

errors arising from this cause. Each group contains six pairs which are used directly for computing the latitude variation, and of which very few have zenith distances exceeding 20 degrees. Each group also contains two pairs introduced for the special purpose of studying the actual refraction, and of which the zenith distance is about 60 degrees. The normal refraction at a zenith distance of 60 degrees is about four times that at 20 degrees; hence the two refraction pairs will furnish an effective method of determining any peculiarities of refraction which are sufficiently great to produce any appreciable effect upon the latitude pairs, provided such effect is one which increases with the zenith distance.

Any refraction effect which is analogous to a displacement of the apparent zenith, by a persistent barometric gradient, for example, will not be put in evidence by this test. To eliminate such an error, dependence is placed upon the fact that the final result is based upon observations at several stations varying greatly in longitude and in the surrounding climatic and local conditions.

It may seem at first sight that an annual variation in refraction would produce an apparent annual motion of the pole. This would be true if the motion of the pole were derived from observations at one station only. It will be seen, however, on further reflection that annual variations in refraction would tend to make all the latitudes along one parallel apparently increase and decrease together, and that therefore the computed motion of the pole would not be appreciably affected if these annual variations were of about the same magnitude at the different stations distributed around the pole.

To sum up, the discovery of the periodic motions of the pole was first made by a purely inductive method. The laws governing those motions have been slowly and

painfully deduced by a continual application of the same method to old series of observations and to many new series made for the special purpose. Now a new campaign of observations, promising results more accurate than any hitherto obtained, has been commenced. The mean position of the pole for each fortnight of the next five years will probably be known within a radius of five feet. There is little prospect for improvement of the observational side of this question for many years. The new observations will furnish material for new triumphs of the inductive method in furnishing a still closer mathematical approximation to the unknown laws of motion of the pole. The interesting feature of this investigation is now that the theorists are at sea, so to speak. Will they at the end of the five years be able to furnish an adequate explanation for the new facts observed or, indeed, for those already known? It is on this theoretical side of the investigation that new energy is needed. Here is a golden opportunity for some one well versed in mechanics, astronomy, and geodesy.

JOHN FILLMORE HAYFORD.

U. S. COAST AND GEODETIC SURVEY.

*THE PLANKTON OF FRESH WATER LAKES.**

For some years I have been interested in the subject of the fauna of our fresh water lakes. This interest was first aroused in regard to the animals of the deeper parts of the lakes. The results of the explorations of the depths of the ocean were just becoming known. I had read in the older works that while the sea was densely populated along shore, and had what has become to be known as a 'pelagic' fauna and flora in the open sea, remote from land, the depths were a barren region utterly devoid of both animal and vegetable life. But later it had been shown that there was, even in the

* Address of the retiring President of the Wisconsin Academy of Sciences, Arts and Letters.

greatest depths, a fauna, not very abundant to be sure, but of great interest because of the strange peculiarities of some of the forms. With others I was profoundly interested in this work, and it led me to conjecture whether there was not a field for investigation in the deeper waters of our lakes. At that time very little had been done in the way of any systematic study of the deeper waters of the lakes. I think the only extensive work on the subject was Forel's 'La faune profonde des lacs Suisses,' published in 1885. Professor Forel had begun his researches on the deep water fauna of Lake Lemman in 1869, and had published various notices in the intervening years. In this country, so far as I know, the first publication in regard to the deep water fauna of lakes was in the first volume of the *Transactions of the Wisconsin Academy*, in a paper by Dr. Hoy, of Racine. He detailed how he had become interested in the food of the whitefish, and had examined their stomachs, finding certain animals that seemed new to science. A company was made up for a dredging expedition consisting of Dr. Hoy, Dr. Lapham, Professor Stimpson, Professor Andrews and Mr. Blatchford, and put in a day's work dredging on Lake Michigan in June, 1870. The result was the collection of a considerable number of animals. Especial importance was attached to the discovery of a *Triglopsis* and a *Mysis*, as they are marine genera, and their presence was supposed to indicate a former direct connection of Lake Michigan with the ocean.

In 1874 Professor Smith published a paper on the 'Invertebrate Fauna of Lake Superior,' reporting the existence of the same crustacea in Lake Superior which Dr. Hoy had found in Lake Michigan. The *Mysis* there, however, occurs in somewhat shallow water as well as in the greater depths. In both lakes it forms an important—perhaps the most important—constit-

uent of the food of the white fish and lake trout. As I was located near a lake of considerable depth, a depth reputed to be anywhere between 400 feet and infinity, it occurred to me that I had an opportunity to carry out similar researches.

My own work on lakes, then, originated in a desire to know more about the abyssal animals. I soon found, however, that the problem was a serious and complicated one, involving a complete faunistic study of the lake. I was fortunate in finding on the bottom of Green Lake the same *Mysis*, which makes its home in Lake Michigan. These animals have not been definitely reported from any other lake in the United States, although *Mysis* is said to live in a lake in New York connected with the St. Lawrence. Here was a pretty problem in animal distribution. How did these animals make their way into Green Lake? Was it by way of the Great Lakes, or did they come at some time by a connection through the Mississippi Valley? I could not tell, and I cannot to-day, for it becomes a problem for the geologist rather than the zoologist. With this as a starting point I attacked the problem of lake faunæ, and the battle is still in progress with no indications of a conclusion of hostilities for many years to come.

