On the Spatial Difference of the Primary Production in the Lake and its Relation to Environmental Factors

by Shun-ei Ichimura*

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Regarding the horizontal distribution of phytoplankton in the lake, the noticeable information has been provided by many investigators. The features of the horizontal distribution should be formed by the interplay of the physical actions, such as wind, in- and outflowing streams and contour shape of lake basin, and the spatial difference in growth rate of phytoplankton in the lake. However, so far almost all of the illustrations for the causes which determine the horizontal distribution have been made only through the physical actions and they have slightly been touched from the ecological viewpoint.

The spatial difference of the productivity must precisely be examined in relation to the study of the primary production in the lake, but the data in this field are still inadequate as to Japanese lakes.

Concerning the above subjects, therefore, the present study has been carried out in several lakes with different morphometries, and the features of the horizontal distribution of phytoplankton were pursued on the basis of the dry matter production.

**Types of horizontal distribution of phytoplankton in the lake**

The standing crop of phytoplankton was measured in chlorophyll amount. Fig. 1 shows the representative features in the distribution of chlorophyll in a vertical section from the top to the end of lakes and the spatial difference in the mean value of

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* Botanical Institute, Faculty of Science, Tokyo University of Education, Otsuka, Tokyo, Japan.
the chlorophyll amount in euphotic layer. The patterns of the horizontal and vertical distributions differed from one another according to the contour shapes of lakes and they were classified into three types, the uniform, regular and irregular ones.

The uniform distribution type is found usually in the oval-shaped lakes with simple shore line and uniform depth such as Lake Suwa (Nagano Prefecture), in which the effect of the inflowing water is insignificant. The phytoplankters in these lakes scatter homogeneously in all part of the lake.

The regular distribution type is common to the slender lakes such as Lake Kitaura (Ibaraki Prefecture) with simple shore line. As for this type, the standing crop measured in the upper region, especially in the area surrounding the mouth of the inflow, is relatively small in comparison with the middle part, where the standing crop is generally higher, but it decreases successively from the halfway region to the lower end of the lake.

The irregular distribution is obtained in the lakes with a complicated shore line and also in the reservoirs, in which some part of the water is exchanged continuously through the inflow and discharge. In this pattern, the standing crop of phytoplankton is more abundant in the lentic environments than in that of the lotic environments. But the irregular distribution pattern is only of conditional character.

**Spatial difference in productive structure of phytoplankton community in the lake**

According to recent theoretical analyses performed by some investigators, the pattern of the vertical distribution of phytoplankton can be summarized as being the two general types following; the one is the homogeneous type and the other is the stratum one (cf. Fig. 2). The homogeneous type is usually established during the circulation period, while the stratum one, during the stagnation period. Among the stratum types, L-shaped pattern stratifies slightly in the euphotic layer but chlorophyll is extremely abundant in the destrophic layer, in which photosynthesis is normally not performed. This L-shaped pattern has usually been found in the deep lakes during the stagnation period. The foregoing two distribution types have been ascertained practically in situ and it has also been confirmed that these types appear
alternately in the course of the year in the lake. However, the productive structure differs spatially in one and the same lake. Such variation was observed remarkably during the stagnation period in the deep, slender lakes. As an illustration, the results obtained in Lake Kitaura are indicated in Fig. 3-A. The productive structure observed at the location near the top of the lake was of the homogeneous type and the same type could be found everywhere in the littoral regions. With the increasing distance from the mouth of the inflow, the homogeneous type transformed gradually into the stratiform type which was converted further into the L-shaped type at the middle of the lake. In the lower shallow region of the lake, the L-shaped type transferred again into the homogeneous one.

