

vary greatly from one year to another is difficult to understand, yet such a condition has been clearly demonstrated. Lundbeck (1926, p. 262) shows that the total weight of fauna in a bay of the Plöner See was, in the growth season 1924-25, almost twice as great as the total for 1923-24. Alm (1922), working on Swedish lakes, had demonstrated a decrease of similar proportions between the total quantity of fauna of the season 1918-19 and that of 1919-20.

Changes of a lesser magnitude might be explained on a basis of the ecological succession within the lake or as a result of the periodic fluctuations. An increase of nearly 75 to 100 per cent. in the amount of fauna present in successive years is yet to be explained and suggests a fruitful field for investigation.

ANNUAL PRODUCTION OF BOTTOM FAUNA IN LAKE SIMCOE

Using Lundbeck's determinations of yearly productivity, *i.e.* three times the summer average for chironomid larvae, one-third for molluscs and twice for the remainder, we may calculate the annual production of bottom fauna in Lake Simcoe as follows:

Organism	Average amount fauna May-October kgm/ha	Rate of productivity (after Lundbeck)	Annual production kgm/ha
Chironomida larvae.....	8.06	x3	24.18
Mollusca.....	2.22	x1/3	0.74
Remaining fauna.....	2.10	x2	4.20
		Total.....	29.12

At this rate of productivity, Lake Simcoe, with an average summer fauna of 12.38 kgm. per hectare, would have an annual production of 29.12 kgm. per hectare or 25.87 lb. per acre. The fact that the composition of the fauna of the Plöner See resembles that of Lake Simcoe might suggest that Lundbeck's rating is not altogether inapplicable, although it

is recognized that the lakes of northern Germany have a somewhat longer growing season than Lake Simcoe.

RÉSUMÉ OF THE GEOGRAPHICAL AND LIMNOLOGICAL FEATURES OF LAKE SIMCOE

Lake Simcoe is a part of the Trent valley system of waterways and drains into Georgian bay through the Severn river. It is situated about 40 miles north of Toronto in a drainage area of 1,100 sq. miles, most of which is cultivated land; some, however, is swampy and wooded.

The area of the lake is 280 sq. miles, its average depth 17 metres (54 feet) and its maximum depth 44 metres. With the exception of two long bays, the lake is an open expanse of water about 15 miles in diameter, the shores being mostly exposed and of a sandy or rocky nature.

The water is somewhat alkaline, pH 8.1, cool and fairly well oxygenated. At midsummer a moderate stratification occurs and the bottom water has an oxygen content as low as 2.0 p.p.m. The temperature of the bottom water at this time is about 10°C. at the average depth, 17m. As a result of a fairly high transparency, the light penetration is somewhat deeper than in most lakes of similar size.

SUMMARY OF PART I

THE BOTTOM FAUNA

(a) *Composition and Distribution*

The bottom fauna is largely composed of six major groups which are considered in order of their numerical abundance as follows:

Chironomid larvae belonging to at least 8 species and subgenera, make up more than 60 per cent. of the total fauna. *Chironomus plumosus* being the largest and most abundant species. The chironomid larvae are abundant at all depths but show a minimum number in the lower sublittoral zone.

(12m.) and a maximum abundance in the profundal zone (14-45m.).

The **Mollusca** taken include 40 species of gastropods and 15 of pelecypods, the latter group being slightly more numerous as to individuals but less varied as to species than the former. The Gastropoda are mostly confined to the upper 20 metres while the Sphaeriidae are most numerous at 20 metres and decrease gradually in shallower or deeper water. The molluscs constitute 13.9 per cent. of the total bottom population.

The **Oligochaeta** (Tubificidae) make up about 8 per cent. of the total fauna numerically. They are present at all depths but most constant and abundant in the deeper water (25-45 m.).

The **Amphipoda** of Lake Simcoe are practically confined to the littoral and sublittoral zones (0-14m.) and they are accordingly much less important than the amphipods of lakes in which the deeper living forms (*Pontoporeia*) are found.

The burrowing **ephemerid nymphs** are numerous in the sublittoral zone of Lake Simcoe. All the mayfly nymphs (Ephemeroptera) are confined to the upper 20 metres.

Corethra larvae make up a small proportion of the bottom fauna of Lake Simcoe. They are most numerous in the lower profundal zone (25-45m.).

The distribution of the chironomid fauna has been indicated above. The non-chironomid fauna is fairly constant in numbers in all depths. In the littoral and sublittoral zones this non-chironomid fauna is largely composed of Gastropoda, Ephemerae and Amphipoda, while in the deeper water these forms are practically absent and the fauna is made up of Oligochaeta, Sphaeriidae (*Pisidium*) and *Corethra* larvae.