During the decade in which I have been interested in limnology there has been a very considerable advance in our knowledge of the subject, and it will be my attempt to-night to summarize this knowledge, and make as clear a statement as I can in the brief time at my disposal of what is now known of the fauna and flora of fresh water lakes. Russell, in his work on North American Lakes, enumerates ten agencies which, acting separately or in combination, may produce lakes. So far as our Wisconsin lakes are concerned, the most important of these agencies is glacial action. Most of our lakes are simply the depressions caused

by the unequal distribution of the glacial drift, or by interference with preëxisting drainage lines. Inasmuch as Wisconsin is not a mountainous state, it follows that these depressions are nowhere of great depth, and that we have no lakes which compare in depth with those located in mountainous regions. Most of our lakes are extremely shallow, few being more than forty or fifty feet in depth. Lake Geneva 142 feet, and Green Lake 237 feet, are our deepest bodies of water, while our largest lake, Lake Winnebago, probably does not exceed twenty-five feet. All lakes are temporary features of the topography. The outflowing water is all the time deepening the outlet and increasing the amount of drainage, while the inflowing water is bringing in material which gradually fills up the lake bed. This process goes on with comparative rapidity, and even in our new lake areas there are numerous examples of dead lakes where swamp vegetation entirely covers what was formerly an open sheet of water. The physical processes involved in the lives of lakes and the relation of the lake vegetation to these processes are very interesting, but this is not the time or place to discuss them, and they can only be referred to in passing.

The subject of the fauna of fresh water lakes has not been especially attractive to zoologists. This is but natural when we consider the great wealth of life in the ocean, and the comparative poverty of fresh water. Of the more important divisions of the animal kingdom the echinoderms and tunicates are entirely absent in fresh water, and the coelenterates and molluscoidea are represented by few forms. Even the crustacea, which form the greater part of the plankton, and are present in such enormous numbers, have very few forms compared with the crustacea of the sea. It is to be expected that zoologists will be attracted by this wealth of material in the sea, and that

most of them will in the future as in the past resort to the sea for their study. It was in the ocean that the ancestors of our fresh water animals dwelt, and it is amongst those animals that the student may expect to find the most information in regard to the development of life on the earth.

But the lakes have their fauna, a fauna of great numbers if not of great variety, and because of their isolation and somewhat peculiar conditions, present a very interesting study in the distribution of animals. Of course the best known members of this fauna are the fishes, whose numbers, habits, and food are fairly well known. Fish are so important for human food that a study of their habits comes to be a matter of commercial importance, and our Federal and State governments expend large sums of money for this investigation and for the practical work of rearing and distributing the spawn or young fish. In Wisconsin, too, as well as in some of the other northern States, it is a matter of great practical importance to maintain the numbers of game fish in our lakes simply for the purposes of sport. Until one has made the rounds of the summer resort lakes one has little idea of the multitudes of people who come to our State in the summer season, attracted largely by the opportunities for fishing. Hundreds of thousands of dollars are brought to us every summer in this way, and it is a good business policy which leads us to do all in our power, and even spend large sums of money, if necessary, to maintain our stocks of game fish.

It has long been known, of course, that fish are dependent for their food upon smaller animals, and it has also been known that a knowledge of these same small animals was necessary to any accurate and complete knowledge of fish, but this study was so difficult and involved so much drudgery that for a long time it was neglected.

Anything like an exact knowledge of the

crustacea may be said to date back only half a century to the writings of Fischer and Claus, although some papers upon this subject had been published previously.

In 1817 Say published a somewhat extended article on the crustacea of the United States, in which he speaks of one *Ostracod*, two *Daphnias* and one *Cyclops*, as inhabiting the waters of the southern states. In 1843, in the 'Natural History of New York,' was published an article by DeKay on the crustacea, which was beautifully illustrated, but added little to our knowledge of the fresh water crustacea. In fact, though *Cyclops* and *Daphnia* are mentioned, they are spoken of as 'extra-limital,' in spite of the fact that not a lake in New York would have failed to furnish him countless numbers of these genera, had he looked for them. To Professor Forbes, of the University of Illinois, is due the credit of making the first extensive collections of these animals in this country, and publishing accurate descriptions of them. His first paper was published in 1876, and was followed by a series of very valuable investigations, culminating within the last few years in the establishment of a floating laboratory on the Illinois River for the continued study of the fauna and flora of that river and the shallow lakes adjoining.

In Europe large numbers of investigators within the last few years have devoted themselves to the study of fresh water animals and plants. Preëminent among them have been Forel and his co-laborers on Lake Lemán, and Zacharias and his fellow-workers in the station at Lake Plön in Holstein. This station at Plön was, I believe, the first permanent fresh water station in the world. Since its establishment in 1891, a considerable number of permanent stations have been established in various parts of the world. It is not my purpose here to give a history of these establishments, for that has already been

exceedingly well done by Professor Ward. I may call attention in passing, however, to the fact that the work in this country has been done almost exclusively in our immediate vicinity, Illinois, Wisconsin and Michigan having published by far the most material on this subject. Similar work has been prosecuted in Minnesota, Ohio and Indiana, but very little has been done in the other states, if we except the exceedingly valuable work of Whipple.

In Wisconsin, work has been prosecuted on the Madison lakes and Green Lake for many years, and now, under the auspices of the Natural History Survey, a more extensive and systematic biological survey of the lakes is being made, probably a more extensive comparative study than has been attempted elsewhere. While this study is of especial scientific interest, as has been intimated before, it is of great practical interest in connection with the problems of fish culture. It may not be likely that, as suggested by a recent writer in *Forest and Stream*, the future angler will carry with him a thermometer and chart with a statement of the laws of vertical and horizontal distribution, but such study does give a fundamental knowledge which is of vast importance to the angler as well as to the fish culturist.

The terminology used in the study of the fauna and flora of fresh-water lakes, as in the sea, was formulated by Hæckel. Under the term 'plankton' is included all living things, animal or vegetable, found in the water which do not move from place to place by their own volition. Fishes are not considered a part of the plankton. The life of the sea may be considered as 'littoral,' 'pelagic' and 'abyssal.' To these terms Hæckel adds 'zonary,' to include those animals which are supposed to occur at zones of different depths in the open ocean. In the littoral and pelagic planktons we may have both animals and plants, but in the abyssal

noplants are found. The study of the pelagic and abyssal faunas has been entirely within the last half century; in fact the very knowledge of their existence dates back hardly fifty years.

