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A STUDY OF THE MAY FLIES (*HEXAGENIA*) OF LAKE WINNIPEG

BY

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ABSTRACT

The economic status of the May flies (*Hexagenia*) of lake Winnipeg is discussed. The nymphs are particularly important as food for sturgeon (*Acipenser fulvescens*), whitefish (*Coregonus clupeaformis*), light-backed cisco or tullibee (*Leucichthys zenithicus*), goldeye (*Hiodon chrysopsis*), and sauger (*Lucioperca canadense*). Two species are present in abundance, *H. limbata occulta* and *H. rigida*, but the former outnumbers the latter by a ratio of 7 to 1. Characters are given for the separation of all stages of these species and their habits are described. Eggs of *occulta* were hatched after artificial insemination. Later development of both species was followed by statistical measurements of nymphs secured at different seasons. The life cycle extends over two years. Sizes at which moults take place are indicated. Maximum growth is in August and is correlated with the amount of phytoplankton in the lake. No growth takes place in winter. The number of nymphs of *occulta* of 10 mm. and more is estimated at 62,000,000 per sq. kilometre in the southern part of the lake, and 93,000,000 in the neighbourhood of the Narrows. Corresponding estimates for *rigida* are 4,500,000 and 44,000,000. Both species are scarce or absent over a large area in the north part of the lake. *H. occulta* shows a 10 per cent. preponderance of females but is probably not parthenogenetic. Males and females of *rigida* occur in equal numbers. Parasites are noted, but are local in distribution. *Occulta* is of greater economic importance than is indicated by the numerical ratio between the two species.

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INTRODUCTION

The data for the present paper have been gathered during the past four years (1927-1930). The collections of material have been made by the writer and others as part of a larger scheme of investigations undertaken by Mr. A. Bajkov for the Biological Board of Canada. Mr. Bajkov's assistance, both as a collector and in the provision of facilities for the work, is largely responsible for the accumulation of the necessary data. Most of the detailed information was obtained during 1929 and 1930.

Although the early stages of North American Ephemeroptera have received a certain amount of attention, published accounts have usually been limited to external descriptions or notes on habitats. The species of *Hexagenia* have not been made the subject of detailed study.

Various references to the habits, food, etc., of nymphs of this genus have been made by Needham (1901, 1920), Morgan (1911, 1913), Clemens (1915), Rawson (1930), and others. Unfortunately, until McDunnough's (1924, 1927) recent papers, the taxonomy of the genus was not understood, a number of species having been grouped together under a single name. Consequently it is not always evident which species (or how many) the previous writers had in mind. In fact, at the present time there are no published descriptions which serve to distinguish the nymphs of any of the species except *H. recurvata* Morg.

Alike from the scientific point of view and from the standpoint of its considerable economic importance, indicated below, *Hexagenia* provides good material for further investigations.

ECONOMIC STATUS

It is evident to anyone who has witnessed the extraordinary summer flights of the imagines, that these May flies must play a part of great importance in the general ecology of lake Winnipeg. A series of dredgings gives an even more striking picture of their predominance in the nymphal phase over large areas of the bottom. A study of the stomach contents of the commoner fishes of the lake shows that the nymphs constitute a very valuable food supply, being eaten to a greater or less extent by all the important commercial species.

Whitefish (*Coregonus clupeaformis* Mitch.)

Bajkov (1930b, pp. 4-7) gives details of the stomach contents of 246 whitefish from various localities in lake Winnipeg. The most important organism is the amphipod *Pontoporeia*. Next in importance are insect nymphs and larvae, among which *Hexagenia*, *Chironominae* and certain trichopterous larvae are represented in nearly equal numbers. Of these *Hexagenia* is of larger average size and probably provides a more continuous food supply throughout the year, as indicated on a later page. It certainly holds second or third place in the food of this very important commercial fish. The stomachs of the 246 listed by Bajkov yielded 679 nymphs, an average of 2.76 per fish.

CISCOES OR TULLIBEES (*Leucichthys*).

