FRESH-WATER BIOLOGY

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PREFACE

For the ordinary student and teacher on this continent fresh-water life has a significance heretofore greatly underestimated. In most parts of the country it lies at one's very door, readily accessible, and is indeed the only type of aquatic existence which can be studied living and at work. This fact gives to fresh-water life, once the student has been introduced into its domain, an appealing interest that fetters his attention and stimulates his desire to know something more of it. Among the most remarkable of early works that followed hard upon the first use of the microscope are some great classics which represent work in this very field.

Various European countries possess elaborate monographs on fresh-water organisms as a whole and on single groups, but no attempt has been made heretofore to deal with North American fresh-water life in its entirety, and few treatises have essayed to cover completely any group of fresh-water organisms. American workers in general have accordingly avoided this field and the few who have attempted to engage in its study have found their problems very difficult to solve.

The preparation of the present work was undertaken many years ago with the purpose of stimulating the study of the material so easily obtainable and of aiding workers of all grades to acquire some definite and precise knowledge of the organisms met in such study. Each chapter has been handled by a specialist on the group and the results achieved by this method have a significance that could not have been attained in any other way. Conditions entirely unavoidable led to the completion of the different parts of the work at somewhat different dates. It is believed that this will not, in fact, impair the value of the work as a whole and will find an excuse in the magnitude of the task. Individual chapters represent a survey of the group treated that is complete for this continent up to the time at which the chapter was closed.

The first few chapters are devoted to a discussion of general biological factors. Evident space limits prevented extended discussion of many most interesting biological topics, which are at best only outlined here. The exact citation of sources at the close of these chapters will aid the reader to pursue such topics further if desired. Not all discussions on general questions have been confined to the introductory chapters. The chapter on Rotifera, by Jennings, presents an admirable description of life processes, which, altho written specifically for that group, applies with appropriate modifications to all groups of many-celled organisms. In the chapter on Copepoda, Marsh has treated with some detail the general question of distribution as illustrated by this group; yet the very factors which he shows to be operative in it are those that lie at the basis of the distribution of most if not all other groups. The discussion of the aquatic vertebrates by Eigenmann is purely biological and the systematic outline is omitted entirely, since that of itself would demand an entire book for its adequate presentation. The same is true of the chapter on Bacteria, by Jordan, and of that on the higher aquatic plants which are treated by Pond in the physiological (chemico-physical) aspect primarily.

Apart from those just mentioned all chapters conform to the same general plan. Each is devoted to a single group of organisms and opens with a general account of the occurrence and history of the group. The description of the anatomy of the forms treated is very brief and deals chiefly with such features as are of special value in the key. Similarly the life history is given in condensed form. More attention is devoted to the biological relations which at this point are discussed with reference to the entire group, whereas individual features are left for later record under individual species except as they are needed for illustrations of general questions. Care has been exercised to include descriptions of special methods for collecting, preserving, and studying the organisms of each particular group.

Special details both biological and morphological regarding genera and species are included under a synoptic key which comes at the close of each chapter except as noted above; in some cases it is carried to species but in others only to genera. The form utilized for the keys has been in constant use for many years at the University of Illinois, having been applied to many aquatic types by Professor S. A. Forbes and his associates. The introductory number of each key line is followed by an alternative number printed in parentheses and on reaching a decision that this line is not acceptable, the student proceeds at once to the line introduced by the alternative number; in case a given alternative is accepted the further course of the inquiry is indicated by a number at the close of the line.

In order to achieve maximum ease in use and perspicacity in grasping the facts presented, all the information on a given form, viz., the illustration, the description, and the biological features with the frequence, range, and other special data, are included between the key line which introduces the name and the key line next following. The total information on a single type forms thus a solid panel and appeals promptly and as a whole to the eye and mind of the student. Each chapter closes with a brief list of the most essential references to the topic. No textbooks are cited and only such works are noted as may be considered indispensable for present-day study of North American forms. The student is cautioned not to regard any such list as in any sense a bibliography of the subject.

To encompass such a mass of material within the limits of a single volume, even tho it be generous in size, has necessitated brevity of treatment at every point. Technical terms are defined or discussed only once and no glossary is introduced. The index includes important terms and all of the scientific names used in the keys so that the reader can find every item promptly.

A serious effort was made to attain uniformity in the use of names thruout the entire work but the worker will find that this end was not fully achieved. The most conspicuous failure in this particular obtains in the citation of host names for various parasitic species. In all such cases that name is employed which was used by the authority from which the record is cited. It was felt that in the absence of monographic revisions of the species of parasites noted any other method would have been indefensible in a brief treatise.

