FUNDAMENTALS OF
LIMNOLOGY

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PREFACE

THE "FUNDAMENTALS" laid down here will in no way replace the introductions to limnology (Thienemann, Brehm, Lenz, and Welch) but complement them in certain respects. The great progress which has been made in recent years in the field of the chemical and physical properties of water and the dependence of the life processes on these makes it appear desirable to take water as an environment as the central theme, and this subject occupies half the text. This method of giving an introduction to limnology seems appropriate to me, because a complete understanding of the biological phenomena in a body of water cannot be attained without a comprehensive knowledge of the environment.

The section of this book on biotic communities will be useful merely as a review and as an illustration of causal relationships. It has been possible to make this section short because the works mentioned above contain much information on this subject.

This book has grown out of the course in Hydrobiology which has been given at the Biological Station at Lunz for some decades. This circumstance will make it clear why the text may seem to be overburdened with examples drawn from conditions in the lakes of Lunz and from work carried on at the Lunz Station.

To my old friend, my collaborator for many years at the Lunz Station, Professor V. Brehm, I owe my heartfelt thanks for many valuable suggestions. Further thanks are due Dr. F. Berger for the careful preparation of the figures, and not the least to my dear wife for the wearisome task of proof-reading.

F. R.

Biological Station, Lunz,
February 1940

PREFACE TO THE SECOND EDITION

THE TREATMENT of the subject and arrangement of the text has not been essentially changed from the earlier edition. However certain sections have been rewritten because of the progress made in the field in the last decade. Through these changes the book has been enlarged from 167 to 232 pages and the number of illustrations increased from 39 to 51. The author is again grateful to those mentioned in the preface to the first edition for further generous help. In addition he wishes to thank also Frau Dr. T. Pleskot (Vienna) for valuable references, Fräulein M. Wimmer (Vienna) for the execution of numerous illustrations and Dr. David G. Frey (Bloomington) for his contribution of American literature.

F. R.

Biological Station, Lunz,
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TRANSLATORS' PREFACE

In spite of the large number of colleges and universities in the English-speaking world which offer courses in limnology or hydrobiology, there have been woefully few books available in English that could serve as suitable texts in such courses. Furthermore, especially in recent years, progress in limnology has been so rapid along certain lines that none of the texts could claim to be up to date.

Shortly after the war the present translators became aware of the 1940 edition of Dr. Ruttner's book and independently began translating it for use in their respective classes in limnology. Soon realizing that this was perhaps the best book available in any language on the principles of limnology, they combined efforts so that the book might become generally available to beginning students as well as to those previously trained who had not kept abreast of new developments in the field. F. E. J. Fry is responsible for the physical and chemical half of the book, and D. G. Frey for the biological portion.

The translators wish to express their gratitude to Dr. Ruttner for co-operating with them in many ways, and particularly for making the manuscript of the revised edition available for translation long before it was even set in type.

This book is not just another book in limnology. It is a mature and balanced treatment of the principles of limnology, written by one of the foremost limnologists of the world, and leavened by his many years of field and laboratory experience. In fact the book is Ruttner. The translators hope that not a few readers will share their general enthusiasm for the book, and will find in it many stimulating suggestions as to the directions in which limnology will develop further.

D. G. Frey
F. E. J. Fry

Autumn 1952

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BRIEF TABLE OF GERMAN-ENGLISH EQUIVALENTS

MOST OF the German terms used by Dr. Ruttner already have accepted English equivalents. A few terms were encountered, however, expressing ideas for which there are no counterpart single words in the English language. Furthermore, the German terms used in the description of the various features of bogs and also in the description of the profile of a lake bottom do not have widely used English equivalents. It was necessary, therefore, to more or less adopt words with approximately equivalent meanings, and these are listed below for the benefit of anyone wishing to refer back to the German edition of the book. The translators would be interested in learning of any English words already used for these various German terms which they have overlooked, or of any English words that would possibly be more suitable than the ones used in this translation.