(b) *The Quantity of Bottom Fauna*

The average number of macroscopic organisms over all depths is 820 per sq. metre (776 per sq. yard). The average dry weight of macroscopic organisms over all depths is 12.38 kgm per hectare (11.0 lb. per acre). The greatest number of organisms (1,097 per sq. metre) is found in the lower profundal zone (20-25m.) and the greatest dry weight (14.8 kgm.

per hectare) in the upper sublittoral (5-10m.) The least number (562 per sq. metre) and the least weight (6.3 kgm. per hectare) are found in the lower sublittoral zone (10-14m.). A summary of the total quantity of bottom fauna and its composition is found on page 99.

(c) *Factors in the Ecology of the Bottom Fauna*

The factors affecting the distribution and constitution of the bottom fauna which have been considered, include bottom deposits, water conditions such as temperature, oxygen content, waves, currents and light penetration and biological conditions such as the protective, nutritive or competitive relations with other animals and with plants. A résumé of the principal factors affecting the fauna of Lake Simcoe appears on page 90. It has been demonstrated that the non-biological factors are inter-dependent and that they can be traced back to two fundamental conditions, the size of the lake, including its depth, area and shore conformation, and its geographical position, including the nature of its drainage area and the climatic conditions of the region.

Lake Simcoe has a fairly rich plankton and bottom fauna, a low supply of oxygen in the deep water and a thoroughly decomposed bottom ooze. In the classification of lake types developed by Naumann, Thienemann, Lundbeck and others, these life conditions would indicate that Lake Simcoe is an eutrophic type with oligohumus bottom deposits. That the distribution and quantity of bottom fauna support this conclusion is shown by the comparison between Lundbeck's theoretical distribution of fauna in an eutrophic lake and the actual distribution in Lake Simcoe, diagram 2, page 94. Lake Simcoe differs slightly from the typical eutrophic lake in having a lesser deficiency of bottom oxygen in the deeper water, which results in a larger number of species and a greater total fauna in its profundal zone than in that of other eutrophic lakes.

The minimum number and quantity of several groups of organisms were found to be in the lower sublittoral zone

(10-14m.) as was the minimum for the total fauna. Lundbeck suggests that the life conditions in the sublittoral zone are transitional between those of the littoral and profundal zones. Since the sublittoral zone has little fauna distinctly its own, it is populated largely by stray littoral and profundal species, neither of which thrive in the sublittoral conditions. The three main features which mark the distribution of fauna in eutrophic lakes, *viz.*, a maximum in shallow water, a sublittoral minimum, and a second maximum in deep water, were each found at slightly lower depths in Lake Simcoe than in Lundbeck's north German lakes. This appears to be the result of Lake Simcoe's greater size and exposure and the corresponding deeper effects of wave action and other surface conditions. In Lake Nipigon the sublittoral minimum was present at a level still lower than that in Lake Simcoe, which might be expected in a still larger lake subject to more active water movement.

The factors affecting the quantity of bottom fauna are necessarily the same as those which affect its quality and distribution, but they may be considered from another point of view. It has been demonstrated that the depth and area exert such a fundamental effect on the "factors" limiting the bottom fauna that the quantity of bottom fauna may be correlated directly with the depth and area, graph X, page 104. These two factors cannot be correlated separately with the amount of bottom fauna but their product shows a definite relation to the latter quantity. Certain factors, chiefly irregularity of the shore line, may cause a deviation from this relation.

A consideration of the seasonal variation and rate of growth of bottom organisms has resulted in an estimated annual crop or production of 29 kgm. dry weight per hectare (25.8 lb. per acre) over all depths in Lake Simcoe, as compared with the average standing amount of 13.8 kgm. per hectare (11.0 lb. per acre).

PART II

THE ECOLOGICAL RELATIONS OF THE BOTTOM FAUNA IN A LAKE

THE CIRCULATION OF FOOD MATERIALS IN A LAKE

Our conception of the amount of living matter and potential food-forming material in a body of water as large as Lake Simcoe is likely to be somewhat inadequate. Besides the myriads of living plants and animals there are the dead organic matter and the nutritive inorganic materials which have been accumulating in the lake for the last 20,000 years.* In comparison with this great "capital" the amounts of organic or nutritive inorganic materials added in any single season from the drainage basin, or the amount swept away at the outlet of the lake can be ignored while we discuss the transformations which proceed within the lake itself.

In the water, as on land, the principle of food chains and the nitrogen cycle have long been recognized. The photosynthetic activity of the phytoplankton providing food for microscopic animals and these minute animals providing food for the larger members of the fauna has been a matter of common knowledge and frequent reference. In spite of this knowledge few realize the complexity of the whole system and there are certain features of the circulation which have received very little attention.

Diagram 3 is an attempt to organize the available knowledge of the circulation of food materials into a single comprehensive picture. The scheme is chiefly applicable to the open waters of the lake since in the shore area additional factors render the relationship even more complex.

