TROPICAL FRESHWATER PLANKTON

by

A. Thienemann*

No genuine limnological investigation of a lake, of the circulation of its substance and of its " production-biology " is possible without consideration being given to plankton, that floating universe of minute plants and animals which inhabit the open waters of a lake. The importance of plankton for existence as a whole in an inland lake is all the greater, the deeper such a lake is. This is because original creation (" Urproduction "), that is to say, the formation of organic matter through the chlorophyll of the green plant, with sunlight serving as source of energy, occurs in the littoral zone mainly through the intermediary of higher vegetation, and in the bulk of the open water—the pelagic zone—through the intermediary of single-cell plankton-algae. And the deeper a lake is, the smaller will be the extent of the littoral zone in relation to the bulk of the open water, and the more important will be, in proportion to the vegetable substance produced in the littoral zone, the rôle of plankton as supplier of the organic substance which, directly or indirectly, serves all the living creatures of the lake (including fish) as food.

But it is not only as the main producer of organic substance that plankton occurs in these deep lakes : it also forms the biological community which, after dying and sinking to the bottom, determines the nature of the mud deposits in the depths of these lakes. The depth sediments of such lakes are the product of plankton, and where diatoms form the main component of plankton, the depth sediment frequently consists of recent " Kieselgur ". In the course of the German Limnological Sunda Expedition (1928-29), we discovered such diatomaceous mud in most of the deep crater lakes of Java and Sumatra, and all around Lake Toba—in some places up to nearly 500 metres above the present lake-level—we saw huge stratified kieselgur deposits, which would fully repay exploitation, as residue of the mud of a very old, much larger and much deeper Toba Lake.

When we set out in 1928 to study for the first time in a tropical region, namely Java, Sumatra and Bali, inland waters of every type by the methods and for the purpose of modern limnology, the study of plankton was, of course, included in our programme. For, practically nothing was then known about the biology of plankton in tropical lakes, especially in respect of its seasonal and spatial distribution under the influence of changing environmental conditions. Professor Ruttner, the head of the Lunz Biological Centre in Lower Austria, carried out this task with profound expert knowledge and untiring zeal, completing the major part of his statistical work and of his biological investigations on the spot. Yet it was necessary before anything could be published to await the completion by research specialists of a systematic analysis of all the categories of organisms found in the plankton. Ruttner's manuscript, which was completed in 1944, experienced many vicissitudes during the post-war period, and it is almost a miracle that it was preserved ; at last, in November 1952, as part of our expedition's report " Tropical Inland Waters " [vol. X. (Archiv für Hydrobiologie, Supplementary Volume XXI)], there appeared Franz Ruttner's " Plankton Studies of the German Limnological Sunda Expedition ". It would thus have been most appropriate for my expedition-companion Ruttner, instead of myself, to stand here in order to report in the light of his own experience. As this was not possible, I should like to say something about these plankton studies which will probably for a long time to come provide a firm basis for all tropical plankton work. Naturally I can discuss here only the most general conclusions, considering that Ruttner's work comprises a volume of 274 pages, 9 plates, 20 illustrations, 29 charts and numerous synopses.

The first thing that strikes the European when investigating tropical freshwater plankton is this—and it applies not only to the Indonesian lakes investigated by us, but to all tropical lakes : " Standing at the shore of a tropical lake, we notice only species foreign to us, hardly a species or type familiar from home, among the trees of the forest girdling the water in immense diversity, among the animals who live there, or among the marsh plants—in short, among all the organic life belonging to the *land*. In the *water*, however, we meet quite a

* Professor Hydrobiologische Anstalt der Max-Planck-Gesellschaft, Plön, Germany.