Aufwuchs—*Aufwuchs* (the closest English equivalent is periphyton; see footnote p. 158)
Austausch—eddy diffusion
Benthal—benthal (as noun) or benthal zone
Blänke—bog pool
Bülte—bog hillock
Durchflutung—inflow-outflow
Eulitoral—eulittoral (as noun) or eulittoral zone
Flachmoor—flatmoor
Halde—slope (of a typical lake bottom profile)
Hochmoor—highmoor
Kampfzone—ecotone
Lagg—bog moat; marginal fossa or ditch
Lebensgemeinschaft—community
Litoral—littoral (as noun) or littoral zone
Moor—bog, moor
Pelagial—pelagial (as noun) or pelagial zone
Profundal—profundal (as noun) or profundal zone
Schlamm—ooze
Schlenke—bog puddle
Schweb—central plain (of a typical lake bottom profile)
Schwingrase—quaking bog
Sprungschicht—thermocline
Sublitoral—sublittoral (as noun) or sublittoral zone
Uferbank—shore terrace; littoral bench or platform

FUNDAMENTALS OF LIMNOLOGY

INTRODUCTION

WATER is the basis of life. Only in resting stages such as in seeds, spores, and the like does its proportion in the structure of plants and animals fall below 50 per cent and it normally makes up 60 to 90 per cent and even more of the total weight. The living substance of the cell, the protoplasm, is a highly complicated colloid system of which the dispersion medium is water. The complete absence of water indicates death.

The first life doubtless arose in water or at least in dampness, and the first organisms were aquatic; the land was first populated after further differentiation. The organisms which embarked on this course of development were only able to do so by taking with them, as it were, their original environment in their body fluids, in the blood and cell sap. The ability to retain the indispensable amount of water, or to replace repeatedly that which is lost, spells the difference between the presence and absence of life under the various climatic conditions of the wide land spaces of the earth.

As can be imagined, since water is an essential element for the life of terrestrial as well as aquatic organisms so that there is scarcely a single organic function in which it does not play some part or other, it would not be incorrect to consider the whole science of life as Hydrobiology. However, in the system of the sciences this subject is rather narrowly restricted. Hydrobiology is limited to the investigation of the plant and animal associations (biocoenoses) which dwell in the aquatic biotopes.

The composition of plant and animal stocks of these biocoenoses is in no way an accident. They are first of all primarily determined by geography and history. These are questions of historical plant and animal geography (Chorology). But within these limits the selection of species is primarily through the biotope, the sum of the environmental conditions which impinge upon them. Of all species which reach a given place, for example a newly created body of water, only those which find their optimum near the prevailing conditions can succeed in the competitive warfare. Thus a "biocoenotic equilibrium" (Thienemann, 1918) is causally related to the conditions in the environment so that a species living in a given biotope remains there only so long as no substantial change takes place in the environment. If the environment changes, so also necessarily is there a displacement in the composition of the biocoenosis. On the other hand we find biotopes widely separated geographically which are equal in their ability to support very similar life associations (for example, the springs and brooks of the temperate latitudes, the thermal springs and the upland moors of all zones).

The investigation of the causal relationship of the biotic communities to their environments (when environment is taken not only to mean the physical and chemical conditions but also to include that dependence which is given by the inter-association of organisms) is recognized as the sphere of interest of Ecology, and ecological considerations form, thus, a fundamental of each hydrobiological investigation.

Hydrobiology is concerned with fields of science other than biology —with physics, chemistry, geology, and geography—for a comprehensive knowledge of the environment is essential to a full consideration of the subject. Thus we must in our case discuss the physical and chemical conditions in water and in waters in so far as these are important to life as well as the biological phenomena.

The part of the earth's surface which is covered with water is subdivided into two very unequal zones, the oceans and the inland waters, each of which is a special field of endeavour, Oceanography serving the one and Limnology the other. Both sciences follow somewhat parallel courses, but their subjects are in many ways so different that they must differ to a certain extent in both treatment and methods. A few of the most essential differences between the two environments can be dealt with briefly, although the fact known by all, that the seas contain salt water and the inland waters generally (but not always) consist of fresh water, will not be in the foreground.

The oceans which cover seven-tenths of the earth's surface are a continuum in both space and time. They have always existed since water was possible on the cooling globe of the earth and have always formed a spatially continuous unit, in spite of the great changes they have undergone in the course of the earth's history since its origin. As a consequence, the development of life in the sea has proceeded from its first beginning without ever being entirely disturbed by any catastrophe. The inland waters, on the other hand, which make up scarcely one-fiftieth of the earth's surface, are ephemeral bodies measured by the standards of geological time. Only a few large lakes (for example, Lakes Baikal and Tanganyika) extend back beyond Quaternary times into the Tertiary. Most of them originated in the Pleistocene. Through the processes of filling and sedimentation, and through tectonic changes, the inland water surfaces disappear in an appreciably short time, and with them goes the community which populated them. Newly arisen bodies of water are seeded and repeat the fate of their predecessors. Because the continual change occasioned by these entrances and exits of biotopes can be followed only by especially adaptable organisms, the inland waters have a very restricted fauna in comparison with the sea.

