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THE AQUATIC HABITAT

WILL SCOTT, Indiana University

Two fundamental problems of biology are: (1) the nature of living matter and (2) the conditions under which organisms can and do exist. So far as we know, living matter is confined to a thin shell about the earth. This stratum is probably never more than twelve miles thick. Mt. Everest is 29,002 feet high. Little if any life exists on its frigid summit. A few spores may be blown across it, but at such a point the layer of living matter must be very tenuous. The Swire deep of the Pacific is 32,089 feet, and little life exists above the surface of the open ocean, so that the limit in this situation is a little over six miles. On the land surface life extends but a few feet into the soil and to an unknown height above it. Birds are usually confined to the first half mile although some have been observed occasionally at the height of approximately two miles. Spores have been collected by aeroplanes flying at an elevation of 18,000 feet.

In this thin layer, organisms exist in one or the other of two habitats, air or water. It is incorrect to speak of land and water organisms, because the land or lithosphere underlies both the air and water oceans, that is, the atmosphere and the hydrosphere.

The differences between these habitats are rather obvious, but the import of their differences is not always seen, possibly because they are so obvious. Water has a specific gravity near that of protoplasm. As a consequence, organisms exist at any level in the water—not only one-celled organisms but relatively large ones. More than twenty species of fish live in the ocean at depths exceeding a mile. Many groups of organisms fly (or swim) in the water. In the air ocean only four groups of animals have been able to leave the bottom for any length of time. These are the Pterodactyls of the Mesozoic and the insects, birds, and bats of modern times.

Air varies in humidity from saturation to the extreme aridity of some of our deserts. No animal was able to invade this environment until it had developed a device which would enable it to keep its respiratory surface moist in air of varying humidity. Only four of the five classes of arthropods and three of the seven classes of vertebrates have been able to do this. With rare exceptions, members of the other eighteen or twenty phyla remain aquatic.

In air there is always a sufficient amount of oxygen for life at any level of metabolism. Moreover, air is extremely mobile, never stagnant. On the other hand, water at 20° C, saturated with oxygen, contains only about four per cent as much oxygen as an equal volume of air at the same temperature. Water is always less mobile than air, and in ponds and lakes it is often stagnant for long periods, so that in its lower levels the amount of oxygen is reduced or may entirely disappear. It is no accident that the only warm blooded animals which we have breathe air. There never has been and never will be an animal of constant temperature with aquatic respiration.

Carbon dioxide constitutes only .03 of one per cent of the air. However, under a given pressure it is more easily absorbed by water than is oxygen; although small amounts of carbon dioxide can be absorbed by water from the air because of its slight pressure, many natural waters have a large reserve of this gas available for photosynthesis in the second radical of the bicarbonate of calcium and to a lesser extent of magnesium. In most of the natural waters of our state photosynthesis is not limited by the lack of carbon dioxide. The amount of carbon dioxide and oxygen in natural waters is influenced by three processes, photosynthesis, respiration, and decay. The first reduces the amount of carbon dioxide and increases the amount of oxygen. In respiration and decay the process is reversed. In lakes photosynthesis takes place in the well-lighted upper levels, respiration occurs at all levels, while organisms disintegrate chiefly at or near the bottom where the amount of oxygen is limited and often exhausted. This distribution of these three processes is the basic cause of the filling up of our lakes with organic matter. Because of the availability of carbon dioxide photosynthesis is not limited, while decay is limited by the amount of oxygen near the bottom of the lake, which is in turn limited by the summer and winter stagnation of the lake. So much for the comparison of these two habitats.

Now a word about some of the characteristics of water. The physical chemists are agreed that it is not simply H_2O. Declaux ('12) has pointed out that because of its atomic weight such a compound should boil at about — 100° C. It may be H_4O_2 or H_6O_3 or a mixture of all three of these compounds to which Sutherland ('00) has given the names of monohydrol, dihydrol, and trihydrol. Water dissolves most substances. Whatever our notion of the nature of a solution, the fact remains that any substance dissolved in water can be recovered in its original amount and form.

Another striking and biologically important characteristic of water is its high surface tension of seventy-five dynes. In this it exceeds all other substances save mercury. It is this property that has made possible the invasion of water by many adult insects.

In the further discussion of the aquatic habitat I shall confine my remarks to fresh water. The fresh waters of the earth are divided by the presence or absence of gravity currents into ponded waters and flowing waters.