Bajkov (A systematic study of the genus *Leucichthys* in the prairie lakes, *MS.*) has recently made a systematic study of the tullibees of the prairie region and recognises five forms in lake Winnipeg. With the exception of *L. hoyi* Gill (a small species) these have all been of great and increasing commercial importance during the last few years. In a further paper (The food of tullibees (*Leucichthys*) in the prairie lakes, *MS.*) he discusses the food of these species. *L. nigripinnis* Gill, *L. nipigon* Koelz and *L. hoyi* Gill are plankton and surface feeders, and as such rarely take *Hexagenia* except in the winged phases. *L. artedi tullibee* Rich. is an omnivorous form and some individuals were found to have eaten *Hexagenia* nymphs in numbers. Imagines were also present in some stomachs. Nevertheless, *Hexagenia* cannot be regarded as a main food of this species.

On the other hand, *L. zenithicus* Jord. & Everm., the "light-backed tullibee," which is considered to be the best species from the commercial standpoint, is a bottom-feeder and subsists on the same organisms as the whitefish; 249 stomachs yielded 818 *Hexagenia* nymphs, an average of 3.3 per fish. Among all other organisms only *Pontoporeia* probably exceeds *Hexagenia* in the amount of food which it provides for this fish.

PICKEREL (*Lucioperca vitreum* Mitch.).

In lake Winnipeg this species apparently subsists to a large extent on small fishes. Out of a considerable number of stomachs examined, some contained *Hexagenia* nymphs, but these did not constitute an important part of the total food.

SAUGER (*Lucioperca canadense* Smitt).

Out of 30 stomachs (from Doghead to Bloodvein R.) examined by the writer, only 17 contained food. Of these, 11 had eaten *Hexagenia* nymphs, the total number being 23. No other organism occurred in so many of the stomachs, though *Mysis relicta* was represented by 29 specimens.

GOLDEYE (*Hiodon chrysopsis* Rich.).

The alimentary tracts of 80 fish were examined. These were from Wells harbour, in June 1929 and 1930. The food of the goldeye is more varied than that of the preceding fishes and includes many adult insects captured at the surface as well as a large number of bottom organisms and free-swimming forms. These stomachs were remarkable for the enormous numbers of *Sialis* larvae which they contained. As these fish were caught, however, just at the season when these larvae are swimming ashore in numbers to pupate, their preponderance in the stomachs probably represents a seasonal rather than an average condition. *Hexagenia* nymphs were present in 54 cases—a high degree of constancy for a fish with such catholic tastes—the number of individuals being 243. Probably they constitute an important standby during seasons when surface supplies are cut off and after the emergence from the water of various species of aquatic insects.

PERCH (*Perca flavescens* Mitch.).

A series of eleven stomachs from the lagoon at Gimli (July) contained no *Hexagenia*, the food consisting chiefly of Odonata nymphs, trichopterous and dipterous larvae and amphipods. On the other hand, six specimens taken in February, on the fishing grounds in the open lake east of Gimli, had fed almost exclusively on *Hexagenia* nymphs. The total combined stomach contents of these six fish were: *Hexagenia* nymphs 60, trichopterous larva 1, *Mysis relicta* 1, amphipods 2.

STURGEON (*Acipenser fulvescens* Raf.).

Bajkov and Neave (1930) have recorded the results of an examination of twenty-five fish from lake Winnipeg and connecting waters. The nymphs of *Hexagenia* were found to be "by far the most important single form" (*loc. cit.*, p. 45). Seven alimentary tracts were empty. The remainder yielded a total of 2,061 *Hexagenia* nymphs, an average of 114 per fish.

In addition to the fishes mentioned above, which are all of considerable commercial value, certain others which are of much less importance from the point of view of the fish industry find a staple food in *Hexagenia* nymphs.

Among these may be mentioned the ling (*Lota lota maculosa* Le Sueur), the northern sucker (*Catostomus catostomus* Forster), and the sheepshead (*Aplodinotus grunniens* Raf.), all of which appear to utilise *Hexagenia* nymphs (at least on the fishing grounds in the southern part of the lake) more extensively than any other food supply.

The winged phases of the "fish flies" as *Hexagenia* is termed locally, are eaten by tullibees, as already noted, and also by goldeyes, but owing to the limited season during which they are available and because most of the marketable fishes are bottom feeders, their direct importance as a food supply is negligible as compared with the nymphal stages. In fact, an estimate of their value based on the winged phases alone might be unfavourable to the May flies, for during the few days when the swarming season is at its height they frequently become somewhat annoying owing to sheer force of numbers. After swarming, the masses of dead bodies form feeding grounds for dipterous maggots, though whether these belong to objectionable species of flies, the writer has not determined.

