THE BIOLOGICAL RELATION OF AQUATIC PLANTS TO THE SUBSTRATUM; PP. 485-526

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U. S. COMMISSION OF FISH AND FISHERIES,

GEORGE M. BOWERS, Commissioner.

CONTRIBUTIONS TO THE BIOLOGY OF THE GREAT LAKES.

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RAYMOND H. POND.

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INTRODUCTION.

This investigation was undertaken at the suggestion of Prof. Jacob Reighard, in charge of the biological survey of the Great Lakes under the auspices of the United States Fish Commission. It was carried on during three years, chiefly in the summer, partly at Put-in Bay, Ohio, and partly at Ann Arbor, Mich., under the direction of Prof. F. C. Newcombe, of the University of Michigan, to whom I am indebted for constant guidance. To Mr. A. J. Pieters, of the U. S. Department of Agriculture, I am indebted for the use of his very complete bibliography of aquatic plants. The discussion of the papers by Forel, Hoppe-Seyler, Seligo, and Stockmayer, constituting the introduction as well as the larger portion of the chapter on economic significance of results, is from the pen of Prof. Jacob Reighard.

One of the objects of the biological survey of the Great Lakes was to ascertain the factors which determine the quantity of food fish it is possible for these lakes to support. To this end it was necessary to study not only the fishes themselves, but all forms of animal and plant life in the lakes, for upon these, directly or indirectly, the fishes depend.

That the larger aquatic plants play an important part in the biology of fresh water has been long recognized, and at least two rôles have been assigned to them. The first of these is mechanical. Often the plants growing submerged are so abundant as to cover the bottom. Their fine rootlets give to the bottom soil greater coherence, while their stems and leaves protect it from the mechanical action of the waves. Such plants, moreover, form aquatic meadows in whose dense growth multitudes of small animals and young fish find shelter and concealment from pursuing enemies. Some fishes select these meadows as localities in which to lay their eggs, and the minute plant and animal forms there present furnish a plenteous food supply for the young fish. Although the larger plants as such are, while living, little used as food by the aquatic animals, yet they greatly increase the surface available for the attachment of microscopic plant forms, which are eaten by the smaller animals, and the latter in their turn by the fishes. This relation of the larger plants to the food supply is, as Seligo (1890, pp. 46, 47) pointed out, chiefly mechanical and indirect.

The second rôle usually assigned to water plants is that of aeration, in which the plants by their carbon assimilation remove carbon dioxid from the water and give out oxygen in its place. Aquatic animals use the oxygen which is in solution in the water and give off carbon dioxid, which passes into the water, and which, if it should accumulate excessively, would become fatal to the animals. The water must, then, be constantly supplied with fresh oxygen and as constantly freed of the greater part of its carbon dioxid. In sunlight plants absorb carbon dioxid, and in using it for the manufacture of carbon compounds give off oxygen to the water in equal volume to the carbon dioxid absorbed, so that green plants during sunlight not only keep the proportion of carbon dioxid down, but actually become aerating agents by reason of their contributions of oxygen. Hence it has been the current belief that aquatic plants are necessary to furnish the oxygen needed by aquatic animals and to remove from the water the carbon dioxid injurious to the animals.

In 1890, however, Seligo indicated that the importance of the aeration rôle of aquatic plants has probably been exaggerated.

> For, as is well known, plants need in their life processes not only the nourishing carbon dioxid, but like all other living things oxygen also, and while the excretion of oxygen takes place only in sufficient light, the absorption of oxygen goes on continuously. If then the oxygen content of water rich in plants must indeed be greater by day, so is it for the same reason much the less by night. At the same time equalization of gases must take place very rapidly in the comparatively shallow shore region of the lake basin, not only by access of the outer air, especially through wave motion, but also by diffusion within the water mass itself; and just as the assumption that forest air must be richer in oxygen than the air in the larger cities, for instance, has been shown by careful air analysis to be erroneous, so can the oxygen content of the shore water rich in plants be scarcely different from that which is free from plants. (Seligo, 1890, p. 47.)

Oxygenation of the superficial layers of water is accomplished by mechanical admixture of air through the action of waves, tributary streams, and rainfall, so that the upper 2 meters, over the entire surface of the lake, is practically saturated with the atmospheric gases. Oxygen thus absorbed from the air has been usually thought, as by Seligo, to diffuse with great rapidity into the deeper layers of the water, but Hoppe-Seyler (1896, p. 15) has measured the rate of diffusion of oxygen into motionless water from the atmospheric air and has found it extremely slow and wholly inadequate to account for the relatively large volume of oxygen present in the deeper water of lakes (about 7.6 c. c., per liter of water). He thinks it probable that the migrations of animals from the superficial water toward the bottom and back again aid diffusion by mechanically mixing the water, thus maintaining the oxygen-content of its deeper layer. He has found that the percentage of oxygen at a depth of 245 meters in Lake Constance is 6.68 c. c. per liter and has shown by experiment (1896, p. 17) that a content of 3.3 c. c. per liter is, if continuously maintained, more than sufficient for the support of sensitive fishes, such as trout. To what extent this oxygen of the deeper layers of water owes its origin to plants of any sort is not known, but there is no reason to believe that any appreciable part of it is due to the larger rooted plants of the shore region. Hoppe-Seyler does not attempt to account for its presence. It is quite possible that the seasonal inversion in which the surface layer is carried to the bottom assists in maintaining the oxygen supply at very great depths. The carbon dioxid present in Lake Constance Hoppe-Seyler found to exist chiefly in the form of carbonates; but little of it (8.14 mg. per liter of water at 147 m. depth) exists free. From these results the conclusion may be drawn with entire definiteness that even at great depths in the lake and very near the bottom only little carbon dioxid is present uncombined, and therefore no hindrance to the respiration of the animals of the lake can occur from the carbon dioxid tension even at such depths.

The observations of Hoppe-Seyler, then, show that the upper layers of the water of the lake to a depth of 2 meters are practically saturated with oxygen, not only where larger aquatic plants are growing, but where there are no such plants. These plants can therefore have no practical effect in increasing the oxygen content of the superficial layer of water. Since his observations show further that in no part of the lake, even at great depths, and in other situations destitute of larger aquatic plants, is there more than a small quantity of uncombined carbon dioxid present, it is clear that the larger plants are not essential for the removal of this gas from the water. It is removed rather as a free gas, by the formation of carbonates. The statement, however, that the larger aquatic plants can not be regarded as essential for the furnishing of oxygen to the animals of a lake or for the removal of carbon dioxid injurious to those animals must be understood as applying only to lakes of considerable size—not to small ponds nor to standing aquaria.

Since the larger plants are scarcely used directly as food by fishes and are of no demonstrated aeration importance in lakes, it remains to determine whether they form one of the links in the chain of nutritive relations that stretches from the water and the soil to the higher fishes; whether, in other words, the plants have, in addition to their mechanical rôle, a nutritive rôle also. If we follow it backward from the fish,