Lakes. A lake is probably the most self-contained autonomous habitat on earth. About forty years ago Eigenmann ('95) referred to this characteristic of a lake by calling it a unit of environment. About the same time Forbes ('87) called a lake a microcosm. Salts and, in swampy areas, organic compounds in solution are carried into lakes by its affluents. Smaller amounts of these materials are removed by its effluent. There is an exchange of gases with the air. With these exceptions a lake is a closed metabolic system.

In a field, a pile of leaves decays. Carbon, in the form of carbon dioxide, and nitrogen, probably in the form of ammonia, become a part of the great mobile air ocean and are widely distributed. The salts are either washed away by water or become a part of the soil. You pass this slowly decaying debris with no offense from odors because its products are so rapidly and widely distributed.

In a lake a similar mass of organic material would produce carbon dioxide, which would go into solution, as would the ammonia. This ammonia would be oxidized into nitrites into nitrates, to be used again by plants and then by the animals. Some of the mass would go into solution as colloids. Most of the contained salts would go into solution. If this occurred in a stagnant region of a lake, the available oxygen might become exhausted with the disintegration continuing under anerobic condition. As I have already pointed out, there is often a residue which becomes a part of the permanent lake deposit.

The degree of autonomy varies widely. At one end of the series might be placed the so-called Lake Pepin, which is caused by the partial damming the Mississippi River by the delta of the Chippewa River. It receives the drainage of the whole upper Mississippi Valley, and its entire volume is discharged in a relatively short time. The opposite extreme is found in Crater Lake of Oregon the area of whose drainage basin but slightly exceeds the surface of the lake. Except for gaseous interchange with the air it is almost wholly autonomous.

Almost all physical and chemical peculiarities of lakes are the result of the relation of the specific gravity of water to temperature. The fact that the point of maximum density is approximately 4°C. (3.98°) accounts for the formation of the ice at the surface of the lake. In the process of warming, the heat, of course, is received at the surface. Until a temperature of 4° is reached, this surface water is continually becoming heavier, and the lake would finally mix by convection, although actually the wind assists in the mixing process.

After the point of maximum density is passed, the heat can be carried to the lower levels by wind alone. This becomes increasingly difficult as the temperature increases above this point. The difference in weight per cubic centimeter of two layers of water whose temperatures are 4°C. and 5°C., respectively, is .000008 gm., while the difference between two layers of 24° and 25° is .000252 gm. It will, therefore, take thirty-one times as much energy to mix the two layers having the higher temperature as it would the two layers having the lower temperatures.

By late spring or early summer this thermal resistance to mixture becomes so great that the highest winds are not sufficient to mix the water of a lake to more than a limited depth. This upper layer that can be disturbed by the wind during the summer is five meters thick in Winona Lake. Its thickness varies with the size of the lake and the exposure of its surface to the wind.

The result of this peculiarity of water is that, during the late spring, summer, and early autumn, lakes in temperate latitudes are thermally stratified. There is a warm upper layer, an intermediate layer in which the temperature declines rapidly from top to bottom, and a lower layer which is relatively cold. These three layers are called respectively the *epilimnion*, the *thermocline* (mesolimnion) and the *hypolimnion*.

The water of the epilimnion is periodically exposed to the air and receives the maximum amount of illumination. The thermocline is not exposed to the air but usually receives some light. The hypolimnion is sealed from the air and receives little or no light.

The oxygen is gradually reduced in the hypolimnion. In about one-

third of the lakes examined in Indiana the oxygen is entirely exhausted from the lower levels by mid-summer. Some chironomids, annelids and protozoa are able to survive from four to five months under these conditions. Just how they are able to do this has not been satisfactorily explained. When this condition becomes too severe, the bottom macrofauna disappears. Heriff Lake has an area of about 4 acres (1.6 hectares) and a depth of 4 m. Its original area was about 200 acres. It is surrounded by a marsh covered with maple trees about 50 feet in height. As a result of its small size and the protection it receives from the wind, its stratification is extreme. On July 18, 1934, it had dissolved oxygen at .5 meters but none at one meter. On the same day, 1935, it was examined after a severe storm and a trace of oxygen was detected at 1 meter. Although the bottom was dredged extensively, no macroscopic organism was detected except Corethra, which is known to migrate vertically. May I add a few incidental remarks concerning this unique and interesting lake? The Secchi's disc disappeared at 5.6 cm. The water was deeply stained. In this thin epilimnion was a dense plankton population which included Diaptomus, *Daphnia longispina*, and Ceratium. Several fishes were seen. One bass, twelve inches long, was taken. Scale examinations showed that it had grown rapidly for the first two years and thereafter very slowly.