Nutritive matter occurs in the lake in five conveniently separated states, represented by the contents of the five circles on the diagram. They are: 1. The inorganic nutritive materials dissolved in the water. 2. The plankton, the higher aquatic plants and the microfauna which is sheltered

*Estimated age of Lake Simcoe from data given by Coleman (1922).

by these plants. 3. The fish fauna. 4. The bottom fauna. 5. The organic detritus of the bottom deposits.

The lines connecting the circles represent processes by which food materials are transformed, *i.e.* the paths by which nutritive materials circulate in the lake.

Path **a** represents the fundamental process of photosynthesis, the only means by which inorganic materials can be elaborated into organic or living substance and thereby be made available as food for the animals of the lake.

The Circulation of Food Materials in a Lake

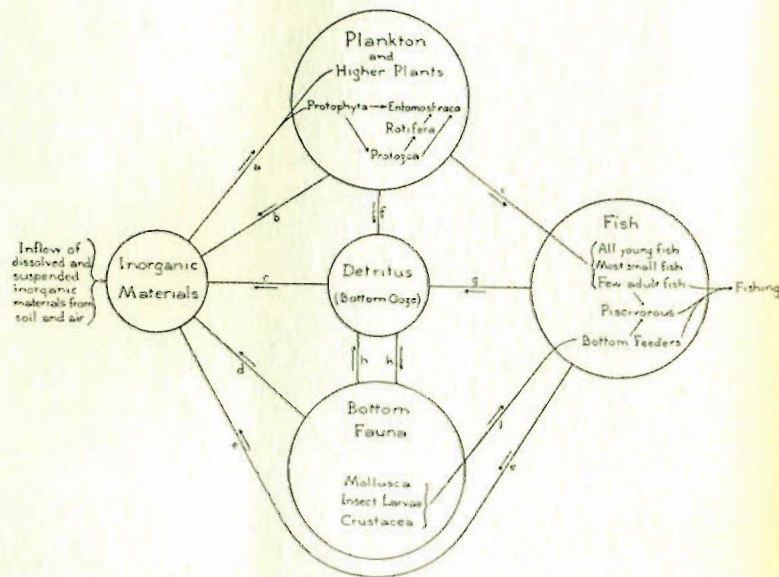


DIAGRAM 3. The circulation of food materials in a lake.

Paths **b**, **c**, **d** and **e** represent the processes of decomposition, largely due to bacterial activity which result in the destruction of organic matter. Decomposition does not always result in the immediate production of inorganic materials. It is known that large quantities of dissolved and colloidal organic matter are present in the water at all times. Since this material is rarely if ever utilized by living organisms

without being further broken down into inorganic salts it is not necessary to represent the dissolved organic materials in our scheme of circulation.

Paths **f**, **g** and **h** indicate incomplete disintegration and settling of plant and animal materials to form the organic detritus of the lake bottom.

The remaining paths, **i** and **j**, represent the feeding of fish on the plankton and on the bottom fauna, while path **k** indicates that the bottom fauna is made up for the most part of detritus eaters. The processes represented by paths **a**, **c**, **f**, **i**, **j**, and **k** are so well recognized as to need no further comment. The remaining five are admittedly less important but still worthy of consideration. Of these, **b** calls our attention to the fact that some of the decomposition products of dead plankton may be dissolved out before the remains settle to the detritus layer; **d** indicates that some of the bottom fauna, *e.g.* larger pelecypods and gastropods, on decomposing, are not scattered as detritus but dissolved as they decompose; **e** and **g** represent the decomposition of fish which die in the lake. Just how many fish come to this fate cannot be estimated but it is thought that the number of fish caught is much less than the number which reach maturity, and we know that some of the most abundant fishes of the lake (ling, perch and sucker) are rarely caught. From this evidence it would seem that the quantity of fish dying in the lake is not to be disregarded. Path **h** represents the fate of the bottom organisms which fail to be eaten by fish or by other bottom organisms.

The arrow on the left indicates the inflow of nutritive materials from soil and air. Especially important in this connection are such nutritive salts as the nitrates and phosphates. The chart does not mention the organic material which is washed in to add to the detritus since in a large lake the amounts of such allocthonous detritus is negligible. On the right a second arrow represents the loss of organic material from the circulation through the agency of fishing. In a simple chart it is not possible to represent other losses, due to emerging adult insects, or the outflow of water. In each case

there appears to be some compensation for the loss, *e.g.* many of the insects drop back into the lake and for everything swept out at the outlet of the lake a similar or greater amount is washed in by the inflow of streams. The outflow of a lake is therefore not to be thought of as a leak in the circulation system, and in a large lake the outflow is not sufficiently rapid to produce marked effects even on the life near the outlet. A calculation has indicated that at the average rate of outflow from Lake Simcoe it would take roughly 22 years for the present volume of water to pass through the Narrows at Atherley.

