THE FAUNA OF LAKE MENDOTA:

A QUALITATIVE AND QUANTITATIVE SURVEY WITH SPECIAL REFERENCE TO THE INSECTS

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INTRODUCTION

The present paper deals with the macroscopic fauna of Lake Mendota. In the fall of 1913 Mr. C. Juday for the Wisconsin Geological and Natural History Survey proposed the following problem to the writer, "A quantitative study of the insect fauna of Lake Mendota as a source of fish food." Certain phases of the ensuing investigations are incorporated in the present paper.

I am indebted to Professors W. S. Marshall and A. S. Pearse, and to Mr. C. Juday for their constant advice, aid, and helpful suggestions; I am also beholden to them and to Professors W. N. Steil, R. H. Denniston, G. M. Smith, and J. J. Davis for faunal and floral determinations, and I take this opportunity to extend my sincere appreciation and thanks for many kindnesses.

Apparatus and Methods.—The Wisconsin Geological and Natural History Survey provided the writer with a row boat and detachable motor. The motor made it possible to reach even the most outlying portions of the lake in less than an hour and to work with the greatest dispatch. Dip-nets, aquatic nets of various kinds, rake-nets, dredge, sifting pan, bottles, rubber boots, tape-line, thermometer, sounding line, and note book formed the chief collecting paraphernalia.

In general, a "square meter" method was employed in col-
lecting. A square meter was laid out; the surface layer of
the bottom and the fauna and flora within the area were gath-
ered as completely as possible, placed in a sifting pan, the
plants sorted over, and the whole sifted down to the compass
of a liter jar (quart jar). Two to three stations,—that is,
points, selected at random, each within one of the fifty areas
(see fig. 1) into which the lake was divided,—were visited on
a trip; the “hauls,” each covering a square meter of bottom,
were taken at successive depths. After all the jars were filled
in the field, they were taken to the laboratory where the or-
ganisms were sorted and counted while still alive and active;
the sorting of “dead” collections offered too formidable dif-
ficulties to be attempted, for so many of the recognition char-
acters of living specimens, such as position, method of locomotion,
and color, are lost in dead material.

Some reference seems appropriate as to methods of col-
lection in the littoral area. In the shallower depths, up to
three meters, the water of the lake was sufficiently transparent
to permit accurate work. Beyond this collection was more
difficult. To achieve a fair degree of accuracy a rake-net of
25 cm. width was drawn over a strip of lake bottom, sufficient-
ly long to make a square meter. This method was employed
primarily in depths exceeding 3 meters.

Investigations.—The main collections were made in spring,
summer and fall of 1914 and 1915. During this time the li-
toral area of the lake was explored, both qualitatively and
quantitatively; the aphytal area of the lake is now being
studied from a quantitative standpoint.

The work soon resolved itself into a series of phases: (1)
A qualitative survey of the macrofauna; (2) A quantitative
survey of the commoner macrofauna; (3) Ecological distribu-
tion, and the criteria of lake life; (4) The breeding of un-
known forms, and biological data on various species; (5) The
actual use of insects as food by fish, and the reciprocal food
relations of the fauna.

With respect to the qualitative survey of the macrofauna, it
was the original plan to consider only the insect fauna, but it
soon proved desirable to include the remaining macrofauna,
if only as a basis for comparison, and the quantitative meth-
ods were extended to the other macrofauna, except fish. The
lake was divided into 50 approximately equal divisions, or
"stations", from which quantitative collections were made (fig. 1); over 350 quantitative hauls were obtained from depths of 0–7 meters from these stations. In addition over 400 qualitative catches were made from about 30 selected habitats in various parts and at various depths of the lake. Thus qualitative, quantitative, and ecological data were obtained.

Observations were made in the field and in the laboratory as to the criteria of life in Lake Mendota. To ascertain in what respects they differed from those of other bodies of water, collections from the following places were made:

Merrill Spring, Merrill Creek, Pheasant Branch Creek, Six-Mile Creek, Yahara River and Swamps, Yahara Spillway, Yahara Rapids, and Yahara Canal, Tenney Park Lagoon and Pond, University Brook, and Picnic Pond, all lying around Lake Mendota;

Lake Monona, its bays and outlet, the Yahara River;
Yahara Swamps and Lake Waubesa to the south;
Lake Wingra and its springs and pools to the north and south.

Each place was visited a number of times in different seasons. Over 1,500 additional collections, some of them quantitative, were made from these various bodies of water.

To the fourth phase, that of the breeding of unknown forms, only little time could be given. In general, the breeding was restricted to the species of Lake Mendota, known as well as unknown forms, the known ones for verification. Except for a beetle larva, all of the commoner species were reared successfully. A considerable number of species from other waters was reared thru some or all of the stages. The waters about Madison abound with little known aquatic species, and offer a fertile field to the investigator. Each pool, spring, swamp, and river contains its quota of species whose stages are unknown to science.

The fifth phase, namely the role of insects in fish food, has received considerable attention, thanks to an arrangement with Professor Pearse, who very kindly turned over to me the contents of fish stomachs examined by him. Over 1,700 fish stomachs, representing over 25 species of fish, have been examined and the insect contents specifically and numerically determined. In the study of reciprocal food relations probably several thousand insect stomachs (Chironomidae, Tri-
Fig. 1.—Map of Lake Mendota showing 1 m. and 5 m. contour lines and the various stations. Circles indicate regular quantitative stations and squares show special stations selected for comparative studies. Scale about 1 : 50,000.
choptera, Odonata, Ephemeridae, Coleoptera, Corethra, etc.) were examined; the food habits of the living insects were further observed in aquaria and in the field. This examination was extended also to leeches, Crustacea, Oligochaeta and other aquatic animals.

It is impossible to treat all of these phases together in a homogeneous manner. Even in restricted form, it is difficult to deal otherwise than in the most general terms with the several phases. For inclusion in the present paper the following topics have been selected:

I. Criteria of Lake Life,—that is, the lake as a physiological body, its ecological divisions, factors controlling the lake and its biota.

II. Qualitative and Quantitative Survey of the Macrofauna, its distribution, factors which decide the complex, biological notes and food relations.

III. Ecology of the Lake,—that is, the ecological habitats and their biota, food relations, and seasonal succession.

IV. General Comparisons,—with other hydrobiota and with other lakes.

PART I. CRITERIA OF LAKE LIFE

1. LAKE PHYSIOGRAPHY

A. PHYSIOGRAPHY

Lake Mendota is the largest of a chain of four lakes in the Yahara Basin in the middle portion of southern Wisconsin. It is of glacial origin, lying near the southern edge of the drift. The lake is an irregular body of water (fig. 1), its greatest length being 9.5 km. (about 5.9 mi.), and its greatest width 7.4 km. (4.6 mi.). The circumference of the lake is 32.4 km. (21.9 mi.), its total surface area 39.4 sq. km. (15.2 sq. mi.). Its greatest depth is 25.6 m. (84 ft.). The areas of the various depths are shown in table 1, page 471.

Shores.—A considerable portion of the shore line of Lake Mendota consists of cliffs of limestone with bold and rocky subaqueous terraces in front of them. Another large portion of the beach line consists of sand with an admixture of
pebbles. The remainder, which constitutes about 60 per cent. of the total, is made up of gravel with an admixture of boulders of various sizes. The sand beaches are situated chiefly in the bays while the rock beaches are found at the most exposed points.

**Bottom.**—The bottom of the lake in the littoral area usually consists of coarse material, such as sand, gravel, and boulders of various sizes; rarely it is made up of mud which is covered with a thin layer of sand as in University and Catfish bays. Some detached shoals possessing rugged bottoms are of some ecological interest also. A shell zone several meters wide marks the lower limit of wave action. This zone is found at a depth varying from 4 meters in less exposed areas, such as University Bay, to 7 or 8 meters on the steeper shores; at Picnic Point, probably the most exposed point on the lake, it lies at a depth of 14 meters. Usually the substratum preceding the shell zone contains a large percentage of marl, but in the zone proper shells constitute almost 90 per cent of the bottom deposit.

In general the bottom is nearly pure mud below 8 meters, but in the more exposed places a considerable admixture of sand may extend to a depth of 10 or more meters.

**Sources of water.**—Lake Mendota receives its water supply through several creeks and the Yahara River and from a number of springs. Some of the springs are of fair size and of considerable local interest; they are situated chiefly at the west end of the lake.

**B. Ecological Habitats.**

The lake as a whole may be divided into three general regions,—the littoral, or phytal region; the aphytal region; and pelagic region. The bottom of the lake may be best classed as follows: The littoral, with its two subdivisions, the eulittoral (euphytal), and the sublittoral (dysphytal); and the aphytal area. (See table 1).

**a. The Littoral Region.**

In Lake Mendota the ecological, physiological, and physiographical features are to a great extent parallel. The plant zone, the littoral area, and the zone of photosynthesis are ap-
proximately identical. Comparably, the aphytal area, and the zone of decomposition are identical.

The littoral area in Lake Mendota extends to a depth of about 7 meters. Usually, the littoral area is accepted as the region of plant growth. In the present paper, the littoral area is regarded as composed of two major divisions, the eulittoral and sublittoral. The eulittoral area is the region of photosynthesis,—hence the region of plant growth. Below this lies a region of variable extent, a region of heaping refuse, a place where a minimal amount of photosynthesis may take place, but which is characterized by the absence of spermatophytes among plants; this is the sublittoral area. Parallel to the nomenclature of pelagic waters into euphotal, dysphotal, and aphotal regions, these two divisions may be termed euphytal, and dysphytal.

In Lake Mendota the eulittoral area extends only to a depth of 5 or 6 meters. This is rather surprising in comparison with some other lakes, such as the alpine lakes of Europe, where vegetation may extend to a depth of 25 and more meters. Lake Mendota presents the conservative extreme in this respect. As an example of the other extreme, Ekman (1915) reports green Characeae from a depth of 50 and more meters in Lake Vaettern, in Sweden, hence from a depth greater than twice the maximum depth of Lake Mendota.

The eulittoral area has three well-defined regions, or zones: shore line, rachion (breaker line), and plant zone.

*Rachion (Breaker Line).*—The rachion marks the point where the interaction of waves and returning undertow is greatest. In Lake Mendota this is at a depth of about 1 meter. The rachion may be continuous with the shore line (on steep grades) or entirely disconnected (shoals). In the latter places it is frequently divided into an “inner” and “outer” bar, a few meters apart from each other, and often many meters distant from the shore proper. In its physical aspects the rachion resembles the stony and gravel shores.

*Shore Line.*—The shore proper offers three varieties of habitats: (a) the rock beaches, characterized by shattered rocks and large boulders, which are not easily dislodged by waves; (b) the gravel (stony) beaches, composed of pebbles and stones, with an admixture of sand, the latter having the effect of smoothing the available surfaces; and (c) sand beaches,
made up of sand and of finer pebbles. Physically, bars are continuous with shores, are subject to the same conditions, and are therefore included under that head. The shore is devoid of vegetation, except the plumes of the alga Cladophora on rock and gravel.

**Plant Zone.**—The plant zone in Lake Mendota extends from the breaker line to a depth of hardly more than 6 meters, as a whole not exceeding 5 meters. The upper delimitation is the rachion in the steep parts of the littoral area, but it is rather less marked in the shoals; yet even there the shore proper and the breaker line are always barren, and the vegetation between rachion and beach is comparatively scant.

In many lakes there exists a definite plant zonation. There may be a succession of areas characterized by the dominance of some plant, e.g., Lemna, Chara, Myriophyllum, etc. In Lake Mendota there is but one spot, where such a zonation is at all indicated. This is a small area along the western end of the bar in University Bay. Here a zone of pure Chara is followed by submerged hummocks of Lemma, this in turn by Myriophyllum and Ceratophyllum, and finally by Potamogeton amplifolium. Small areas may be found in other portions of the lake where some plant species may attain a slight dominance, as Chara does opposite Merrill Springs; but a true zonation is entirely absent.

There is, however, a secondary zonation, not so much of plant species, as of types of plants. This consists of a zone of "upright" or standing vegetation, e.g., Potamogeton amplifolium, Najas, and Vallisneria, which tend to reach the surface (but do not emerge); and a zone of "recumbent" vegetation, composed of Chara, Myriophyllum, Ceratophyllum, and some Potamogeton species, all of which tend to recline.

As incidental, but of direct ecological importance, the heavy incrustation of carbonates on the leaves of Potamogeton and Vallisneria should be noted. After some days of quiet weather the leaves of these plants are covered with a layer of lime, which breaks off in heavy weather and is swept to the bottom. In places the bottom is covered with a very appreciable deposit of this "plant marl." It forms a type of bottom which is little frequented by animals.

**Shell Zone.**—The lower limit of wave action is marked by the shell zone. In Lake Mendota this also marks the lower limit
of plant distribution. As an ecological habitat it is fairly distinctive and has its own association. The zone is identical with the sublittoral area of more transparent lakes.

b. The Aphytal Region

The aphytal area is the area below the shell zone and includes the depths below eight meters. (I have used the word *aphyal* = plantless, in preference to "abyssal" which is used by Forel and others to designate the area below the plant zone; the latter word has been used in oceanography in a very special sense, and is therefore inapplicable and somewhat confusing when applied to limnology. Strictly applied, a shallow body of water, such as turbid ponds or streams, would then have an abyssal,—i.e., plantless, area).

The aphytal area presents the greatest uniformity of conditions and comparatively low ranges of variation. Its main features are the presence of mud and debris, the latter largely of organic and coprogenic origin. Because of the difficulty of making exact quantitative collections this area has been studied only qualitatively; but quantitative collections are now being made.

c. The Pelagic Region

This is the open water and the distinctive abode of the plankton organisms. In a quantitative study of the macroscopic fauna this region affects only Corethra among insects and Limnesia histrionica among Hydrocladina. Yet both of these forms are more or less concerned with substrata and will be taken up from that view-point.

C. HABITAT DISTRIBUTION

In general, the habitats in the lake are fairly evenly distributed. Uniformity of conditions makes for uniformity of response. Yet it continually happens that we find a different fauna in places which appear to be alike as regards external conditions. Quite a number of species are locally abundant in the lake, forming so-called "distribution islands." This localization of species is sometimes very difficult to account for.

It is also worthy of note that the seasonal distribution and
the seasonal representation are not identical. According to the stage of life history a species may attain a periodic abundance,—generally during the warmer months of the year. Again, owing to the peculiar conditions of winter,—that is, ice on the shore line, and a more equal distribution of gas in the aphytal area,—the horizontal distribution of the species frequenting these regions will vary from that of other periods of the year.

Seasonal representation or seasonal succession of dominant faunal types is apparent to the collector. More will be said of this later, but it is desirable to call attention to the fact that in a quantitative study the seasonal element plays a very important part. To cite an instance, the collections made during late June and July show a remarkable scarcity of the case-building Trichoptera; yet collections made a month later will show them as the dominant faunal type of the plant zone. The same is true of Platyhelminia, of Annelida in general, of Hydra, Ephemerida, etc. This feature has had to receive attention in averaging the quantitative results.

2. Lake Physiology

A. EXTRINSIC FACTORS

Molar Agents.—Under this term are grouped eroding agents, such as winds, waves, currents. Waves are the result of surface disturbances caused by winds. The size of the wave is proportional to the wind pressure on the surface, and to the distance traveled, less so to the velocity of the wind. On Lake Mendota the largest waves do not exceed 1.5 meters in height and may reach a length of 15 m. in storms.

The daily winds are an important feature of lake physiology. These light winds are frequent, occurring at various times during the day, even during summer calms, and may persist for brief periods. They may be of varying intensity, frequently covering the lake with choppy, crested waves of 7–8 meters length and half a meter's height.

In their effect on the lake physiognomy the waves are of primary importance. On the sandy shores there is a constantly moving film of sand. Rock and gravel shores are clean-swept, and the floating rubbish pulverized. On gravel shores pebbles and stones are torn loose and form a movable substratum with
the sand which serves to smooth the shore. The rachion resembles the gravel shore with its fluctuating rubble. It is composed of smooth stones and marks the point where the interaction of waves and undertow is most violent. In shoals the rachion is entirely detached from the shore proper, sometimes a hundred or more meters distant. Furthermore, in such shoals there are "secondary" breaker lines found toward the shore, usually a short distance behind the first. The two rachia are comparable to the "outer" and "inner" bars of the ocean shore.

The lower limit of wave action is marked by the shell zone. Sand and other heavier particles carried by the waves are soon deposited, while the lighter shell fragments are carried farther down the slope to the limit of wave action. In Lake Mendota this lies immediately below the plant zone.

Winds and waves dominate the complex and the upper distribution of the littoral fauna and flora. Wave action determines the floral complex in that it banishes all emergent and floating vegetation from the lake proper (by "floating," plankton flora is not meant); it controls the upper distribution in that it banishes all plants from the shore area and the rachion, except the filamentous alga Cladophora.

Among the fauna the determining influence of molar agents is equally potent. Wave action controls the complex in that it banishes all surface breathers (with a few exceptions); it limits the distribution of water-breathers in that it permits only clingers and burrowers on the shore and in the rachion.

Waves furthermore aid the circulation of the lake, and thru the roiling of the bottom affect the clearness of the water, and hence the penetration of light for photosynthesis.

Temperature and Circulation.—In early spring after the ice goes out the water absorbs heat; thru the influence of the wind and convection currents the water is set into complete circulation so that the heat is distributed thruout the entire depth of the lake. As the days grow warmer, the surface water absorbs heat faster than can be communicated to the lower depths of the lake. There is a concomitant change in the quantity of the dissolved gases. This difference in dissolved gas and circulation increases as the summer progresses, and a zonation is established in the lake: (a) an upper, well oxygenated, warm layer, the epilimnion, comparable to a zone of photosynthesis;
(b) a thermocline, or *mesolimnion*, a zone of rapid decline in temperature and in oxygen content; and (c) the *hypolimnion*, a bottom layer, which is poor in oxygen, cool, and constitutes a zone of stagnation and decomposition.

As an essential of life the distribution of oxygen exerts a decisive influence on the distribution of plants and animals. Despite the fact that bottom areas of the lake are without oxygen and exceedingly rich in carbon dioxide for several months of the year, a fair number of species live in the decomposition area throughout the year; all of the species are present in large numbers.

*Light and Mineral Matter.*—The relation of these two is not a direct one, but may become so. The depth to which light may penetrate water depends on the clearness of the water. Particles of solid matter in suspension control its clearness and hence its penetrability. This is well illustrated by a comparison of Lake Mendota and some of the alpine lakes. Lake Mendota contains a large amount of matter in suspension; a white Secchi’s disk of 15 cm. diameter can be seen at a depth of about 2.5 m. in the open lake, and about 3 meters near the shore. In some of the alpine lakes a similar disk can be seen at 10 and more meters. Ekman (1915) reports 18 meters as the limit of vision in Lake Vaettern.

The degree of penetrability affects the photosynthesis of plants. Aquatic plants receive a more ideal light for photosynthesis than those on land. That is, the best light for photosynthesis is a diffuse or dispersed light of about the intensity of bright moonlight, or one twelfth of sunlight. Such a diffuse condition prevails in the water. The light is dispersed by the particles; much of the light is reflected by the surface so that the intensity is somewhat lessened. This intensity decreases with the depth, and we actually find an increase in growth as depth increases, up to an optimum point, until we finally come to the minimum where light is too insufficient for photosynthetic activity. That is to say, plant growth is more luxuriant as the depth increases, and the optimum is not found at the surface, but some distance below; in Lake Mendota this optimum lies between 3–5 meters.
B. INTRINSIC FACTORS

Respiration.—Aquatic animals can be conveniently divided into surface-breathers and water breathers. The latter obtain their oxygen directly from the water. Surface-breathers, however, must come to the surface for the replenishment of their oxygen supply. Many surface breathers attach themselves to the free surface film by means of hydrophue bristles, plates, and rosettes, and bring their stigmatal opening into contact with the atmospheric air; others cling to some object in the water, usually a plant, while they push their breathing apparatus above the water. In the first case a quiet surface film is essential, in the second an emergent vegetation,—two conditions which do not exist in the lake for a continuous period.