In the epilimnion there is usually plenty of oxygen. Theoretically, there should be a diurnal oxygen pulse, but it is very difficult to demonstrate due to the mixing of the water by wind. After many trials, I succeeded in demonstrating it in Winona Lake (Scott '23). The pulse is always higher in the weedy littoral than in the pelagic region. The maximum was reached at 5:30 p. m.

Supersaturations of oxygen may occur in both the epilimnion and the thermocline, but their development and duration are quite different. In the epilimnion the supersaturation may develop whenever there is a period of calm weather and there are sufficient algae. With the first wind the supersaturation is obliterated.

In some lakes the position of the thermocline and the transparency of the water are such that considerable light reaches the thermocline. Under these conditions an algal flora may develop which produces a little more oxygen each day than is consumed in respiration and decay. This slight excess of oxygen, being under some hydrostatic pressure, does not escape. It is not influenced by wind. The effect, however, is cumulative, and a relatively high supersaturation may occur. This supersaturation may persist for some weeks. It remains for some time after the algae which produced it have disappeared.

In Lake Gage on July 6, 1929, at 8 meters the oxygen amounted to 158% saturation. This was associated with a rather dense flora of Lyngbya. Four weeks later the amount of Lyngbya had declined, but the oxygen saturation had decreased only slightly to 153%. A similar observation has been reported by Birge and Juday ('11) for Garvin and Knights Lake.

The thermoclinal supersaturation differs from that of the epilimnion in that it is not subject to the influence of wind. The oxygen accumulates over a longer period. The supersaturation is usually higher and lasts

much longer. The complete history of a thermoclinal supersaturation has not been determined. The saturation in the epilimnion develops during relatively calm weather and is terminated by the first windy day. This condition is most likely to develop in small lakes which are protected from wind.

What I have called the thermoclinal oxygen notch is an interesting phenomenon. It developes in mid-summer in lakes of considerable depth and with a rather rich plankton. In these the amount of oxygen declines rapidly in the supper part of the thermocline and then increases in the lower part of the thermocline or the upper part of the hypolimnion. This is followed by the usual slow decrease to the bottom of the lake. In some lakes the oxygen entirely disappears at the level of this notch. In such a lake there usually is a region near the bottom without oxygen, then a level with oxygen, above this, the oxygenless level of the thermocline, and finally, the well-oxygenated epilimnion

Snow Lake and the third basin of James Lake of Steuben County develop this condition and also have cisco. The cisco prefer cool water and, of course, must have oxygen. In early summer they live in the hypolimnion; as the oxygen begins to disappear from the lower levels of the lake, they are forced upward. In early August they are trapped between two oxygenless levels. Soon after the first of September their oxygen supply becomes so reduced that they are partially asphyxiated and come struggling to the surface. Here they soon recover and descend as far as the oxygen of the upper levels permit.

The most characteristic element of the fauna and flora of a lake is the plankton. The word *plankton* was first used by Heusen to include all small organisms floating in the sea, "Alles was im wasser treibt."

In lake work the term *plankton* has come to mean a very definite association of organisms found in the pelagic or open part of the lake. The organisms are small and have a specific gravity near or quite identical with the particular water in which they occur. Some of them migrate vertically, but their horizontal movements are for the most part passive.

A rather large element of the plankton is cosmopolitan in its distribution. *Daphnia longispina*, *Bosmina longorostrus*, *Cyclops leuckartii*, *C. serrulatus*, *C. phaleratus*, and *Keratella cochlearis*, for example, may be expected in any lake in the world. The wide distribution of this group of organisms, this sameness of the plankton of lakes, is associated with the similarity of the pelagic region of different lakes. There is less difference between the pelagic region of a lake in Indiana and one in Holstein than may be found in the littoral of almost any lake. Not only that, but the pelagic area changes very slowly. This cosmopolitanism is the result of rapid distribution, or age, or possibly both. If the distribution is very rapid, the length of time required for cosmopolitan range need not be so great.