Further, because of the world-wide expanse of the sea, its waters are in permanent and active interchange over all zones of the earth. The sea is very little influenced by the land masses, but often, on the other hand, it determines the climate of these. In contrast, the inland waters are relatively limited enclosed bodies of water, strongly influenced by the local climates of the land masses which surround them. Because of their small extent and depth, the regular change of the physical and chemical properties and the distribution of organisms dependent on this change are compressed into a much narrower space than in the sea and are in much less measure disturbed by currents. For the investigation of the relations between living conditions and biological phenomena the inland waters are thus more easily reviewed and they are, in many respects, more suitable objects of study for the investigation of causal relationships than are the oceans in spite of the smaller variety of life in them.

Part A
WATER AS AN ENVIRONMENT

If an attempt is to be made here to sketch limnological investigation in its fundamentals, it follows, as was pointed out in the Introduction, that it must begin with a consideration of the environment. If this is to be discussed under the title "Water as an Environment," then it must be realized that this refers, not to water *per se,* but to waters in their manifold forms which produce the biotopes in question—biotopes in which the conditions for life are fixed, not by the water content alone, but by the suitability of the bottom, and the form and location of the basin, or (in running waters) of the channel. However, these factors are in general of less importance than the "hydric limitation" (Hentschel, 1923) of life in water, and we therefore first consider the peculiarities of water as an environment in contrast to the conditions under which the land (or better, aerial) organisms exist. Therefore, we shall first consider that biotope in which the "hydric limitation" finds its purest expression, the open water of the large lakes.

Water has a two-fold effect on the life within it: (1) through its physical properties, as a medium in which plants and animals extend their organs and move or swim; (2) through its chemical properties, as a bearer of the nutrients which produce the organic from the inorganic through the primary production of the plant kingdom.

I. Physical Properties of the Environment

It is these which above all most strikingly separate the environment of water from that of air. The vast differences in specific gravity, mobility, specific heat, and humidity—factors which have the greatest of influence on life—have many divergent effects on the plants and animals in the two environments.

1. *Specific Gravity, Viscosity, Surface Tension*

The specific gravity of water is 775 times greater than that of air (at 0°C., 760 mm. Hg) and correspondingly its buoyant effect on a body within it is also greater by the same ratio. This means a considerable saving to the organism in the energy required to support its own weight and makes possible the reduction of supporting tissue. A *Potamogeton* or *Myriophyllum* which raises its stems and spreads its leaves in water collapses when taken out; freshwater polyps or jellyfish become formless and motionless masses in air.

The density of water in our lakes, brooks, and rivers is not quite the same in different places and at different times. Although the differences which do occur are generally small in themselves, they are nevertheless of great importance to the events in the waters under discussion. The differences in density are mostly brought about through variations in temperature and salt content.

The increase in specific gravity with increase in the content of dissolved substances is shown in the following table which gives the relation in dilutions of sea water.

Salt content ‰ (g. per litre)	*Specific gravity* (at 4°C.)
0	1.00000
1	1.00085
2	1.00169
3	1.00251
10	1.00818
35 (Mean for sea water)	1.02822

It follows from these data that the specific gravity increases nearly linearly with increasing salt content. The figures given above are not strictly applicable to inland waters since these not only generally contain far less salt but also contain the salts in different proportions. However, we can estimate the change in specific gravity due to this factor with greater exactitude. The content of dissolved substances in normal inland waters (when we omit the saline ones) generally lies between 0.01 and 1.0 g/l., values of the order 0.1 to 0.5 g/l. being most common. In a single lake, spatial and temporal differences in salt content are seldom greater than 0.1 g/l. Correspondingly, variations in specific gravity arising from this cause are very small (about 0.00008, i.e. 0.08 g/l.), but these cannot be wholly disregarded, as will be shown later.

The density changes which take place through changes in temperature are of much greater importance. It is well known that water occupies a special position in this respect. Its specific gravity does not increase continuously with decreasing temperature as is the case with all other substances, but reaches its maximum density at 4°C.,[1] after

[1]This is true at normal pressure. At *high pressures* the temperature of maximum density is lowered. An increase in pressure of 10 atmospheres (hence about 100 m. below the surface) decreases the temperature of maximum density by about 0.1°C. (the values of the physicists do not all agree exactly). For this reason in

which it decreases in density, at first gradually and subsequently, on freezing, suddenly. Ice is about one-twelfth lighter than water at 0°C.