In the lakes we use a similar set of terms. The regions are 'littoral,' 'limnetic' and 'abyssal.' The characteristics of these regions are somewhat known, but still our knowledge is far from perfect.

A list of the plants and animals found in any one lake seems quite formidable because of its length, but the species that are present in any considerable numbers are very few. From a limnetic collection, for instance, we may find in abundance the following: Four or five copepods, five or six cladocera, three or four protozoa, and perhaps two rotifers. This would be a fair average fauna in one of our lakes. Of the plants, we would find two or three diatoms and as many algæ.

Not only are the animals and plants of neighboring lakes very much alike, but the same animals may be found distributed over wide territories, and even over different continents. This is true even of some of the higher animals of the plankton, like the crustacea. Of our fifteen species of *Cyclops* nine are found in Europe. In the case of one species it is not only found in Europe, but in Asia and in Africa, and literally does not vary a hair in these widely separated localities. On the other hand, the genus *Diaptomus* is very variable. We have not a single species which is common to the European lakes. Not only that, but there are many localized species in the United States. One species occurs, so far as known, only in a few lakes in the northern part of the lower peninsula of Michigan. A second is widely distributed in all the smaller lakes across the continent in the northern States. Another goes from the center of Wisconsin north into the Arctic regions. In the Rocky mountain regions are several peculiar spe-

cies. Through the southern States two species are found which never come north. Mexico has at least one peculiar species. Of the other organisms, both animal and plant, most are world-wide in their distribution. From this fact of the general uniformity of fauna and flora over wide regions, it is clear that the study of a lake which simply produces a faunal and floral list is of very little value. There was a time when such lists were important, before this uniformity of distribution was determined, but that time is long since past, and those European authors who continue to fill the proceedings of learned societies with lists resulting from desultory explorations of one or more lakes are almost wasting printers' ink.

In the littoral region we find usually an abundant flora. Those plants which need an anchorage find it in the mud of the bottom, and the unattached plants are protected by those that are stationary. Protected by these plants and living upon them is an abundant fauna in which crustacea are the most prominent, although we find great numbers of rhizopods, infusoria, sponges, hydrozoa, worms, true insects and mites, mollusca and bryozoa. This abundance of the lower animals forms a rich supply of food upon which the higher animals can live. It is in this littoral region that the fish get the most of their food, and every fisherman knows that marshy borders are necessary to maintain the supply of fish. The animals of the littoral plankton are opaque, and generally are so colored that when they are at rest they are inconspicuous. Those that swim about and then drop to the bottom to rest are ordinarily so colored that they are not easily distinguished from the mud. Frequently in littoral regions the bottom is covered with a thick mat of *Chara*, which, in turn, forms hiding places for enormous numbers of the invertebrates.

The flora of the limnetic region can be, of course, only of floating plants. Among

these are an enormous number of diatoms. *Chlorophyceæ* are present in larger or smaller numbers and sometimes large numbers of the *Cyanophyceæ*. Generally speaking the limnetic flora is not sufficiently abundant to attract attention, but on some lakes they are sometimes multiplied in such quantity as not only to attract attention but even to excite alarm. The surface of the lake has a thick coat of bright green, and as this is cast up on the shore by the waves it forms thick ridges which in their decay become very offensive. This phenomenon has been known in England as 'the breaking of the meres,' in Germany as the 'wasserblüthe,' and in this country as the 'working of the lakes.' The appearance is sometimes ascribed to the seeds of littoral plants. Only a few species of plants are concerned in this phenomenon, and the species differ somewhat in different lakes. Certain diatoms may be present, too, in sufficient numbers to produce an unpleasant 'fishy' smell in the water. This exaggerated growth of the limnetic flora is most pronounced in shallow or comparatively shallow lakes, and is frequently a source of great annoyance to cities which get their water supplies from such bodies.

The limnetic fauna, as I have said before in this address, has but few kinds of animals, by far the most numerous and characteristic being the crustacea. These are beautiful, transparent and nearly colorless creatures. It is not true, as is sometimes stated, that the limnetic fauna is entirely distinct from the littoral. The general character of the limnetic animals is certainly different, and distinctly different, from that of those found in the littoral region, but many individuals are common to both. It is true, however, that while there is hardly a radical distinction between the two faunæ, certain species are common in the limnetic regions and only rarely found in the littoral, while some that

are everywhere in littoral collections are rarely found in those taken in the open water. There is, of course, no clear dividing line between the two regions, but one insensibly merges into the other, while, under the influence of the winds and waves, such limits as exist are continually changing.

In the species of crustacea there is a certain distinction between the limnetic fauna of the deeper lakes and that of the shallower. One species of *Diaptomus* is found everywhere in the Great Lakes, but in only three of the Wisconsin lakes—Lake Geneva, Green Lake, and Cedar Lake. The shallowest of these lakes—Cedar Lake—is about a hundred feet in depth. One of the species of *Cyclops* is very abundant in the Great Lakes, but is seldom found elsewhere except in comparatively deep lakes.

In a paper published in the Transactions of the Academy, I made the suggestion that lakes might be divided according to their faunæ into the deep water and the shallow water, suggesting as a possible limit between the two 40 meters. I have since found that Elhart Lake, 117 feet, and Cedar Lake, 95 feet, have many characteristics of the deep water fauna, and it is possible that the dividing line should be nearer 30 meters than 40.