number of old acquaintances: *Potamogeton* species, *Myriophyllum*, *Hydrilla*, *Ceratophyllum*, *Najas and Utricularia* are to be found here, partly in the species in which they occur at home. Passing on to study the micro-flora of the lake, we meet almost entirely with forms widespread in temperate waters, too, and strangers are few and far between. The same applies in the case of the water animals, though not to the same extent. Apart from fish, higher crayfish and some other categories of animals, the tropical freshwater fauna greatly resembles ours. Thus we find among plankton the same species of Cyclopidae, the same Cladocera and Rotifera. We are confronted here with the well-known phenomenon that organic life in inland waters is more or less cosmopolitan . . . . The factor which differentiates land-bound organic life in the tropics from that in the cold zones is, above all, frost, the influence of winter so hostile to life on land . . . . Conditions are quite different in the water where there is no frost destructive of life even in arctic regions. Below the ice sheet of lakes, there prevail temperatures which the majority of organisms can bear without harm. The impact of environmental factors of differentiation between the tropical and the temperate zones is, therefore, much weaker in the water than on the land. Taken in this sense, life is governed by tropical conditions even in our temperate waters. . . . . This far-reaching identity bestows a quite particular importance on tropical limnology within the scope of our efforts to obtain an adequate view of life in inland waters no matter where situated. This approximate identity enables us above all to make comparative studies of the part played by the temperature factor in biological communities composed of very similar constituent parts when other outward conditions are virtually alike" (Ruttner).

Roughly one quarter of the 267 species of the Sunda-plankton investigated have up to now been found only in the tropics; among the mass forms which account for 46 per cent of the total plankton, the proportion of tropical species amounts to one-third; their percentage is largest in the case of crayfish (75 per cent), and smallest among the Rotifera (4 per cent). Twenty to twenty-five per cent of the mass forms are strongly developed in both temperate and tropical lakes; the remainder of the mass forms of the Sunda-plankton, i.e. approximately 50 per cent, have their optimum development, as regards temperate zones, not in the pelagic zone of large and deep lakes but in small waters, shallow lakes and in the littoral zone. It seems that only few species are endemic. Cold-water-stenothermal species which play a great rôle in the population of temperate lakes are, of course, lacking. The major part of the organisms which occur as true cosmopolitans in both zones, belongs to eurythermal forms. The species which occur in the tropics only, are warm-water-stenothermal. But even among the cosmopolitans there are warm-water-stenothermal species; for water temperatures can rise to tropical degrees even in temperate zones, above all in shallow waters or waters of small extent. Some species which normally inhabit only the littoral zone, like diatoms and Cladocera, develop in great masses in the plankton of some Indonesian lakes: here, the fact that the limno-plankton originates in the littoral zone is demonstrated before our very eyes. The predominance of small and even minute species in the phyto-plankton of tropical lakes is striking; for this reason, the plankton net fails to provide a true image of the nature of plankton in tropical lakes. While diatoms make up the largest proportion in the volume of phyto-plankton (25 per cent), Entomostraca make up the largest proportion (20 per cent), and Rotifera the smallest, in the volume of zoo-plankton.

Ruttner has investigated the quantitative vertical spread of the plankton very thoroughly. We find in the Sunda lakes the same types of vertical spread as in temperate lakes, even though its characteristic features are not always marked as sharply in the former as in the latter. We did not notice any genuine water blossoms. The overwhelming majority of the species occur epilimnically, but *Trachelomonas*, *Difflugia hydrostatica* and *Anuraeopsis fissa* were observed metalimnically; furthermore, at the lower oxygen limit, Rotifera and sometimes also crayfish were discovered. Aerobic species (three diatoms) occurred hypolimnically only in Lake Toba, whereas anaerobic species, above all iron and sulphur organisms, as well as Ciliata, were regularly found in all lakes and behaved similarly as they do in temperate lakes. As is well known, the typical vertical stratification of the constituents of plankton is completely blurred in times of full circulation. Lake Bratan on Bali was in full circulation down to the bottom during our visit, and the stratification of the plankton was almost entirely wiped out. Part of the zoo-plankton moves vertically every day in response to light conditions, exactly as it does in temperate lakes; thus, *Cypria javanica*, one of the Ostracoda, and a *corethra* larva withdraw deep down into the oxygen-free meta- and hypo-limnion during the day (in temperate lakes there are no planktonic Ostracoda). The bulk of the constituents of zoo-plankton do not normally descend below the oxygen-rich epilimnion; any reduction in the oxygen contents below 1 milligramme per litre constitutes an impenetrable barrier to them. In temperate lakes, this limit lies in general near the lower O_2 values; thus, in the Lunzer Obersee in Austria, crayfish descend below the 0.5 mg limit, Rotifera even below 0.25 mg. But the respiratory value of the O_2 contents of 1 mg is at least four times as large at a temperature of 5 degrees centigrade in a temperate lake as it is in a tropical lake at a temperature of 25 degrees C.