The outstanding feature of lake physiology is the constant commotion of the surface. Periods of perfect quiet are exceedingly rare; for even on the calmest days of summer light breezes disturb the surface for short periods. The fairly constant wave-action does not permit the growth of an emergent vegetation,—the second essential. The two conditions, quiet surface film and emergent vegetation, necessary to the surface breather, are absent from the lake—hence an absence of surface-breathers from the faunal complex.

There are a number of insects which would seem to form exceptions to the rule, i.e., some aquatic beetles and Hemiptera. Certain of the beetles, however, have readapted themselves and have become water-breathers (not in a direct sense) again, as will be explained elsewhere. Other forms will readily seize oxygen bubbles secreted by plants instead of going to the surface,—an ingenious method of replenishment which is practiced also by hibernating surface-breathers under the ice.

In the lake, this method of bubble capture applies to most beetles and some of the Hemiptera. Some of the latter, however, regularly swim to the shore during a blow; as do most beetles during prolonged blows, altho they are able to stand prolonged submersion.

Locomotion.—A second characteristic of the lake habitat is that the animals are either clingers directly, or indirectly so thru artificial aids, such as burrows, tubes, webs, and other fastenings. Free swimmers except fish and plankton organisms, are rare indeed. Corethra and the Ceratopogoninae are the
only ones among insect larvae, and Corethra is confined to deep water while the others seek shelter in algae (Cladophora, Spirogyra, Batrachospermum, etc.).

Food Supply.—Nutrition is of less influence on the lake complex than on the distribution within the lake. Phytophaga among animals are restricted entirely to the zone of photosynthesis,—while secondarily sarcophaga are restricted in their distribution by the same factor. To escape such limitations, some species have become necrophagous and coprophagous, and may occur wherever organic waste is present.

Currents.—It is essential to consider the relative strength of currents and their frequency in discussing the lake complex. Many water-breathers are restricted to waters which have a continuous flow, such as rapids and falls; these species are homiophilous. In the lake the habitat which most nearly approximates this condition is the rock shore, and the gravel beach and rachion to a lesser extent, where intermittent takes the place of continuous wave action. Hence it is not surprising that many of the inhabitants of the rock beaches are found also in the rapids.

This statement must not be made too categorically, however, for the condition of the bottom may perhaps be a more decisive factor than the current. In the case of the inhabitants of the rock beaches it may be the presence of rough surfaces, especially rocks, that is really the determining feature. For instance, Psephenus lecontei, certain may-flies, and other petrophyllous species are found on the stones of rock beaches and in the Yahara Rapids. If current were the decisive factor, then they ought also to be found in the short rapids of Merrill Springs and Merrill Creek; yet they are absent from these places.

Special Habits.—Certain special habits seem to influence the lake complex. This is notably the case among Trichoptera, Ephemeridae, and Odonata. Several species of caddisflies are confined to the springs along the lake shore, never occurring in the lake proper. The same is true of some Ephemeridae. The dominance of a habit, however, is best illustrated in the case of Odonata; here the habit of oviposition is, I believe, decisive. Most Zygoptera, Aeschninae, and some Corduliinae oviposit in plants,—therefore a habit necessitating the presence of emergent vegetation which is of course absent
from the lake. Enemies, behavior, and other factors may influence the complex and distribution of the fauna, but usually in combination with one of the major factors already discussed.

PART II. QUANTITATIVE AND QUALITATIVE SURVEY OF MACROFAUNA

In the following pages I have not attempted to give the details of the quantitative work. In all of the tables I have merely noted the final averages. Thus, if a species occurred in 20 out of 50 catches, the latter number was used to average it, and from this the total has been computed. In a number of instances, however, the total average was so obviously inconsistent with the actual representation, that the totals had to be revised and raised or lowered arbitrarily, according to the findings of the qualitative catches. This was especially the case with the Hydroptilid caddisflies. These occur in the lake for a very short period. But since it was impossible to visit all of the stations during the time of their maximum, the final averaged total was proportionately much too low. Hence a lower number was used as a basis for average for these and some other species. In general, however, the averaging was strictly adhered to.

THE MACROFLORA OF LAKE MENDEOTA

Because of their importance as a substratum and as a food supply, it seems advisable to give a list of the larger plants in the lake. I am indebted to Professor Denniston for the use of certain tables showing the distribution of the plants in Lake Mendota. The following is a list of the species taken:

1. From Shore line and Rachion.
   Cladophora glomerata L.

2. From Plant Zone. True lake species which are quite general in their distribution. All are submerged plants.
   Potamogeton pectinatus L.
   " zosteraefolius Schum.
   " richardsonii Bennett.
   " lucens L.
   " alpinus Balbis’ (a rarer species).
   " amplifolius Tuckerm.
Najas flexilis Rost. & Schmidt.
Vallisneria spiralis L.
Ceratophyllum demersum L.
Myriophyllum verticillatum L.
Chara crispa L.

3. Swamp, pond and river species which may be found locally, in places where the lake tends to swamp, and also opposite the mouth of rivers and creeks. Largely emersed species.

Lemna minor L.
Lemna trisulca L.
Seirpus lacustris L.
Castalia odorata Wood & Wood.
Utricularia vulgaris, var. americana Gray.
Typha latifolia L.
Radicula nasturtium-aquaticum L.
Ranunculus delphinifolius Torr.
Nymphaea advena Soland.
Philotria canadensis Britt.
Wolffia columbiana. Karst.
Zizania aquatica L.

THE MACROFAUNA

I. INVERTEBRATE PHYLA (EXCL. ARTHROPODA)

1. Porifera.

Spongilla fragilis Leidy.

Only the encrusting form of this sponge occurs in the lake, on the rocks of Maple Bluff, Governors Island, and Picnic Point, and in parts of the Yahara Spillway.

2. Coelenterata.

Hydra fusca Linne.

No numerical data of this species are given. It is ubiquitous in the littoral area of the lake, and locally may be found in enormous quantities. A Myriophyllum plant with seven branches totalling a length of four meters was found to hold over 15,000 specimens. In late fall the sexual individuals are especially abundant. Hydra may hibernate, but in quite reduced numbers. Probably the greatest representation of Hydra may be found along the channel of the Yahara River to
the north, where it passes thru the swamps; that region seems to present optimal conditions for Hydra.

A few specimens of Hydra viridis Linne were taken on Chara at the mouth of Merrill Spring in August, 1914. This rare species has been obtained elsewhere only from spring-fed pools north of Lake Wingra.


Plumatella repens Linne.

Like Spongilla, this species encrusts the under side of rocks along rocky shores and in the Yahara Spillway. Some distance up the Yahara River I have found palmate growths of Plumatella on the underside of lily-pads; such growths are infrequent in the lake on plants, altho they may be occasional on Potamogeton amplifolium. More minute growths of Bryozoa, belonging to the genus Fredericella, and probably also to Lophopus, occur plentifully on the plants of the lake, and frequently on the bottom to a depth of eight meters.

4. Platyhelminthes. (Table 5, p. 474.)

Planaria maculata Leidy.

This ubiquitous species is found practically everywhere in the lake. The color variations are considerable and one may be tempted to consider the extremes of specific distinction. It is possible, indeed probable, that several species have been lumped as P. maculata in the numerical estimates. A relative, P. doritocephala, is abundant in Merrill Spring; another species, P. agilis, is frequent in the springs and occasional in the lake.

Polycelis nigra Ehrenberg.

Dendrocælum lacteum (Müller).

These two species, so interesting because of their colors, apparently find conditions optimal in Merrill Spring, where they are thick on the stones in the channel. Both species are occasional in the lake, confined apparently to the rocky areas.

Mesostoma ehrenbergii (Focke).

This form was taken in four of about 350 catches. It is very common in Picnic Pond in May and June, but disappears as
the temperature of the water rises. Its transparency makes it
difficult to see and it is probable that it has been overlooked
in some of the collections from the lake, where it was found in
late July and August. Like its relatives it travels on slime-
trails, but when irritated will go thru a violent flapping motion
free in the water,—in fact, an actual swimming reflex resembl-
ing the vertical wave-motion of some leeches.

5. Nemathelminthes. (Table 5, p. 474.)

Gordius aquaticus Linne.

“Pink” Nematode.

During late June large numbers of young Gordii and of some
other, “pink” Nematode may be found coiled on plants or on
the bottom of the lake. Most of these occur in the shallower
parts, but they are also quite frequent at greater depths. Ap-
parently they have just left their intermediate hosts to search
for others. Many are of course destroyed during this “free”
period, which lasts not more than two weeks, while others suc-
ceed in finding a second host.

Especially Chironomus tentans larvae and pupae are found
to be infested with Gordius, some containing as many as three
individuals. Other Chironomid species may also be infested
with them, notably the larger species C. lobiferus, tentans var?,
and plumosus; I have not found the worms in the smaller species,
nor in any other lake insects, (they probably occur in Eph-
emeridae) altho I have repeatedly observed the unsuccessful at-
tempts of Gordius to enter caddis-worms.

The “pink Nematode” may be a form of Mermis; I have
found it in Chironomus palliatus, lobiferus, and viridis. No
mature specimens were obtained. Gordius adults are not un-
common in the lake and especially its tributaries and basins in
September.

6. Chaetopoda. (Table 5, p. 474.)

Only the larger Annelids have been considered individually
in the numerical counts. Except for Sparganophilus eiseni
Smith, which is a purely littoral form, the data given cannot
be considered complete, for they apply only to the littoral area,
while at least the Lumbriculids are quite general in their dis-
tribution.
A distinction must be made for the small Oligochaeta which are given in bulk. They form a very conspicuous percentage of the numerical total of the August fauna, altho less prominent as regards their bulk. As a rule they live in loosely constructed cases of accretions and secretions on the aquatic plants, and were it not for the difficulty of gathering them and freeing them from their cases, an individual count might be attempted. They are not difficult to recognize, for each of the several species of Chaetogaster, Nais, Pristina, etc., which make up their membership, has a distinctive locomotion, usually of the S-type, which makes identification of living specimens comparatively simple. Fish eat a large number of them, but it is difficult to estimate the percentage, for only the minute setae remain undigested.

Of the bottom Oligochaeta, Limnodrilus claparedeianus Ratzel, Tubifex tubifex Müller, Lumbriculus limosa, etc., are eaten with the mud by perch, suckers, and other fish. Sarcophagus eiseni Smith, the blue earthworm, is confined to gravelly areas and has been taken up to depths of 2.5 m.

7. Hirudinea. (Table 5, p. 474.)

The distribution of leeches in the lake was found to be more uniform and less restricted than at first suspected, except for Erpobdella punctata (Leidy) and Nephelopsis obscura Verrill. Altho the percentage of specimens is much larger in rocky areas a great many individuals are found among the plants of the littoral depths.

Erpobdella and Nephelopsis, curious to say, find their optimal conditions on the shore margin, where coarse gravel and stones are intermixed. Stones buried at the point where water and shore meet seem their favorite habitat choice; for under these rocks, of about a size of 25 by 15 cm., one may occasionally find clusters of as many as 85 individuals on a single rock. The stones are often tightly wedged and the leeches evince surprising agility and strength in burrowing under them. The egg-cases of Erpobdella and other species are common on the stones of rock and gravel shores.

The food of leeches is variable, and may consist of the microfauna and flora of the lake as well as of some of the larger lake forms. Thus I have found may-fly larvae (Hexagenia,
Caenis), and Trichoptera larvae (Polycentropus) in Erpobdella punctata, while other leeches contained Chironomid larvae, Hydrachnida, Hyalella, etc. On several occasions I found small leeches of the genus Glossiphonia attached to the under side of the beetle larva Psephenus lecontei; whether the leech was feeding or whether it was a mere accidental relation I am unable to say.

8. Mollusca. (Table 5, p. 474.)

Not all of the species occurring in the lake have been listed in table 5. For some reason Lamellibranchia are comparatively little represented (if one excepts the enormous numbers of the minute Corneocyclas which occur in the aphytal area.) Amnicola limosa Say is by far the most abundant of Gastropoda. In early summer its favorite spot seems to be the rachion (breaker line) where at a depth of two meters it covers the stones in immense numbers.

The general distribution of the Gastropoda in the littoral area is fairly uniform. Certain species evince a preference for the bottom,—at least I have rarely found them elsewhere; while others are quite common on plants, busily feeding on the Oligochaeta and Chironomids. In the aphytal area I have not found any Mollusca except Corneocyclas; very rarely one may meet a specimen of Limnaea stagnalis. This is rather surprising because of the fact that in so many of the European lakes, especially the deep alpine lakes, many Gastropoda have become permanently aphytal. (Feler, Roszkowski, Zschokke).

II. ARTHROPODA.

1. Crustacea. (Table 5, p. 474.)

Dikerogammarus fasciatus (Smith).

This Amphipod is confined to the rocky and stony shores of the lake. A relative, Gammarus limnaeus, is very abundant in the slack water of the springs and creeks at the western end of the lake, and also in the Yahara Spillway.

Hyalella azteca (Sauss).

As will be seen from table 5, this species is of comparatively wide distribution in the littoral area. Yet despite the formid-
able numbers found, the optimum conditions appear to be those of the Yahara River, entering the lake on the north. In the lateral parts of the stream, where it shallows over the mud of the swamps but still retains a fair current, Ceratophyllum and Myriophyllum are very abundant and line the channel with thick waving mats. These “mats” form the feeding and breeding ground of Hyalella; among the leaves and stems of the two plant species they live in such tremendous quantities that the plants appear gray from the living encrustation. On an area approximating a square meter with a depth of one-half meter I collected between seven and ten thousand Hyalellae one August day.

Hyalella is avidly eaten by fish, insect larvae of various kinds (Odonata, Gyrinus, Dytiscidae, Hydrophilus), and also by leeches. On their own part they eat diatoms, and other microfauna and microflora, and will not spurn eggs of Hydrochids, damselflies, Trichoptera, and other insects. In aquaria I have repeatedly seen them gnawing Chironomid pupae, even when other food was plentiful,—on several occasions resulting in the death of some cherished specimen which I was attempting to breed.

Cambarus propinquus Girard.

This is the commoner of the two species of crayfishes listed. Young specimens form an item of the spring food of fishes. They are not at all uncommon in the stony and gravelly portions of the shore. There they may be found wedged under stones, with smaller pebbles heaped around them,—a type of incipient burrow. In the less exposed depths they are not so cautious and seek only the slight shelter of plant leaves. C. virilis Hagen, another species, seems to be restricted to the deeper portions of the lake, where Prof. Pearse has secured it in gill nets.

Asellus communis Say.

I have only a single record of this isopod in the lake, and this, I believe, was an accidental occurrence after a freshet which carried much of the Merrill Creek fauna from its original location. Its absence from all lake catches is rather peculiar, for it has been reported from European lakes. It is very common in the slack water of Merrill Creek and the Yahara Spillway.
2. Hydrachnida. (Table 5, p. 474.)

The great bulk, I may say 99%, of the Hydrachnid contingent of the lake is composed of members of the Hygrobatidae. The commonest of all forms is Limnesia histrionica (Hermann), which occurs as practically the sole representative of the subfamily. Other common forms are Curvipes turgidus Wolcott, Atax ypsilophorus (Bonz), etc. The genus Arrhenurus especially offers a large field, for quite a number of species have been taken, several of them apparently new to science.

Except for an occasional Arrhenurus, Limnesia histrionica forms the chief Hydrachnid contingent of fish food. However, on a number of occasions I have found Eylaits and Hygrobatides present, especially in creek fishes. It is of interest that altho the red Hydrachnida and their scarlet eggs are shunned by fish, insects, and other Hydrachnida, they—the red ones—appear to enjoy their own eggs as food. They also will readily attack other Hydrachnida, but usually not the red species.

In general, the Hydrachnid food consists of their own kind, of Chironomid larvae, and of other animals whose pellicle they can pierce. All of the nymphs, most of the larvae, and a few of the adult mites are parasites. The symbiotic relation with sponges suggested by some writers is probably inapplicable; the sponge merely offers transient shelter, for mites will hide as readily in empty shells, in larval cases, and in egg clusters (Odonata, Trichoptera, Gastropoda, etc.).

Of all groups present in the lake their distribution seems most uniform. Respiration seems a slight factor with them; most of them have lost their tracheae entirely and breathe through their skin. Their free swimming habit makes them independent of a substratum except as a source of food, while their small size permits easy access to shelter.

III. INSECTA.

A. Order Plecoptera.

At least three species of stone-flies occur in Lake Mendota. Each of these appears to be fairly abundant, the adults appearing in April, June, and July, respectively. Yet for some reason unknown at present, I have failed to find any evi-
dence of the larvae, or of the exuviae at the time of emergence, notwithstanding very careful search.

B. Order Ephemeroidea. (Table 5, p. 475.)

All may-flies are water-breathers during their larval existence. They seem, for the larger part, to be stenoeaphic,—that is, with a small range of substrata. The lake species are for the larger part petrophilous, a few species are essentially phytophilous.

Specimens representing various species of the genus Baetisca, Baetis, Callibaetis, Siphurus, and Ephemera are occasional in the lake, but occur so sparingly that they have not been considered in the quantitative estimates.

Caenis diminuta Walker.

This is a small species, very abundant and quite general in its distribution. It is phytophilous and quite uniformly distributed in the littoral area. Like most other may-flies of the lake, it emerges in early June. It is common in fish food.

Ecdyurus maeulipennis Walsh.

Heptagenia canadensis Walker, H. interpunctata Say.

The three species named form a conspicuous part of the rock community of the lake. Their depressed form, as well as their strong claws, makes them particularly adapted to turbulent waters. H. canadensis in Lake Mendota has been found chiefly in depths exceeding two meters, hence beyond the influence of the greatest wave action. This indicates that the condition of the substratum and not the current is the controlling habitat factor for this species. All three are true petrophils of the infra-petral type (i. e., found on the underside of rocks).

The food consists of micro-organisms, Hyalella, some Hydarchnids, and occasionally one of their kind.

Ephemera varia Eaton.

This species in its general habitus recalls Sialis, with which it appears to divide the distribution area. That is, Ephemera is a littoral form, and Sialis begins its distribution at the shell zone, where the other leaves off. Ephemera varia is a bur-
rower, and its fore-legs show a distinct spatulation for the purpose of burrowing in sand and gravel. It is worthy of interest that there is a change in habitat with the growth of the larvae. Young larvae frequent the sandy bottoms at depths exceeding one meter, hence are distinctly ammophilous (sand-loving); I have no records of young larvae from rocky areas or from any part of the shore line. Older larvae, however, are found chiefly in rocky and stony areas, especially on the shore line,—hence are petrophilous.

The situation amounts practically to this: the adults appear during the first days of June, young larvae will be found several weeks later in the deeper sandy bottoms, while at the same time an occasional full grown larva may be found in the rocky regions of the shore line; after the middle of August older larvae will be very common on gravel and rocky shores, and exceedingly rare on sandy bottoms, especially those below the racchion. A second flight of adults occurs in early August; that is, the specimens which failed to emerge in June emerge in August.