The circulation of nutritive material or food relationships as indicated in the chart is not a simple cycle but a combination of a number of cycles. For convenience we may represent the five states of food as *I, P, F, B, D*, denoting: Inorganic materials, Plankton, Fish, Bottom fauna, and Detritus, respectively. The cycles represented by $I \rightleftharpoons P$ and $I \rightarrow P \rightarrow D \rightarrow I$ represent the growth and destruction of plankton organisms without any utilization either by bottom fauna or by fish. Similarly, $I \rightarrow P \rightarrow B \rightarrow D \rightarrow I$ and $B \rightleftharpoons D$, represent cycles involving the production of bottom organisms but still no fish. It is thus possible to have a large amount of life and a great food circulation with little utilization by fish. In a similar manner the possibility of five more cycles involving the utilization of either plankton or bottom organisms by fish can be demonstrated.

The diagram is limited in being applicable chiefly to the open water. In the shore areas other factors, chiefly the higher aquatic plants, cause a further complication of the scheme. It also fails to show the relative importance of the different processes, a defect which might be remedied by making the lines (paths) of different intensities, but at the risk of adding to its complexity. The purpose of the scheme, however, is to show the intricate nature of the circulation and something of the processes through which it is accomplished. In addition it demonstrates the unity of the whole process, a view well expressed by Dr. Forbes (1887) in his "Lake as a Microcosm."

THE FOOD OF FISHES IN LAKE SIMCOE

In the general nutritive system of the lake the question of fish food is of more than ordinary interest, especially from an economic point of view. Since this investigation was centred about the bottom fauna, the food of bottom-feeding fish received more attention than that of the piscivorous or of the plankton feeders. The following conclusions as to the food of various fish are based upon an examination of the stomach contents of 214 fish. Unless otherwise stated, the specimens were taken during the period between May 1 and October 30. This distribution of the observations is necessary since the food taken by fish at a particular season may not represent its usual diet. It is also noted that the fish were of average adult size, the food of young fish being examined only in exceptional cases.

THE WHITEFISH (*Coregonus clupeaformis*)

The stomach contents of 42 whitefish of average size (1 lb. 2 oz.) taken from eight different parts of the lake between May 1 and October 30, were made up of the following organisms:

Molluscs (chiefly *Pisidium*) occurred in 37 stomachs in an average quantity of 28%.

Ephemerae—large nymphs occurred in 27 stomachs in an average quantity of 35%.

Chironomid larvae occurred in 18 stomachs in an average quantity of 14%.

The molluscs eaten by the whitefish were largely composed of *Pisidium* with small numbers of *Amnicola*, *Valvata*, *Planorbis*, *Physa* and young *Campeloma*. Although the average quantity of Mollusca per stomach was smaller than that of the ephemera nymphs, the molluscan part of the food was more constant, occurring in a larger number of the stomachs examined. The ephemera nymphs varied at different seasons from a mere trace to 95 per cent. of the contents of individual stomachs. They were the large burrowing forms, mostly *Hexagenia* with some *Ephemera*. Three less important food organisms, Ostracoda, Hydracarina and

Amphipoda, were found in the stomachs. The ostracods were often numerous but they are so minute that their nutritive value is negligible. Hydrachnids were unusually plentiful, occurring in 18 of the stomachs and averaging 6 per cent. of the total contents. Small quantities of *Chara* and *Cladophora* were found in several stomachs, but they are thought to have been taken by accident while the fish were feeding on the bottom organisms for which these plants provide a shelter.

Seven whitefish caught by angling at Jackson's point on November 7, 1928, were found to have eaten ephemerid nymphs 80%, chironomid larvae 10%, caddis and other insects 5%, *Pisidium* and *Amnicola* 5%. These specimens were taken in 10 metres of water and indicate the abundance and the utilization of mayfly nymphs at such depths. Although spawning had just begun, most of the fish appeared to be feeding freely.

The stomachs from whitefish taken at Beaverton on February 15, 1927, contained a number of lake shiners, *Notropis atherinoides*, and sticklebacks, *Eucalia inconstans*. While most of the former were undoubtedly those supplied as bait by the fishermen, it is improbable that the sticklebacks were from this source. The remainder of the contents were composed of ephemerid nymphs, chironomid larvae with a few caddis larvae and *Pisidium*.

A lot of 12 stomachs from whitefish caught at Jackson's point, March 1, 1928, contained large quantities of rice used in "prebaiting," page 157. Ephemerid nymphs, chironomids and *Pisidium* were present, a single specimen of *Mysis relicta* and a specimen of the Iowa darter, *Poecilichthys exilis*. It was of greater interest to discover that the stomachs contained eggs of the cisco, *Leucichthys artedi*. The eggs were in the eyed stage of development and were present in 5 of the 12 stomachs examined, in an average number of 16 per stomach.

A summary of all the available data indicates that the food of adult whitefish throughout the year in Lake Simcoe is composed of molluscs, 36%, ephemerid nymphs, 30%, chironomid larvae, 16%, caddis larvae, amphipods, hydrachnids, ostracods and fish eggs, 18%.