In the shallow lake as well as in the round-shaped deep lake with uniform depth there is no spatial difference in the pattern of productive structure, but the structure is usually represented by the homogeneous type in the former and by the stratiform one in the latter. Fig. 3-B and -C show the productive structures obtained from the various stations of Lakes Kasumigaura and Suwa. The areas of these lakes are large but the depths are rather small in proportion to the volumes of the lakes. The upper and lower regions of the lakes are 2-3 m. in depth, and the middle regions, 6-7 m. The productive structures in the slender Lake Kasumigaura were found to be the homogeneous type in both its upper and lower regions and the slightly stratiform one in the deep, middle region. In the round-shaped Lake Suwa, the productive structure indicated the homogeneous one at every place. The mode of the stratification may be determined by the morphometric difference of the basin.

Spatial difference of photosynthetic activity of phytoplankton in the lake

As reported in a previous paper6), the photosynthetic activity of phytoplankton in the ocean differed regionally but it was approximately the same in a restricted area. As compared with the area of the ocean, that of a lake is small in a scale, but here the photosynthetic activity of phytoplankton community differs place to place even within a lake. In a small lake, such activity difference is rather slight but it appears clearly in a large lake. Fig. 4 shows the photosynthesis-light curve obtained under the laboratory condition in the sample waters taken from the surface of three stations of Lake Kasumigaura. The photosynthesis was measured by the Winkler method. Sample A was taken at the upper region, sample B at the middle and sample C at the lower region, and the distance between the two stations is about 10 km. The Samples A and B were entirely the same in the light-photosynthesis reaction
as well as in the maximum rate, and were a little higher than that of sample C.

The successive decrease in photosynthetic rate with the downward stream flow was measured more clearly during the stagnation period in long slender lakes with complex shore lines. For example, the photosynthetic rate measured in Lake Jonuma in September 11, 1957 was 14–17 CO₂ mg./chl. mg./hr. in the sample taken at the region near the mouth of inflow, but only 6–8 CO₂ mg./chl. mg./hr. at the lower region of the lake. As will be illustrated in the next chapter, these variations in photosynthetic rate are referred to the varying environmental conditions, especially nutrient gradient.

As pointed out in a previous paper⁶), the photosynthesis pattern of natural phytoplankton concerning light intensity varies with the difference of its habitat: the phytoplankters in the surface layer are the sun form, and the samples in deep layer, the shade form. Such differentiation of photosynthesis pattern, however, was found only in the samples taken vertically from the stations with deep basins and no differentiation was observed in the samples from the shallow regions. Therefore, it can be deduced that the degree of the differentiation alters according to the difference of the depth at each region in a lake.

The features of the vertical change in the photosynthetic rate in situ also varied with the difference of the stations. Fig. 5 indicates the depth-photosynthesis curves measured in situ at the said three stations in Lake Kasumigaura. The Secchi disc reading at that time was 1.7 m. at station B, 0.7 m. at station A, and 0.9 m. at station C. The photosynthetic rate decreased rapidly with the increasing of the depth both at stations A and C, and the compensation depth was found at about 1.2–1.5 m. The vertical change in the photosynthetic rate occurred more slowly at station B than at stations A and C, and the compensation depth was 2.5 m.
For these reasons, the unit areal production at the middle region may be surmised to be more large value than that obtained at the shallow regions of the upper and lower regions of the lake. The same phenomenon had also been observed by Steinmann Nielsen in Lake Fure, Denmark.

**Factors determining horizontal distribution of phytoplankton in the lake**

Since the phytoplankters are scattered in the water, the horizontal distribution of phytoplankton may correspond mainly to the features of the water current and it may also result from the difference in the production rate of phytoplankton due to the spatial difference of the environmental conditions in the lake.

Simple relationship between the horizontal distribution and the environmental factors can be found in a shallow lake with simple shore line and flat basin. The entire water in the shallow lake is agitated completely by the natural actions of wind and water current, thereby the environmental conditions in such a lake being continuously in a uniform state and the phytoplankton is scattered homogeneously all over the lake. Because of the uniform condition in the lake, the photosynthetic activity of the phytoplankton is equivalent everywhere and the spatial difference of the unit areal primary production is little worth considering, consequently the standing crop would always maintain the homogeneous distribution pattern.