C. Order Odonata. (Table 5, p. 475.)

From the standpoint of adaptation to amphibious life the Odonata as a unit have reached the highest development among insects. Amphibious existence is ancestral with them, and they have equipped themselves for both terrestrial and aquatic life during their larval state. For aquatic respiration they have the rectal gills (Anisoptera) or caudal gills (Zygoptera), while both suborders possess open thoracic spiracles for aerial respiration. The latter are impermeable to both water and miscible oils (Portier 1911) so that an exchange from an aquatic to an aerial medium, and vice versa, can be effected immediately.

In spite of their perfect adaptation to any type of aquatic life the Odonata are very sparsely represented in the lake complex. I believe that this is due to the ovipositional habits of the adults. Odonata lay their eggs on a free substratum or in plants. It is of course obvious that in the second case the eggs must be laid in plants which emerge from the water. Hence we find this type of species restricted more or less to habitats showing emergent vegetation; this includes most Zy-
goptera, Aeschninae, and many Corduliinae. But even those species which lay their eggs free on a substratum (sand, matted algae, scums, etc.) or in the open water are largely confined to the more quiet habitats. This may be due to the food varieties, more of which are offered in ponds, swamps, and quiet streams, than in turbulent waters. However, it is important to point out that it is not the respiratory factor which restricts the Odonate lake complex, but purely that of food and a special habit, oviposition.

Habitat relations, general form, and method of locomotion are closely interrelated in the Odonata. This relationship is expressed in table 2. Both positions at rest and methods of locomotion are combined in order properly to designate the main types of larvae. Many genera or subfamilies are comparatively restricted; thus, the Zygoptera in general, and also Gomphinae and Petalurinae, are poor swimmers, and have primarily a sedentary, "clinging" mode of life, and the Gomphinae and Petalurinae a burrowing habitus. (See p. 471.)

Argia putrida (Hagen).

The nymph of this species is easily recognized from its stout, depressed form; it is slate-colored, with white-tipped caudal gills. It belongs to the category of rock-clingers and is one of the characteristic forms of turbulent waters. While it occurs in the rocky areas of the lake, its optimal habitat seems to be in rapids.

Enallagma antennatum (Say).

This species is fairly abundant in the lake, together with Ischnura verticalis. It is a true plant clinger. Other species of Enallagma occur in restricted areas of the lake, especially where a river fauna enters or a swamp fauna lies nearby. In such spots Enallagma hageni, carunculatum, ebrium, signatum, and pollutum may be found in fair numbers. No Lestinae occur in the lake, but they are abundant in spring-fed ponds and in clear creeks.

Gomphus fratermus (Say).

The nymph burrows into the sand or rubble at the point where wave-action is strongest, hence at the breaker-line. Like Argia putrida, it is much more abundant in rapids than in the lake.
Epicordulia princeps (Hagen).

In parts of the lake, especially opposite rocky shores, the larvae of this form are not at all scarce. During July one may see the exuviae clinging to the face of the cliff for a height of 10 meters, while the spotted adults are busily engaged hunting for prey or ovipositing. The eggs are laid in long strings, usually at the surface on the floral beds of Potamogeton and other plants.

D. Order Hemiptera. (Table 5, p. 475).

Hemiptera are not conspicuous in the lake community. Few of them are hardy enough to withstand the severities of lake conditions. Two species of Corixa, one of Notonecta and of Pelocoris, and the ubiquitous Plea striola form the Hemipteran contingent of the lake; and for the first three it must be noted that they are abundant only in the tiny nooks one may find along the shore line, where the immediate shore forms an accessible shelter during adverse conditions.

Experiments have shown that Corixa cannot endure any prolonged submersion in disturbed water, two hours being the maximum; Notonecta is a little more hardy, while the minute Plea is hardiest of all, enduring a submergence of five hours without much damage. That the true habitat of all five of these species is not the lake, is indicated by the fact that in flowing streams, and especially in the swamps of the Yahara River, the same species of Corixa, Notonecta, and Pelocoris are enormously abundant, at least three times as abundant as in the most favored spots of the lake. Fish caught in such regions will be found gorged with specimens of one or all species. Belostoma, Nepa, and Ranatra are entirely absent from the lake. They are adapted to an emergent or floating vegetation and hence do not occur in the lake. Only the fact that Notonecta, Corixa, etc. may rapidly change from an aquatic medium to the shore permits them to stay in the lake, but then always within a short distance of the shore, as indicated by the quantitative hauls.

E. Order Neuroptera.

Sysira umbrata Needham.

This is the only spongilla fly I found in the lake. At Maple Bluff it is occasional in the encrusting sponges. No numerical
estimates have been made, as it forms a negligible item. Various species of Hemerobius occur in the sponges of other waters, but I have not found the larvae.

**F. Order Megaloptera.**

*Corydalis cornuta* Linne.

I have on several occasions taken larvae behind the bar of University Bay, but never in the lake proper. It is not an abundant species.

*Sialis infumata* Newman. (Table 5, p. 475.)

The larvae of this species constitute one of the major items of insect fish food. Late in April, or in early May, during a very brief period, the larvae migrate to the shore, emerging there in immense numbers to pupate in the earth. After two weeks the adults emerge; they may be so abundant in places along the shore as to be an annoyance to the pedestrian or boatman frequenting the spot. In oviposition the females lay their eggs in thick, velvety masses on the branches of trees, on sticks, and on piers along the water’s edge.

In emerging the larvae drop into the water, where fish are attracted in numbers, apparently relishing the feast. The larvae immediately migrate through the plant zone to the sub-littoral area, where they are very abundant. On the bottom they will wander downward as far as the oxygen content of the water will permit them to go. As the oxygen goes out with the warming up of the lake, they migrate to the shallower regions; vice versa, they go downward with the fall overturn.

Pereh brought up from the deepest portions of the lake in winter were found to contain many of these larvae.

A two-year cycle is indicated by the fact that shortly after the annual shore migration half-grown larvae are quite abundant in the lake. I secured them freely with the dredge throughout the summer.

The larvae live chiefly upon organic detritus of various origin. They do not refuse live Chironomids and worms, however. They are water-breathers and may descend to any depth, controlled by the oxygen supply.

The numbers quoted are incomplete, since they do not account for the distribution below 6 meters, altho the maximum is found below the depth indicated.
G. Order Hymenoptera.

Several parasites have been caught or bred from insects obtained from the lake. With the exception of Diapria columbana Ashmead (kindly determined by Prof. C. T. Bruces) they still await identification.

As an extraneous source of food supply the Hymenoptera are not without some importance in the lake economy. The variable winds of the summer blow thousands of insects of all sorts into the lake, where they become water-trapped and drown, or may be directly eaten by fish. As regards drowning I estimated in the summer of 1914 that 2% of the bulk of insects collected was formed by dead insects,—most of them Hymenoptera. At the time of their summer flights millions of winged ants are blown into the lake and become the toll of the water and of the fish. That the latter will eat ants greedily, is attested by the gorged stomachs of perch and other fish which were filled with Camponotus, and Formica. Other forms which are very common in the lake toll but rarer in fish stomachs are Pelecinus polyturetur, Apis mellifica, various species of Bombus, Polistes, Vespa, Bembex, Ammophila, Pompilus, Ichneumon, etc.

The important fact, however, is that the fish should eat ants in such quantities whenever available, since this brings up the question of nauseous emanations, similar to those by which the Hemiptera are supposedly protected.

H. Order Lepidoptera.

Two species of Lepidoptera have been taken in the lake. Nymphula maculalis larvae were secured in different parts of the lake in various depths. But the optimal situation seems to be the sheltered portion of University Bay, at the point where the bar joins the Picnic Point peninsula. There the larvae of N. maculalis and N. allionalis occur in large numbers on Potamogeton and Vallisneria. In Picnic Pond close by Hydrocampa sp. is also abundant.

As an item of fish food the Lepidoptera are negligible.

I. Order Trichoptera (Table 5, p. 475)

During the latter half of summer and early fall the Trichoptera form the greater bulk of the littoral fauna of Lake Men-
dota. One species, Leptocella uwarowii, is especially common, occurring in amazing numbers. Each haul of a square meter contains a fair number of individuals, often as many as 85 to 100 (over 500 in two instances).

In their general ecology the caddis-worms are more uniform than any other group of aquatic insects. In food habits they are primarily phytophagous; all of them live in shelters of some sort,—from those formed by a loose accumulation of refuse to the most elaborately constructed webs and cases; all are water-breathers and are supplied with lateral gill-filaments or anal blood-gills for respiration.

Family Hydroptilidae.

Agrayleia multipunctata Curtis; Hydroptila sp.; Ithytrichia clavata Morton; Orthotrichia sp.; Oxyethira sp.

These five species of Hydroptilidae occur in Lake Mendota, the first three quite commonly; the last two rarely. In June and early July when all other caddis-worms have pupated, they are in their larval stage and form one of the characteristic seasonal complexes of the lake.

Agrayleia, Hydroptila, and Ithytrichia are very abundant in the rocky areas of the lake among the Cladophora, while the first may be more or less generally found on the filamentous algae which cover the bottom and vegetation of the littoral area to more than three meters’ depth.

Agrayleia is distinctive because of the bean-shaped green case, woven from parallel algal filaments; Hydroptila has a case of similar shape, but made up of extremely fine sand granules; while Ithytrichia makes a case of clear green secretion, bottle-shaped, with the wider end open. The other two species, Oxyethira and Orthotrichia, have cases which are shaped as a poppy seed, or like a flat flask, respectively. In pupation the caddis-worm usually merely closes the open end of the cases, making sure beforehand that the case is firmly attached to a rock or plant. Ithytrichia, however, forms a pupal case of two tapering ends which resembles a leech cocoon remarkably, fastening the two ends each with two bands to the under side of rocks.

In places the various species may be quite abundant. On an Elodea plant of about three meters stem length, including all

26—S. A. L.
branches, I counted over 1,500 specimens of Agraylea multiplicata. As an item of fish food they are negligible, not because of their inavailability but because of the difficulty of capture.

The adults are often taken for Microlepidoptera. I have bred four of the species listed, two of them in quantities. A peculiarity noticed for Ithytrichia and Agraylea is that the pupae may swim about in the water for quite a while before ecdysis. The adults of both of these species have also been observed to swim actively.

**Family Hydropsychidae.**

*Polycentropus* sp.

The species is restricted to the rocky shores and the breaker line, altho on several occasions specimens have been taken some distance out on plants. The web spun by the larva is a funnel with fluted ends, the whole covered by a woven sheet.

Its relative, *Hydropsyche alternans* Vorhies, is very abundant in the rapids of the Yahara Spillway, where it constructs a loose network into which it anchors some of the flotsam sweeping over the falls.

**Family Molannidae.**

*Molanna uniophila* Vorhies.

The larva is an inch long, and builds a tubular case with lateral extensions. The larva lives on sandy bottoms and despite its "obvious" adaptations to strong molar agents is much more common in depths below the breaker line than above.

**Family Leptoceridae.**

*Leptocerus ancylius* Vorhies.

The larva is small, half an inch or less in length, and builds a case consisting of a tube imbedded in a concave shield. This species is confined to the rocky shores where it is found on the under side of the rocks.

*Leptocerus* sp.

This species which was bred from material obtained from the shell zone proved to be different from known American species, and may be identical with the European *L. fulvus*. Its case
is of sand and shell fragments. The species seems confined to the sublittoral area.

Leptocerus dilutus Hagen.

The minute, curved, and hooded cases are characteristic for the rock and gravel shores, though less common on the latter. This is not an abundant species.

Leptocella uwarowii Kolenati.

This is the characteristic caddis-fly of the lake, especially in the plant zone, and occurs everywhere in amazing numbers. It is adapted to a variety of aquatic conditions, for it seems also to be able to maintain itself to a fair extent on the rocky shores and in the rapids of the Yahara Spillway.

Only the larger fish eat the caddis-worms, for the long cylindrical tubes are somewhat difficult to manage. In fall, at the time of the heavy equinoctial storms, myriads are swept onto the shores and killed in the surf. After such a storm a thick lake drift lines the shore, while a secondary drift may be found in places in the water; a large portion of the accumulation will be composed of the dead Leptocellae.

Setodes grandis Banks.

Though occurring sporadically in the lake, the true habitat of this species is the Yahara River north of the lake. There the larvae in their translucent green cases may be found abundantly on Myriophyllum, etc.

Triacnodes flavescens Banks.

The spiral case is characteristic for this species. It is fairly abundant in somewhat sheltered spots, such as the small bayou north of the Yahara Spillway.

Family Sericostomatidae.

Helicopsyche borealis Hagen.

This is a small species, which is quite common on sandy bottoms. The characteristic case is built like that of a snail, as which it has been repeatedly described. First instar larvae build a slightly twisted case, while that of the second instar larva is like the case of the older stages. The species is eaten frequently by fish.
Family Limnephilidae

Limnephilus sp.

I attempted to breed this species, but overlooked the final ecdysis until too late. The case is square like that of Limnephilus rhombicus Linne, and composed of fine bits of crossed twigs, fibers, etc. This species, however, is much smaller than its relative of the springs.

The larva is the only active "swimmer" among the lake caddis-worms, most of which are too heavily encumbered by their cases to be able to swim at all (except the first and second instar larvae of caddis-worms which are all good swimmers.) The species is not infrequent in the lake.

Platyphylax subfasciatus Say.

This is the largest species found in the lake, although rare. In places it may be abundant, at a depth of about a meter. Its congener, P. designatus Walker, and relative, Neophylax autumnus Vorhies, are quite thick in the waters of Merrill Spring.

Family Phryganeidae.

Phryganea interrupta Say.

A single specimen of this species was taken in the lake, in a sheltered part of University Bay. Like Neuronia postica Walker, it is more characteristic of smaller streams and ponds, and is not uncommon in Pheasant Branch Creek. Here it lives among the roots of the plants or buried in the fine silt of the bottom.

J. Order Diptera

The Diptera have adapted themselves to a greater variety of conditions than any other order of insects. These conditions range from aerial and terrestrial to subterranean and aquatic, from ectoparasitic to endoparasitic. On a taxonomic basis none of these conditions can be stated as characteristic exclusively of the different groups of the order. For instance, all transitions from a damp habitat to a semiaquatic and holaquatic habitat may be found. These transitions take place within close relationships, and the facility with which members of a single family pass from one extreme to another is extraordinary, and de-
notes great plasticity. The attempt to select the aquatic representatives of the Diptera for inclusion in the present study proves this strikingly. Table 3 is a compilation intended to show the degree of "aquativeness" of the larvae—that is, the extent to which larvae have adapted themselves to an aquatic mode of life. This is evidenced most strongly in the respiratory adaptations,—whether the larvae have remained surface-breathers (i.e., come to the surface to breathe the air above it), or whether they have become water-breathers (i.e., obtaining their oxygen directly from the water.) (See p. 472.)

It is surprising to find that seven of the families are only in part aquatic; again, it is interesting to note that several families have members under the extremes of terrestrial and water-breathing habits (Leptidae, Ceratopogoninae); or, that of a partial and a total aquativeness as in the Psychodidae, Corethridae, and Anthomyiidae.

On the one hand, this classification indicates that the transition from a purely terrestrial habitat to an aquatic one is not very difficult; it also indicates that the final step from surface-breathing to complete water-breathing is, after all, not so very great. On the other hand, the presence of water-breathers alone in the lake complex demonstrates the dominating influence of respiration; while a further specialization of the aquatic habit is found in the limitation of some species to a constant current.

In the present paper only two of the Dipteraous families can be considered, the Corethridae and the Chironomidae.

Family Corethridae. (Table 5, p. 475).

A single species of this family occurs in the lake, Corethra punctipennis Say. The Corethridae are of interest in more ways than one. In the first place, the presence of semi-aquatic and holochronic larvae distinguishes the family. Secondly, the fact that Corethra is one of the few insect genera whose species are pelagic is of considerable interest. In addition the peculiar anatomy of the larva, its remarkable transparency, its physiology, and its importance as an item of fish food make it noteworthy.

Corethra punctipennis occurs in the lake in enormous numbers. Due to its pelagic habits, it is possible to give only an approximate estimate of its numbers. The figures given in the
table are littoral catches made at pupation periods and of no value in estimating the deeper distribution. (Some of the catches made in the summer of 1916 by means of a clam-shell dredge show numbers ranging from 2,000 to 18,000 individuals per square meter.)

Corethra begins to pupate about June 10th and enormous swarms emerge continually during the summer weeks of June 15th to about August 20th; the numbers then decrease to September 10th, when they become small, the last adults emerging about September 30th. Corethra emerges at night, beginning early in the evening and continuing through the night. Large swarms of them fly to the lights of Madison or gather in the tree-tops, especially in the vicinity of the lake. In the morning, if the lake is quiet, the females can be seen resting on the surface, ovipositing through the surface film.

From observations made since 1912, it seems that there are about six great periods of swarming or emergence, alternating with an equal number of minor "pulsations." In each case the adults live about three to five days.

The larvae, while primarily pelagic, hunt their food chiefly at the bottom, where they nestle into the soft ooze. The food consists of small worms, and the various components of the plankton. In Picnic Pond, where specimens of Corethra are quite abundant, I have watched them feed on Volvox. The method of feeding is curious. Bits of food are rasped off the prey, taken into the stomach, and digested. After digestion the waste is ejected through the mouth (Frankenberg 1915), an observation which can be easily verified.

Transparency is the greatest protection of the larva and pupa. Despite this transparency Corethra is eaten in large numbers by the fish of the lake, especially by the bottom feeders of the deeper waters. One frequently finds specimens of perch which have gorged themselves on Corethra larvae.

Corethra is unique in its system of respiration. At each end of the body are found two twisted air-chambers, which are entirely detached from the surface. Their structure is tracheal, and they function primarily as static organs, and possibly as storage organs for oxygen used in respiration. The general tracheation is very meager and appears insufficient. In respiration the oxygen must be taken from the water through the skin and carried in the blood wherever needed. In contrast
to the larva the pupa has an elaborate tracheation which communicates with a pair of external air-chambers from the thorax.

Pupal life is very short, and lasts one to three days, at most.

The daily migration of the larvae needs mention. In daylight the larvae are found below the thermocline and in the bottom mud, while at night they come to the surface. Aside from the considerable adjustment entailed by the change in pressure (at least two atmospheres), there is the change from aerobic to anaerobic conditions which perplexes us and leaves us in doubt as to the precise status of the air chambers.

The larval history lasts about six to seven weeks. Hence there may be three generations during the summer, the wintered larvae pupating in May and June, the second generation appearing in late July and early August, the third generation in September. Wintering larvae are uniformly larger before pupation than are summer larvae.

Family Chironomidae. (Table 5, p. 475).

The species of Chironomidae about Madison are legion. The various waters,—lakes, ponds, springs, creeks, swamps, whichever they be—all contribute their share to the Chironomid complex. Only a small portion of this complex has been studied, and a still smaller portion only can be referred to in this paper. In practically all of the species listed it was possible to breed the species and verify previous work. Additional species from other waters were also bred, some in all of their stages, some in part only,—wherever opportunity offered and time would permit. An idea of the richness of the Chironomid fauna may be gained from the fact that I have taken at least 35 species from the lake, and that each of the surrounding waters contains several other species. The contents of fish stomachs from various localities have apprised me of further unknown stages.

Ceratopogoninae.

Palpomyia longipennis Loew; Probezzia pallida Malloch; Probezzia glaber Coquillett.