This special position of water among the fluids arises because its molecules tend to form swarms or aggregations as a result of their electrical properties in a manner which is dependent on temperature. While the molecules of all other liquids arrange themselves as spheres packed compactly together somewhat as peas pack in a container, water molecules take up a tetrahedral arrangement at lower temperatures (one molecule in the centre and four in the corners of a tetrahedron). This "tridymite" structure is the sole arrangement in ice. In water in the liquid state the tetrahedra are broken down into other forms of aggregation and with increasing temperature gradually pass through intermediate stages to that of spheres in the most compact arrangement as is found in other liquids. The tetrahedral arrangement takes up the greatest volume of any of these states and therefore has the lowest density, while the densely packed spheres provide the greatest density. If these processes operated *alone* the volume would thus *decrease* and the density *increase* on heating. However, as in any liquid, the ordinary thermal expansion takes place at the same time. The resultant of these two opposing forces is the anomalous temperature-density curve given in Figure 1.

This anomalous behaviour of water is the cause of some very striking and, for life, important natural phenomena. Of these, the facts that our limnetic waters can only freeze on the surface (since water at 0°C. is less dense than water at 4°C.) and that the temperature in the deeper parts of lakes is generally only a little under 4°C. in winter, are of prime importance. For these reasons, the animals and plants in the water under the ice are exposed to far smaller temperature fluctuations than are the land forms, and are not exposed at all to destroying frosts whose occurrence presents an impassable barrier to the geographic distribution of many species. Of course, there are many small shallow bodies of water which freeze to the bottom. The populating of such a biotope can only be by species which can protect themselves from the frost by the formation of resistant resting stages. In the case of some species, for example many phyllopods, winter eggs are produced which require freezing before they will develop further; this is also the case in the seeds of certain plants.

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very deep lakes, as for example Münster-Strøm (1932) has shown in Norway, temperatures below 4°C. are frequently found without the stable stratification being upset as a result.

The salt content also lowers the temperature of maximum density, there being a decrease of about 0.2°C. for each increase of 1‰. Thus, in sea water (35‰) the temperature of maximum density lies at —3.52°C. and accordingly is not reached in the liquid phase at normal pressures. (The freezing point of sea water is —1.91°C.)

However, even apart from this anomaly, the small differences in density with changes in temperature are of very great and indeed of overwhelming importance to the course of events which take place in the waters. It can be said without exaggeration that the great processes which regulate the water and chemical economies of lakes are primarily a function of the differences in density. Because of the great importance of this relationship, variations in density between 0° and

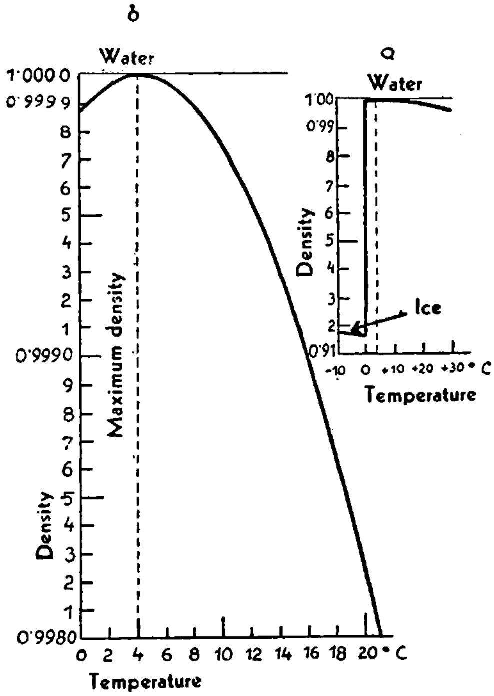

FIGURE 1. *a*. The dependence of the specific gravity of water and ice on temperature. *b*. Section of the curve between 0 and 20°C. with the density scale magnified 20 times and the temperature scale 5 times.

20°C. are shown in Figure 1*b* (which has the vertical scale of 1*a* enlarged by twenty times and the horizontal one by five times). The density corresponding to any temperature can be easily ascertained from this diagram. The fact that the density changes more rapidly at higher temperatures than it does at lower ones is especially important. Thus, the change in density between 24° and 25°C. is thirty times as great as that between 4° and 5°C.