The uniform type was found also in a small, deep lake with round contour shape, in which the environmental conditions are horizontally the same. The circulation of the water in such lakes occurs only in the upper layer and it is relatively gentle, thereby the breakdown of the productive structure being slight and progressing slowly. As is well seen in Fig. 6, under these conditions, the developmental process can clearly be observed in the productive structure which indicates an analogous structure constructed theoretically.

The lakes, in which the phytoplankton distributes with regularity, resemble each other in their slender and deep forms. In such lakes, both upper and lower regions are usually shallow, while middle region is much more deeper than the former ones and the regions widely differ from each other in their aquatic environments such as light, nutrient concentration, etc. In the shallow regions, the turbidity of water is very high and through which the penetrating light is usually absorbed rapidly by the water, while the rapidity of light extinction decreases in the middle region with deep water as the result of the low turbidity. On the other hand, the chlorophyll content in the shallow region is small in spite of the high turbidity. This may suggest that the ratio of the non-living matters to the phytoplankton in amount is much larger in the shallow region than in the deep region due to the rising of bottom mud induced by water stirring, the light penetrated into the water being reduced mainly by the non-living matters. As indicated in Fig. 7, the features of the vertical change in
photosynthetic rates, which are calculated for the said three stations in Lake Kasumigaura by means of combining the photosynthesis-light curve in Fig. 4 and the light-depth curve measured in situ, coincided fairly well with the results in Fig. 5. The gross primary production calculated by the combination of the depth-photosynthesis curves in Fig. 7 and the chlorophyll amount in situ were 2.95 O₂ g./m²/day at station A, 6.25 O₂ g./m²-day at station B and 2.47 O₂ g./m²/day at station C. Therefore, it seems reasonably certain that the unsuitable light condition in the shallow regions may contribute directly to the reduction of the organic matter production per unit surface area in the phytoplankton community there.

Another conceivable reason for the small standing crop in the upper region may be referred to the effect of the inflowing water. Since the upper region is replenished with the inflow stream, the phytoplankton growing there is diluted always with the inflowing water and a large part of the phytoplankton is carried away with the stream from that place to the halfway down region. Hence, the standing crop hardly reaches a maximum equilibrium level at the upper-stream region.

In the middle region of moderate transparency, the light can extend to considerable depth of the water and the compensation depth is much deeper than those both in the upper- and downstream regions. In addition to this suitable light condition, the nutrients in the water have not yet been exhausted in this region (see Fig. 8), thereby the photosynthetic activity of phytoplankton being also high. Besides the facts mentioned above, the velocity of the current is slow in the middle region where the amount of production surpasses the amount which has escaped from there to the downstream region. Under these circumstances, the dry matter production in the middle region can be expected to give high yield as compared with that in the other regions. Because the wave action is rather weak in the middle region of the lake, the vertical shift of phytoplankton is minor and only the precipitation of phytoplankton progresses, and thereby the L-shaped structure can be formed at a region somewhat lower than the halfway down region. Simultaneously, the accumulation of nutrients proceeds in the middle region through the biological production and a large part of the nutrients accumulated in phytoplankton cells is stored in deeper layer in the form of organic deposits, some of which undergo decomposition and consequently the bottom water is enriched. As a result of the accumulation of salts in the deeper layer of the middle region, the lower end of the downstream stream of the lake is conserved usually with the exhausted water, especially during the summer stagnation period. This phenomenon could be speculated clearly in deep, slender lakes. Fig. 8–A indicates the values of phosphate-P content both in the surface and bottom waters of Lake Kitaura at various stations in the summer stagnation period. The amount of phosphate-P decreased rapidly in the surface water with the gradual downward flow, while its value in the bottom water rather increased at the middle region. According to the data measured in Lake Jonuma, the magnitude of the nutrient gradient
depends upon the lake contours and it is extremely great at the growing period. Since the nutrient elements of this lake were mostly exhausted at station 1, the effect of the enriched sewerage did not reach to the narrow, slender part (station 2) of the lake. As illustrated in Fig. 8-B, the highest value was obtained at the mouth of the inflow of the sewerage and the next was measured at the middle part (stations 4 and 5) and finally nutrients were scanty or practically of a negligible amount at the lower end of the lake, while the gradient was not distinct during the circulation period. Beside the gradient of nutrient concentration, it is interesting to note that the feature of the distribution of the standing crop and the difference of the photosynthetic activity coincides very well with the nutrient gradient. Judging from the fact that the photosynthetic activity in the raw water increases with addition of nutrients, it can be deduced that the reduction of primary production in lower region may be partly caused by the deficiency of the nutrients. As one of the essential factors determining the horizontal distribution of phytoplankton, therefore, some understanding is necessary on the horizontal distribution of the nutrients in the lake.

