summer stagnation period. He concluded that the vertical gradient is due to adaptation of algae such as Oscillatoria and Anabaena to low illumination and to favorable supply with nutrient salts.

The nutrient level in the thermocline of Lake Haruna, especially phosphate content, is much higher than that in the surface layer during the stagnation period. Under such a nutrient condition, the photosynthesis of phytoplankton can be expected
to give a relatively high value in the thermocline as compared with that in the surface layer of minor nutrient content. Steemann Nielsen\textsuperscript{10} made the same observation in the marine environments.

As mentioned already, the chlorophyll maximum was found in the thermocline of Lake Haruna during the summer stagnation period. This maximum might be related to the profuse growth of Cryptomonas sp. which is able to live under weak light in the depth of water. The midwater chlorophyll maximum has commonly been observed in marine environments\textsuperscript{11,12}. Steele\textsuperscript{12} has speculated that chlorophyll maximum near the foot of the euphotic zone in the sea may be due to an accumulation of sedimented plankton. It is a common fact in terrestrial plants as well as in algae that chlorophyll content in shade plants is usually much higher than in sunny plants. This seems to be another possible reason for the chlorophyll maximum in Lake Haruna.

At any rate, there exists a significant correlation between the maxima of oxygen and chlorophyll in the thermocline of Lake Haruna, and characteristic photosynthesis of Cryptomonas sp. would certainly be responsible for these maxima.

The authors express their deepest thanks to Professor Hiroshi Tamiya for his kind help in preparation of this manuscript.

References