The German authors make a distinction between 'plankton-poor' and 'plankton-rich' lakes, which very nearly corresponds to my deep-water and shallow-water lakes; for the total amount of plankton in the deep lakes is very much less than in the shallow lakes. This is easily explained. For the number of animals is, of course, dependent on the number of plants. Inasmuch as plants are dependent upon sunshine, they will grow in water only in those places that are reached by the sun's light. As the light of the sun penetrates in deep water only to a limited distance, the deeper parts of our lakes are entirely de-

void of plant life. On the other hand in shallow lakes not only do we find the floating vegetation as in the deep lakes, but as the light reaches the bottom over a larger proportion of its surface, we have in addition a very large flora flourishing on the bottom. In some of the very shallow lakes nearly the whole bottom is covered with a rank vegetation. This is true, for instance, of Lake Vieux Desert. In Green Lake, on the other hand, inasmuch as the shores are somewhat precipitous, there is only a comparatively narrow margin on which can be supported a flora growing upon the bottom, while the larger part of the lake is so deep that only the floating vegetation can exist. It is easily seen, then, that a shallow lake will be 'plankton-rich' as compared with a deep lake. Fishermen recognize this fact, and expect the shallow lakes to be better for their sport.

It is evident, then, that the living limnetic vegetation must be at or near the surface, where it can have an abundance of light. Animal life, however, is not limited in this way. It was long ago shown that in the sea there was an abundant surface fauna and an abyssal fauna, but in regard to the condition of the intermediate region there has been some dispute. Agassiz has claimed that there is a region intermediate between the top and bottom, which is entirely devoid of life. This has been disputed by some authors, and late explorations seem to indicate that no region between the surface and bottom is entirely free from animals. A similar condition exists in the lakes. By far the most abundant fauna is at and near the surface, but animals are found in greater or less numbers at all depths. The larger part of the plankton is found within thirty or forty feet of the surface; but the same kinds of animals that form the fauna of the upper waters may be found at all depths, although in small numbers. *Limnocalanus* is an ex-

ample of an animal which belongs to the intermediate regions. It, too, may be found in small numbers at any depth from the surface down, but it seldom occurs in any considerable numbers outside the intermediate region.

Limnocalanus and *Daphnia pulicaria* are perhaps the only animals in fresh water which belong distinctively to the zonary plankton, although *Cyclops brevispinosus* is much more abundant between five and twenty meters than it is near the surface.

Collectors of plankton material have known that they could ordinarily make much more abundant collections at night than in the daytime. This has led to a belief that there is a vertical migration of the plankton, towards the surface at night, and away from it in the daytime. It was supposed that the whole body of the plankton moved up and down. This idea has been proved to be false. What movement there is is within quite narrow limits near the surface, and all members of the limnetic fauna do not, by any means, behave in the same way. They have most decided individual peculiarities, so that we cannot speak of the movements of the fauna as a whole, but each species must be considered by itself. Some of them do not move at all vertically, but have the same distribution from one end of the day to another. Others, like the larval forms of the copepods, are more numerous at the surface in the daytime than in the night. Some have a very pronounced migration. This is particularly true of *Leptodora* which is rarely found at the surface in the daytime, but appears at almost exactly forty-five minutes after sunset, remains at the surface during the night, and disappears again at just three-quarters of an hour before sunrise.

Most of the larger crustacea which form the great body of the plankton do migrate in this way, and it was natural, perhaps, to

infer that the whole plankton moved up and down.

The limits of this vertical migration it is very difficult if not impossible to fix. Most of the movement is within one meter of the surface, the most marked changes being within one-half meter of the surface, and below three meters the amount of movement is very slight. Eight determining factors have been listed by Professor Birge as controlling the vertical distribution of crustacea: food, temperature, condition of the water in respect to dissolved oxygen and other substances, light, wind, gravity, age and specific peculiarities. Of these factors, by far the most important are food, temperature and light. Inasmuch as the food supply is controlled by temperature and light, we may speak of these two factors as, in the main, controlling the vertical distribution of the limnetic plankton. Of these two factors, temperature is the most important, although light has a marked effect on many species. In the winter season when the waters of all the lakes are very nearly uniform in their temperature from top to bottom, the vertical distribution of the limnetic fauna is much more uniform than in summer.

In the summer season the most marked changes in vertical distribution are correlated with the vertical changes in temperature. This is most distinctly seen in the deeper lakes. In these lakes it is a surface layer of greater or less depth which is warmed, the deeper layers feeling the effect of the summer's sun only very slightly. In Green Lake below 40 or 45 meters the temperature never rises above 6.11 degrees Centigrade, although the surface may run as high as 26.67 degrees C. In Lake Michigan the bottom temperature at depths of 360 feet is 4.2 degrees C., with a surface temperature of 18.3 C.

The change in the temperature from the top to the bottom is not a gradually decreas-

ing one, however. A layer of water at the surface, which may be in midsummer some ten or twelve meters in depth, is very nearly uniform in temperature. From the lower surface of this layer there is a very rapid decrease in temperature for a short distance, and then a gradual decrease until a minimum is reached. This layer of sudden change in temperature is known as the 'thermocline,' and its position varies in depth with the season and the size of the lake. As the summer season progresses the thermocline grows lower. In the very shallow lakes the temperature during the summer season is nearly uniform through the whole depth. In Lake Winnebago, for example, there is seldom a difference between top and bottom temperatures greater than two degrees. In small lakes the thermocline is considerably higher than in large lakes. This is doubtless due to the influence of the winds, by which the small lake is less affected. This was very prettily illustrated in a comparison of the Waupaca lakes with Cedar Lake and Green Lake about August 1st of this last summer. In three of the Waupaca lakes—Rainbow, McCrossen and Beasley's, of which Rainbow is the largest and Beasley's the smallest, the thermocline was respectively at six meters, five meters and three meters. At the same time the thermocline of Cedar Lake was at eight meters, and the thermocline of Green Lake at eleven meters. The vertical distribution of the plankton has a very close relation to the thermocline, most of the animals being above it. *Limnocalanus*, *Daphnia longiremis* and *Daphnia pulex*, however, are found below the thermocline, and in some plankton-poor lakes the proportion of the other organisms below the thermocline is much larger.