The mosaic pattern in the horizontal distribution of phytoplankton within a lake is resulted mainly from the partial difference in the flowage. As reported by Kojima and Stepanek et al., the irregular distribution is common in the reservoirs, where the water body is divided distinctly into two parts, one is the running water and the other is the dead water. In the former, the water is continuously renewed with the inflow and through which the standing crop of phytoplankton is diluted and moreover it is removed with the discharge. On the contrary, the phytoplankton in the dead water region increases successively within the same region.

**Summary**

Concerning the difference of the primary production in vertical and horizontal directions in the lake, the present researches were carried out in several lakes which differ from each other in their contours. The main factor determining the features of the distribution pattern was elucidated through the analysis of the interrelationship between the dry matter production by phytoplankton and the environmental conditions.

1) As for the horizontal distribution of the phytoplankton, three types can be observed. The first is the uniform distribution that is found in the shallow lake. The second is the regular one and observed in the slender lake with a simple shore
line, lacking in any large inflows and outflows. The third type is the irregular one and is obtained in the lake and reservoir with a complicated water current.

2) The different productive structures are found in different parts of the lake. The homogeneous structure is found in the shallow region of the lake and the stratified one can be observed in the regions with deep water.

3) The photosynthetic activities of phytoplankton differ spatially in a lake. Generally, the photosynthetic activities of phytoplankton sampled from the upper and middle regions of the lake are entirely the same, but that from the lower region shows usually low activity than those of the samples from the former two regions. Differentiation of phytoplankton to the sun and shade forms is observed in the region with deep basin, but not noticed in the shallow region.

4) The spatial difference in the light and nutrient conditions in a lake has been confirmed as the factors determining the horizontal distribution. Unfavorable light condition of the shallow region, which is caused by high turbidity through the bottom mud shifting, reduces the photosynthesis of phytoplankton, and consequently the dry matter production. The light condition in the region with deep water is suitable for the production.

5) Since the nutrients are exhausted at the upper and middle region of the lake, the lower region is replenished usually with the poor nutrient water. The nutrient gradient in the lake affects remarkably the spatial difference in the productivity of the slender lake with complex shore line.

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References

構 摘
市村俊英：同一湖沼の異なった場所における基礎生産のちがい
同一の湖沼内において、植物プランクトンの場所による基礎生産のちがいを調べた。円形の単純な湖沼形態をもつ湖沼では、著しい相違は見られず、全水域にわたってほぼ均一であった。長形の湖沼では流れとともに現存量、生産力ともに減少する規則的な変化がみられた。複雑な湖沼形態と湖沼をもつ湖沼では場所によるちがいは全く不規則であった。本論文ではこのような変化様式が湖沼形態によって規定される環境条件と、これにともなう物質生産の相違によって定まることを明らかにした。（東京教育大学理学部植物学教室）