Specimens of these three species were bred in large quantities. All three are common in the lake and appear to show a special preference for Cladophora and other filamentous algae as a habitat.
The larvae of Palpomyia longipennis and Probezzia pallida resemble each other in form, but differ greatly in size; both are white, and have a vibratile method of locomotion,—like that of a rod which is fastened at one end and permitted to vibrate freely at the other. Probezzia glaber is pale green, and extremely attenuated; it swims in regular, worm-like undulations.

For emergence the pupa of P. longipennis climbs up the sides of rocks and rubbish, while the other two species emerge from the water surface. Parallel to this is the ability of the Probezzia species to rest on the surface-film and oviposit through it, while Palpomyia breaks thru the film and must therefore oviposit from solid objects.

These larvae have an interesting method of letisimulation. When grasped while in the water they straighten out and become rigid; this is one of the few cases where aquatic insects feign death in their normal environment. Since their color resembles that of the filamentous algae among which they live, the larvae may be said to be doubly protected. In spite of this, they are quite frequent in fish stomachs. They are quite resistant to digestion, specimens having been taken alive from perch stomachs several hours after capture of the fish.

The Ceratopogoninae are among the free-swimming insect larvae although not pelagic. They do not build tubes or shelters such as the Tanyptinae and Chironominae. Their range appears to be limited by the oxygen distribution of the lake; in winter, like the fish, they go to deeper waters, but with the advance of the thermocline they migrate toward-shore. For respiration they ever retractile gills from the anal opening.

They pupate in July, and during June and early July form the chief Chironomid contingent of the littoral catches. Three other species of Ceratopogoninae have been found in Lake Mendota, but I have been unable to breed them; they are not abundant. According to the sex, the larvae show a dimorphism in size, the female larvae being uniformly larger than the males.

Tanyptinae.

The habitus of the Tanyptinae is more Chironomid-like. The larvae resemble those of the true Chironomids, while the pupae bear a strong resemblance to the Corethra type. In many
forms the head of the larva is elongate, and the antennae are frequently retractile. The following forms have been found in the lake.

Protenthes choreus Meigen.

The distribution of this species is practically identical with that of Chironomus tentans in the lake. It is fairly abundant in the bottom mud and forms an important item of fish food.

Tanypus decoloratus Malloch; Tanypus monilis Linne; Tanypus carneus Fabricius.

These three species occur in the lake, but only T. monilis in appreciable numbers. All three are littoral forms. The larva of T. monilis is remarkable for its retrogressive locomotion, resembling that of a crayfish. None of the species build true cases, but live free or in concretions which are loosely put together.

Chironominae.

This subfamily comprises the true "blood-worms," although this designation is somewhat of a misnomer. Most of the species are able to spin tubes, using plant fibers or sand granules.

Chironomus abbreviatus Kieffer.

This is species number 82 of Johanssen (1905). The species is littoral and sublittoral in its distribution.

Chironomus tentans Fabricius.

This is the largest of all Chironomid species that occur in the lake. Its distribution is practically confined to the bottom area of the lake, although it occurs in great numbers in the muddy areas behind the bars of University and Catfish bays. It is stenoeaphic in mud, hence limophilous. Larvae have been taken from the lake, ponds, creeks, in fact wherever a mud bottom occurs.

The larvae are extensively parasitized by Gordius, at times by as many as three individuals, although usually only a single parasite is present in the larva or pupa. The species transforms during late April and May and late September and October. There is a peculiar parallelism between transformation and the amount of available oxygen, transformation de-
creasing in early summer as the oxygen goes out, and increasing with the increase of the oxygen content of the hypolimnion in early fall.

A dimorphism in size of the larvae, which was at first supposed to indicate a two-year cycle, was later found to be a sexual difference, the larger larvae being females. Female larvae may attain a size of 5 cm., while males rarely exceed 3.5 cm.

This species forms a very conspicuous item of fish food, especially during the winter.

In connection with this species it seems appropriate to test out Miall’s dictum, “that only such Chironomus larvae as live at the bottom and burrow in the mud possess the red hemoglobin. Those which live at or near the surface have colorless blood.” As far as Chironomus tentans is concerned, the red color is characteristic of the larva no matter where it occurs,—in the bottom of the lake, pond, or horse-trough. Conversely, Protenthes chorera which it is associated in the lake, shows only occasionally a slight suffusion of pink, no matter where it may be found; usually the larvae are of a cream or pale green color, with the fat body showing through the epidermis.

In general, I have found so much variation as to the color of the larvae of the various species in identical surroundings that it is obvious that no fixed rule can be laid down as to coloration. There is no intensification of color parallel with the increase in depth, such as Miall suggested. I have taken red specimens of C. lobiferus, digitatus, fulviventris, etc., from depths varying from 0.2 to 6 m.; while pale specimens of the same species were found at precisely the same depths (see discussion of color varieties under C. lobiferus). In fact, at any given spot on the shore one may find specimens of these species colored a brilliant scarlet, while at a depth of one meter or five meters the same species may be pale, or vice versa.

What I wish to emphasize is the absolute lack of any correlation of intensification of color and of oxygen supply. Needham (1903) called attention to the fact that the young of the red species when hatched from the egg are pale, never red.

Chironomus digitatus Malloch; Chironomus fulviventris Johannsen; Chironomus lobiferus Say.

These three species are littoral forms of wide distribution. C. digitatus is of special interest in that it is sand loving form
(ammophilous), and is common on sand beaches and in the finer gravel. C. fulviventris is somewhat similar in its predilections, but more isolated in its distribution. C. lobiferus is quite regular in its distribution, and is a ubiquist as regards its habitats,—varying from sand, gravel, and rocks, to plants and filamentous algae.

The larvae of the three species are trimorphic as to color. The larva of C. lobiferus may be a bright red, a very pale green, or reddish transfused with green. In C. fulviventris bright red larvae occur, others that are pale cream, olive green, or red with a transfusion of green. Even more marked are the distinctions of C. digitatus in which a scarlet larva is commonest, white or pale green next frequent, and a rarer form is colored a dark red with green parenthetical dorsal markings on each segment. I have tried to discover a racial character in these markings, but the breedings of all three types for C. digitatus and C. lobiferus proved their identity.

A peculiar feature is that in C. digitatus and lobiferus the variations occur side by side, so that one may find red and green forms of either species in the same locality. In C. fulviventris I have found the red forms only in the short rapids of Merrill Spring and in the sandy parts of the lake shore; the pale cream form seems to be confined to the outlet of University Brook into University Bay.

The food of these three species has been examined in several hundred specimens. Diatoms, Protozoa, algal spores, and in several instances smaller Chironomid larvae, were found in the stomachs. On two occasions larvae of Hydrachnida were found in C. lobiferus; these probably belonged to Limnesia histrionica, for those of other species are less common and generally protected by armor or secretions. In turn, the larvae are eaten by fish; C. digitatus notably forms the food of shore fishes, especially of the darters, and Cottus. I have seen smaller larvae frequently attacked by Hydrachnids, while the crustacean Hyalella azteca at times has the annoying habit of nibbling at the respiratory tufts of the pupae (field and laboratory observation).

Chironomus plumosus Linne; Chironomus tentans var.

Both species are confined to the littoral area. C. plumosus in Lake Mendota is restricted to a few places on the north
shore, while C. tentans var. is more general in its distribution. It is of interest that the Giant Midge, C. plumosus, so common in the muddy depths of Lake Winnebago, should be confined purely to a few rocky and gravelly areas in Lake Mendota,—one of the peculiar contradictions so frequently met with in limnological studies. C. tentans seems to begin its distribution in the lake where C. tentans var. leaves off. That is, it is confined to sandy areas and gravel while C. tentans seems to be restricted to mud bottoms.

Chironomus viridis Macquard; Chironomus pallidus Coquillet.

The former species and its congener, C. palliatus, the latter the rarer of the two, were first called to my attention by their appearance in fish food. C. viridis emerges early in the year and was not met with in 1914. In 1915 I did not find it till August when it was quite common on plants in depths of one or more meters.

Chironomus modestus Say; Chironomus flavus Johannsen.

The two species are not abundant. C. modestus is ammophilous, while C. flavus frequents plants.

Tanytarsus exiguus Johannsen.

This is the only species of Tanytarsus found in more than one locality in the lake. In each case I found it at depths exceeding 5 meters, where the larvae would be fairly common.

It is characteristic of the species of the genus Tanytarsus that they are more or less localized in their distribution. I have taken T. agraylioides (== obediens Joh.?), lauterborni, muticus, bausei?, dives, etc., in the lake, but always confined to a single locality, so that they cannot be considered in a quantitative study. The habits of the larvae of this genus are specially interesting; many of them build cases which are remarkable for their form and variety.

Cricotopus trifasciatus Panzer; Cricotopus exilis Johannsen.

Of the two species C. trifasciatus is especially abundant. It is a shore form, nearly ubiquitous in its habitats, and is much eaten by fishes. It is a common species in creeks and swamps.
K. Order Coleoptera. (Table 5, p. 475).

Adaptation to an aquatic mode of life has reached its greatest differentiation among the aquatic Coleoptera. Table 4 aims to show the progressive adaptations for the families listed. It is difficult to class the Coleoptera into surface-breathers and water-breathers. For on the one hand some of the adult Coleoptera are able to effect a gaseous interchange while submerged; on the other hand some of the water-breathing larvae have stigmata which they are able to use at the surface, although in the latter case primarily in the prepupal stage. In effect, therefore, the adults mentioned (some Dytiscidae, etc.) are true water-breathers, yet in a manner different from that of the larvae. (See p. 473).

Again, many regular surface-breathers are intermittently submerged, for a long period during the winter, and are able to effect a partial oxygenation during their submersion (Wesenberg-Lund, Ege, etc.). This complicates the situation and allowance must be made in a table. The adaptations to the aquatic environment are so manifold among both larvae and adults, that it seems as if each species has developed individual means and methods of aquatic respiration. Among the list of families noted as breathing "submerged air" there is hardly one which follows precisely the same method as any of the others.

Now, with all their manifold adaptations to an aquatic life, aquatic beetles, except for a few species, are scarce in the lake complex. Surface-breathing larvae are entirely absent from the lake; water-breathing larvae, while common to a certain extent, are limited through their adults, which usually are surface-breathers. Beetles, in one or all stages, are surface-breathers; and it is through the surface-breathing habit that the molar agents exert their dominating influence on the lake complex.

The Hygrobiidae, Dysticidae, Hydrophilidae (except Berosus), Donacinae, and Gyrrinidae, the latter despite the water-breathing larvae, are practically absent form the lake community. The typical lake Coleoptera are the Haliplidae in the vegetation zone, and the Dryopidae in the rocky and gravelly areas, while several species of adult Dytiscidae are locally abundant.
Family Dytiscidae.

In the earlier part of summer, late May to the middle of July, adults of Biddessus flavicollis Leconte, Coptotomus interrogatus Fabricius, Hydroporus undulatus Say, and Laccophilus maculosus Say, are not at all uncommon in the lake. Individuals of Agabus and Colymbetes may occur, but rarely. Since adjoining ponds, creeks, swamps, and basins are on the whole copiously provided with larvae of Laccophilus, Acilius, Cybister, Agabus, etc., although entirely absent from the lake, it is probable that such adults as are found in the lake have migrated into it and have not bred there. In specially favored spots where shelter permits some emergent plants to gain a foothold one may find some Dytiscid larvae.

The difference between the lake and other aquatic communities is very marked in late summer, when sheltered water such as the lagoons in the parks and the several ponds and creeks about the lakes teem with young Dytiscid larvae of several species, while such larvae are conspicuously absent from the lake. As a food factor the Dytiscidae are therefore negligible so far as the lake is concerned; but this does not apply to creeks and rivers.

Family Hydrophilidae.

Only a single species, Berosus sp. (probably striatus Say), is represented in the lake, and this species is quite rare. The larva occurs in sandy depths up to six meters. I was able to breed the species and discovered that the pupa is aquatic and a water-breather like the larva; but the emerged adult escaped before I had seen it. In the fast current just below the Yahara spillway, the species seems to thrive; at least, fish taken at the spot frequently contained larvae of Berosus.

Family Gyrinidae.

The larvae of the Gyrinidae, like Berosus, seem to find conditions optimal in the current below the Yahara spillway. In that stream, too, the adults are exceedingly abundant, occurring in enormous swarms composed of many thousands of individuals. Although an adult Gyrinid is occasional in the lake, no larvae have as yet been found.
In fish taken from the Yahara Canal Gyринus larvae are rare, while adults, in spite of their presumably noxious emanations, are more frequent.

Family Haliplidae.

Haliplus ruficollis DeGeer; Peltodytes edentulus LeConte; Peltodytes duodecimpunctatus Say.

These three species are common in the lake, both in larval and adult form (except the larva of the last, which I have not found). The larvae are water-breathers, while the adults can remain submerged for considerable periods. The larvae are microphagous on filamentous algae and are not restricted in their distribution save by that of their sheltering plants. In creeks, basins, and elsewhere the larvae may be quite abundant. Among the Cladophora and other algae just below the Yahara spillway, Haliplus ruficollis larvae are especially abundant and form a favorite item in the food of fish.

Family Dryopidae.

There is no other insect family with aquatic representatives that offers as many points of interest as the Dryopidae. Adaptation to an aquatic life has reached its highest development among them, both in the larvae and in the adults. As will be seen from table 4 there are two groups according to degree of aquaticiveness, both of which have in common holaquatic larvae and terrestrial pupae, but differ in the aquatic habits of the adults. (See p. 473).

Of the five genera given, Limnius is not represented in the American fauna, its place being taken by Stenelmis. Psephenus lecontei and Stenelmis crenatus were bred in large quantities, while a third species (a larva resembling that of Elmis somewhat and which I believe is Dryops lithophilus) did not reach pupation in the various cultures.

Stenelmis crenatus Say; Elmis vittatus Mels.

The larvae of Stenelmis crenatus resemble those of the European Limnius troglodytes. In color they range from a light brown to a deep black, and it was thought at first that two species were represented in the larval material. Extensive breeding proved the identity with Stenelmis crenatus.
The larvae are water-breathers, extruding an anal tracheal tuft for the purpose. In general they live in tiny burrows made in gravel or in sand between stones, but they may frequently be found crawling freely over rocks in depths from the shore-line to 6 meters. Besides crawling, the larvae have a quite unusual method of swimming; this is retro-progressive (i.e., moving backward), but in an inverted position, the recurved caudal segments flapping violently. For pupation the larvae leave the water and in the moist sand make a peashaped burrow in which they transform. Pupation begins in the middle of August and lasts for about 10 days. The adults immediately reenter the water, where they copulate and deposit their eggs on rocks.

In a sense, the adults are true water-breathers. For they remain submerged continually, rarely, if ever, coming to the surface for the replenishment of their oxygen supply. Brocher (1912) in a very interesting paper has shown that Stenelmis adults exchange oxygen very readily through the abdominal plastron of air.

In Lake Mendota Stenelmis adults occur chiefly in plant marl, gravel, and sandy bottoms in depths up to 10 meters.

I have not found a single larva nor adult in any of the eight hundred or more shore fishes examined.

**Dryops lithophilus Germar; Parnid sp. larva.**

I do not know the larva of Dryops lithophilus, but suspect that it is the Elmis-like, or "trilobite" larva found fairly abundantly on rocky shores, and here referred to as Parnid sp. I have failed to breed this larva hitherto although I assembled them in considerable quantities. The optimal habitat of the larva is between one-half and one meter depth on rocky shores, apparently where wave action is quite strong. It also occurs among the rocks of the Yahara spillway.

Dryops lithophilus frequents the moist places of the shore and may occasionally descend into the water.

**Psephenus lecontei Leconte.**

The characteristic larva of this species is the famous "waterpenny" or "stone-penny" of the rocky shore. The larvae occur in depths of 0–6 m. and seem to be restricted to a rocky and stony habitat. They are always found on the under-side
of stones. For respiration they have branched abdominal gills, which, however, unlike the trilobitic Parnid sp. just mentioned, are not retractile (the other also possesses a retractile anal tuft of tracheae).

In late July the larvae emerge in enormous numbers from the lake and pupate in the moist soil under the rocks near the water margin. In 1915 pupation took place immediately before a rise of 17-20 cm. in the lake level, which resulted in the death of great numbers of the pupae, since the latter, like the adults, are terrestrial. If it were not for the fact that the year-old larvae remained in the lake—the species has a biennial cycle—the lake population of the form would be considerably diminished.

The adults are terrestrial. Copulation takes place on land. Oviposition may take place at the water's edge, on stones in the water, or the female may descend some distance into the water to lay her eggs.

Locally the larvae may be exceedingly abundant. On one occasion, in July, 1915, I found over 800 specimens in an area of one square meter at Farwell’s Point. Yet curious to say, I have no records of their being eaten by fish. Whether this is due to their excellent protective adaptation or to some other factor remains to be seen; I have, however, on several occasions, found small leeches attached to the underside of the larvae.

A problem of distribution was revealed during some dredgings made on the shallow reefs in the eastern portion of the lake. Each of the reefs is over half a mile from the nearest shore, hence it is unlikely that larvae might migrate to them. But the dredge contents showed that the larvae were quite abundant on one of the reefs. Since the reefs are covered with at least 3 meters of water at their highest points, the assumption of drift as an explanation for the distributional "island" is out of the range of probability. How the larvae got there, how they pupate (pupae being terrestrial), etc., remains a riddle for the present.

27—S. A. L.
PART III. ECOLOGY OF THE LAKE.

I. ECOLOGICAL ZONATION.

The general ecological zonation has been discussed in part I of this paper. But for the sake of comparison the following summary of the vertical and horizontal sections of the lake is offered:

<table>
<thead>
<tr>
<th>Area</th>
<th>Vertical Section</th>
<th>Depths</th>
<th>Horizontal Section</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eulittoral (Euphytal)</td>
<td>1. Shore line (incl. bars)</td>
<td>0-1 m.</td>
<td>Rocky—barren</td>
</tr>
<tr>
<td></td>
<td>—Sheals</td>
<td>1-1 m.</td>
<td>Stony—barren</td>
</tr>
<tr>
<td></td>
<td>2. Surf line (Rachlon)</td>
<td>1 m.</td>
<td>Sandy—barren</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Sandy—sparse veg.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Stony—barren</td>
</tr>
<tr>
<td>Littoral (Phythal)</td>
<td></td>
<td>1-5</td>
<td>Potamogeton, Najas, Vallisneria</td>
</tr>
<tr>
<td></td>
<td>3. Vegetation Zone</td>
<td>4.6 m.</td>
<td>Chara, Myriophyllum, Ceratophyllum, Potamogeton.</td>
</tr>
<tr>
<td></td>
<td>—Upright</td>
<td></td>
<td>Plant, marl, sand, stones</td>
</tr>
<tr>
<td></td>
<td>—Recumbent</td>
<td></td>
<td>Rock, with encrustation</td>
</tr>
<tr>
<td></td>
<td>—Barrens</td>
<td>Patches</td>
<td>Shell, sand, mud-barren</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mud, with admixture of deflux, (shell, ooze, etc. organic and coprogenic sediment)</td>
</tr>
<tr>
<td>Sublittoral (Daphythal)</td>
<td>—Rock Reefs</td>
<td>3-8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4. Shell Zone</td>
<td>6-8</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>7-25</td>
<td></td>
</tr>
<tr>
<td>Aphyal (Dysphytal)</td>
<td>5. Aphyal Zone</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Practically the entire macrofauna of the lake, except the fish, is bound to one or other substratum; fish, too, show certain habitat preferences conditioned through food, or through reproduction, which delimit their distribution. Since the physical agents operate on the substrata, it is through the latter that we must study the ecological habitat.