SPECIFIC DISTINCTIONS

Needham (1920) recognises only two eastern species of *Hexagenia*, *H. bilineata* Say and *H. recurvata* Morgan. According to his definition, all the lake Winnipeg specimens belong to the first-mentioned species. McDunnough (1924, 1927), however, has separated Needham's "*bilineata*" into several species. Two of these forms are found in lake Winnipeg, and after examining a very large number of adults and nymphs, the writer has no doubt that they are specifically distinct. According to the nomenclature adopted by McDunnough, the two forms represented are *H. limbata occulta* Walker and *H. rigida* McDunnough.

Imagines and Subimagines.

As McDunnough has pointed out (*loc cit.*), the adult males can readily be distinguished by the form of the penes, which are short and hooked in *limbata*, long and nearly straight in *rigida*. The females are frequently very much alike. That of *occulta* is of rather larger average size,—body length 19 to 26 mm., wing length 19 to 24 mm., as against body length 18 to 24 mm., wing length 17 to 22 mm. for *rigida*. (These measurements are of specimens preserved in alcohol, body length being taken to end of abdomen without caudal setae. Specimens of *occulta* from Limestone bay, at the extreme northwest end of lake Winnipeg, average smaller than elsewhere, but are included in these figures). The wings of *occulta* usually show a yellowish tinge. The abdominal markings of *rigida* usually take the form of three sharply defined dorsal brown streaks on each segment, these streaks often, but not always, united posteriorly by a transverse brown band. The corresponding markings of *occulta* show great variation and may closely resemble the above, but usually the contrast between the light and dark areas is less sharp and there is a strong tendency for the mid-dorsal dark patch to become dominant while the lateral ones are reduced to narrow streaks. In extreme cases the abdomen may appear pale, with a broad central dark stripe running throughout its length. In *rigida* the lateral brown streaks are frequently larger than the mid-dorsal one. With the exception of the wing tinge, the same remarks apply to the subimagines, in which, however, the body is frequently of larger size than the imago (up to 28 mm. in the female of *occulta*).

The above distinctions are admittedly not absolute. In the writer's experience, however, female imagines and subimagines can be positively identified by examining eggs taken from the body cavity. In both species the chorion of the egg exhibits a reticular sculpturing. In *occulta*, however, the "strands" of the network are stouter and run straight or nearly so. In *rigida* they are rather finer and, seen under a high power of magnification, distinctly sinuous (figure 8, K, L). It is sometimes necessary to remove the contents of the egg in order to see this clearly.

Nymphs.

So far as the writer is aware the nymphs of these two species have not been distinguished by previous workers. A brief description is therefore presented herewith.

H. limbata occulta Walk.

Length of full-grown nymph (excluding setae): male, 18 to 29 mm.; female, 21 to 32 mm. (measurements are of specimens preserved in weak formalin). Body pale, in small nymphs almost entirely so, in older nymphs with abdominal maculations of same type as in adult, but somewhat fainter; gills brownish with pale fringes. Frontal projection broad, rounded or obtusely pointed, marked with a brown spot of variable size and shape. Mandibular tusks long, with a rather even curve (figure 7, A, B). Legs as described by Needham (1920, p. 281) under *H. bilineata*. For a description of the newly hatched nymph see p. 10,

H. rigida McDunnough.

Length of full-grown nymph: male, 18 to 23 mm.; female, 21 to 26 mm. Very similar to the above, but frontal projection narrower, acutely pointed or truncate at tip. Mandibular tusks more slender, more sharply upturned and hence not projecting so far in front of the head (figure 7, C, D). The older nymphs usually show the characteristic abdominal markings of the adult. The rudiments of the penes and forceps of the male appear at a comparatively early stage in both species, being sometimes distinguishable in nymphs only 8 mm. in length. Frequently the specific difference in the length of the penes can be detected almost as soon as they become visible, the penes of *H. rigida* being usually longer than the forceps for some time after the first appearance of these organs. The males of the larger nymphs can be distinguished as readily by their genitalia as the adults. The other characters mentioned are somewhat variable, but by taking account of them all, one is seldom left in doubt as to the identity of even very small nymphs.