During our Sunda limnological expedition we could investigate each individual lake only once and could therefore only take snapshots, as it were, of the quantitative development of its plankton. We could only determine the biological bulk, the so-called standing crop, and this, of course, is a shaky foundation on which to assess the 'production-biology' of these lakes. In order to gain a rather more certain judgment concerning the plankton production of a given lake, the latter would have to be subjected to observation at regular intervals during at least one year. Nevertheless, a comparison of the standing crops of the 14 lakes investigated with each other and with those of temperate lakes is quite revealing. On the basis of counts, Ruttner has computed the volumes of the phyto- and zoo-plankton both separately and jointly below 1 square centimeter (cm^2) of lake surface and has expressed them in cubic millimeters (mm^3). This resulted in values varying between 19.52 and 1.46 mm^3 the average of all lakes put together amounting to 7.6 mm^3. If the lakes investigated are arranged serially according to the volume established in each case, the series thus obtained in no way corresponds to the order in which we would group these lakes, according to their relative trophical value, as inferred from the transparency and colour of the water etc. Thus, to mention only one example, Lake Manindjau in Sumatra which, with a plankton volume of 19.52 mm^3 below 1 cm^2 of water surface contains the largest standing crop, is undoubtedly closer to the oligotrophic than to the eutrophic type, and the definitely eutrophic Ranu Lemongan in Eastern Java has a plankton volume of only 8.00 mm^3. Observations made in temperate zones, in the north-eastern Lime Alps and the lakes of Karnten, lead to similar results.

"The cause of this phenomenon which at first sight seems paradoxical," says Ruttner "is that in an oligotrophic lake, on account of its much deeper penetrability for radiation, the autotrophic phyto-plankton can populate much more massive strata of water, assimilate them effectively and use their food contents to produce vegetable standing crops." If, for instance, a eutrophic lake contains twice as much utilizable food substance as an oligotrophic one, while the latter has twice the radiation penetrability of the eutrophic lake, both lakes, other conditions being equal, will produce the same volume of standing crops.

If, however, lakes are grouped, not according to their plankton volume below 1 cm^2 of surface, but according to their average contents of plankton per litre of water from the plankton stratum, then a series results which corresponds fairly well to the trophical values inferred from the physical qualities of the lakes. Thus the six lakes with the highest plankton volume (6.67 to 18.7 mm^3 per litre)—situated in Java—undoubtedly have the highest eutrophy, while the three lakes with the lowest plankton volume (only 0.44 to 1.96 mm^3 per litre)—situated in Sumatra—are oligotrophic.

These observations have suggested to Ruttner highly important general conclusions.

" In considering 'production biology,' a clear distinction has to be made between two sets of facts :

1. the plankton production of the lake as characterized by the standing crop produced below a given surface unit, and
2. the water fertility as expressed in the standing crop of the volume unit of the water within the stratum of production.

Water fertility is a potential quantity which is turned into organic production in proportion to the penetration of radiation. Since radiation is screened off by great plankton density, the depth of the stratum where assimilation can occur decreases with increasing density of population. Thus, in a lake containing water poor in feeding substance, the resulting dearth of production can be compensated by the greater depth of the stratum capable of assimilation. Only in proportion as the radiation absorption, characteristic of water independently of the screening-off effect of plankton, sets limits to the further growth of the assimilating stratum, will the total production of the lake below a given surface unit be determined—other conditions being equal—by its food contents . . . . Thus, only the *population density* of the assimilating stratum depends on the fertility, i.e. the trophical value of the water, whereas the *volume of plankton below the surface unit*—fertility being equal—is a function of penetrability to radiation." Ruttner concludes these remarks by saying : " The absolute volumes of plankton found to exist in the Sunda lakes below 1 cm^2 approximate, as regards quantity, to the volumes found to exist in temperate lakes. In 50 per cent of the cases these volumes were within the extremes ascertained in lakes of the Eastern Alps. Whether this holds good also for the *annual amount* of plankton production cannot be determined on the basis of the observations made."