THE CISCO (*Leucichthys artedi*)

The food of the cisco in Lake Simcoe was determined by an examination of the stomachs of 31 specimens. While the plankton formed the greater part of their food it was noted that as they grew larger the amount of plankton eaten decreased somewhat and the quantity of bottom food increased. On the whole, their food was made up of about 81% plankton (largely of entomostracan forms such as *Bosmina*, *Daphnia*, *Cyclops*, *Diaptomus* and *Senecella*), 11% Ephemeridae, 5% chironomid larvae and 3% other insects, some of them terrestrial. Small numbers of *Pisidium*, oligochaetes, amphipods and ostracods were found in some of the stomachs. The Ephemeridae were mostly in the nymphal stage although in June and July the cisco stomachs contained specimens in which the last nymphal skin covered the future subimago. It is concluded that these individuals were proceeding to the surface for emergence when captured by the ciscoes. At the same season whitefish stomachs contained ordinary nymphs, indicating that the whitefish ate only the Ephemeridae in the bottom mud.

A more striking example of the ciscoes feeding on bottom organisms was found by the writer in Waskesiu lake, northern Saskatchewan, in 1928. In that lake ciscoes less than 25 cm. in length ate 76% Entomostraca and 18% insect larvae, while ciscoes between 25 and 38 cm. in length ate only 25% of Entomostraca and 60% insect larvae. The insect larvae were largely those of *Chironomus plumosus*, which was by far the most important bottom organism in the lake.

THE LAKE TROUT (*Cristivomer namaycush*)

The ciscoes form more than 90 per cent. of the food of the lake trout in Lake Simcoe. The length of the ciscoes captured by the seventeen trout examined ranged from 15 to 25 cm. and as many as six have been taken from a single stomach. Other fish found occasionally in the stomachs of trout are young suckers, the whitefish, perch and the brook stickleback.

THE COMMON SUCKER (*Catostomus commersonii*)

The analysis of 27 stomachs of the common sucker has shown that it feeds chiefly on insect larvae. The average composition of the stomach contents was: ephemerid nymphs 49%, chironomid larvae 18%, Mollusca, chiefly Gastropoda, 18%, amphipods 5%, and the remaining quantity, 8%, composed of fish remains, crayfish, isopods and vegetable matter. The gastropods eaten by suckers were chiefly small *Physa* and *Planorbis*, the amphipods all *Hyaella knickerbockeri*.

THE CARP (*Cyprinus carpio*)

The examination of carp stomachs is complicated by the large quantity of mud and unidentified debris which obscures the food organisms. In estimating the quantities of the following organisms the percentages are of the total food organisms exclusive of mud and debris. The food from eleven carp stomachs was made up of chironomid larvae 35%, Mollusca, *Physa*, *Lymnaea*, *Planorbis* and *Sphaeriidae* 27%, algae and higher plants 23%, ephemerid nymphs 9%, other insects, amphipods, oligochaetes and ostracods 6%.

THE CATFISH (*Ameiurus nebulosus*)

The stomachs from four catfish were found to contain *Cambarus* sp. 40%, ephemerid nymphs 36%, fish remains 15%, chironomids, caddis and other insects 9%.

THE PERCH (*Perca flavescens*)

Three large perch, each more than 3/4 lb. in weight, were found to have fed much like the bass, taking chiefly minnows and crayfish. Most of the perch are smaller and feed chiefly on the insect larvae as indicated by the analyses of 13 stomachs, the contents being composed of ephemerid nymphs 43%, chironomid larvae 5%, other insects, adult and larvae 25%, remains of small minnows 11%, the remainder 16% being made up of crayfish, gastropods, hydrachnids and ostracods.

THE SMALL-MOUTHED BLACK BASS (*Micropterus dolomieu*)

The small-mouthed bass feeds upon crayfish and small minnows or young fish. The analyses of 16 stomachs give

the following proportions in its diet: crayfish, *Cambarus* 53%, small fish 29%, dragonfly nymphs 8%, miscellaneous insects, amphipods and gastropods 10%. Since six of these specimens were taken near and in the mouth of the Beaver river where the crayfish is very numerous, it is possible that the average amount of crayfish taken by bass in the open lake is less than 53% of their total food.

THE ROCK BASS (*Ambloplites rupestris*)

Of nine stomachs of the rock bass which were examined, eight were found to contain crayfish. The total contents were composed of crayfish 74%, insect larvae, caddis, Odonata and ephemerid 20%, small fish and terrestrial insects the remaining 6%. Since the rock bass appears to compete with the small-mouthed bass for its chosen food the crayfish, it is fortunate that this species (*A. rupestris*) is not numerous in the lake.

THE LING (*Lota maculosa*)

The contents of twelve ling stomachs were found to be composed of 95 per cent. ciscoes with negligible quantities of chironomid larvae, Mollusca, *Mysis relicta* and Oligochaeta.