RELATIVE ABUNDANCE

To obtain an idea of the relative abundance of these two species, it is obviously of little use to take the winged phases, since the season of maximum abundance is quite short, affected by meteorological factors, and usually does not coincide in the two cases. A chance collection might result in securing thousands of one species, and few or none of the other. On the other hand, a census of the nymphal population, which is present throughout the year, can readily be made by taking a large series of quantitative dredgings. Some details of this work are given on a later page. It may be noted here, however, that out of 2,871 nymphs which were dredged from all parts of lake Winnipeg and carefully examined by the writer, 2,513 were *H. limbata occulta* and only 358 were *H. rigida*,—a ratio of 7 to 1. The only stations at which the numbers of *rigida* approached—and in four cases exceeded—those of *limbata occulta*, were in the region of the Narrows, from Grindstone point to Berens island. Both south and north of this area the disproportion is greater than the ratio indicated above.

HEXAGENIA LIMBATA OCCULTA WALKER

WINGED PHASES.

The first winged flies of this species have been found on dates ranging from June 20 to July 1. The numbers increase fairly steadily until the middle of July, when a tremendous accession marks the height of the swarming season. After a few days the numbers may drop almost to zero, but lesser swarms or scattered individuals appear again at intervals until near the end of August. The greatest numbers of imagines do not appear simultaneously at all points on the lake. Nevertheless, the maximum does not necessarily occur later in the more northern localities, as might be supposed. In 1930, for instance, the height of the swarming at Gimli, near the south end of the lake, occurred from July 15 to 17. At Limestone bay, 220 miles further north, the maximum was passed before the 14th, as attested by the great numbers of dead and dying flies which were present on this date.

The subimagines emerge from the nymphal skins on the open surface of the lake. Though they can, and often do, ride moderate waves with success, a large number emerge during the early morning, a time well known to the local fishermen as being usually the calmest period of the day. Moreover, any light breeze would tend to set on shore at this time, creating favourable conditions for the flight to land. After this flight has been accomplished, the subimagines settle on vegetation, buildings, etc. The subimaginal skin appears to be shed usually on the following day. The numbers vary considerably in different years, but at the height of the swarming season are beyond all comprehension. During the daytime any intrusion into grass or bushes near the shore produces a whirring cloud of May flies. White houses appear blackened and telephone poles show a furry outline due to the vast numbers of clinging insects. The nymphal skins floating in the lake frequently form extensive brown carpets, and when these collect in bays, etc., they may effectively damp down wave action until they are finally cast on shore.

Towards evening, but still in broad sunlight, the imagines take possession of the air for a few hundred yards inland from the shore (see figure 1). During their dancing flight the more remote volitants gradually work towards the lake until at dark the whole flight is massed in a dense column which follows the contour of the lake shore and fills the air with the swishing of countless wings. The dance, however, does not extend over the water, nor even the open beach, but takes place above the outer fringe of vegetation (grass and trees, etc.) at the upper side of the foreshore. Under favourable conditions the greatest concentration of the swarm appears to be three metres or more above the ground. At copulation the pairs leave the swarm and fall through the air almost to the ground before flying towards the lake. The male then usually rejoins the swarm, while the female proceeds straight out over the water or lingers for a time in the neighbourhood of the water's edge. The altitude of the swarm allows room for the initial drop without "crashing." On an evening when conditions were marred by a rather strong breeze, the writer observed a small flight of males which kept low over the tall herbage (1 to 1½ metres above the ground). No copulation was observed on this occasion.

The height of the mating time was about 9 to 9.30 p.m., *i.e.* approximately an hour after sunset. No flights were observed to last later than 10.00 p.m.

It may be noted that in calm weather the breeze tends to set off shore at the time of swarming, due to the cooling of the land, creating favourable conditions for the females to distribute their eggs over the lake. Meteorological conditions, however, are not always suitable, or may change suddenly during the swarming period, and it is probable that on them depend to a large extent the numbers of the resulting generation of nymphs and also the manner in which they are distributed over the lake. The writer has seen mating flights interrupted or cur-