Abundant use has been made of figures to illustrate the forms described. Most of the illustrations are new and many of them drawn by the author of the chapter especially for this work.

In chapter II certain figures and tables are taken with modifications from Shelford's Animal Communities in Temperate America by courtesy of the Geographic Society of Chicago and the University of Chicago Press.

It would be impossible to acknowledge all of the aid which has been extended during the progress of the work. Valuable suggestions from many sources have been freely extended us and as freely utilized.

To all of our colleagues who, in spite of multitudinous difficulties and seemingly interminable delays, have worked so generously to perfect their individual chapters the sincerest thanks of the editors are due. Especial mention should be made of the numerous helpful suggestions and criticisms given outside their own chapters during the preparation of the work by Professors E. A. Birge and Frank Smith. Grateful acknowledgement is also due E. C. Faust and H. G. May for aid in reading and checking proof.

Finally, it is a pleasure as well as a duty to express our appreciation of the work of the publishers. Their forbearance and continued kindly assistance during the long and difficult period of preparation has made possible the completion of the work and its presentation to the scientific worker in attractive form.

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CHAPTER I

INTRODUCTION

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On the surface of the globe, water and life are intimately associated. As water grows scantier life becomes more restricted until with the total failure of water life also disappears. In regions where water is very scarce the few organisms that exist have learned to store water or to discharge vital functions with a minimum supply and thus to meet the natural defects of the situation.

The hydrosphere, or the total water mass on the globe, forms the subject of study for hydrography which is readily subdivided into (1) oceanography, that deals with the vast continuous mass of salt water in the ocean, and (2) limnology, which treats of the various fresh-water units. The term limnology is sometimes restricted in its application to the more stable bodies such as lakes and ponds, in which case rheology is used to cover various types of flowing waters. All fresh water is distributed over the surface of the land and variably grouped into separate series of systems connected with each other only through the ocean to which each system is joined. The rare desert systems, such as terminate in the Carson Sink or the Dead Sea, are exceptional in having no present connection with the ocean.

Fresh water is deposited on the land in the form chiefly of rain or snow, and tends ultimately to reach the sea, though first and last a considerable part is taken up by evaporation and goes back directly into the atmosphere. Much of the precipitation soaks into the ground to reappear elsewhere in springs or by seepage to feed ponds and streams. Activity or rate of movement distinguishes two classes of water bodies: the flowing water of streams and the temporarily quiet water of lakes. The latter almost always form parts of stream systems and have thereby an intimate connection with the ocean that is of fundamental importance in determining the origin of fresh-water organisms.

The more or less actively flowing waters appear in the form of springs or rivulets, then increase and unite to make brooks, creeks, and rivers. The transition is ordinarily gradual and size has only a secondary influence on the biological character of the stream. The rate of flow, and the physical and chemical character of the soil over and through which water drains into a stream and by which its banks and beds are formed are the chief factors in determining its life.

From the tiniest rivulet to the mightiest river one may find every possible intermediate stage, and between the swiftest mountain torrent and the most sluggish lowland stream there exists every intermediate gradation. Biologically considered, the torrent imposes on the development of life within its waters evident mechanical limitations which are not present in the slow-flowing streams. Ordinarily the biological wealth of a stream varies inversely with its rate of flow, and anything which stops or checks the flow makes conditions more favorable for the development of life. Flowing waters are thinly inhabited and also present considerable difficulties to the student; hence they are relatively unexplored territory.

Waters of the static type, characterized by lack of flow, form an equally continuous series from the great lakes or inland seas progressing by insensible gradations through lake, pond, and pool to the morass or swamp. In the first group size permits more wind action; it also provides greater stability in level as well as in thermal and chemical conditions. Possessing only limited communication with the ocean these bodies of water constitute biological units of great definiteness. The lake is a microcosm; a minute replica of the ocean, it responds more quickly to changes in its environment, is simpler to grasp and easier to study. Yet it is withal the most complicated of inland environments (Shelford).

The distinction between water bodies of different size is often indefinite. Puddle, pond, and lake form in fact a continuous series. Yet in a strict sense lakes are characterized by a central region deep enough to exceed the limits of growth of the flora in the shore zone. Ponds are shallow lakes, usually insignificant in area, yet still of relative permanence. They constitute distinct units of environment. These more nearly stable units, the lakes and ponds, are often rich in life. They are exceptionally favorable for study and have been extensively investigated both in Europe and in this country.