It is evident that the circulation of the water is in the layer above the thermocline, and that below the thermocline there is insufficient oxygenation, and that this bottom layer must, too, hold a great deal of the

dead and decaying material falling from the upper layers. It is a curious fact, first pointed out, I think, by Whipple, that the bottom waters of deep lakes are stagnant during both winter and summer, but have a period of overturning in spring and fall. This overturning may come with considerable suddenness when the waters have not been much agitated by the winds. We ordinarily think that water is so mobile that the heavier portions will immediately sink, and thus the water of greater density will always be at the bottom. It may happen, however, as in the fall, that the upper waters will cool off, and yet retain their position, so that the lighter water will actually be below. The lake is in a condition of unstable equilibrium. If, under these circumstances, there comes a heavy wind, the whole body of water will overturn.

It is at these two periods of overturning, as shown by Whipple, that the growth of diatoms is especially pronounced, and they are found present in enormous numbers in the limnetic plankton. This great growth of diatoms is explained in the following way: During the periods of stagnation diatoms or their spores, if diatom spores exist, accumulate at the bottom of the lake, inasmuch as their specific gravity is greater than that of water. They do not grow there, because sunlight is essential to their growth. At the bottom is accumulating during this period, too, a large amount of organic matter from the decay of organisms near the surface, and this, under the influence of bacteria, is transformed into material fitted for food for the diatoms: in this food material the nitrates are perhaps the most important. When the time of overturning comes, the diatoms or their spores rise to the surface, accompanied by these dissolved organic materials, and, under the influence of sunlight, an exceedingly rapid multiplication takes place. As the food

materials are used up the numbers of diatoms decrease again. Other organisms, of course, show the effect of the overturning of the water, for many are directly or indirectly dependent upon the diatoms for food, and, besides, diatoms are not the only organisms which can make use of the food materials which are thus brought to the surface. *Diaptomus*, *Epischura*, *Limnocalanus* and two species of *Cyclops* show quite clearly these two periods of rapid production, although in some of these cases the results are complicated by the fact that the temperature of the surface water has a direct effect on the reproduction.

The matter of the annual distribution of the organisms of the plankton is a very interesting question, but is also a very complicated one. As has just been stated, certain of the diatoms have a distinct spring and fall maximum, and there are other organisms which, because of their dependence upon the diatoms, have similar periods of maximum growth. But there are other causes at work which control the growth of individual organisms, so that their optimum periods may come at very different times of the year.

Generally speaking it is probably true that the largest amount of plankton occurs in midsummer, although Yung says that the maximum development of plankton in Lake Lemman is in May or June, and that the minimum is in March and September. Zacharias states that the maximum period for Lake Plön is about August 1st. Measurements of a large number of collections from various lakes in Wisconsin indicate that the maximum of plankton occurs in these lakes in the latter part of July. The exact period of maximum development may vary from year to year, and in different lakes, because of varying local conditions. The reason for this July maximum seems to be not because any considerable number of organisms have their highest develop-

ment, but because of the fact that there is a greater variety of forms at this time than at any other time of the year. This is undoubtedly because of the peculiarly favoring conditions of temperature. It is this time of the year that seems to be especially favorable to the growth of the algæ. The 'water-bloom' may appear in June and remains sometimes until into September, but it is in July and August that it is present in the greatest quantity. This summer, on Lake Winnebago, it was most abundant during the latter half of August.

The minimum of plankton development is in the winter months, especially in January and February. At no time of the year, however, are either plant or animal forms wanting, and collections made through the ice will give a considerable variety of kinds, as well as numbers of individuals.

It will be noticed that the period of maximum plankton development corresponds to the time of highest temperature of the water, and that the period of minimum development corresponds to the time of lowest temperature, so that we can be certain that the one important controlling factor in the growth of plankton is the temperature.

Hensen and his co-laborers who worked out a very elaborate system of measuring the plankton of the sea claimed that the distribution of the plankton over wide stretches of the sea was nearly uniform. Granting this to be true, it evidently is possible by a series of collections and measurements to compare different parts of the ocean in regard to their productiveness in animal and plant life. This conclusion, that the horizontal plankton of the sea has a practically uniform distribution, has been accepted by the majority of scientists, although vigorously combated by Hæckel.

Apstein has applied the same methods to the examination of lakes, and has concluded from his investigations that the plankton

of lakes is uniformly distributed. It is easily seen that there is very good reason for assuming this to be the case from the actual conditions under which the plankton exists. The plankton consists of organisms that do not move voluntarily from place to place, and therefore do not change their positions. They are dependent upon heat and light for their development, so that their growth is mainly within from twenty to forty feet of the surface, so that a depth exceeding this would not mean any greater production of plankton—or in other words, the amount of plankton depends not upon depth, but upon surface.

This is a most important conclusion, if true, for it gives us an exact method by which we can compare one lake with another and determine their relative productiveness, or from a series of collections, determine the absolute annual productiveness of any body of water. Such determinations would have an important commercial value, for by them could be estimated the possibilities of fish production in a lake. The method was worked out in detail and very elaborately by Hensen. The collection was made by a conical net of bolting silk drawn vertically through the water, thus straining out the organisms of a column of water of the size of the opening of the net. Then the material was counted under the compound microscope by a very laborious process. In this way exact numerical values can be obtained not only for the plankton as a whole, but for the individual constituents. Most investigators use Hensen's methods with greater or less modifications, and they have been productive of very fruitful results. But, unfortunately—I say unfortunately, because we all like to claim exact results, and are prone to think that nature works according to certain inflexible laws—much of the laborious detail of the work is a waste of time.