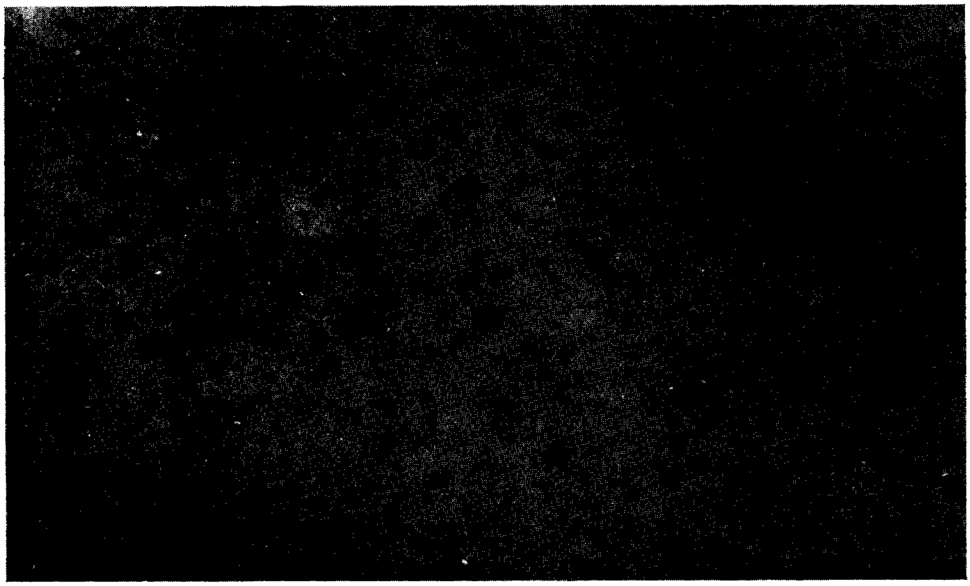

FIGURE 1. Flight of *Hexagenia limbata occulta*, Gimli, July, 1930 (photograph by A. Bajkov).

tailed by thunderstorms and strong breezes and there is little doubt that a series of years with bad weather at the swarming season would greatly reduce the amount of this potential fish food which is present in the lake. The direction and strength of the wind at the time of mating probably determine to a considerable extent the location of the eggs. On several occasions in the late evening the writer has seen females of this species flying downwind over the lake, sometimes several miles from the nearest shore. Doubtless they had come from a swarming party over the land.

EGGS.

The eggs average 0.30 by 0.18 mm. and are somewhat oblong in shape. As mentioned previously, the chorion exhibits a characteristic reticular form of sculpturing (figure 8, J, K). Needham (1920), writing of the composite species

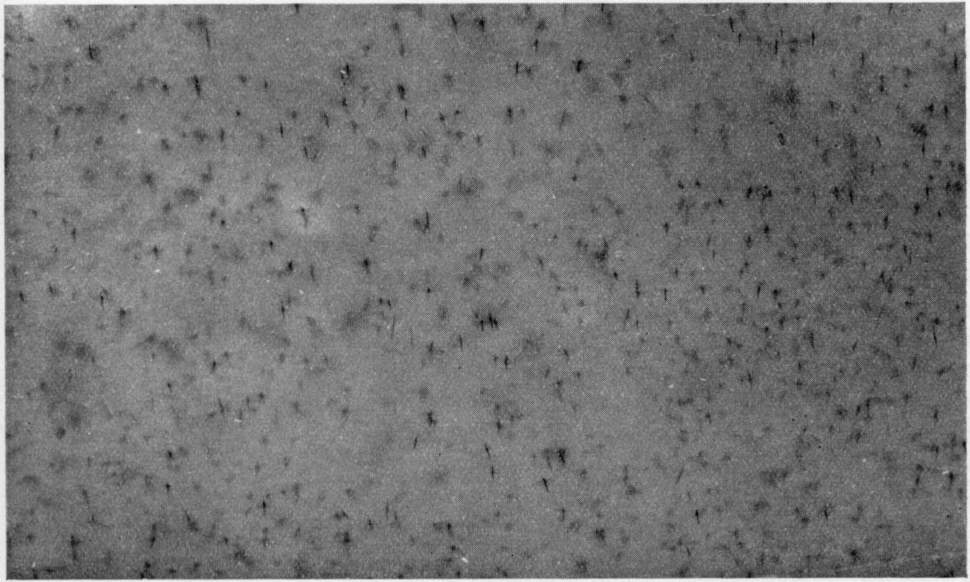

FIGURE 1. Flight of *Hexagenia limbata occulta*, Gimli, July, 1930 (photograph by A. Bajkov).

H. bilineata, puts the usual number of eggs at over 8,000. Counts made by the writer on two newly transformed females of *H. limbata occulta*, gave 3,631 and 3,388, respectively. As described by Needham (*loc. cit.*) they are extruded in two compact masses which disintegrate in water, so that the eggs have a chance to become distributed by currents, etc., as they sink to the bottom.