The *viscosity* of water is a physical property that is not to be underrated. This is the cause of the frictional resistance that a fluid offers to a moving body. The magnitude of this function is proportional to (1) the extent of the surface in contact with the water, (2) the speed, and (3) a constant depending on the temperature and the nature of the fluid. Since the influence of the salt content (thus the nature of the fluid) within the limits occurring in fresh water is only slight, we are chiefly interested in the effect of temperature. As the temperature rises the viscosity falls. It is twice as great at 0°C. as at 25°C. Hence at 25°C. a plankton alga under conditions which are otherwise equal will sink twice as fast (see p. 98). Since the viscosity of water is about one hundred times as great as that of air, aquatic animals must overcome much greater resistance than aerial animals are required to, and the movement of a *Cyclops*, a mayfly larva, or the lightning dart of a trout requires powerful muscular force.

The *surface tension* of water towards gaseous and solid bodies is an important biological factor under certain conditions. It acts at the air-water interface and forms a special biotope to be mentioned later (p. 113). It affects the organs of plants and animals in a different way according to whether they are wettable or not. Young leaves of *Potamogeton* and the shells of the plankton Cladocera are water repellent. Contact of the latter with the water surface is often destructive, since the water draws away from the repellent shells and the tension of the upper surface prevents the submersion of the animal. The ecological significance of the surface tension is also to be seen in the circumstance that organs with a water-repellent surface are far less frequently the substrate for foreign growths which limit movement and metabolism.

Under the heading of physical properties of water are a group of phenomena causally connected with each other, whose importance to life in waters is undisputed.

2. *The Fate of Incident Solar Radiation*[2]

Solar radiation not only determines the intensity and quality of the light, the source of all life, which is available to the organisms at a given depth, but it also affects through the interplay of radiation, evaporation, and conduction the temperatures of waters with their diel and annual variations. Indirectly, radiation phenomena, together with those phenomena which result from them, affect almost all phases of organic and inorganic events, and it must be our task to concern ourselves with a thorough consideration of them.

[2]The diffuse radiation from the sky and clouds is considered under this heading as well as direct sunlight.

(*a*) *The distribution of radiation*

The point of departure for the consideration of relations in nature is made here from the knowledge gained by physicists in the laboratory. They have discovered that a beam of light falling on a water surface at a certain angle is in part reflected and in part penetrates the water simultaneously becoming more vertical.

The proportion reflected depends on the angle of incidence (calculated from the perpendicular) and is considerable when the ray is very oblique. With an angle of incidence of 60° it is only 6 per cent; at 70°, 13.4 per cent; at 80°, 34.8 per cent. In our latitudes about 2.5 per cent of the noon sunshine in summer and 14 per cent in winter is reflected. It is evident that during the change in the altitude of the sun in the course of the day there are major alterations in the proportion of light reflected. A result of this process is, for example, that —of course only when the sun is shining—the intensity of illumination in the evening decreases more rapidly under the surface of the water than above it. The increasing path travelled by the light from the descending sun with its more rapid extinction (see below), plays an appreciable part in this more rapid darkening as does the greater reflection. The diffuse light from the sky, which according to the degree of cloudiness and the height of the sun amounts to from 8 to 100 per cent of the total radiation, strikes the water surface from all angles, and of this on the average 6 per cent is reflected. Naturally, this holds true only when the horizon is completely free. When the horizon is obscured by hills, trees, and so forth, the reflected part of the diffused light is appreciably smaller. At all but very low elevations of the sun, the spectral composition of the reflected light is substantially the same as the incident sunlight. This, of course, has often been noted, since images mirrored in the water surface are colour-true.

The light which represents the fraction of the rays which penetrate the water does not pass through it unaltered; some of it is dispersed and some is absorbed and transformed into another form of energy, heat. The percentage held back in one metre we term the *extinction coefficient*;[3] that transmitted, the *transmission coefficient*.[4]

[3]That is, the part lost through absorption and diffusion.

[4]Mathematically expressed the intensity of light I at a given depth may be derived from the following formula:

$$I = I_0 \cdot e^{-\epsilon h},$$

where I_0 = the intensity at the surface;
e = the basis of natural logarithms;
ϵ = the extinction coefficient;
h = the length of the light path in the water column.