The question of the uniformity of horizontal distribution has been discussed by various authors and with considerable vigor, but I think it must now be acknowledged, that while there is a certain amount of uniformity, so that, by a considerable number of collections, we can express within rather wide limits the amount of plankton at any time on a lake, uniformity in any exact sense does not exist. This lack of uniformity is largely due to a difference in the number of crustacea, although there are marked differences in the distribution of the other organisms. Surface growing plants, for instance, are moved about under the influence of the winds, and accumulate on the leeward side of a lake. If one part of a lake is deeper than another and the lake is not much disturbed by the winds, at the period of maximum growth the number of diatoms will be much greater over the deeper part. Crustacea may be in ill-defined aggregations which may be called swarms, and these swarms are not stationary in all cases, but move slowly, perhaps under the influence of extremely weak currents. Not only is there a considerable variation in collections made at different locations on a lake at the same time, but if a series of collections is made at the same place, the amount of the plankton in some collections may be twice as much as in others. An examination will show that these large variations are generally due to a difference in the numbers of some of the crustacea, showing conclusively that not only do the numbers of crustacea vary at different locations, but that these swarms are not stationary. It follows, then, that conclusions in regard to the plankton drawn from a few collections may be quite erroneous. If, however, a considerable number of collections is made, especially if they are made from widely-separated localities, the average of all these collections, allowing something of a margin for

error, will give a fair idea of the amount of plankton in a lake. Of course, the larger the number of collections the less the amount of error, but anything like very exact results can not be expected. We are able, in this way, to compare the plankton of one lake with that of another, or to determine the relative amount of plankton at different times of the year on any single lake. But any estimate of the actual amount of plankton produced by a lake at any time or during the year must be acknowledged to be only an approximation. Care must be taken, too, in comparing one lake with another, that they be compared under similar conditions. The maximum of one lake may not be reached at the same period as that of another. The conditions of a deep lake are very different from those of a shallow lake, and a fair comparison can be made only by averaging collections continuing over a considerable period.

In the abyssal region, because of the lack of light, plant life is impossible, and the fauna is very meager.

It is true that the list of animals which have been found in the abyssal regions of lakes is a long one, including, as it does, protozoa, cœlenterata, worms, molluscs, bryozoa, crustacea, arachnida, insect larvæ, and some few fish, but an examination of any single lake shows that not only is the number of kinds small, but the numbers of individuals of any kind are very small. In Europe the abyssal fauna of Lake Lemán has been worked up with great thoroughness. In this country very little detailed work has been done on this subject. It is not a fruitful field for research, and it is not strange that it has been neglected. In shallow lakes it is doubtful if there is any distinctive abyssal fauna. The most abundant animals in the mud of the bottom are worms, insect larvæ, gasteropod and lamelli-branch molluscs, and amphipods. With these may be associated at times great

numbers of other animals, as occasionally one finds in the mud of shallow lakes large numbers of fresh-water hydra. Most if not all these animals are identical with the littoral forms, and the difference between the littoral fauna and the deep-water fauna is that in the deep water those forms which are especially dependent upon the weeds for food and protection are lacking, while we find in abundance the mud dwellers.

In the abyssal regions of deep lakes, however, we find forms which are characteristic of those regions, although they may be mingled with others that are also found in the littoral region. In the abyssal region of Green Lake, which may be considered the typical deep-water lake of Wisconsin, are found, besides some undetermined worms, a little lamellibranch, *Pisidium*, ostracods, amphipods, insect larvæ and *Mysis*. There are some protozoa in the mud, but they have not been studied. The ostracods are so numerous that their shells form a conspicuous part of the bottom deposit.

In the smaller lakes of a depth ranging from 60 to 100 feet, like the Waupaca lakes and Elkhart, a different condition of things exists. The bottom is composed of a dark mud, and is almost completely devoid of life. This has been a puzzling fact, and has been to me personally a matter of considerable disappointment because of my interest in abyssal animals. The probable explanation seems to be that these depths are rendered unfit for life by reason of the more complete stagnation of the deep water in small lakes, and because of the larger amount of organic matter which is being decomposed there. Because of the small areas of such lakes, leaves are carried from the shore all over their surfaces, and, sinking to the bottom, increase largely the amount of decaying organic matter. Partly decomposed leaves are common in the bottom collections of small lakes but rare in lakes of the size of Green Lake or Lake

Geneva. This may account largely for the black color of the bottom mud. Then, in a large lake, the winds indirectly produce slow bottom currents. A prevailing wind will pile up the water at the end of a lake; this water must return in some way, and there is good reason to think that at least a part of it returns by a slow bottom current. Professor Birge tells me that his temperature observations give evidence of such a movement of the water. It follows, probably, that in the large lake there is not perfect stagnation, and hence the conditions of the bottom are more favorable for animals than in a small lake. The larger the lake, then, other conditions being equal, the greater would be the abundance of abyssal life. While there have been no accurate means of comparing the abyssal fauna of the Great Lakes with that of the smaller lakes as to quantity, such collections as have been made would indicate that it is much greater in the Great Lakes, and decreases in proportion to the degree of stagnation. If my explanation proves to be the correct one, as I feel quite certain it will, it will follow that the small deep lake will be limited in its fauna in two ways: because of its steep shores it will have a small littoral fauna and flora, and because of its stagnant deep water it will have little or no abyssal fauna.