The temporary water body, a puddle or pool, whatever its area, affords only conditions for transient existence that are sometimes irregular in their recurrence and sometimes present themselves with considerable regularity. They are fitted for organisms that reproduce very rapidly during the favorable season and also have special means of tiding the species over the unfavorable period. Purely temporary water bodies, such as pools that form in hollows after a heavy rain or in a wet season, develop little if any life. Such places on poor soil are most barren of all; the aquatic life increases with the fertility of the soil, the age of the water body, and the consequent accumulation of organic debris. Residual ponds, water bodies in which the drying out is more gradual and often incomplete and in which a central area may be protected from complete desiccation by vegetation or proximity to the general water level, afford conditions at the opposite extreme. The wide stretches of lowland subject to periodic overflow from great inland rivers like the Illinois, Missouri, and Danube in certain regions, develop a rich flora and fauna which equals or exceeds in abundance that found under other circumstances (Antipa, Forbes). Similarly among ponds adjacent to a lake basin the permanent are poorer than those which dry out for a time (Shelford).

The smaller water body presents nearly uniform conditions throughout and therewith also a single series of inhabiting organisms. The entire area falls within the shore or shallow water zone which is limited to such parts as support fixed plants. In this general region are readily distinguished two zones, (*a*) that of the emergent vegetation where the larger plants reach conspicuously above the water level and constitute the dominant feature to the eye, and (2) that of submerged vegetation in which the plants rarely project at all above the surface and in consequence the water itself dominates the view. Both of these regions may be subdivided on the basis of the particular form of vegetation which is common in a given portion. In a swamp these regions are often the only ones that are present. But in a pond one can usually determine the existence of a third zone in which the fixed vegetation is lacking.

With increase of the water body in size or more especially in depth, new conditions are presented. The littoral region passes over insensibly into a deeper bottom region with its own biological series and to a free open-water area known as the limnetic region. The corresponding region in the ocean is designated the pelagic and this term is also used by some for the fresh-water area. The plants and animals in this region are characteristic; they constitute what is called the plankton, the floating life of the water. Such organisms remain suspended in water during their entire existence; they live and die "on the wing." In the larger lakes the shore zone loses in prominence whereas the pelagic and bottom regions gain in distinctness and relative importance.

Lakes vary widely in character and abundance in different regions. They are infrequent in areas that are physiographically old and most abundant in glaciated territory, where they occur in eroded rock basins, in partially filled rock valleys, in hollows over the moraine, and more rarely at the margin of the ice sheet. Sometimes lakes are found in old volcanic craters, in the depressions of a lava-covered area, or behind a lava flow dam. They occur regularly in streams as mere expansions in the course or are formed by the inflowing delta of a lateral tributary or when the stream breaks through a narrow neck and leaves an ox bow or cut-off lake at the side. One finds them often on low coastal plains some distance from the shore, more commonly close to the sea and even on the same level with it. Old lakes without an outlet become strongly alkaline or saline and develop aquatic life of a type peculiar to each. Most lakes, however, are fresh and shelter organisms of the same general type.

Taken together lakes compose one-half the fresh water on the surface of the globe. They present an infinite variety of physical features in rocky, sandy, swampy margins, in steep and shallow shores, in regular and broken contours with no islands or many, with shallow water or depths that carry the bottom far below the level of the sea.

They vary in the chemical character of the soil in the lake basin as well as in their banks and bed, in the degree of exposure to wind and sunshine, in the relative inflow and outflow in ratio to their volume, in their altitude as well as in geographic location. All of these and many other factors modify and control the types of living things and their abundance in the waters. Lake, pond, and swamp are successive stages in change from the water-filled hollow to the terrestrial plain that ultimately occupies the same location. Along the margin of the lake, especially at the points where tributary streams empty into it, the inflowing water brings detritus of all sorts that builds out the shore and forms a shelf on which the littoral vegetation gains a foothold. As the lake grows old this region increases at the expense of the pelagic and bottom areas, until the latter disappears and the former persists only in reduced amount. Finally the entire area is conquered by deposits of silt and growth of vegetation. The swamp comes and is made over into dry land traversed in winding channels by the stream system that is responsible for these changes. In other cases the outflowing stream cuts down the level and ultimately drains the lake.