These two factors are difficult to separate. Viable eggs of these crustacea have been taken from the stomachs of fishes. It has been suggested that if the fishes were eaten by birds, the eggs would probably survive. This has not been demonstrated. Some of these forms have been found attached to birds' feet. I have found a colonial protozoan

attached to aquatic beetles. These protozoa were active after remaining in the air all night. Migula ('88) enumerated 23 species of algae from aquatic beetles.

We do not have adequate data on the influence of birds on the distribution of aquatic invertebrates. Experiments are needed to determine what eggs or spores of these forms pass through the alimentary tracts of various water birds. If such experiments give affirmative results, it will help to answer a long discussed question.

Some genera are cosmopolitan while their species are strikingly local. In a closely related group the species may be widely distributed. The American species of the copepod genus Cyclops are almost if not quite identical with those of Europe, while in the genus Diaptomus there are more than thirty species peculiar to America and none identical with those of Europe. Practically all of the lakes of the northern hemisphere came into existence with the melting of the ice of the last Pleistocene glaciation. Lake Tanganyika of Africa is much older, and a comparison of their faunas is of interest.

Tanganyika is the most southern of the series of deep African lakes lying in the "great rift" whose formation Suess places in the Miocene. The finding of a jelly fish in this lake first suggested a marine origin for the fauna. Moore ('03), who led the first two expeditions of the Zoological Society for the exploration of this lake, concluded from the study of the fauna, and especially the molluscs, that the fauna was closely related to that of the marine Mesozoic. The geology of the region does not support this view. The subsequent work of Cunnington ('20) and others indicates that here, in a lake fauna that has been pretty well isolated since the Miocene, many of the forms have become unique. The long spined gastropods, for instance, closely resemble marine shells. Not only is it a case of convergence, but they suggest the bizarre characters of senescence familiar to every paleontologist. In the plankton of this lake are the following cosmopolitan forms: *Cyclops leuckartii, C. albidus, C. serrulatus, C. phaleratus, Branchionus angularis,* and *Keratella cochlearis.* The question of the relation of the cosmopolitan to the endemic species is complicated by the systematist. Of the twenty species of copepods listed by G. O. Sars ('09), fourteen were described as new. Two of these were described from single individuals and four of the remainder from single collections.

This question is further complicated by seasonal variation. In temperate latitudes where this has been studied, the Cladoceras, for instance, are much more alike in winter than in summer. Wesenberg-Lund ('08) has said that in Denmark during the summer, he can usually tell from what lake a daphnid has come, while in winter they are nearly if not quite identical.

This seasonal variation of the plankton has been attributed to changes in viscosity, specific gravity, and locomotion in relation to food.

Some light on the question of cosmopolitanism of plankton may be obtained by a study of the development of the plankton in a new artificial lake. When a pond or lake is first formed, it is usually some years before a typical lake plankton develops. Either the organisms are unable to reach the lake, or something must happen in the lake to make it suit-

able for the plankton. In one of our state forests there are three lakes, recently constructed. Last summer I planted in one of these lakes a complete complement of lake plankton. A recent examination showed that the plankton is surviving in this lake, while in the control lake the only plankton forms are blue-green algae. The question of the cosmopolitanism of lake plankton, its age, and its methods of distribution, remains intriguing, complicated, unanswered.

Streams. Streams differ from lakes in the presence of current and their greater dependence on land. Green plants occur in streams in one of three situations. In clear well-aerated streams, with stony or gravelly bottoms, Cladophora and similar attached algae are found. In streams whose rate of discharge is relatively constant, aquatic phanerogams develop if the current is not too rapid. Such streams are often the outlets of lakes. In our state the upper Tippecanoe, the Pigeon and the Fawn rivers are good examples. Last summer we weighed the plants from fifty-two quadrats in the upper Tippecanoe. The average weight was 2.9 Kilos. per square meter, which is a trifle less than 13 tons per acre wet weight. The dry weight was approximately 10% of the wet weight.

Streams rich in organic matter, domestic sewage, for example, with proper temperature, produce a dense growth of blue-green algae.

In other situations, streams are wholly dependent on land for their basic organic material. In small streams, where the relation of shore line to area is high, a considerable number of insects and bits of plants reach the stream more or less by accident. In larger streams whose levels fluctuate, much organic material is washed into the stream bed from its flood plain.