I have thus far spoken as though all lakes had the three faunæ: littoral, limnetic, and abyssal. Generally speaking this is true, even small bodies of water showing this distinction. But occasionally the distinction is almost lost. This is true in Lake Winnebago. In spite of its great size—the lake is some twenty-eight miles long by ten or twelve broad at its greatest width—it is only about twenty-five feet deep. In its fauna there is a curious mingling of littoral and limnetic forms, littoral forms being found in the open lake, and limnetic forms even among the weeds along

shore. The explanation seems to be this: because of its slight depth the environment, even far from shore, is favorable to the growth of littoral forms. Then there is good reason for thinking that the winds have a profound effect on its waters, thus thoroughly mixing limnetic and littoral waters, and consequently causing a similar mingling of the organisms. Lake Winnebago has the characteristics, in many respects, of an enormously overgrown puddle. I do not say this, however, to show a lack of respect for this lake, for from a practical standpoint it is a most valuable possession to the state. It can support, and does support, an enormous number of fish. Few lakes can compare with it in productiveness.

All the inhabitants of fresh water are, of course, descendants of marine forms. In some cases the modifications have been very great but in others they are hardly to be distinguished from their salt-water relatives. This is true, as has already been stated, of some of the crustacea: in some of these it is difficult to make a specific distinction between the fresh-water and marine forms. Most of the environmental conditions in fresh water are so different, however, from those in the sea, that we should expect a fauna to develop itself which would differ widely from its ancestors.

It will be noticed that the most pronounced likeness to marine animals, perhaps, is found in the abyssal forms. So far as that is true, it may be explained, I think, by the uniformity of conditions existing in the depths of lakes. The temperature varies but a few degrees from one end of the year to another, and such currents as exist are slow and almost imperceptible. The abyssal fauna of a lake is subject to nearly the same conditions as that of the sea, except for the difference in the composition of the water. If, as has been supposed, the deep-water fauna of the Scandinavian lakes is descended directly from the deep-water

fauna of the sea, coming from the sea into lakes having a communication with salt water, and surviving there after the lakes were cut off from the sea, and their waters had become fresh, we can see how the animals could gradually adapt themselves to their surroundings, inasmuch as the conditions of light, temperature and food supply would remain with very little change.

With the limnetic and littoral fauna, however, a very different condition exists. In our climate the temperature of the surface varies during the year from the freezing point to eighty degrees or more Fahrenheit. In shallow lakes, not only is there this variation of the surface, but the lake may be frozen to the bottom in winter, so that all forms which can not go into a resting stage of some kind are destroyed. The conditions of life are hard, and especial fitness is required in order to make survival possible. In the sea, on the other hand, the conditions even of the littoral and pelagic fauna and flora are much more uniform. It is not strange that the fresh-water animals and plants are of few kinds, and that generally they are very different from those of the sea. It is perhaps more strange that so many resemblances remain, and that the forms are so varied as they are.

To trace out the connection of the individual forms with their marine ancestors is, of course, the work of the specialists in zoology and botany. It may be noticed, however, that the present population of our lakes has come since the glacial period, in fact the lakes themselves only date from that period. So far, then, as the fauna and flora pass from one body of water directly to another, we may assume that the present animals and plants are descended from those that were pushed south by the ice, and that as the ice retreated they followed again towards the north.

Currents carry organisms from one part of a lake to another, and from one lake to

another by connecting streams: in this way animals or plants introduced at the source of a river may be carried through its whole length.

From lake to lake, too, seeds, eggs and living animals are carried by water fowl attached to their feathers or in the mud upon their feet. This is not simply from one lake to its neighbor, but many of these birds take long flights before alighting, so that the organisms are scattered over a wide stretch of territory. It is in this way, probably, that we can account for the uniformity in the fauna and flora of the lakes and the wide distribution of some of the forms. Where conditions are similar, then, we may expect likeness in the fauna and flora. As we have seen already, temperature is the great controlling factor in distribution, so that in lakes of the same latitude or the same elevation, other conditions being equal, of which the principal is depth, we may expect close similarity in fauna and flora.

We may assume, then, that the littoral fauna and flora have had their origin from neighboring bodies of water, and that as the ice retreated, the lakes were populated, partly by direct migration between contiguous bodies of water, and partly by the aid of the winds, currents and water fowls. The limnetic fauna and flora is descended either from littoral forms which have gradually adapted themselves to limnetic conditions, or from pelagic forms, which, in bays where the water was less salt or brackish, have become adapted to the conditions of fresh water and have been distributed by the same agencies as the littoral forms.

Part of the abyssal fauna is descended from marine forms directly, as in the 'fauna relicta' of the Scandinavian lakes, and in the case of some of the animals in our Great Lakes. Another part of the abyssal fauna is descended from littoral forms which have gradually moved into deep water, and have been modified to suit their new en-

vironment. All the abyssal fauna of the Swiss lakes is supposed to be of this character.

What I have said thus far applies almost exclusively to lakes of the temperate zones, for it is there that lakes exist in the greatest numbers, and it is upon such lakes that most of the work of investigation has been done. But there are lakes in warmer climates, and we may expect that a thorough study of them will give us much that is new and interesting. A striking example of the extraordinary interest that may be attached to such lakes is Lake Tanganyika in Africa. Some years ago it was reported that a jelly fish was abundant in its waters. This excited the curiosity of zoologists, for the medusa is a marine form, and very rarely is found in fresh water, the most noted case being of the one found in the basin in Regent's Park, which is supposed to have been brought with plants from some tropical country. The *medusa* of Tanganyika is one of four jelly fish known to live in fresh water, and the other examples are very rare. A special expedition was organized to make an exploration of Lake Tanganyika, and although this work was very imperfectly done, the results appear to be of great interest. Along with the ordinary lacustrine fresh-water fauna there is a fauna of marine origin, but this marine fauna is not closely related to modern forms. It does, apparently, closely resemble Jurassic forms. Indeed, it is said that were some of the forms referred to a paleontologist, he would not hesitate to say that they belonged to Jurassic times. Have we here, then, a 'fauna relicta' which dates back to Jurassic times? It is too early to answer this question with any certainty, both because of our imperfect knowledge of the fauna of Lake Tanganyika, and because of our great ignorance of the geology of that part of Africa. But the mere possibility that this may be true is startling, and should incite scientists to a

thorough study of the fauna and flora of Lake Tanganyika and the other lakes of Central Africa. So far as explorations have gone this 'halolimnic' fauna as it has been named, is peculiar to Lake Tanganyika, but we may expect to find more or less of it in other lakes.