This leads us to the problem, equally important from the theoretical and practical viewpoints, of the *productivity of tropical lakes*. At any given moment, the volume of the standing crop of a tropical lake is about the same as that of a temperate lake. But what about annual production?

Immediately after returning from our Sunda expedition I delved into the problems of the concept of production in biology (Archiv für Hydrobiologie 1931, Volume 22, pp. 616 to 621), and in a further essay entitled "Tropical Lakes and Theory of Lake Types" (Archiv für Hydrobiologie 1931, Supplementary volume 9, pp. 205 to 231), I have attempted to view the theory of lake types, which was developed in temperate zones, from the tropical aspect. Ruttner in his great work on plankton has commented on this.

What do we understand by "production of organic substance"? My definition is as follows: "The production by a 'biotope', in our case a lake, of organic substance within a given period is the total quantity of the organisms including their organic excretions formed during this period within the biotope concerned." Although in the tropics the year does not constitute a natural climatic time-unit for the development of organisms as is the case in the temperate and cold zones, we must nevertheless, if we want to compare the productivity of lakes of different climatic zones, use the year as our time-unit for any considerations on production. We are accustomed to regard the production of tropical countries as considerably higher than that of the other zones. Having found that at any given moment the volume of plankton in a tropical lake is about the same as in a temperate lake, we are led to the conclusion that the former's annual production can be larger only if the turnover speed of its organisms, i.e. their sequence of generations and speed of growth, is higher than in a temperate lake. Other things being equal, the speed of development and growth of organisms depend on relative temperature. According to Van T' Hoff's well-known RGT law, turnover speed increases between two and three times if the temperature rises by 10 degrees C. Since the temperatures of the plankton-producing, so-called trophogenous, surface stratum of the Sunda lakes investigated by us are about 10 degrees C higher during the year as a whole than the corresponding summer temperatures of temperate lakes, two to three times as much plankton must logically be produced per time-unit in the former. If, in addition, we assume that only summer is really productive in temperate lakes while winter causes a more or less complete interruption of production, then the relative annual production of tropical lakes must be even larger. As against this, Ruttner points to the longer duration of sunshine enjoyed by temperate lakes during the summer, "i.e. the substantially larger supply of light energy during the warm season when assimilating performance is least restricted by temperature and a far-reaching utilization of the energy radiated into the water is guaranteed. It may, therefore, be said that at least the warmer among the temperate lakes are superior to tropical lakes in respect of potential assimilation performance during the warmest summer months." Our present knowledge scarcely permits us to establish the relative weight of these different factors, so that Ruttner "leaves to future investigations the final determination of proportionate total production in the pelagium of tropical and temperate lakes, respectively". Once the limnochemical and planktological conditions of tropical lakes have been investigated during at least one entire year, it will be possible to arrive at definite conclusions in this matter.

I must refrain here from dealing with the many details which must be taken into account in such studies of biological production, as well as with the considerable methodological difficulties which such studies offer in both the temperate and tropical zones. I should, however, like to draw your attention to a phenomenon which surprised us even during our first investigations.

When plankton dies, it drifts from the epilimnion, the trophogenous surface stratum, through the intermediary stratum, the metalimnion, down into the lowest watery stratum, the hypolimnion, where it more or less disintegrates; we therefore call this last-named stratum the tropholytical, i.e. food-decomposing stratum. Finally, the residue of this plankton settles on the bottom as sedimentary mud. Now, if the volume of water of this decomposition stratum is small in relation to the water constituting the "feeding stratum", decomposition gets concentrated, as it were, in this lowest watery stratum, which is thereby largely, and indeed often completely, deprived of oxygen. If however, the volume of the tropholytical stratum is larger than of the trophogenous stratum, decomposition is diluted, the dwindling away of oxygen in the hypolimnion is checked or even virtually prevented as far as the bottom of the lake. This is the customary picture offered by our temperate lakes; we call the latter type of lake, which is mostly quite deep, oligotrophic, whereas the former type, which is predominantly shallow, is called eutrophic. In Java and Sumatra, however, even lakes more than 100 metres deep showed the phenomenon of oxygen dwindling down to nil in the hypolimnion. It was tempting to explain this by the higher turnover speed, i.e., greater plankton production of the epilimnion conditioned by temperature. This factor plays a certain rôle to be sure, but I have no doubt that the difference in temperature itself is the main reason.