In a study such as the present it becomes necessary to make sweeping statements without considering possible, and more probable, exceptions in the way of habitat preferences and associations. These preferences are deduced largely from the quantitative averages. While a quantitative method tends toward exactness, it carries with it an element of uncertainty in that it necessarily restricts itself to the exploration of a very definitely circumscribed area; hence qualitative catches have been used to supplement the findings.
DEPTH DISTRIBUTION.

Table 7 (p. 477) indicates the distribution of the species of the various groups in the order of their depth occurrence. The optimum depth has been noted in italics. Distinction should be made for species whose depth distribution extends below 7 meters. In many of these it means that they extend over the entire lake bottom beyond the depth of 7 meters; for others the distribution may be limited according to certain bottom conditions, and, more especially, by the gas content of the hypolimnion.

ECOLOGICAL DISTRIBUTION.

In its larger aspects the lake is divided into two areas, the littoral, and the aphytal area. The littoral area is assumed to extend from the shore margin to the lower limit of photosynthesis,—hence of plant growth. Below this is a region of comparative quiet, of relatively mild changes, of no plant growth—the aphytal region.

The littoral area permits of two subdivisions,—a eulittoral region, reaching from the shore margin to the lower limit of photosynthesis,—in Lake Mendota nearly synonymous with the limit of wave action; and a sublittoral region, a region of heaping of refuse and drift, lying next to the vegetation area, and synonymous in Lake Mendota with the lower limit of wave action.

In the following the ecological habitats of these areas are taken up in both their vertical and horizontal aspects. The littoral area in vertical section can be regarded as composed of (1) The shore line, (2) the breaker line, and (3) the plant zone,—comprising the eulittoral area; and (4) the shell zone,—comprising the sublittoral area.

The Eulittoral (Euphytal) Area.

1. The Shore Line.

The physical characteristics of the shore line vary somewhat in the different parts of the lake. In this paper the shore line is distinguished as that narrow strip of lake border which owing to the exposure to molar agents has a “clean-washed” appear-
ance. This strip is rarely more than nine meters wide, and in Lake Mendota is easily recognized, even where separated from the breaker line by extensive shoals.

Physiologically, it is a region of great molar activity, and, with its more or less shifting bottom, presents certain definite ecological aspects. The animal (or plant) that desires to live there must be able to meet (a) great molar action of wave and undertow, (b) a partly shifting bottom as a result of molar action, (c) extremes of temperature, and motion, (d) prolonged periods of hunger,—in general, sudden changes to which other parts of the lake, except the breaker line, are not subject.

In horizontal section, the shore line may be classified into rocky shores, stony or gravel shores, and sandy shores. The lake shallows will be treated as part of the vegetation area. Each of the shores is more or less distinct in its conditions and associations, and will be treated separately.

A. The Rocky Shores.—In Lake Mendota these occupy about a fifth of the lake circumference. The physical aspect is that of large boulders, shattered rocks,—in general an appearance of roughness. The width of the rock shore is usually from 8 to 10 meters, its depth often being continuous to 6 or more meters; for the purposes of ecological association the depth to 1 meter alone will be considered. The slope of the rock shore is usually considerable, and the surf line is practically always continuous with it, generally marking the lower edge.

In its physiological aspects the rock shore indicates the greatest exposure to molar agents found in the lake. The heavy waves, the surf, the strong undertow and its accompanying drift, the swift changes from quiet to turmoil, present conditions which relatively few animals are equipped to meet.

The only plant found is Cladophora, a filamentous alga, the plumes of which are conspicuous at all times of the year. An elaborate system of clinging rhizoids, and great pliancy of the plumes enable it to meet the conditions of wave action. Since it needs the sunlight for food manufacture it is never found on the underside of rocks.

The animals in turn, except the visitors, are practically confined to the underside of rocks (see table 8, p. 471). They must, therefore, not only meet the action of the general molar agents, but must protect themselves from the undertow and the shifting rubble. To meet wave action, the prime response is to
offer as little resistance as possible. This means that the animals
have a flattened body, or that they enclose themselves in flat
structures, or that they apply appression methods. In addition,
they must be supplied with strong clinging devices.

The mayfly nymphs Heptagenia interpunctata, Eddyurus
maculipennis, and Siphlurus alternatus, and the Odonate nymph
Argia putrida offer good examples of depressed body structure.
Depression in a secondary sense is attained by Psephenus
lecontei and a Parnid larva in that the segments of the body
are supplied with lateral extensions, which are very efficient in
permitting the animals to appress themselves. Compression
laterally is again the means by which the Amphipods Hyalella
azteca, Dikerogammarus fasciatus, and Gammarus limnaeus
adapt themselves; however, these belong to the category of mi-
grants or visitors.

Caddis-flies form a characteristic element of the petrophilous
fauna, but their submission to conditions is shown more in the
structure of their protective cases than in their own morphology.
Thus, the flat, Ancyclus-like case of Leptocerus ancyclus forms
one of the finest instances of shore adaptation. Leptocerus
dilutus usually seeks some tiny depression in a rock in which it
anchors its curved, hooded cases. Similar in character to Lep-
tocerus ancyclus are the flat leech cocoons which are numerous
under the shore rocks.

A number of petrophilous species meet the factors by other
types of appressed structures. Thus the tubes of Chironomids,
especially of Chironomus digitatus and C. lobiferus, are quite
common on the underside of rocks, where they are invariably
built of sand granules and firmly anchored by means of some
secretion. A more marked instance is that of Polycentropus sp.
which weaves a funnel-like tube and over this spreads a broad
sheet of webbing. Appression, too, is the growth method of the
stone sponges and bryozoans. All of these forms are equipped
with strong clinging devices, in the way of claws, suckers, cement-
ing substances, and minor adaptations.

During certain months of the year the fauna among the
Cladophora plumes is quite abundant. It consists of the cadd-
disworms Hydroptila sp., Ithytrichia clavata, and Agraylea
multipunctata, and occasionally an Oxyethira sp., which feed
on Cladophora. Chironomus lobiferus may frequently be found
in cases built of algal filaments. Still more marked is the pres-
ence of free-swimming Ceratopogoninae larvae of Palpomyia longipennis, and especially of Probezzia glaber and P. pallida. Yet except for Ithytrichia clavata none of these forms is truly petrophilous; they are to be regarded as primarily algophil, since they are found on filamentous algae in the lake wherever these occur. In the shore area they may occur on the under as well as the upper side of rocks and stones.

Some burrowers are frequently found on the rocky shores. These are Stenelmis crenatus larvae and the older larvae of Ephemerella varia. Here also may be found Cambarus propinquus, which wedges itself under stones and heaps gravel about itself. All three are more common on gravel shores.

Among vertebrates Cottus and Etheostoma flabellare are characteristic of the rock beaches. These and the Crustaceans Hyalella, Dikerogammarus, and Gammarus can be called migrants or visitors, for most of them migrate in unfavorable weather. Other visitors are the Hemiptera and adult Coleoptera. These very readily climb the rocks and leave the water during unpropitious conditions.

A secondary zonation is indicated. While most of the species on the list are primarily petrophilous, they seem to prefer certain regions of the shore. Thus, at the immediate shore margin one may invariably find hundreds of leeches that have burrowed under the rocks at a depth of about 10–15 cm. below the surface. Most of the petrophilous fauna prefers the middle ground between the shore margin and the lower edge which marks the breaker line. This is illustrated in the case of Psephenus leontei and its relative, Parnid sp.; Psephenus prefers the upper middle ground, while the Parnid may be found more abundantly toward the breaker line.

Owing to the peculiar conditions of this shore area, and especially because of the lack of vegetation except Cladophora, the food conditions are necessarily somewhat uniform. Alimentation is possible only during relatively short periods. Since even then many of the forms do not wish to leave their shelter under the rocks, they must feed on the micro-organisms found in their immediate vicinity. This means a mixed diet. Several species, however, such as Polycephasmus sp., Hyalella, and the Ephemerid larvae, quickly mount to the upper side and feed on the Cladophora or on the very abundant microfauna and flora which breeds among the algal filaments.
Before passing on, note must be made as to the extent of the fauna of the rock shore. Vertically, the fauna extends downward below the breaker line, often for several meters. Thus, Psphemus lecontei, Ephemeraria varia, Heptagenia, Ecdyurus, Stenelmis crenatus, Chironomus digitatus, C. lobiferus, etc., are found not only occasionally, but in fact quite frequently on rock bottoms at depths exceeding two, three, and even six meters. This is an important phenomenon. These same species are also found under the rocks of milder rapids, in creeks, rivers, and falls. If we note in addition that several of the species have been found on the rocky reefs in the middle of the lake, it must be evident at once, that current can hardly be considered the primary factor in the distribution of these forms; that on the contrary it is probably the condition of the substratum,—namely the rock bottom,—which is the determining factor, and that current and the ability to respire under difficult conditions are secondary factors.

B. The Cobble (Gravel) Shores.—Cobble shores occupy over one half of the shore lines of Lake Mendota (inclusive of bars). Their physical character is that of stones of varying size intermixed with gravel and coarse sand, all worn to smoothness by molar agents. Hence they are analogous in their conditions to those offered by the rock shores, and the difference is a relative one, expressed mainly by the facts that there are fewer and smaller and also smoother rocks, that there is an abundance of pebbles and of coarse sand,—in general, that there are fewer clinging surfaces.

Physiologically, the same conditions hold true as for the rocky shores. Yet the finer composition of the substratum permits a comparably greater activity of the molar agents upon it; in heavy weather there is a steady oscillation of sand and gravel carried by waves and undertow. And this fluctuation of the rubble may be said to accentuate the need of protective shelter for this association.

Thus, soft-bodied animals,—such as Planarians, various Oligochaeta, Ceratopogonine larvae, the larvae of may-flies,—and adult bettles are much rarer in the stony association than among the rocks. However, it is necessary to distinguish between absence due to molar agents and absence due to food supply. The alga Cladophora, so conspicuous on the rocky shores, is found in more isolated patches; like soft-bodied Planaria, it cannot
withstanding the grinding wear of the rubble. But since it is the sole food supply of the phytophagous petrophilus it is obvious that these will not be found where no suitable food supply exists. Thus the caddis-worms of the rocky shores are for the greater part absent, or at least much rarer among cobble-stones,—due primarily to the absence of their food-plant.

In a measure, this absence of caddis-worms may be due also to the lack of sufficient protection; for while their cases are built strongly enough to withstand the impact of waves and spray, most of them would fare only indifferently well in the gravelly areas. As a matter of fact, the majority are absent, except Leptocerus ancylus, an occasional Leptocerus dilutus, and the Hydroptilids Agraylea, Ithytrichia, and Hydroptila, which live on Cladophora. But all of these are proportionately much less frequent, even among their food-plants, than in the rocky areas. The scantier representation of the may-flies,—that is, of Heptagenia, Eddyurus, Baetisca, and Caenis, is probably due directly to the undertow and its drift,—for these larvae have no further shelter beyond their chitinous covering. Hyalella, and the irregular component of beetles and Hemiptera are all more scattered.

The characteristic of the cobble and gravel fauna is, therefore, that its representation of clinging forms is much smaller than that of the rocky areas. On the other hand, the number of burrowing species is much greater. In fact, burrowers may be said to dominate,—for the moving sands and gravel are much more favorable to their existence in tubes and burrows than to the exposed clingers. Thus, Sparganophilus eiseni, the "blue earthworm," is practically confined to the pebbly shores, while burrowers and tube-builders like Stenelmis, Gomphus fraternus, Ephemera varia, Argia putrida, Chironomus digitatus, C. lobiferus, C. modestus, C. plumosus, C. tentans, Cambarus propinquus, Erpobdella punctata, and Nephelopsis obscura find the gravel shores apparently optimal,—for nearly all of these are much more frequent here than anywhere else in the lake. It is especially true of Chironomus digitatus, C. tentans var?, and C. plumosus, and of Stenelmis crenatus larvae, Sparganophilus eiseni, Cambarus propinquus, and Ephemera varia. Erpobdella punctata and Nephelopsis obscura, as on the rocky shore, here also burrow at the shore margin, some 10–15 cm. below the surface, under flat stones.
C. Sandy Shores.—The transition from gravel shores to sandy shores is nearly imperceptible and is marked primarily by the gradual diminution in the number of larger pebbles and rocks. The absence of the latter means that no clinging surfaces whatsoever are left,—hence also a total absence of any larger plants. Secondly, the sand as a substratum is still more influenced by molar agents, and forms an exceedingly insecure bottom,—in fact, it lacks permanence entirely.

Hence the fauna must cope with, (a) a bottom which is only transient, (b) the absence of clinging surfaces, (c) a bottom which shifts with the slightest disturbance, and (d) a resultant absence of plant food.

Yet it is surprising that even here some species manage to maintain themselves. Thus, I have found Sparganophilus eiseni and a Lumbricusulid burrowing in the sand; Chironomus digitatus, one of our commonest forms, appears to have a predilection for sandy and gravelly bottoms, and builds its tubes copiously along the sandy shores; C. modestus, C. tentans var.?, and C. fulviventris imitate C. digitatus in this respect. Hyalella azteca is quite frequent as a visitor; and the Johnny Darter, Boleosoma nigrum (Rafinesque), patrols the shore quite commonly in search of food; Chironomus digitatus is often the sole element in this food.

D. The Sandy Shoals.—Physiographically, they lie between the breaker line and the shore proper, and are therefore about a meter or less in depth. Their extent may be considerable, in places stretching out nearly 300 meters from the shore. Physically, they are composed largely of fine sand, with a very scanty floral growth of Vallisneria, Chara, Najas, and Potamogeton. Physiologically, they are less exposed to molar agents, since the waves lose their main impact at the breaker line; as a result there is a fair growth of vegetation. Yet even with the loss of their main force, the waves are strong enough to prevent the growth of emergent plants, except in much secluded spots; and in these the waves promptly begin to erect a barrier in the form of a bar, thereby cutting off the foreign complex.

Because of the presence of plants, the fauna of the shoals is in many respects like that of the vegetation zone proper beyond the breaker line. No component characteristic of the shores is found in these shoals, except the Chironomid species
before mentioned. But when we assume that the Chironomid species in question are ammophilous and that by settling on the sandy shore they merely expanded the horizon of their habitat, the apparent discrepancy will be understood.

E. The Bars.—Physiographically bars are continuous with the shore. In all respects the various bars of the lake show the same physical and physiological characteristics as the stony and sandy shores; to all intents they are precisely like these in their faunal makeup. Hence they will not be treated as separate ecological entities, but are to be included in the stony shore association.

2. The Rachion (breaker line).

Physiographically, the rachion is frequently a separate entity, while at times it is a unit with the shore line. This is dependent primarily on the slope of the shore. On steeper shores the breaker line is continuous with the shore line, rocky, stony, or sandy, as the case may be. In shallower areas it is detached from the shore, often several hundred meters from the latter; here, too, it may be frequently divided into two lines,—an "outer" and an "inner bar." Physically, its make-up again depends on its location. If continuous with the shore line proper, it can be recognized by its makeup of rocks, gravel, and sand,—the rocks in the middle, while the smaller ingredients will be piled on either side. In places where a rocky shore extends downward a number of meters, the breaker line is usually recognized by the absence of algal growth at the line and by the gravel heaped on either side. Where the breaker line is detached from the shore, it is easily marked as a stony area some 5–8 meters in width running parallel to the shore. Its middle section is invariably composed of larger stones, while gravel and sand lie on either side. In the larger shallows it is followed some meters closer to the shore by a secondary breaker line.

Physiologically, the rachion, or breaker line, marks the place where wave action and undertow cause the greatest turmoil; it is the point of extremes in lake conditions.

Faunistically, it is comparable to stony shores. Its fauna is largely the same, except that Polycentropus and various Chironomid species are extremely abundant in it. We must dis-
tistinguish, however, between the detached rachion and the continued rachion. Since the latter are found on steeper, hence more exposed, shores, the molar agents will be more violent in these places. Hence, by far the larger number of petrophilous forms are absent from the continuous rachion. On the other hand, the great majority of them are present in the detached rachion. Again, Gomphus fraternus, Epicordulia princeps and Molanna uniophila appear to prefer the sand heaps just beyond the attached rachion, while Amnicola limosa foregather directly on the breaker line in all parts of the lake in early summer.

3. The Plant Zone.

In the plant zone we have to deal with a double problem,—that of two substrata. The composition of the bottom is to be considered, and that of the vegetation growing upon it. Since by far the larger portion of the fauna is phytophilous, the treatment may be simplified into that of the plant areas, and of the barrens. The plant area of the lake extends from a depth of about one meter to the limit of photosynthesis, which in Lake Mendota is at about 6 meters. This area is interspersed with small barren patches of sand, or rock, while in other places the accumulation of plant marl forms large beds to the hindrance of the growth of the plant itself.

The plant zone may be conveniently divided into two divisions according to the habitus of the plants,—upright plants, and recumbent plants.

A. Upright Plants.— These are formed largely by Potamogeton amplifolius, Najas, and Vallisneria, and more rarely by Myriophyllum and Ceratophyllum. Their characteristic is that they tend to reach the surface, but except for their floral heads no part is protruded. They extend to a depth of about 5 meters, usually less.

Physiologically, they offer the following: (a) exposure to molar agents near surface, (b) plentiful clinging surfaces, (c) a food supply, (d) shelter. On the other hand, since this flora is not an emergent one, it offers no foothold for surface breathers.

The fauna must therefore be composed of water-breathers in the first place; beyond this clingers, crawlers, and swimmers of all types may find food, shelter and protection. It is among the
upright plants that Hydra luxuriates; Planarians find food on the slimy cover of the plants; millions of small Oligochaeta, none of them good swimmers, lope and loop along the plant stems; mollusks of all species except the Lamellibranchiata, Ancyclus, and Pleurocera, make these plants their favorite feeding-ground; Hyalella and Hydrachnids are exceedingly numerous among the leaves; among may-flies the ubiquitous Caenis diminuta is prominent; among caddisworms Leptocella uwarowii occurs in prodigious numbers, and much less frequently Triapionodes flavescens, and the small Hydroptilids; among Diptera Chironomus viridis, C. palliatus, and Tanypus monilis are especially phytophilous, while Tanypus fasciatus and Cricotopus exilis will be found less commonly; among Coleoptera Haliplid larvae and the adult of Stenelmis manifest a phytophilous tendency.

B. Recumbent Plants.—These are primarily Chara, Myriophyllum, Ceratophyllum, and the various Potomagetons, except amplifolius; they are most abundant between 4 and 6 meters. Physiologically, they present a more intricate shelter and less exposure to molar activities. Faunistically, much the same biota occur here, but with the difference that Limnea stagnalis may be found more abundant, and that among caddisworms Helicopsychae, Molanna, and other bottom forms will venture on the trailing leaves of Myriophyllum. Comparably, the forms of the upright plants are less abundant.

C. Barrens.—Certain deposits of plant marl (i.e. the carbonate encrustation of aquatic plants) are frequently found among plants; these are frequented primarily by Tanytarsus exiguis, Chironomus digitiatus, and by adults of Stenelmis ereatus. Practically all other species of the littoral benthos favor a sandy bottom. This includes the Lamellibranchiata and Pleurocera among mollusks, Helicopsychae and Molanna among Trichoptera; Chironomus tentans var.?, C. digitatus, C. lobiferus, C. abbreviatus, and Tanytarsus exiguis among Diptera, and Stenelmis adults and larvae of Berosus sp. among Coleoptera.