In the food of the bottom-feeding fish of Lake Simcoe there are three outstanding constituents, ephemerid nymphs, chironomid larvae and Mollusca. The ephemerid nymphs form a large proportion of the food of bottom-feeders throughout the year. In Lake Nipigon, Clemens *et al.* (1924) found that the Ephemeridae were much more abundant in fish stomachs at certain seasons than at others. In Lake Simcoe this is only partly true. During June and July, when the ephemerids are about to emerge, the stomachs of ciscoes and perch show a larger percentage of mayflies than at other seasons. That these individuals are caught while on their way to the surface is indicated by the fact that most of them are in the last instar with the subimago complete inside the nymphal skin. In the stomachs of whitefish and suckers the quantity of ephemerid nymphs is fairly constant through-

out the year. Since these nymphs are all large in size, it is clear that the duration of the nymphal stage of these burrowing forms over a period of at least two years is of importance in providing a constant supply of large nymphs for the consumption of the bottom-feeding fish. Such a condition would be impossible with a life cycle of one year.

The amounts of the three staple bottom foods eaten by the bottom-feeding fish in Lake Simcoe are shown in table 14.

TABLE 14. Comparing the composition of the more important food organisms of bottom-feeding fish in Lake Simcoe.

	1 White- fish	2 Sucker	3 Carp	4 Perch	5 Catfish	6 Average 1 to 4
Chironomid larvae....	16%	18%	35%	5%	5%	19%
Ephemero nymphs....	30%	49%	9%	43%	36%	33%
Mollusca.....	36%	18%	43%	18%

In the food of three of the five species shown above the ephemero nymphs are the most important source of food. For the whitefish they are almost as important as the Mollusca, but the carp, because of its shallow-water feeding habits, is unable to make use of the burrowing nymphs which abound in the deeper water.

Column 6 shows the average amounts of each food organism taken by the four more important bottom feeders. The catfish has been excluded since its numbers are too small to be comparable with those of the other fishes. If it were included the resultant average would be distorted accordingly. In the combined food of the remaining four, the proportions are: Chironomidae 19%, Ephemeridae 33%, and Mollusca 18%. In comparison with the food of bottom-feeding fish we may consider the bottom fauna, which was composed of Chironomidae 64.7%, Ephemeridae 5.8% and Mollusca 18.3% (page 99). The two series are not altogether comparable since in averaging the food requirements of four species we assign equal values to each, which is somewhat

inexact, *e.g.* the whitefish probably outnumber the suckers and their food demands are greater accordingly. The comparison does show, however, a striking difference between the supply and the demand as represented by the fauna present and the organisms eaten. The ephemero nymphs make up only 5.8 per cent. of the total bottom fauna and yet they supply 33 per cent. of the food of bottom-feeding fish, not to mention those eaten by the ciscoes during the period of emergence. A further reason for the discrepancy between food taken and food supply is to be found in the fact that a part of the fauna is not available as fish food. It has already been noted that the carp do not feed in deep water and are thus denied the larger mayfly nymphs and chironomid larvae. The evidence from fishing in the lake indicates that even the whitefish rarely feed deeper than 30 metres. Accordingly, a considerable quantity of the chironomid and other fauna of the deeper water is not available to them. This condition is most marked in greatly stratified lakes such as those in northern Germany studied by Lundbeck (1926). He found that the "frasszone" or range over which the fish fed was quite limited and that it was cut off fairly sharply at its deeper limit by the oxygen deficiency below the thermocline. In Lake Nipigon, on the other hand, whitefish are known to feed at very great depths, 90 metres or more, the bottom oxygen at these depths being sufficient for their needs. From these considerations it may be seen that a lake with an abundant food supply does not necessarily produce a large quantity of fish since the availability of this food is dependent upon other conditions in the lake.

The composition of the food of three important bottom-feeding fish in various lakes is compared in table 15.

To prevent any ambiguity it may be explained that at the upper left corner of the table, Whitefish, Mollusca 36%, Lake Simcoe, indicates that of the total quantity of food taken by whitefish in Lake Simcoe the Mollusca make up 36%.

The table indicates a considerable variation in the food of the same species in different lakes, a situation which is

TABLE 15. Comparing the composition of the more important food organisms taken by three bottom-feeding fish in four lakes.

		Lake Simcoe	Lake Nipigon	Oneida lake	Waskesiu lake
Whitefish	Mollusca.....	36%	14%	26%	23%
	Ephemered nymphs.....	30%	5%	8%*	
	Chironomid larvae.....	16%	28%		62%
C. sucker	Mollusca.....	18%	20%	30%	18%
	Ephemered nymphs.....	49%	20%	21%*	
	Chironomid larvae.....	18%	25%		68%
Perch	Ephemered nymphs.....	43%	30%	25%*	1.8%
	Chironomid larvae.....	5%			53%

*Insect material of all kinds.

readily explained. In Lake Nipigon, the whitefish food contains a small proportion of ephemered nymphs because, as indicated by Adamstone (1924), these nymphs are largely confined to the upper 10 metres. As has been mentioned above, the whitefish in Lake Nipigon feed at great depths, eating chiefly *Pontoporeia hoyi*. The quantities of this species, *P. hoyi*, taken in the deep water accounts for the lower proportion of all other bottom foods as compared with Lake Simcoe, in which there are no deep water amphipods. The common sucker, in Lake Nipigon, takes only 20% ephemered nymphs as compared with 49% in Lake Simcoe where the ephemered are more abundant. In the food of the perch the two figures, 30% in Lake Nipigon and 43% in Lake Simcoe, show a greater agreement, because in Lake Nipigon the ephemered are most numerous from 0-10 metres, in which zone the perch are also most frequent.