Lakes are thus in a geologic sense only temporary features of the river system to which they belong. Similar influences direct the evolution of the stream from the violent instability of its youth to the sluggish stability of its age. During this process of evolution the life in the waters undergoes parallel changes. At first the fauna is scanty but increases in numbers and variety as new habitats are created. Unstable and intermittent conditions indicate paucity of life; but when the aquatic environment becomes more permanent organisms more easily invade the territory successfully and its life grows increasingly complex as time goes on.

Lakes influence noticeably the life of a stream system in that they act as filters or settling basins for inflowing waters and also regulate the volume of the discharge; thus the outflowing stream is free from sediment and approaches constancy in level. This greater permanence militates against the development of certain types of life but favors others. The continued dilution of the stream by the addition of water free from life and the removal of such organisms as are produced at a given point by the constant flow of the water make the river plankton scanty in amount, but many fresh-water lakes produce an immense number of plankton organisms. These have been much studied in recent years and about them alike in ocean and fresh water has grown up a new study, Planktology, the Planktonkunde of the Germans.

Among the forms of the open water are some, primarily the fishes, which manifest individual power of movement adequate to make them independent of water movements, storms, and distances. They can thus determine their own distribution in an active fashion and stand in marked contrast with the plankton, for the latter is unable to regulate effectively its location, and is dependent upon the winds and waves for its dispersal. Typical plankton organisms, in fresh water known together as the limnoplankton, are found only in water bodies of some size, whereas in small lakes or ponds the circumscribed open-water area contains life which consists of migrants from shore and shallow water regions. Whereas on the land higher forms, especially domestic animals, depend on the higher fixed plants for food, in the water the higher types depend upon the smaller floating plant and animal organisms which transform inorganic materials and organic debris into available food substances.

The floating organisms which taken together constitute the plankton are grouped into two purely artificial classes according to methods used in collecting. The constant use of fine nets (cf. p. 74) for collecting plankton organisms led to a conception of this type of life that unconsciously assigned a minimum limit in size. Thus the organisms taken in the plankton net are all that the older authors included under the term plankton, an assemblage which should be termed more correctly the net plankton. It is well known through the work of many investigators during recent years and includes a great variety of Crustacea and Rotifera with many Protozoa and Protophyta, and less regularly some other types.

Within very recent times there has been obtained by more precise methods of collecting what has been termed by Lohmann the nannoplankton (dwarf plankton) with a size limit he set arbitrarily at 25μ. It consists of the most minute organisms only, those that (Fig. 1) pass through the meshes of the finest silk gauze, Swiss bolting cloth No. 25,* having meshes that measure 0.04 to 0.05 mm. square. The nannoplankton is composed chiefly of flagellates and algæ; although bacteria are constantly present they apparently form but a minor constituent in bulk and weight. The number and variety of these organisms is truly astonishing even in the clear waters of Alpine lakes where according to Ruttner they stand to the organisms of the net plankton numerically in the ratio of 160 : 3 and at least two-thirds of them are still undescribed and difficult to include in known genera. The maximum number of nannoplanktonts thus far recorded is from Lake Mendota, Wis., where Cyclotella has been found to the number of over 30,000,000 per liter of water.

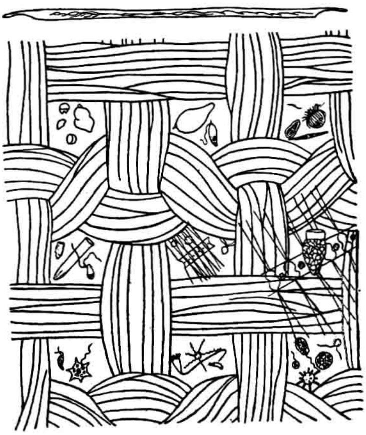

FIG. 1. A piece of bolting cloth No. 20 with plankton organisms drawn between the meshes to show relative size. Above, *Rhizosolenia alata*. Upper row, left mesh: *Gymnodinium*, beneath *Amphidinium rotundatum* and *Exuviaella baltica*, right *Pouchetia parva;* middle mesh: *Prorocentrum micans* and *Rhynchomonas marina;* right mesh: *Nitschia sigmatella*, *Achradina pulchra*, *Halteria rubra*, *Nitschia closterium*. Middle row, left mesh: *Tintinnopsis nana*, *Tintinnus steenstrupi*, *Oxyrrhis phaeocysticola;* middle mesh: chain of small *Chaetoceras* species, above it on the left *Thalassiosira nana* and *saturni*, on the right *Carteria;* right mesh: chain of large *Chaetoceras* species (*Chaet. didymum*), *Tintinnopsis beroidea*. Lower row, left mesh: *Rhodomonas baltica*, *Distephanus speculum;* middle mesh: *Strombidium caudatum* (?), *Meringosphaera mediterranea*, *Amoeba;* right mesh: *Coccolithophora wallichi*, beneath on the left *Pontosphaera huxleyi*, on the right *Coccolithophora leptopora*, above on the right Chrysomonadine without shell, at the very bottom *Rhabdosphaera claviger*. × 110. (After Lohmann.)