A few words in regard to the work on plankton which remains for the future investigator. It will, I think, be evident, that so far as exact and comprehensive knowledge is concerned, we have but entered a vast field. We know so little, that we can say that we are just beginning to place limits on our ignorance.

A systematic knowledge of the fauna and flora is a first and fundamental condition of comparative biological work. We need accessible manuals by which the animals and plants dealt with can be identified. Systematic work may not be the highest or the most satisfying to the investigator, but it is very necessary. The plankton student is met, at the very beginning of his work, with a difficulty that is almost a complete block to further progress; although the number of forms with which he has to deal in his plankton work may be very few, he has to have the knowledge of a specialist in each group in order to identify them. If a laboratory has a company of specialists, the material is quickly identified by passing from one to another. But if the investigator is by himself, he finds himself in a most discouraging situation. The literature of the various groups is scattered and fragmentary, and frequently is utterly useless to any one but a specialist. There is need of a manual, or rather a series of manuals, that shall so treat of the fresh water fauna and flora, that any well-trained biologist shall have no difficulty in identifying his material outside the group which he may have made his special study.

It seems to me that we have nearly reached the time when the publication of

such a manual should be possible. Most of the preliminary work has been done. More, perhaps, remains to be done on the botanical side than on the side of zoology, for the exact study of the lower aquatic flora has been much neglected. I hope that the time is not far distant when we may have such a manual produced in this country, with the coöperation of our best specialists. Nothing would do more to further the study of plankton, for it would furnish the student with a tool of inestimable value.

In regard to the plankton itself, very little is really known of the abyssal fauna and its controlling conditions. I have spoken of the fouling of the water at the periods of stagnation, but our knowledge of the conditions of the water at those times is very imperfect. There should be a systematic examination, by chemical analysis of the water and its contained gases, and of the mud of the bottom, and an exact comparison should be made between the lakes with sterile bottom waters and those with a comparatively abundant fauna. In connection with this should be a study of the currents of the abyssal region. A more careful and thorough examination should be made of those lakes whose geological history indicates that they were formerly connected with the sea, and may contain a 'fauna relictæ.' I may say that it is not likely that such explorations will yield any startling results. The time for that is probably past, and the lake student of the future must content himself with hard work, without the satisfaction of brilliant discoveries.

Our quantitative knowledge of plankton is only a beginning. We know something of the conditions on a few lakes, but only on a few, and we do not know what variations may be caused by the peculiarities of individual lakes. Even in the same lake the conditions may change from year to

year, and in only a few instances have observations continued through a series of years. We are all prone to generalize on the facts in our hands, but it must be acknowledged that the facts upon which we can build theories of fresh water plankton are very meager. There is need of a series of examinations of typical lakes carried on for a term of years, before we can build with certainty.

There remains the great problem, or complex of problems, of the relation of the different elements of the plankton to each other and to the fish. We see, frequently, an apparent overproduction of one of the elements. In shallow lakes—at least in many of them—there is apparently a great overproduction of vegetation. How is this explained? How is the balance of life restored? What constitutes an ideal relation between the vegetable and animal growth? When we plant a new species of fish in a lake, we, of course, disturb the existing balance of organisms, may we not, in some cases, at least, work actual damage? To what extent is this balance between animals and plants maintained in a lake that is not interfered with by man?

These and similar questions, now without answers, offer a field of almost unlimited work, and work that is worthy the best efforts of our students. For while my address, in treating of the present condition of the study of lakes, has dealt largely with isolated facts, after all it is not the facts which the student pursues as his ultimate aim, but the general laws underlying the facts. He is an unfortunate man who sees the trees, but cannot perceive the forest, who can see the stones of which the cathedral is constructed, and show how they were lifted to their places, but cannot perceive the beauty of the structure as it stands in its exquisite proportions, its massive masonry and wealth of sculptured detail only serving to express the

idea of beauty and harmony in the master mind of the architect.

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SCIENTIFIC BOOKS.

The Cambridge Natural History. By DAVID SHARP, M.A. (Cantab.), M.B. (Edinb.), F.R.S. Vol. VI. *Insects* (Part II.). London and New York, Macmillan & Co. 1899. 8°. Pp. xii+626, and 293 cuts.

The completion of that portion of the Cambridge Natural History which is devoted to insects is an event of unusual importance to entomologists; for these two volumes constitute the most useful work of its kind that has appeared since the publication of Westwood's *Classification of Insects*.

The most striking feature of this work is the same as that which characterized Westwood's *Classification* and has made it an indispensable part of every entomological library; that is, it includes the results of a careful sifting of the greater part of all entomological literature. In a word, these two volumes of the Cambridge Natural History constitute an encyclopædia of entomology, written by one who has thoroughly studied the more important contributions to all departments of entomology, and who also contributes much that is new.

An admirable feature of the work is the fact that it is well-balanced; the morphology, the taxonomy, and the œcology of insects have each received sufficiently full treatment. The student of any phase of entomology is almost sure to find something on his subject here and to find also references to the more important literature.

The author has placed entomologists under so great obligations to him that one does not feel like saying anything but praise of his work. I cannot help feeling, however, that it would have been better if in some respects he had been less conservative. This is especially true of his treatment of the larger divisions of the class of Insecta; his conclusions on this subject are hardly an advance on what might have been written a quarter of a century ago. In fact this is the weakest part of his work. Thus, in his discussion of Brauer's classification (Vol. V., pp. 175-176), he has apparently failed to