In Oneida lake the mollusc content of the stomachs is very great as compared with the insect food taken by each of

the three species. This is the direct result of the composition of the fauna, which was found by Baker to be more than 50% Mollusca.

In Waskesiu lake the burrowing mayflies are scarce and the chironomid larvae make up 94% of the total weight of the fauna. As a result of this situation the three species of fish under consideration all eat large quantities of *Chironomus plumosus*, while the ephemered nymphs are practically negligible as food.

It is evident that the diet of whitefish, sucker and perch is modified, depending upon the availability of bottom organisms. The fact that the larger ciscoes both in Waskesiu lake and in Lake Simcoe take a considerable quantity of bottom food may be regarded as further evidence of this adaptability.

The discussion of fish food may be summarized in the following manner: The bottom fauna of Lake Simcoe provides the major part of the food of whitefish, sucker and carp; it also supplies a considerable quantity of food for the perch, small-mouthed and rock basses and a small part of the food of the cisco.

Of the three staple bottom foods, ephemered nymphs, chironomid larvae and Mollusca, the latter two are of about equal importance, with the ephemered nymphs much more important than either. This is surprising in view of the fact that ephemered nymphs make up only a small percentage, 5.8, of the total fauna.

A comparison of the food of bottom-feeding fish in different lakes indicates that each species of fish is able to exist on very different diets if the fauna makes it necessary to do so.

THE AMOUNT OF NUTRITIVE MATERIALS IN THE DIFFERENT STATES

THE BOTTOM FAUNA

The total quantity of bottom fauna has been calculated and discussed on pages 95-99. The final estimate indicated

that the average dry weight of macroscopic organisms over all depths was 12.38 kgm. per hectare or 1,238 mgm. dry weight per sq. metre. From a chemical analysis of the organisms from thirty dredgings, the total organic nitrogen of the bottom organisms was found to be 7.5 per cent of the dry weight. The total organic nitrogen of the fauna may therefore be expressed as 0.93 kgm. nitrogen per hectare or 93 mgm. organic nitrogen per sq. metre.

THE PLANKTON

The purpose of the plankton investigation was to obtain an estimate of the total plankton present during the summer in order to compare it with the amount of plankton in other lakes and with the other forms of organic matter in Lake Simcoe. With this end in view the samples were taken over the whole period from May to October in order to minimize the effect of minor fluctuations or pulses in the plankton. A number of series of vertical hauls have not been completely examined but as yet they indicate nothing unusual in the vertical distribution of the plankton forms.

Twenty-eight total vertical hauls taken with the 18-inch net (page 27), in various parts of the lake have been weighed and submitted to chemical analyses. About five hauls were taken in each month from May to October inclusive and they were distributed over the 15-20 metre depth zone. Since the average depth of the lake is 17 metres it is thought that these total vertical hauls are quite representative of the plankton in the lake over the five-month period.

The average weight of plankton in the total vertical hauls was 34.5 mgm. dry matter and the average of the total organic nitrogen content was determined as 4.5 mgm. The shape and construction of the net was such that its efficiency, (page 28), was very low, the correction factor being 4.32. The column of water through which the net was drawn had a volume of 106 cubic feet or 3.0 cubic metres. The plankton collected was therefore 11.6 mgm. dry weight per cubic metre. Applying the correction for the efficiency of the net,

the total net plankton throughout the summer is seen to be 50.11 mgm. per cubic metre.

In order to make this value comparable to those given by Juday for Lake George (1922) and for Green lake (1927), the percentage of ash was determined by the method described by Juday (1922, page 44). Representative plankton samples from Lake Simcoe had an ash content of 27 per cent. (dry weight basis) as compared with 32 per cent. in the plankton of Lake George. The difference is apparently due to the larger proportion of diatoms in the plankton of the latter lake. The quantity of dry organic matter in the net plankton of Lake Simcoe is therefore 36.58 mgm. per cubic metre. In Lake George it was 21.2 mgm. and in Green lake 62 mgm. It is seen that the quantities of plankton in three lakes are related in the same manner as their bottom faunas (page 103), *i.e.* Green lake contains the greatest fauna and plankton, Lake George the smallest fauna and plankton. Attention has already been drawn to the fact that Lake George, a smaller but deeper lake than Lake Simcoe, supports a smaller fauna probably because of its greater depth. It would appear that for the same reasons it supports a smaller quantity of plankton.