Ruttner also calculates the volume of the nannoplankton in the Lunzer lakes as three times that of net plankton. According to Birge and Juday the weight of its dry organic matter varies in three Wisconsin lakes from slightly less (rarely) to 15 or 20 times more than that of the net plankton and is ordinarily 5 to 6 times as great. This amount is unquestionably of marked importance both scientifically and practically, and the character of the organisms indicates even more clearly their fundamental importance in the problems of aquatic biology.

Plankton organisms are characterized by transparency, delicate colors, and above all by their power of floating due to buoyancy and

* New No. 25 is identical with No. 20 of older authors (Lohmann).

form resistance in contrast with related organisms. The buoyancy is achieved by oil droplets and gas bubbles formed in the cells whereas heavy cell walls and skeletal structures are wanting. Flotation-apparatus in the shape of lateral wings, bristles, spines, or a body form like a parachute, a spiral thread, or a gelatinous cover — provides against rapid sinking. Ostwald has determined that the rate of sinking is equal to the excess weight of the organism above that of an equal water volume divided by the product of the form resistance and the viscosity of the fluid.

Generally speaking great depth in a water body and large inflow in proportion to volume are unfavorable to the abundant development of the plankton organisms whereas minimal depth and scanty inflow favor the production of plankton.

When water is first deposited on the earth it is almost absolutely pure, containing only the minute amount of materials which it has leached out of the atmosphere. From the ground over which it flows or the soil through which it percolates come substances organic or inorganic, in solution and suspension, here of one type and there of another, that serve to enrich it and make of it an environment capable of supporting life. "The aquatic population of a lake or stream is thus sustained by the wastes of the land, materials which would otherwise be carried down practically unaltered to the sea; and rivers and lakes may be looked upon as a huge apparatus for the arrest, appropriation, digestion, and assimilation of certain raw materials about to pass from our control" (Forbes).

For the determination of physical data on the character of bodies of water, methods and apparatus of considerable complexity have been devised, largely by students of oceanography, and adapted later to fresh-water conditions. By such means the investigator is enabled to measure in a comparative way, and sometimes in absolute fashion, and to record environmental conditions such as the depth, temperature, turbidity, and other physical features of the water body. Some of these determinations are simple and require only limited apparatus; others are complex and beyond the powers of the ordinary student of aquatic biology. The application of such data to biologic problems is discussed in part in the following chapter. An adequate consideration of methods and apparatus demands more space than is available here and for further information the student is referred to manuals dealing with that phase of aquatic investigation. General methods of collecting and photographing aquatic organisms form the subject of a separate chapter while such methods as are applicable to the study of each special group are discussed in the chapter on that group.

The environment of water organisms as of all others is a complex of many elements. The physical factors are determined by the materials held in suspension or in solution in the water, by its temperature, depth, movement, illumination, shore and bottom. Chemical factors are found in the acidity or alkalinity of the water and in the gases, salts, and other materials in it. The organisms themselves make the biological environment. Living or dead, as food or feeder, parasite or host, friend, enemy, or neutral, each living thing contributes to the sum total of the biological complex by which each living unit is surrounded. It is the problem of science to unravel this tangle and to determine the relation of each constituent, living or non-living, to the others. The conditions of existence to which organisms are subject in different aquatic environments and the influence which these environments exert on organisms in general are discussed in the following chapter. In subsequent chapters an attempt has been made to present these relations as illustrated by each group of organisms. To become thoroughly acquainted with a single group involves a knowledge of the relations its members bear to every other organism in the community.

No climate is too rigorous for fresh-water life. It exists in fresh-water lakes at 77° N. L., hardly if ever free from ice, often only slightly melted and with a maximum temperature of less than 2° C. at the bottom. The Shackleton expedition described an extensive microfauna at 77° 30′ S. L. from Antarctic lakes that are frozen solid for many months, often for several years. At the other extreme of temperature evidence is less complete but Cypris is recorded from hot springs at 50° C., ciliates and rotifers from waters at 65° C., Oscillaria and nostocs from places that are recorded at 70° to 93° C.