D. The Rock Reefs.—These reefs occur in various portions of the lake, and because of their varying depth are difficult to classify. Primarily, they consist of rocks, slabs, and boulders of considerable size that may come within 3 meters of the surface. In practically all places the reefs are without any admixture of sand or gravel; but their naked surfaces are cov-
ered with a thick encrustation of an alga. This encrustation gives shelter and food to a considerable number of micro-organisms, so that it can offer some attraction to the fauna of the lake. Hyalella azteca, Psephenus lecontei and several ubiquitous Chironomids are the only members of the macrofauna that I have found on the reefs. Psephenus lecontei was the biggest surprise of all. This is a rock shore species, which pupates, copulates, and oviposits on land. How it gets to the reefs, how it reaches the land to pupate is indeed a mystery. It is evident, however, that the condition of the substratum is of decisive influence upon Psephenus, for it occurs on most of the reefs, even at 8 meters depth.

The Dysphytal (Sublittoral) Area.

Physiographically, this area lies immediately below the plant area, and marks the limit of photosynthesis. It is characterized by a heaping of slowly decaying plant and other organic matter. It may lie above, or below, the wave limit. In Lake Mendota it happens to coincide with the limit of wave-action (wave-base) and is specifically characterized by the great amount of decomposed shell,—a shell zone. In some of the clear lakes of the north the euphytal or photosynthetic region may extend considerably below the normal wave-base and the shell zone then lies within the euphytal area.

The Shell Zone.—As just stated, in Lake Mendota the shell zone is physiographically coincident with lower wave action, and is marked physically by the great accumulation of shell, with an admixture of mud and sand. The heavier particles carried by the water have been deposited during their transportation from the shore and only the lighter fragments of shell are swept farther downward, where they accumulate by their own weight. Beyond this point only mud is carried.

The shell zone is also marked, in Lake Mendota, by the organic offal from the plant area above. Many of the plants, though uprooted, will be able to maintain themselves for a while, but will finally succumb to the lack of sufficient continued light for photosynthesis.

Hence the following conditions are offered to the fauna: (a) absence of molar agents, (b) absence of clinging surfaces, (c) absence of living plant food, (d) organic waste, i. e., organic
matter swept from the plant zone above, and slowly decaying below, (e) a bottom composed of shell, mud, waste, giving ready shelter, but also permitting easy access to enemies.

The fauna meets these requirements in the manner outlined. By far the larger number of species are tube-builders and burrowers, while the remaining ones are well protected by cases. Molluscs are very common in the shell zone, especially the Gastropoda; Leptocerus sp. frequently attaches its cases to the shells of the larger snails, and is carried about by them. Swimmers are the Hydrachnida, and Corethra frequently. Outside of these the fauna consists largely of the tube-builders: worms, Limnodrilus and Tubifex; Diptera, Chironomus tentans, lobi-
ferus, and Protenthes choreus; the Lamellibranch, Corneoclyclus idahoensis; and of the burrower Sialis infumata. In food habits practically all of these are scavengers, or carnivores; among the latter Sialis and Corethra are dominant.

The Aphytal Area.

This signifies the plantless area. Physiographically, this area merges imperceptibly with the dysphytal area. It is more easily definable on a physiological basis. Its area covers that part of Lake Mendota below the shell zone and extends to the greatest depth of 25 m. Physically, its makeup is of fine mud with an admixture of shell, silt, grit, organic and coprogenic waste, varying in different parts of the lake. This composition of the bottom seems to have considerable influence on the horizontal and vertical distribution of the fauna, as shown by S. Ekman for Lake Vaettern (1915); in Lake Mendota, however, it is not this physical factor which determines the vertical distribution of the aphytal area, but the physiological factor of thermotic stagnation. This stagnation results in the establishment of a region of variable extent for a variable period,—the hypolimnion, a region of low temperature, in which the oxygen content has been used up in the formation of CO₂ and methane by decaying organisms.

The aphytal area therefore offers the following conditions: (a) an absence of O₂ from the bottom waters for several months of the year, and a corresponding increase in CO₂ and CH₄—hence anaerobic conditions; (b) low range of temperature—hence stenothermal; (c) a bottom of mud of varying admixture; (d) food consisting of deflux.
It will be seen that the decisive factor here is respiration. Unless the animal can escape or withstand the periodic anaerobiosis it is obviously barred. Once having adjusted itself to this condition the composition of the bottom will determine its horizontal distribution. Food will be of tertiary importance.

If, bearing this in mind, we examine the macrofauna of the aphytal area we find that adjustment to anaerobiosis is effected by two methods: migration and aestivation. Migration applies to pelagic forms like Corethra and Limnesia histrionica, which swim directly upward to oxygenated water; and to Sialis infumata, which retreats as the hypolimnion progresses outward and upward.

Aestivation, coupled with the storage of oxygen, is the more common adjustment. Species like the Chironomids Chironomus tentans and Protenthes choreus, are able to store oxygen.

Since the aphytal area adjoins the dysphytal area (here the shell zone), the fauna of the two are related. That is, the species of the aphytal area and the shell zone are alike to a certain extent, but there are more species in the latter; for quite a number of these have been unable to adjust themselves to the deoxygenation of the summer months. Although the shell zone marks the lower limit of wave action, this activity is too little to affect the composition in any other way than through its selective heaping of débris.

**DISCUSSION.**

Notwithstanding the fact that the lake taken as a unit is a place of relatively slight and slow changes, it contains within itself a series of well defined habitats, each with its own controlling factors and its own biota. For the lake as a whole molar agents through their influence on respiration are undoubtedly most decisive. But for the species established in the lake certain additional factors must be taken into consideration.

For example, why should certain Chironomid species prefer plants as a substratum, others mud, and still others sand and rocks? Why should certain species, especially of the genus Tanytarsus, be extremely localized in their distribution? Of Tanytarsus I know of four species in the lake, and five or six elsewhere, all of which are found in numbers in a very definite spot and nowhere else. Again, why should certain forms be
so varied in their diet, others so restricted? Why should certain caddisworms be algophagous, while others feed on any plant and will readily eat animal food?

It is evident that the commoner forms have a wide range in more than one respect. Thus, for instance, Chironomus lobiferus is nearly an ubiquist as to distribution, and holophagous as to food. It should then follow logically that the most widely adapted forms are the most plastic; that this plasticity will result in the numerical preponderance of the plastic form.

Table 8 shows that many species are found under widely differing conditions. Yet in every single case one habitat seems to offer the optimal conditions, and it is in this habitat that the species attains its maximum representation. But it is rarely indeed that a plastic species dominates in its optimal habitat. What I mean to emphasize is that plasticity may insure continuation of the species, but that it does not necessarily result in dominance. To illustrate, Chironomus digitatus and C. lobiferus are both plastic forms, the latter more so than the former; yet while both are very common in different areas, neither of the two dominates in any area, and their numerical total for the lake is inferior to that of many species that attain a local dominance. (See p. 480).

Dominance is relative in each group. Twenty Hyalellae per square meter along the shore I would regard as a small representation, while an equal number for Leptocerus aeneylus would mean dominance. Yet Hyalella dominates among the Crustacea of the shore, while Psephenus lecontei dominates among Coleopterous larvae. But no single species dominates among the biota of the shore line. Psychologically, any impression of dominance is linked to bulk,—fifty Heptagenia larvae will look more numerous than a hundred Hyalellae,—so that an estimate can only be relative.

No species dominates the biota of the entire lake. But for the plant zone the caddisworm Leptocella uwarowii comes nearest to complete dominance of any form in the lake, while Sialis infumata is prominent but not truly dominant in the dysphyal area. In the aphytal area, however, we have a curious simultaneous dominance of Corethra, Chironomus tentans, Protenthes choreus, Corneocycallas, and of Limnodrilus and Tubifex. These biota of the aphytal area form a bigger contingent of the lake complex than nearly all other forms taken together. It is
probably by virtue of their resistance to anaerobic conditions that they attain their eminence. But in every instance it is rather the stenoplastic species which may dominate than the euryplastic one.

On the basis of physiological, physical, and biotic aspects it is possible to divide the lake into the various habitats listed. The following summary presents in briefest form the major evidence. The animals can be included in this summary only according to habitus and type, not according to species.

28—S. A. L.
### Ecological Summary of Lake Zonation

<table>
<thead>
<tr>
<th>Area:</th>
<th>Physiography Depth</th>
<th>Characteristics</th>
<th>Biota</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Littoral—Phytal</strong></td>
<td></td>
<td></td>
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<tr>
<td>A. Eulittoral—Euphtal</td>
<td></td>
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</tr>
<tr>
<td>1. Shore Line</td>
<td>0-1 m.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a. Rock</td>
<td>0-1 m.</td>
<td>Varied... Strong molar agents, extremes of temperature, intermittent feeding.</td>
<td>Forms with shelters, clingers, burrowers; visitors=swimmers. Cladophora-plant and clinging. Animals either flattened, or with shelter, or with appressed methods; clingers. Fewer clingers, no crawlers, many burrowers and visitors.</td>
</tr>
<tr>
<td>b. Cobbles (stony)</td>
<td>0-1 m.</td>
<td>Stones, pebbles, sand, smooth aspect... Fluctuating rubble, food-scant—less Cladophora, fewer clinging surfaces.</td>
<td></td>
</tr>
<tr>
<td>c. Sand</td>
<td>0-1 m.</td>
<td>Sand, with pebbles. Shifting bottom, no clinging surfaces.</td>
<td></td>
</tr>
<tr>
<td>2. Rachion (breaker line)</td>
<td>1-1 t</td>
<td>Stones with pebbles. Greatest wave action and undertow, little plant food.</td>
<td></td>
</tr>
<tr>
<td>3. Plant Zone</td>
<td>1-6 m.</td>
<td>Upright plants, Potamogeton, Najas, Vallisneria, Bottom sand... Exposed to molar agents, clinging surfaces, abundant food, shelter.</td>
<td></td>
</tr>
<tr>
<td>a. Upright plants</td>
<td>1-5 m.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b. Recumbent plants</td>
<td>4-6 m.</td>
<td>Plants bent and trailing. Less exposure to molar agents, greatest photosynthesis.</td>
<td></td>
</tr>
<tr>
<td>c. Bottoms</td>
<td>Various</td>
<td>Sand, plant marl, rarely mud. No exposure, food waste and plants</td>
<td></td>
</tr>
<tr>
<td><strong>B. Sublittoral—Dysphytal</strong></td>
<td></td>
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<tr>
<td>4. Shell Zone</td>
<td>6-8 m.</td>
<td>Shell, with sand and mud. Lower limit of wave action, food waste, dying plants.</td>
<td></td>
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<tr>
<td><strong>Aphytal—Plantless</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. Aphytal Zone</td>
<td>7-25</td>
<td>Mud, with deflux... No molar action, slight activities anaerobic for several months, thermoneral.</td>
<td>An aerobes, tube builders, burrowers, swimmers, aestivators.</td>
</tr>
</tbody>
</table>
II. THE SEASONAL CYCLE.

Probably the most characteristic feature of the annual cycle is the brief ascendancy of plant life during the summer months, and the synchronous maxima of many forms of animal life. So closely are these two connected, so interdependent, that the plant ascendancy may be assigned as the direct cause of the faunal ascendancy. The seasonal succession is not continuous, but really composed of a series of maxima.

Vernal Succession—Period of Elimination and Transformation.—After the ice has gone out, a very small number of plants will have survived; most of them are but a few inches in length. Growth is rapid, and by middle June most of them are able to send their floral heads to the water surface. But in the meantime the filamentous algae of the lake, especially Cladophora and various Spirogyra, have increased to a prodigious extent. If molar agents have not been too severe, the great waving plumes of Cladophora will form a miniature wilderness along the shores, while Spirogyra, Anabaena, Hydrodictyon and other algae will cover the plants and the bottom of the vegetation zone with a green film, and also form immense mats of scum in the shallow cut-offs. Among higher plants Castalia, Nymphaea, Lemna, and Myriophyllum, dominate behind the bars; in the lake Myriophyllum, Ceratophyllum, and Potamogeton species, though short, send forth long spiral stems with floral heads protruding above the surface.

This period lasts until the water temperature rises above 16° C., after which Cladophora decays very rapidly and disappears; by the time a temperature of 18° is reached only the younger and more resistant growth will be found.

The animal life of this algal period is characterized chiefly by a series of periodic eliminations rather than by any distinct dominance. In April large series of the less common Chironomid species leave the lake, including Cricotopus exilis, Chironomus modestus, and a varying number of C. tentans and C. plumosus. Early in May the annual shore migration of Sialis larvae takes place; in certain parts of the shore armies composed of many thousands may be observed climbing up some small drain or ravine. Two weeks later the adults may be seen laying their eggs everywhere on branches overhanging the water's edge.
Coincident or slightly before the appearance of the adult Sialis, Chironomus digitatus will emerge, followed shortly afterwards by C. tentans, plumosus, and lobiferus. A little later, about the time the eggs of Sialis hatch,—that is, in early June,—there begins the exodus of mayflies. Usually about the first week of June Ephemerella varia emerges, followed at once by millions of Caenis diminuta, and in quick succession by Ecdyurus and Heptagenia. Before the middle of June their flights are past.

In the lake shallows, that is, in the cut-offs behind the bars, the imagos of Enallagma, Ischnura, Nehalennia, some Libellulidae, and Chrysops are conspicuous. They may be seen flying up and down, mating and ovipositing. The leaves of Castalia especially will show large batches of eggs of the various Zygoptera, Chrysops, and Donaciinae on the upper or under surfaces.

So many species have been eliminated from the lake by this time that the remaining ones attain a temporary dominance. Thus, the encrusting sponges and Bryozoa are conspicuous in the rocky areas, while among Cladophora and Spirogyra millions of the small Hydroptilids and the Ceratopogonine larvae will be found. For a fortnight the migration of young Nematodes, Gordius aquaticus and a pink Nematode, makes them quite conspicuous in all parts of the lake. Of other species Amnicola limosa is eurydaphic at this time, but seems to favor especially the breaker line where it gathers in clusters exceeding a thousand specimens per square meter.

*Summer Succession—Period of Multiplication and Growth.*—With the disappearance of Cladophora there is an intense growth of spermatophytes. Various species of Potamogeton, but especially P. amplifolius, Myriophyllum, Ceratophyllum, Vallisneria, Najas, and Chara luxuriante and with their rise begins the tremendous ascendancy of Trichoptera and small Oligochaeta.

When the temperature of the water reaches about 15°, there begins the long series of wave-like “flights” of Corethra. These occur in pulses about ten days apart, and last throughout the summer until the middle of September. Their climax is reached about the middle of July.

These Corethra flights initiate what may be termed the “summer succession,” in contradistinction to the “vernal succession” which ends with the appearance of the may-fly species
and the first damselflies. Since pupal and adult stages of the various species overlap, and since many of them have a very brief pupal stage, I shall refer to these explicitly.

In late June and early July the Ceratopogonine larvae pupate and after two to four days appear as adults. The case-building caddisworms which have pupated during late May and June leave their cases about the same time and appear as adults, being conspicuous for a few days. In the latter half of the month the Hydroptilid caddisworms emerge after a brief week of pupal life. The larvae of Psephenus lecontei go to shore to pupate and their adults emerge in the early part of August. Simultaneously with their emergence, the pupal life of Stenelmis crenatus is begun, lasting for about ten days. Dikerogammarus for some reason is quite conspicuous at this time, while the young Hyalellae (fertilization takes place in late June) appear to dominate for a brief period.

All of these may in a way be said to prepare for the great climax of late August and early September. The eggs of caddisflies which were laid in early and middle July hatch at once (I exclude those of the Hydroptilids which do not hatch until the following year) and grow in quick stages. It seems little more than a month before the caddisworms have attained their full size. Hence by late August practically all of them are full grown.

Now, this maturity is practically synchronous with the numerical culmination of the small Oligochaeta and the greatest proliferation of plant life. To the student it seems as though the caddisworms and Oligochaeta received a sudden impetus which carried them to a rapid climax. This climax is indeed a remarkable one. Every plant, each leaflet, the bottoms of the plant zone, all will be found covered copiously with caddisworms,—especially with Leptocella uwarowii and Helicopsyche borealis,—and with small Oligochaeta. But while the Trichoptera appear greater in bulk, the small Oligochaeta outnumber them a thousand times, although they seem less in mass by reason of their transparency and their smaller size. So great is this multiplication of the Oligochaeta that they cover the leaves and stems of some plants like an animate scum.

This ascendency is paralleled to a lesser extent in other groups. Hydra proliferates in enormous numbers, but seems to attain its climax somewhat later in the season. Planarians,
so scattered early in the season, are extremely abundant and practically ubiquitous. The same is true of leeches, Hydrachnida, and smaller Bryozoa. Among insects the shoreward migration of the larvae of Ephemera varia is of interest; that is, the younger larvae have lived in the sands of the plant zone during early summer, and the older larvae now migrate to their habitat in the rachion and stony shores. Among Chironomids Chironomus digitatus, lobiferus, fulviventris, viridis, palliatus, and others reach their larval maxima at this period.

*Autumnal Succession—Period of Diminution.*—The ascendancy lasts till early September, when there is a falling-off throughout the lake community. While the falling temperature may effect this to some extent,—for instance, in the case of Corethra,—it is probable that the molar agents in the form of equinoctial storms are the most important factors. Lake circulation is quickened by the storms and the falling temperature, and the return of oxygen to the aphytal area stimulates the anaerobes and adjoining bottom fauna to renewed activity.

Sialis at once migrates downward to the newly accessible feeding-ground. The return of the oxygen stimulates Chironomus tentans and Protenthes choraeus to pupation and there follows an autumnal flight of these species. Some of the Tanypodius species of the dysphytal area are also stimulated to transformation, but they do not form any conspicuous element such as their relatives.

Some of the autumn storms are of great violence and the havoc wrought by them among the plant and animal life of the lake is immense. Potamogeton, Najas, Vallisneria,—practically the entire upright vegetation is broken loose; much of it is cast ashore, portions are set adrift on the lake and later on sink to the bottom.

Much of the faunal life of this vegetation is cast on shore or battered to death in the surf. In November, 1914, after one of these storms, there was a great shore drift in Sunset Bay, between Picnic and Sunset Points. This drift was some 30 meters long, about 2 meters wide and 15 cm. deep, and was composed almost entirely of dead Leptocellae in their cases. A second drift, even greater in extent, lay in the water. According to an estimate, there were at least five million specimens in this drift. And this was only for a very small portion of the lake off Sunset Bay.
The same storms bring about the death, no doubt, of many other aquatic animals. Dead crayfish, Hyalellae, Ephemeroptera larvae of various kinds, and other forms are a common sight along the shores after a vigorous storm, not only in the autumn, but also at other times of the year. But the autumn storms bring about a rapid stripping and cleansing of the entire littoral area, and by late November only a very short young growth is left in the different parts of the lake.

The Winter Period—Period of Torpor, Suppressed Activities. There remains the winter life of the fauna. The removal of the greater part of the flora has destroyed the clinging surfaces for most of the species, and they are obliged to become bottom dwellers for the winter months. Plant growth goes on during the winter, even under the ice, but it is so slight that it cannot be regarded as a direct factor.

In general, the winter period can be regarded as beginning at the time of the greatest density of the water,—at 4° C. This water sinks to the bottom, and hence there is the reversal of the summer condition,—namely, warm water below and cold water above. The lowered temperature inhibits the activities of many species and these may become more or less dormant. As a whole, physiological activities are lowered, and hence there is a corresponding lowering of food requirements.