There has been a notion that temperature is the principal factor influencing the amount of oxygen in streams. Butcher, Pentlow, and Woodley ('30) have called attention to the influence of plants, pollution and turbidity in their work on three small rivers of England—the Itchen, Lark, and Tern. These influences are most marked during the summer. The Itchen is "clear, rapid and unpolluted." On July 27 its oxygen content was 121% saturated at 2:00 p. m. and 69% at midnight. The Lark, which is slow-flowing, contains plants in abundance, and is polluted by a beet sugar factory, had the following per cents of oxygen saturation on June 27; at 6:00 p. m., 165%; at 6:00 a. m., only 36%. The Tern, which is "moderately rapid", often turbid, and never clear, varied from 96% at 4:00 p. m. to 87% at 11:00 p. m.

In winter they were much more alike, and the diurnal variation was less. On December 14 the Itchen varied from 88% to 84%. On February 16 the Lark varied from 77% to 66%. The variation in the Tern on January 29 was from 87% to 79%. In each instance I have given the maximum and the minimum.

Denham, working on White River, found that clouds for an hour during the day made a notch in the diurnal curve.

At some distance below the point where sewage is discharged into a river there occurs what is known as the oxygen sag. That is, some oxygen is in solution at the point where the sewage enters but the decay of the organic material soon depletes this supply. However, algae soon

begin to develop in this rich solution and suspension of organic material and the influence of photosynthesis is soon apparent. Denham traced this influence from the Indianapolis plant to a point 169 miles down the river. He was able in eight days to complete five 24-hour series at points approximately 6, 26, 61, 113, and 169 miles from the point of discharge. The diurnal variations in oxygen expressed in per cent of saturation were for these five stations, respectively, 4-0, 118-18, 295-94, 151-64, and 132-72. So far as these observations go, the maximum diurnal variation occurred at 61 miles, which is just below the town of Gosport.

The plankton of streams is a puzzling subject. Current seems to be inimical to its development and maintainance. It is well-known that in an effluent of a lake the plankton soon disappears. Whenever a river is rich in organic matter, especially in that which produces ammonia, blue-green algae are numerous. Rotifers are usually associated with these. With a slight rise in level, and consequent increase in velocity, the number of diatoms in the plankton increases.

Kofoid ('08) in his work on the Illinois River decided that its plankton was derived from the shallow lakes of its flood plain. I found a similar thing in studying the plankton of a cave stream. Here the source was a particular type of solution pond. These ponds are formed by the occlusion of a sink hole. In some of these a second opening at a higher level was formed. In rainy weather the pond overflowed into the cave below through this secondary opening.

Allen ('20) studied the plankton of the San Juan River from three stations. Two of these stations were located on lateral canals. The third station, located on the main stream, occasionally had Cladocera and similar typical lake plankton forms. Tulare Lake is sometimes flooded into the San Juan. In the upper course of King's River, the principal tributary of the San Juan, there are at least seven mountain lakes. The relation of these lakes to the river plankton was not determined.

Eddy ('34) has held in a recent paper that the amount of plankton in a stream is proportional to the age of the water. He based this conclusion on a study of the plankton in a reservoir in the Sangamon River. The river was not studied below the dam, which would have helped determine whether it was the age of the water or the ponding which was associated with plankton development.

Behning ('29) finds in the lower Volga, near the delta, a very complex plankton similar in its components to lake plankton. Even delicate forms like Leptodora are present.

The Volga has a low gradient and consequently slow current. If there are not tributary ponded waters, it is difficult to see how a floating society like the plankton can be maintained. The Volga has very high summer floods, on the recession of which, Benring points out, many eggs and spores of these forms are left on the banks and flood plain. It is thinkable that waterfowl, migrating north, might carry these eggs upstream and thus complete the cycle.

It is obvious that this phenomenon should be studied over a whole river system through all the seasons.

I am forced to omit many things. I should like to have told you something of the studies of Birge and Juday ('29) in the penetration of

solar energy, of various wave-lengths in different types of water, of the work of Woltereck ('28) in the modification of daphnids by transplantation, of the refined experimental work now being done at Aneboda (Nauman, '28), the factors that are involved in the vertical immigration of plankton, the factors influencing the distribution of bottom fauna, and many other interesting and important phases of fresh water and its organisms. However, I trust I have given you a little glimpse at what Sir John Murray once called the most ancient of organic habitats.

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