Whereas at the bottom of our deep temperate lakes temperatures are at 4 degrees C or a little more, they are at 20 to 27 degrees in Java, Sumatra and Bali, i.e., some 20 degrees higher. This results in a turnover speed—i.e., decomposition in this case—which is 4 to 6 times as great according to the RGT law. Even while drifting down, the dead plankton bodies to a large extent decompose, so depriving the lowest watery stratum of oxygen. And thus, in these deep Indonesian lakes, the sedimentary mud often is a deposit of almost pure silicic acid formed by diatom shells, showing little resemblance to the sedimentary mud of our temperate oligotrophic lakes. This speeded up decomposition of plankton results, of course, also in an intensive concentration of decomposition products of albumen, ammonia and phosphates in the lowest watery stratum of tropical lakes. Ruttner has made the following computation. The Javanese lake, Ranu Lamongan, with a diameter of 750 m and a depth of 28 m, is one of the smallest of the lakes investigated by us. Nevertheless, its lowest 20 m contain some 1,400 kg of phosphorus and some 12,000 kg of nitric ammonia. Lake Manindjau in Sumatra, with a surface of 97 sq. km, contains the following gigantic quantities in the stratum situated below a depth of 60 m : 1.5 million kg of phosphorus and some 7 million kg of nitric ammonia. In the mountain country of Java, the lakes are frequently dammed up artificially and then used to irrigate the rice fields. The surface water, poor in nutritive substances, is used for this purpose. But should not rather the dead capital buried in the fertilizing substances of the lowest watery strata of such lakes be activated by being used for irrigating and fertilizing the rice fields ? The technical difficulties inherent in this are likely to be small, but the economic results would be considerable.

I have reported briefly on the knowledge concerning the plankton of Indonesian lakes obtained by the German limnological Sunda expedition—thanks to the labours of Ruttner. I may perhaps be permitted to point out the kind of plankton investigations in tropical Southeast Asia which seem to me particularly important now. Above all, one major deep and one shallow tropical lake should be investigated according to the methods of present-day limnology at short regular intervals for at least one year in respect of their physiography and population. Only thus will it be possible to get near a solution of the problem of the productivity of such lakes.

May I now turn to the question of plankton as food for fish, a question of great economic importance. In the course of our expedition we assembled a vast collection of fish. Up to now, however, a quarter of a century since our tropical expedition, I have not been put in a position by the American ichthyologist who was to establish the nature of this collection to do any research work on these fish. This is all the more to be regretted since it was my intention to investigate the contents of the stomach and entrails after having defined the species. Are there fish in Southeast Asia which feed exclusively on animal plankton as do some of our species of *Coregonus*? I do not know. I do know, however, that in tropical Africa, for instance, certain Cichlidae feed on the freshly sedimented phytoplankton which has sunk down dying but has not yet decomposed, the so-called "Afja". These fish utilize original vegetable food directly, omitting the stage of eating animals which feed on phytoplankton—doubtless a very rational method. This problem still requires much study.

Above all, however, such studies of tropical plankton should also take into account the viewpoint that the tropics are the cradle of life. Our branch of science has taken rise in temperate zones where all biological phenomena are of a secondary, derivative nature in comparison with those of the tropics. The biologist and limnologist who has experienced a year in the tropics looks at nature at home with entirely different eyes. What formerly seemed self-evident now becomes a problem to him and general biological concepts, as e.g., the concept of production, appear to him in an entirely new light.

May I therefore, in conclusion, express the wish that, even more than before the war, young scholars of the science of biology should be enabled by actual experience to get to know other zones—Europeans the tropics, and scholars from the tropics the temperate zones. Indeed, the year in the tropics which I was privileged to spend on research in Indonesia has been the happiest in all my life.