That there is no complete cessation is evidenced by the activity of fish, plankton Crustacea, Corethra, Ceratopogoninae, and other groups. There is, however, a general diminution or deferment of activities. Once the ice covers the lake, many species become entirely inactive. The amount of light penetrating the ice depends on its quality—whether smooth, rough, or stratified,—and the amount of snow upon it. The problem of continued darkness makes the feeding of animals precarious and, in general, the discriminating feeders become dormant.

For the surface-breathers of the lake shallows, ponds, streams, and other waters, a new era sets in,—the period of dormancy. For a while, indeed, many of the surface-breathers are very active under the ice (Wesenberg-Lund), hunting to and fro in quest of food. Their oxygen is obtained from the bubbles secreted by the plants under the ice. Soon, however, the ice will be too thick and the light for photosynthesis will be insufficient,—hence no more secretion of oxygen,—and the animals will dig into the mud and become dormant for the winter.
This dormancy appears to be a definite seasonal instinct and persists even among the surface-breathers frequenting homiothermal waters which never freeze. But curious to say, while the Gyrini, Dytiscidae, Tipulid larvae, and other surface-breathers occurring in these waters may be evident a little longer than their relatives of the frozen ponds, sooner or later they, too, burrow into the mud or silt of the homiothermal waters and remain so for several months.

For the shore animals winter brings a new problem which is as difficult as any offered by more temperate conditions. This is the problem of ice,—of the freezing of their habitat. Many forms such as some species of caddisworms, may-flies, and leeches, appear to recognize the danger by migrating downward toward the breaker line or even below that point. This migration apparently occurs between 4° and 1° C. But to my surprise I have found that many other species, including Psephenus lecontei, Stenelmis crenatus, Erpobdella punctata, Nephelopsis obscura, Heptagenia, Sparganophilus eiseni, and others, make no attempt at all to escape downward. I have found them close to the shore margin, with less than 2 cm. of water between the ice (then 15 cm. thick) and the bottom; later on I have found them packed for days and weeks in mush ice which had been forced under the ice-sheet proper by heavy winds. The mush ice in the shore area would be practically continuous with the surface ice.

It can therefore be supposed that they die by freezing, or that they can resist the influence of cold, or that their survival is purely accidental. One thing is certain,—and that is, when spring comes the identical shore will have its normal biota, and apparently without numerical impairment. Whether this biota is a "survival," or newly recruited, I have been unable to ascertain with certainty, although I believe that the former is the case. There is always the possibility that the ground temperature is sufficient to keep a thin sheet of water between the ice and the bottom proper, in which case a "zone of safety" would be established; this would explain the survival of the shore dwellers, and some condition like this "zone" seems to be indicated by various examinations made in the winter of 1914–15.

Before the ice goes out in the spring, animals become active again. Ground radiation raises the temperature of the water during late winter, so that it approximates 4° C. at the bottom.
Long before the ice goes out completely, some early insect species become active. In places where the entry of homiothermal spring water keeps an open area in the lake, insect larvae will begin to transform. As a matter of fact, such transformation (pupation) may take place even when the lake is completely covered with ice. For instance, Pearse (1916) captured perch from Lake Wingra in early March, which contained largely Tanytarsus dives, half of them pupae; this was at a time when the lake was completely covered with ice, which did not go out until a week or more afterward. A similar condition exists in ponds and other waters, and some species appear to be able to measure the time so closely that the period of their emergence and the going out of the ice seem to be synchronized to the hour.

To other species the disappearance of the ice means the inception of larval life. There are not many such species in the lake, the Hydroptilid caddisworms being the most prominent. But especially among surface-breathers of the other waters spring means the beginning of active life; while in the lake it means primarily a continuation of larval life for at least the insect biota.

III. FOOD RELATIONS.

A. Reciprocal.—With the varying influence of molar and other agents it is not to be wondered at that the averages of food supply fluctuate from month to month and from year to year. The greatest fluctuation, however, is the seasonal one, and is best expressed in a table of comparative percentages. These percentages can refer to bulk, not to numerical representation. In table 9 I have attempted a bulk calculation for two seasonal periods, and an annual estimate for comparison. The seasons represent the two great floral periods of the lake,—namely the algal period of May-June and the spermatophyte period August-September; or, from an animal standpoint, the elimination period (= transformation) and the multiplication period referred to in the discussion of the seasonal cycle. I have not included the fish in the summary of the macrofauna; too little is known of their numerical representation. (See p. 482).

A comparison of the bulk percentage and the food relations of the various groups shows two important results: (1) The scavengers are the dominant forms of the lake; (2) Trichop-
tera are dominant in the littoral area, hence in the region of plant food. A third point is indicated,—and that is the ready passage from a microphagous diet to any other. Among the scavengers can be listed Annelida, Gastropoda, Corethridae, and Chironomidae; while among the phytophaga the caddisworms have attained a single dominance. It is indeed surprising that of phytophagous aquatic groups only the caddisworms attain a prominent place in the lake complex; and since even caddisworms will readily resort to a sarcophagous method of life, the place of plant food in the lake complex becomes minimized as a primary source of food, while emphasized rather unexpectedly from the viewpoint of waste food.

B. Fish Food.—The greatest element of surprise of the food relations lies in the study of fish food items. These items are not linear in their proportions to the available food supply; I mean to say that the different groups do not form the same percentage of fish food that they form of the lake complex. In the way of food fish will naturally choose first the free-living forms, secondly plant clingers and crawlers, thirdly burrowers and tube-builders. But the depressed and appressed clingers and protected types of the shore areas seem to be quite absent.

The commoner supply of food is formed by the Diptera primarily among insects, next to which come Sialis and Hemiptera (the latter in the lake shallows). Along the shore line Chironomus lobiferus and C. digitatus are the main source, while in the aphytal area Protenthes choreus, Chironomus tentans, Corethra, and Sialis infumata are the chief representatives.

Again, certain faunal types are comparatively rare in fish diet. Thus, while Leptocella uvarowii forms practically 90% of the caddisworm fauna of the lake, it forms probably less than 25% of the caddisworm diet of fish, while the whole caddisworm diet amounts to hardly more than 2% of the total fish food. This proportion is not at all commensurate with their availability and we have to look elsewhere to account for this disparity. Perhaps it is the secretions which make them less agreeable as a diet, although along this line other species and the notably repellant Hemiptera form a favorite diet wherever available. To me it seems that the length, rigidity, and general unwieldiness of the cases play a big part in the selection of this particular item; small fish cannot manage the cases at all, while
larger fish have difficulties in breaking and swallowing them because of their rather pointed ends and the considerable stiffness of the tubes proper.

As for repellant secretions, most of the red Hydrachnida are refused by the general macrofauna, but not by the red Hydrachnida themselves. Apparently, therefore, they are obnoxious or distasteful; yet individuals of Atax turgidus, Eylais, Hygrobes, and other red genera are too frequently present in fish diet to permit a sweeping statement as to their offensiveness. This applies equally well to other types, such as the various Corixae and Gyrini, especially to the adults of the latter. Fish of various species frequently gorge themselves on Corixae, and adult of Gyrinus are not uncommon in fish stomachs. Yet these are all well-known instances of supposedly well-protected species,—at least that has been the assumption of the purpose of the emanations from these species. The facts of fish food would tend to force a change or modification of these assumptions.

As a whole, the place of insects in the fish diet is a variable one, and fluctuates with the habitat and the species of fish. Insects compose about 60% of the macrofauna of the lake, excluding fish, and their bulk percentage in fish food is equal, or near, to the same figure. Taking the insects as a unit, the Trichoptera form 30%, and the Corethridae and Chironomidae 65% of the supply. The actual use, however, appears to be Trichoptera 5%, Corethridae and Chironomidae 90%.

The Lake Toll.—As an irregular source of fish food must be mentioned the thousands of insects which are blown from the land, and such that venture too near the surface in the chase of food and become water-trapped.

In the first category can be placed myriads of Lachnosterna, mayflies, Corethra, bees, ants of various species, wasps, and many other, less common insects. In the second category belong primarily Odonata and Asilidae. Although expert fliers, Odonata frequently become water-trapped in a too eager quest of prey, often of their own kind. Yet they are often able to free themselves, especially if the surface is somewhat disturbed; it seems that they wait for an opportune wave-crest to lift them slightly above the surface and this is sufficient to give them the initial freedom of wing movement.
As for Asilidae, these have a penchant for damselflies which invariably try to escape over the water. The latter are able to fly exceedingly close to the surface film without touching it and this ability is an effective means of protection. The pursuing robber-fly frequently ventures too close and becomes trapped by the water. It is surprising that in the ensuing struggle to escape from the water the robber-fly should come to lie helplessly on its back, the wings held firmly by the surface film. Here, too, slight wave action may overturn the captive Asilid and give an opportunity to escape from the water. Hundreds of robber-flies were observed during the summer of 1914 trapped in the fashion described.

The Role of the Scavenger in the Lake Economy.

In a previous portion of this paper I mentioned the fact that from a bulk standpoint, and much more so from a numerical standpoint, the scavengers predominate among the lake fauna. The supply of fresh plant food is comparatively restricted in the lake, not only in quantity but also in time, while great amounts of waste are accessible in the way of decaying plant and animal matter and inorganic waste.

Thienemann (1911), Lauterborn (1905, 1912), and especially Rhode (1912) have pointed out that certain halophilous species of Chironomids are regularly associated with the sulfuretted inorganic waste of certain manufactories, while others are invariably associated with the sewage and drainage systems of many cities.

Among the halophilous species Rhode found several which are able to exist in inorganic waste of an especially high concentration of Na and K; in fact, of a concentration exceeding that of sea water. (This recalls some species of Ephydridae—Aldrich 1912). There they were associated with fungi, flagellates, and bacteria.

Other species were found in tremendous numbers in the sewage water of cities, where they were associated with Tubifex, and some rare fungi. In both cases, that is, in the presence of inorganic and organic waste, the concentration of certain mineral compounds was quite abnormal, and it is difficult to understand the possibility of life under some of the conditions found. For instance, an extreme was Chironomus gregarius which was
found in mineral waste containing a concentration of 5.5% NaCl.

Chironomids have been found so regularly in drainage and sewage water (they are constantly mentioned in reports on sewage) that it has been suggested that they play an important rôle in sewage disposal,—indeed, a part akin to the sewage bacteria. Such a rôle appears to be held by the Chironomids and worms of the aphytal area of the lake. They are scavengers in the broadest sense, even coprophagous, and that they may aid if not entirely take the part of, the sewage bacteria in the lake seems not unlikely.

Part IV. COMPARISONS AND SUMMARIES.

In discussing lake life, the prime question confronting us is: "What are the advantages of aquatic life, particularly of lake life?" Why have so many insects reverted to aquatic life? It is easy to understand why animals which are holaquatic in the first place should remain so, but once a terrestrial mode of life is acquired a change is more difficult to understand.

Except for Odonata, Ephemeroidea, Plecoptera, and some Neuropteroidea, aquatic life is secondary among insects. That is, while the insect progenitor was aquatic, and the oldest insects were amphibious, their descendants largely adopted a terrestrial mode of life. The above mentioned orders, however, appear to have retained their primitive amphibious life. Other orders, such as Diptera, Coleoptera, Hemiptera, and Lepidoptera, became holoterrestrial, but many of their modern representatives have again adopted an amphibious life.

As to the why and wherefore, we have not far to seek. A terrestrial mode of life entails adaptations to a series of extremes. Sudden and often extreme changes of temperature, of winds, variations from drought to flood, from dust to mud, and the like, are all of a kind to require considerable adjustment on the part of the organism. When we consider the additional need of food and of shelter from enemies, we cannot wonder that so many insects,—indeed, the greater number of them—have acquired some means of procuring additional shelter at least for the larval stages.
The most general methods of concealment adopted have undoubtedly been subterranean and endophytous shelter,—chiefly among the holometabola; endophytous life is in certain respects (plant-borers and miners) a variant of subterranean life. Both modes are successful in that they offer shelter from extremes of climate and protection from enemies, less successful in that they largely restrict the self-feeding larvae to a limited supply of plant food.

The ease of burrowing in soft or moist ground led animals to a wet substratum, and finally to a purely aquatic environment. We find within several orders, even within families, practically all of these transitions (see tables 3 and 4, Diptera and Coleoptera). Other species may have adopted an aquatic life more directly.

The advantage of aquatic life is that this environment offers a greater uniformity of conditions and a plentiful food supply. Conditions are not extreme, changes are slow, and the animal is easily able to adjust itself to these without any special morphological adaptations. But the aquatic environment necessitated certain physiological adjustments, especially along respiratory lines, and it is by the perfection of these adaptations that species indicate the degree of aquativeness (i.e., adjustment to aquatic life) attained by them. This aquativeness has been developed to its highest point in lake life and in rapids, where molar agents have forced a complete separation from aerial respiration and a resultant total aquativeness.

Rapids.—When comparing other hydrobiota with the lake, we find a rather marked resemblance between the rapids and certain exposed portions of the lake,—i.e., the shore and the rachion (Wesenberg-Lund 1908, Steinmann 1907). The same may-flies, leeches, beetle-larvae, and caddis-worms are found in the rapids. On the other hand, certain stenophilie species such as Simulium, Chironomus tenellus, Baetis pygmaea, Hydropsyche alternans, and others, are conspicuously absent from the lake shore. For while the latter offers current at intervals, these stenophils demand a persistent current, hence are homoioophilous. Experimentally, I have placed Simulium and Hydropsyche alternans larvae in a jar where the current would sweep around the jar, but not into it; most of the larvae died within two or three hours, despite thorough oxygenation and repeated change of water.
Yet the community of forms and adaptations of both habitats is sufficiently pertinent to indicate a probable common origin (Steinmann 1907). Both faunas consist largely of appressed clingers and some burrowers, all are well protected or sheltered forms (except Simulium, which is specialized in an entirely unique direction.) Both complexes do not admit of air-breathers, that is, as residents; for the air-breathers so frequently found in the slack water of rapids are not residents in the sense of permanence. They exist because the current does not reach them; and if it should they would be unable to maintain themselves. No emergent plants or submerged spermatophytes will be found; Cladophora and some other filamentous algae are able to maintain an appressed growth where the current is not too strong.

The current considerably modifies the shelter, and the food and breeding habits of the biota. The constant current prevents the biota from wandering about; as a rule an individual remains fixed for the greater part of its life. Strong fastholds in the way of strong claws, suckers, and other means are possessed by most of the biota, while the few swimmers (Hydarchnida, fan-tail darter) have especially elaborate swimming structures. Shelter must be sought under rocks, where the force of the current is somewhat broken. The eddies behind the rocks are favorable feeding grounds, since much of the flotsam passing over the rapids finds its way into the tiny eddies and whirlpools about the rocks. Some animals have elaborated their holding devices to trap this flotsam; such are the caddis-worms of the rapids, whose webs are generally supplied with sieves and nets for food-capture. Other animals of the rapids, such as Simulium and the may-flies, have elaborated their mouthparts into "nets" through which the water is strained for the micro-organisms which comprise their food.

Most of the insects of the rapids at the time of their final ecdysis float to the surface, where the pupal skin opens at once and the adult flies upward, an adaptation insuring the safety of the species. In oviposition some species (Odonata) dip their abdomen into the water and let the current carry the eggs away; others (caddisflies) may lay their eggs at the water's edge or enter the water and fasten the eggs to rocks. The latter applies especially to stenophilic species.
More than any other fauna that of the rapids is in danger of extinction during the winter period. Frequently the rapids may freeze solidly, and with the friction of slowly moving rocks and ice pressure all animate life is destroyed. As a matter of fact, the insects do not hibernate in the larval stage in the rapids; long before the rapids freeze up, the fauna has become reduced, and the larvae present are comparatively few.

Springs.—The outlets of springs are frequently miniature rapids and may approximate the conditions of rapids. But they are nearly always characterized by an abundant growth of water cress, among which one is certain to find air-breathers such as Hemiptera and Tipulid larvae. This is a striking example of the dependence of surface-breathing species on plant growth for their maintenance.

The most important character of springs is the temperature, which as a rule is constant throughout the year. The numerous springs about the Madison lakes are all homiothermal, with a temperature of 8–10° C. the year round. The outlets contain an abundance of water-cress, in which caddis-worms, snails, crustacea, and planarians are exceedingly plentiful. Some of the typical representatives are: the caddis-worms Neophylax autumnus, Platypylax designatus (more truly a rapids form), Limnephilus rhombicus, the latter with both vernal and autumnal cases at the same time, an interesting persistence and overlapping of a seasonal instinct. Among planarians Dendrocoelium lacteum and Polycelis nigra are especially common, while Planaria doritocephala and P. agilis are quite frequent, all four species occurring also in the lake; Physa gyrina and P. heterostropha among Gastropoda; and Gammarus limnaeus among Crustacea.

It is difficult to decide which factor controls the fонтicolar association, whether it is current, food supply, temperature, or chemical composition of the water. This much is certain: the springs about the lakes vary as to their biota. Thus for instance, Merrill Spring outlet contains an abundance of caddis-worms and Planarians, while Merrill Creek close by, which is fed by springs, contains not a single Trichopteron or Planarian. The conditions appear to be similar to Merrill Spring, but differ in the chemical makeup of the water, due to additional drainage water and the composition of its basin. In places the Merrill Creek rapids exceed those of the spring’s
outlet in swiftness, and Simulium has established itself in such spots, an indication that current may be the decisive factor for Simulium, while the chemical composition of the water appears to be the only factor which prevents its associates of the Yahara spillway from establishing themselves also.

This situation further indicates that the conditions required by even a stenophilic species are relative and that the fluctuation of conditions resulting in an intergrading of habitats is paralleled by a corresponding intergrading of the respective biota.

In their general makeup the associations of the lake, rapids, and spring outlets are distinctly related. They may be said to form the water-breathing communities. In contrast to them may be placed the communities of streams, creeks, ponds, swamps, and shallows, as typified by air-breathing animals.

_APPENDANT LAKE SHALLOWS.—Certain parts of the lake have shallowed out and have been cut off by means of bars so that they no longer need be considered a part of the lake proper. Yet these shallows are of enormous importance as food sources to fish, especially to the shore fishes, and as breeding places for a great number of species, especially among vertebrates and surface-breathing insects.

The shallowing process, frequently a result of sedimentation by inflowing streams or of the swamping due to the invasion of an emergent vegetation, and the lessened exposure to molar agents favor the abundant growth of an emergent and floating flora, such as Lemna, Nymphaea, Castalia, Typha, and others. In this respect the outlying lake shallows are akin to the swamps which line the Yahara River along its course. It is to be expected, therefore, that the fauna of the shallows will also be similar to that of the swamps, and that is precisely the case.

The fauna consists chiefly of surface-breathers of various kinds, including vertebrates, but it also includes many of the water-breathers found in the lake, especially inhabitants of the mud bottom. It is marked by the considerable number of Culicidae, Chironomidae, Syrphidae, Anisoptera, Hemiptera, and Dytiscidae, but it has a very scant representation of Ephemeroptera, Trichoptera, Zygoptera, and Hyalellae. Stagnation is, of course, very great in the swamps, and this means that to some extent anaerobic conditions may prevail on the bottom for short periods. This may be an important factor in determining the faunal complex.

29—S. A. L.
Decaying plants, and mineral matter tend to form an organic sediment of varying thickness. In places this sediment may constitute a layer of considerable thickness; it will be a false bottom, for while it may bear a fair amount of stress, any considerable pressure will pierce this layer. This sedimental layer is quite impervious to heat, absorbing little and permitting none to penetrate, so that the wet soil beneath will be found quite chilly by comparison with the warm water above. Decomposition and acidification are important factors in swamp physiology and probably of great importance in determining the faunal complex; yet too little is known of this phase of the subject to permit any detailed analysis.