This correlation between the amount of plankton and the amount of bottom fauna in different lakes is of special interest from three viewpoints:

It is an indication of the essential interdependence of the two groups of organisms.

It throws some light on the question of indices to the richness of lakes (page 142).

It is a confirmation of one of the basic assumptions in the trophic classification of lakes (page 91), *i.e.* that certain lakes are characterized by rich plankton, rich bottom fauna and a low supply of oxygen in the deeper water while others have a scanty plankton and bottom fauna and plenty of oxygen.

Juday (1922) found in examining the plankton of a large number of lakes that the net plankton represents about 1/10 of the total plankton, the remainder being made up of the nannoplankton which may be separated by centrifuging. On

this basis the total plankton of Lake Simcoe from May to October would average about 365.8 mgm. dry organic material per cubic metre. The annual crop as distinct from the amount of plankton present during the summer months is too complex for our present methods of calculation.

THE NITROGEN OF THE BOTTOM OOZE

As an index to the organic content of the bottom ooze and detritus layer, samples were submitted to a chemical analysis which determined the total organic nitrogen. The relation of the amount of nitrogenous material, presumably an indication of the nutritive value of the detritus, to the amount of bottom organisms present in different parts of the bottom of Lake Simcoe, is dealt with in the following section under indices to the richness of lakes. The average amount of total organic nitrogen present in the upper 5 cm. of the bottom deposits in Lake Simcoe was 1.045 mgm. per kgm. dry weight. This is equivalent to 156.7 gm. per sq. metre or 1567 kgm. per hectare.

In his investigation of the connecting lakes of the Illinois river, Richardson (1921) found that the mud of the "deeper bottom land" lakes contained 2.7 mgm. organic nitrogen per kgm. dry weight. The mud of shallow weedy lakes contained 3.9 mgm. organic nitrogen. Deep water bottom deposits in Lake Simcoe show an average of 1.04 mg. organic nitrogen per kgm. dry weight.

It is not known what proportion of the nitrogenous material represented by 1567 kgm. organic nitrogen per hectare (1393 lb. per acre) is available as food for the bottom organisms. It is interesting, however, to note the great excess of this organic material over the organic nitrogen content of the macrofauna which amounts to only 0.93 kgm. per hectare (0.827 lb. per acre).

In the aforementioned "deep bottomland" lakes, Richardson found a bottom fauna of 396 kgm/ha live weight, about 79 kgm/ha dry weight. While the life conditions in these lakes are somewhat different from those in Lake Simcoe,

it is noteworthy that the bottom muds contained three times as much organic nitrogen and supported more than six times as much fauna.

Of the states in which organic materials may occur we have still to consider the nannoplankton, the dissolved organic material and the fish. The fish are as yet an unknown quantity but the work of Birge and Juday and their associates has provided a considerable body of data on the other two materials. Their work indicates that the nannoplankton of Lake George collected by a high-speed centrifuge, contained as much as forty times the organic matter of the net plankton. This amount is greater than usual for the nannoplankton in most lakes is from six to ten times the net plankton.

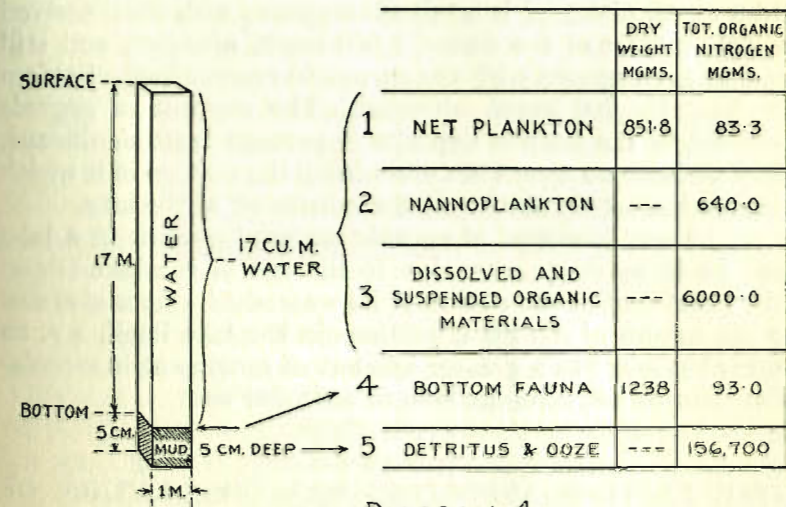


DIAGRAM 4

DIAGRAM 4. The vertical distribution of nitrogenous organic matter (exclusive of fish) in Lake Simcoe.

The dissolved and colloidal organic matter in the lake has been shown to make up about 85 per cent. of the total organic matter in the water, the remaining 15 per cent. being made up of plankton (Birge and Juday, 1927). This relation between plankton and total dissolved organic material, and