These two values are by no means the same for all wave-lengths. Line *DW* in Figure 2 shows the percentages of the various wave-lengths in the region of the visible spectrum that are transmitted through one metre of distilled water when the light falls normal to the surface. It will be seen that in the short wave-lengths the transparency is high and rather constant. At about 550 mμ and up, that is in yellow, orange, and red, it decreases rapidly. Even before the infrared is reached, which is beyond the visible region at wave-lengths of 900 mμ and above (heat rays), the radiations do not penetrate to any extent through a metre thickness. On the whole about 53 per cent of the total solar radiation is absorbed and turned into heat in one metre.

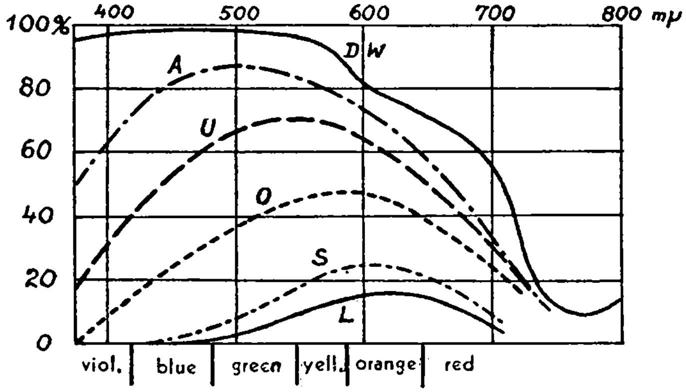

FIGURE 2. The transparency of a stratum of water 1 m. thick with respect to different regions of the spectrum. *DW*, distilled water (after James); *A*, Achensee (Tyrol), *U*, Lunzer Untersee; *O*, Lunzer Obersee (Lower Austria), after Sauberer; *S*, Skärshultsjön (South Sweden), after Åberg and Rodhe); *L*, Lammen.

Results of laboratory experiments cannot be applied directly to conditions in natural waters, as Aufsess showed long ago. Lakes, brooks, and springs do not contain chemically pure water but a dilute solution of inorganic and organic substances, together with suspended material of various sorts consisting of both plant and animal organisms and mineral and organic particles. All these circumstances affect the transparency of the water.

The technical difficulties which attend the exact measurement of light under water kept us from more than a meagre knowledge of the radiation climate of our waters until within the last three decades or so. Even now our knowledge is in a state of flux and is far from being complete. The older investigators had to use simple methods of measurement and these are often still in use today.

One such method of investigation that is often employed is the determination of *the depth of visibility* by means of a *Secchi disc.* A white plate of 20 to 25 cm. diameter is lowered on a calibrated line until it just disappears. The depth thus found is the depth of visibility and gives a measure of the transparency of the water. Consideration will show that the changes which the light undergoes on its way from the surface to the disc and then back to the eye are of two sorts, absorption due to the water itself or substances dissolved in it (colour) and the scattering due to turbidity. Each condition can affect the visibility of the disc independently. In the first case for example, in the clear but dark coloured waters of a bog lake the light intensity is low at the point where the disc disappears. In the second case in the milky water of a glacier lake the water can be quite well lighted as if under a ground glass, even when there is a high level of opacity. The determination of the limit of visibility does little in this latter instance to elucidate the light conditions in the lake. Nevertheless when properly employed, this simple and portable apparatus serves as a useful means of describing waters, and the Secchi disc will long remain a limnologists' tool.

The natural differences in transparency found in the waters of different lakes are very considerable. The highest values, 50 metres and more, are found in tropical and subtropical seas. However, in clear mountain lakes (Lago di Garda, Walchensee) the visibility is not infrequently 20 to 25 metres. In general, the white disc disappears at 10 to 15 metres in our alpine lakes, and in the lowland lakes at depths from a few decimetres to 10 metres. In the alpine lakes the transparency is generally greatest in the winter at the time of the snow cover of the drainage area and of the plankton minimum. In the Baltic lakes, because of the turbidity resulting from the winter rains, it is least at this time.

People have also tried to measure the decrease in light intensity with increasing depth by lowering photographic plates and sensitized paper. Thus for example, in Lake Geneva 200 to 240 metres is the limit at which a day's exposure will produce a recognizable darkening. However, these methods give unsatisfactory results for various reasons (for example, because of differences in the sensitivity of the plates).

Birge and Juday, working on North American lakes in the decades following the First World War, should be credited as the first actually to employ exact methods to investigate the penetration of light. These investigators used sensitive thermopiles suitably arranged so they could be lowered to various depths by a cable. A galvanometer was used to measure the thermal current produced. Thermopiles have the very appreciable advantage of being equally sensitive to all wave-lengths