Whatever the factors be, given a slight current, the fauna immediately changes certain of its aspects, perhaps because of the removal of the chemical deterrents. This can be observed admirably in the swamps of the Yahara to the north of Lake Mendota and south of Lakes Monona and Wanbesa. Where the water is stagnant the fauna lacks Trichoptera, Zygoptera, and Hyalellae; but in presence of a fair current these groups are well represented.

Streams.—As just stated, a stream differs from a swamp in that it flows, while the swamp is stagnant. The degree of flow is, of course, relative. Much also depends on the composition of the bottom. Given a sandy bottom and another of mud it is probable that the muddy stream will support little plant life while the sandy stream will be choked with vegetation.

The composition of the substratum is of the highest importance to the biota of the stream. No better examples of this exist than Pheasant Branch Creek at the western end of the lake and Six Mile Creek flowing in at the north. Pheasant Branch Creek is a narrow, rapid stream, about 6 meters wide, a little over a meter deep, with a bed of mud covered with silt. The water is clear. The creek contains a luxuriant vegetation of Lemna, Myriophyllum, Ceratophyllum, and Elodea, in which a very rich fauna maintains itself.

Six-Mile Creek is a slower stream, with a very tortuous channel, varying in width from 8–12 meters, with a depth of 1–2 meters. Its bottom is mud and clay. Its water is murky and no vegetation exists in the bed of the stream, except for an occasional Nymphaea and Castalia; hence the animal life is essen-
tially that of the lake shallows, chiefly Ephemeridae, Aeshnidae, and Libellulidae.

Again, the Yahara River, passing through the swamps on the north, of Lake Mendota, carries with it a great deal of sediment, which makes it murky in its middle portions. Through its own force it is able to keep its channel unobstructed to a depth of about 3 meters. In this murky part no vegetation and an exceedingly scant fauna exist. But in the shallower portions on its side the fauna and flora are of the stream type, with an especially large representation of caddis-worms (chiefly Setodes grandis), damselfly larvae, and Hyalellae.

This relation shows that current, while of so great an influence in changing the complex of the fauna, nevertheless is not an absolutely decisive factor, but that photosynthesis may affect distribution and makeup in the establishment of a different substratum. To what extent the makeup of the plant substratum is able to affect the faunal composition is indicated by a comparison of the Yahara River, as just described, and Pheasant Branch Creek.

In the latter Lestes forcipatus and other Zygoptera larvae abound. Hyalellae are few, Setodes grandis scarce, beetle larvae plentiful, Culicidae rare, Nymphula larvae numerous; while in the Yahara River these faunal proportions are exactly the converse.

Ponds.—It is a curious circumstance, that to a considerable extent the fauna of Pheasant Branch Creek and Picnic Pond have much in common. But while Pheasant Branch Creek has a strong current, Picnic Pond is stagnant, being maintained by seepage from the lake. Lepidoptera larvae, beetle larvae of various kinds, except Gyrinidae, Chironomidae, Lestes, Sympetrum, and Libellula basalis among Odonata, and other species, are common to both regions. As for differences, Corethra is common in the pond (recruited from the lake); so are Culicidae larvae, Dytiscidae, Cyphonidae, Tipulidae, Stratiomyidae, Ephrydidae, and certain other forms which are more or less limited in their distribution.

Again, Tenney Park contains a large lagoon and a small pond. The lagoon contains flowing water, supplied from the lake, and its fauna is that of a stream. But the pond, small as it is (10 m. diameter) is noted as a depository of toad eggs, and harbors several faunal forms which agree with those of Picnic Pond, while
differing in its larger representation of certain Dytiscidae and Anisoptera.

The character of the ponds therefore appear to be chiefly stagnancy, shallowness, and the tendency toward swamping. Only the fact that there is open water (generally) in the middle prevents acidification. Circulation is minimal in the vegetation areas, with the tendency toward local centers; that is, little isolated patches of warmer and cooler water. In a swamp such warm patches would soon form decomposition centers, while in ponds the periodical disturbance of the open water in the middle is sufficiently strong to suppress such centers. Yet even in ponds, especially in dry summers, the vegetation may gain the upper hand and cover the entire pond area. In such instances acidification is strong, decomposition advanced, and the remaining water becomes untenable for the major part of the fauna.

Summary of Lake Characters.

It is evident from the brief survey of types of aquatic habitats that the interrelations are comparatively easy to outline and so are the larger differences; but it is extremely difficult to fix the precise points at which differences begin. No habitat can be set forth as a unit which is well-definable in every respect; I have rather attempted to show what might be used as criteria by calling attention to the interrelations. Physical and physiological conditions intergrade everywhere; for the environment is labile. Correspondingly, there is an intergradation of biota; for the organism, too, is labile.

Therefore, in attempting to define a habitat such as the lake the intergradation with surrounding habitats must be kept in mind and not too strict an emphasis laid on any single characteristic. The following is an attempt to define the lake as an aquatic unit, distinct from other aquatic bodies:

The lake is body of water
1. Of sufficient depth and area to permit strong wave action.
2. Without emergent or floating vegetation. This is due to condition number one.
3. With a shore line destitute of plants, except Cladophora, and harboring only clingers and burrowers among animals. A
result of condition number one. This region shows the greatest specialization among lake animals.

4. Without surface-breathers among animals.

5. With a plant zone of variable depth (according to clearness of the water) which is barely indicated in winter, but luxuriates during summer. Parallel with plant growth a great summer proliferation of phytophagous animals.

6. With a thermal stratification for a portion of the year.

In part, these conditions apply to rapids and spring outlets, especially those pertaining to the fauna. In part, they may also apply to streams. We have, therefore, a gradual merging of lake to pond and swamp in one series, and lake to swamp directly. Rapids, springs, and lakes form the water-breathing associations, while ponds, swamps, and appendant lake shallows form the air-breathing associations, with streams occupying an intermediate position.

From the definition given above it will be seen that the term "lake" for certain bodies of water is inapplicable. At best, the term has been used in a relative sense as applicable to any broad and enclosed expanse of water. Thus, the shallows of streams when spread over large areas have been called lakes, although lacking every true characteristic. Again, the vegetation character is not always distinct. Shallowing of lakes produces "swamping," a feature which is invariably characterized by emergent growth of plants. Yet there are lakes where this shallowing process is so gradual that a breaker line or rachion is barely indicated on the bottom, and the transition from lake to swamp is practically imperceptible.

The absence of surface-breathers is a good characteristic, but is applicable also to the open water of ponds, and rivers, that is, to a large extent. Again, stagnation coupled with the formation of a thermocline may be characteristic of a great many lakes; yet so large a body of water as Lake Vaettern in Sweden has only a very gradual thermocline and the bottom waters contain oxygen the year round.

Hence this definition will be found inadequate for some lakes, and inapplicable for certain others. But for the "plains" lakes it will probably be generally acceptable. Alpine lakes have certain special conditions; but even here the conditions present some similarities.
In respect to faunal and floral distribution Lakes Mendota, Monona, Waubesa, Cedar, Nagawicza, and most others in southern Wisconsin present a similar situation. Practically all of these lakes have a low degree of transparency and hence have a shallow zone of photosynthesis. All of them have similar types of shore, rough in places, sandy in others, and tending to swamp in less exposed situations. The northern Wisconsin lakes are more transparent and show a correspondingly greater zone of photosynthesis. They are more like the Alpine lakes in this respect.

In its particulate aspects, comparison with other lakes can be only relative. For the littoral areas much the same type of fauna and flora will be found in all lakes, except the very large and stormy lakes. Wesenberg-Lund (1908) finds similar types for the rock shore communities of Danish lakes, although Lake Mendota seems more populous. Forel, Zacharias, Zschokke and others have worked on the fauna of alpine lakes and find a similarly typical fauna as far as the littoral area is concerned.

In the aphytal area the situation differs somewhat. From a physiographical standpoint some of the alpine lakes are valleys between mountains which are filled with water. Some of them have a depth of more than 500 meters, and we find conditions at these depths which are somewhat akin to those of the ocean abyss. In the upper portions of the aphytal area (inappropriately termed "abyssal area") the fauna resembles that of the aphytal area of Lake Mendota. Below 50 meters this resemblance ceases. Practically all of these deep lakes harbor a series of glacial relicts, and certain species of worms, in general, forms that never come to the shallower depths above 50 meters. And as a result there is a fauna, rich in its variety and adaptations, which has been called an abyssal fauna (inappropriately so, as just mentioned, since the term is preoccupied in a special sense in oceanology.)

As far as the plains lakes are concerned, these "abyssal" conditions do not exist in them aside from the general conditions of the aphytal area. Their fauna consists largely of species which come to the surface or at least to the shallower waters at some time during their life. No special fauna has been developed which is particulate in its predilections for great depths. In general, the fauna is such as may be found within relatively shallow waters, a fauna which connects distinctly with that of the shores and shallow bodies of water.
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The difference of the areas is indicated is square meters. Ecological Habitats shown for comparison.

<table>
<thead>
<tr>
<th>Depth in meters</th>
<th>Area in sq. km</th>
<th>Difference in sq. m.</th>
<th>Ecological Zone</th>
<th>Ecological Area</th>
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<tbody>
<tr>
<td>0</td>
<td>30.4</td>
<td></td>
<td>Shore to Rachion</td>
<td>Eulittoral (Euphytal)</td>
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<tr>
<td>1</td>
<td>25.4</td>
<td>4,000,000</td>
<td>Plant Zone</td>
<td>Littoral Region</td>
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<tr>
<td>2</td>
<td>23.7</td>
<td>1,700,000</td>
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<td>Sublittoral (Dysphatal)</td>
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<td>3</td>
<td>22.0</td>
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<td>Shell Zone</td>
<td>Plantless Area</td>
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<td>2,500,000</td>
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<td>10</td>
<td>24.0</td>
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<td>..................Aphytal Region</td>
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<td>15</td>
<td>25.8</td>
<td>7,200,000</td>
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<td>20</td>
<td>26.6</td>
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<td>25.5</td>
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**Table 2. Types of Odonate Larvae**

<table>
<thead>
<tr>
<th>Habitat Preference</th>
<th>Form</th>
<th>Group</th>
<th>General Habits</th>
<th>Group</th>
<th>Form</th>
<th>Habitat Preference</th>
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</thead>
<tbody>
<tr>
<td>Phytotphilous</td>
<td>Cylindrical</td>
<td>LESTI-NAE</td>
<td>Rock Clingers</td>
<td>ZYGOPTERA</td>
<td>Depressed</td>
<td>Petrophilous</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Free Swimmers</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phytotphilous</td>
<td>Lanceolate</td>
<td>AESCH-NAE</td>
<td>Plant Clingers</td>
<td>ZYGOPTERA</td>
<td>Elongate</td>
<td>Phytotphilous</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Loping Swimmers</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scaptotphilous</td>
<td>Very flat</td>
<td>GOM. PHINAE PETAL-URINAE</td>
<td>Sprawlers</td>
<td>LIBELLAE LIDAE CORDULE- GASTER-NAE</td>
<td>Squat,</td>
<td>Depressed</td>
</tr>
</tbody>
</table>
### Table 3. Dipterous Families Whose Larvae are Found in Water.

<table>
<thead>
<tr>
<th>Family</th>
<th>Terrestrial Larvae</th>
<th>Aquatic Larvae</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Breathers</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lake</td>
</tr>
<tr>
<td>1. Tipulidae pars.</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>2. Psychopoteridae.</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>3. Psychodidae</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Psychoda, Pericoma pars.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pericoma pars., Ulomyia.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. Dixidae</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>5. Culicidae</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>6. Corethridae</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Mochlonyx.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corethra.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7. Chironomidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ceratopogoninae pars.</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>8. Simulidae</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>9. Blepharoceridae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10. Orphinephilidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>11. Leptidae pars.</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Atherix.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12. Zarthomylidae pars.</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>13. Tabanidae pars.</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>14. Syrphidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15. Ephydridae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16. Scorpionidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>17. Cordyliuridae pars.</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>18. Anthomylidae pars.</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Callophilys.</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>19. Oestridae (endoparasitic)</td>
<td></td>
<td>x</td>
</tr>
</tbody>
</table>
### Table 4. Coleoptera and their Relations to Aquatic Life.

<table>
<thead>
<tr>
<th>Name</th>
<th>Terrestrial</th>
<th>Aquatic</th>
<th>Water Breathers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Surface-air comes to surface to breathe</td>
<td>Submerged air capture gas bubbles</td>
</tr>
<tr>
<td>Hygrobitidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Larva</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Pupa</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Dryopinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Larva</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Pupa</td>
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<td>x</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Hydrophilidae</td>
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<td></td>
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</tr>
<tr>
<td>Larva</td>
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<td>x</td>
<td></td>
</tr>
<tr>
<td>Pupa</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>DONACINAE</td>
<td></td>
<td></td>
<td></td>
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<td>Dryops</td>
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</table>

*The Donacinae live submerged, but obtain their air by sinking the caudal hooks into the air vessels of aquatic plants—hence are indirectly surface-bearers.*
TABLE 5. Numerical distribution of various forms of animals between the shore line and a depth of 7 meters.

The averages are computed on a basis of 50 stations for each of the depths given. The total number of individuals of the various forms may be ascertained by multiplying the averages by the areas at the different depths, viz., 0—1 m. = 4 sq. km.; 1—2 m. and 2—3 m. = 1.7 sq. km. each; 3—5 m. = 3 sq. km.; 5—7 = 2.5 sq. km.

<table>
<thead>
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<th>Name</th>
<th>Averages per sq. m. at depths of</th>
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<td></td>
<td>0-1 m:</td>
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</tr>
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</tr>
<tr>
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</tr>
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<td>Pink Nematode</td>
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<tr>
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<tr>
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<td>Leeches</td>
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<td>Ancylus</td>
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<tr>
<td>Limnaeae stagnalis</td>
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</tr>
<tr>
<td>Physa anciliaris</td>
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<tr>
<td>Physa heterostropha</td>
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<tr>
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<tr>
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<tr>
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<td>C. plumosus</td>
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<td>O. exilis</td>
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<td>Coptotomus Interrogatus ad.</td>
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<td>P. edentulus larv.</td>
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TABLE 5—Continued.

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<th>Name</th>
<th>0-1 m.</th>
<th>1-2 m.</th>
<th>2-3 m.</th>
<th>3-5 m.</th>
<th>5-7 m.</th>
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<td>0.44</td>
<td>0.06</td>
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<td>P. lecontei larva</td>
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</table>

TABLE 6

Estimates of the total number of individuals of the various groups of animals between the shore line and 7 meters, based on the averages obtained from the 50 different stations.

*Platyhelminia* 553,200,000
*Nemathelmia* 18,600,000
*Chaetopoda* 8,690,500,000
*Hirudinea* 103,200,000
*Mollusca* 2,389,700,000
*Crustacea* 2,221,300,000
*Hydrachnida* 815,900,000
*Ephemeridae* 291,300,000
*Odonata* 16,400,000
*Hemiptera* 49,300,000
*Sialidae* 12,200,000
*Trichoptera* 1,862,800,000
*Corethridae* 38,900,000
*Chironomidae* 2,644,700,000
*Coleoptera* 218,400,000
### Table 7.—Showing Distribution by Depth and Character of Bottom

(Abbreviations: r = rare; f = frequent; a = abundant; c = common)

(R = Rock bottom; G = Gravel; S = Sand; M = Mud; P = Plant.

(See p. 419)

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<th>Character of Bottom</th>
<th>Optimum depth</th>
<th>Optimum Hab.</th>
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<td>f c c c c c</td>
<td>2-3</td>
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<tr>
<td>PORIFERA Eupogia officinalis</td>
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<td>c</td>
<td>c</td>
<td></td>
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<td>a</td>
<td>a</td>
<td>0-1</td>
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<tr>
<td>PLATHEMIA Polyclis nigra</td>
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<td>f</td>
<td>a</td>
<td>0-1</td>
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<tr>
<td>Decoeculum lacteum</td>
<td>c c e c</td>
<td>c</td>
<td>f f f c c</td>
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<td>c f f c c c</td>
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<td>f</td>
<td>f</td>
<td>1-25</td>
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<td>f</td>
<td>f</td>
<td>1-25</td>
</tr>
<tr>
<td>Pink Neanptide</td>
<td>a</td>
<td>c</td>
<td>f</td>
<td>1-25</td>
</tr>
<tr>
<td>ANELIDA Sparganopodium eiseni</td>
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<td>c</td>
<td>c f f f c</td>
<td>1-25</td>
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<tr>
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<td>c</td>
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<td>1-25</td>
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<td>c</td>
<td>c f f f c</td>
<td>1-25</td>
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<td>2-3</td>
</tr>
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<td>c</td>
<td>f f f f f</td>
<td>1-2</td>
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<td>Anodonta &amp; Lampsis</td>
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<td>f</td>
<td>f</td>
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### Table 8 — Ecological Distribution of Lake Animals Arranged in the Order of their Habitats

(Abbreviations: a = abundant; c = common; f = frequent; r = rare)

(See p. 432)

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GRAVEL SHORE

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Amnicola limosa. | a   | c      |      |          |           |        |            |               |
Camarurus propinquus. | a   | c      |      |          |           |        |            |               |
Ephebera varia, larva. | a   | c      |      |          |           |        |            |               |
Ephebera variaold larva. | c   | c      |      |          |           |        |            |               |
Arria putrida. | c   | d      |      |          |           |        |            |               |
Chironomus trigonatus. | c   | c      |      |          |           |        |            |               |
Stenelmis cronatus. | c   | c      |      |          |           |        |            |               |

RACHION

Epicordulia princeps. | c   | r      |      |          |           |        |            |               |
Gomphon fraternus. | c   | r      |      |          |           |        |            |               |
Monanima uniofila. | c   | r      |      |          |           |        |            |               |

UPRIGHT VEGETATION

Hydra fusca. | c   | c      |      |          |           |        |            |               |
Planaria maculata. | c   | c      |      |          |           |        |            |               |
Hirudinea | c   | c      |      |          |           |        |            |               |
Campeloma. | c   | c      |      |          |           |        |            |               |
Phanorhis parvus. | c   | c      |      |          |           |        |            |               |
Ph. campanulatus. | c   | c      |      |          |           |        |            |               |
Ph. bicuscanus. | c   | c      |      |          |           |        |            |               |
Hydrachna denticulata. | c   | c      |      |          |           |        |            |               |
Caenis dulcina. | c   | c      |      |          |           |        |            |               |
Ischnura verticalis. | c   | c      |      |          |           |        |            |               |
Eunialla antenatatus. | c   | c      |      |          |           |        |            |               |
Nymphula sp. | c   | c      |      |          |           |        |            |               |
Platygynus multifasciatus. | c   | c      |      |          |           |        |            |               |
Leptocella uncirostris. | c   | c      |      |          |           |        |            |               |
Trianeodes flavescens. | c   | c      |      |          |           |        |            |               |
Protoria glabra. | c   | c      |      |          |           |        |            |               |
Table 8.—Ecological Distribution of Lake Animals Arranged in the Order of their Habitats—Continued.

(Abbreviations: a = abundant; c = common; f = frequent; r = rare.)

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31—S. A. L.
### Table 9.—Comparative Places of the Macrofauna of Lake Mendota.

Expressed in percentages of bulk (= 100%).

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<tr>
<th>Name</th>
<th>Seasonal (litt)</th>
<th>Annual Estimate</th>
<th>Type of food eaten</th>
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