HATCHING EXPERIMENTS

Owing to the difficulty of obtaining newly-laid eggs and following their development in their natural environment, the writer had recourse to a method of artificial insemination not unlike that which is practised in fish hatcheries. On July 26, a female which had been reared alone from the subimaginal condition in a cage, was taken and "stripped" of her eggs. The abdominal contents of a male which had similarly transformed in captivity were applied to the egg masses, which were then placed in a petri dish of water. The eggs distributed themselves on the bottom of the dish and adhered to it, this property making them very convenient for handling, examination under the microscope, etc.

On August 14, and for the next two or three days, nymphs emerged from these eggs, *i.e.*, 17 to 19 days after insemination. Probably this represents a fairly normal incubation period for this locality (Gimli), as the temperature in the laboratory did not differ greatly from that of the lake water during the time of the experiment (18-23° C.). Clemens (1915) obtained eggs of "*H. bilineata*" at Georgian bay and found that they took 36 days to hatch (p. 116).

In the present case about half of the eggs produced nymphs. Another batch, which was not inseminated, showed no signs of any development, and this result, together with observations made at the time of swarming, leads the writer to believe that parthenogenesis does not take place.

NYMPHS.

The nymphs escape from the egg through a longitudinal fissure.

Newly hatched nymph: length (without caudal setae) 0.86 mm., antennae 0.21 mm., caudal setae 0.27 mm. Antennae 5-jointed, bearing two short hairs at the tip; frontal projection not prominent; eye-spots small, frontal tubercles distinct; mandibular tusks not developed; legs not flattened as in older nymphs, abdomen without gills; caudal setae indistinctly 4-jointed (figure 8, M). Owing to the writer's enforced absence from lake Winnipeg during the following month, the early development of these nymphs was not followed. Judging by analogy, it would seem that most of the characteristic nymphal organs are rapidly acquired. Nymphs of the related form *Ephemera* obtained from the same locality on August 17, possessed a prominent frontal projection, flattened legs and abdominal gills, when only 1.5 mm. in length. Even at this early stage it was possible to distinguish them from *Hexagenia*. Mandibular tusks in *Ephemera* were not apparent until a length of 2.5 mm. had been attained.

In view of the difficulties of following out the life-history under natural conditions of nymphs which normally live buried in mud under some depth of water, it was thought that statistical methods might throw some light on the subsequent development. The larger nymphs, it is true, readily transform in captivity, and a number of subimagines were obtained in this way, but the nymphal period is much shortened under laboratory conditions (nymphs obtained from the lake on November 7, 1929, transformed on dates varying from January 27, 1930, to March 31, 1930, instead of waiting until the beginning of July) and the ecdyses, etc., are difficult to observe in these mud-dwelling creatures. The length of the normal life cycle is a matter of considerable importance in estimating the value of the species as a food for fishes. It is evident that if the nymphal period extends over one year only, there will be a season (at the time of swarming and during embryonic development) when only a few or no nymphs are available in the lake. Moreover, a bad swarming season would result in a greatly diminished supply of nymphs during the ensuing year. If, on the other hand, the life-cycle normally extends over two years or more, there would be medium or large size nymphs available at all times of the year, forming a continuous food supply. Also, the effects of a bad swarming season would be palliated if preceded or followed by a good swarming season, since both crops would be available together for the greater part of a year, thus tending to level down violent fluctuations in the total supplies present in the lake.

It was soon obvious, from the large numbers of nymphs of medium size present in August, just after the flight of the adults (the "record" number of nymphs per dredge being taken on August 23, 1929, between Hecla and Black island, when 401 were brought up in 10 hauls of a 9-inch (23.16 centimetre) Ekman dredge, *i.e.*, an average of 743 per square metre), that the life cycle must extend over two years at least. In order to obtain further information on the growth and the length of the nymphal period, a long series of nymphs, collected at different seasons of the year, was measured and the results expressed in the form of graphs. The measurements in every case were taken (to the nearest millimetre) from the frontal projection to the tip of the abdomen, excluding the setae. All the specimens were preserved in weak formalin and individuals which were obviously in an unnaturally extended or contracted condition were rejected.

Since the females, in general, attain a larger size than the males before transforming, it was felt that to obtain the best results the sexes should be separated for measurements. As mentioned previously, the male genitalia can readily be seen in the larger nymphs, but they are not always visible until a length of 14 mm. or more has been attained, necessitating the use of some other character for separating the smaller specimens. The most constant criterion which the writer could find lies in the shape of the eyes, those of the male being slightly larger and having a more distinct angle on their inner margins. The shape changes somewhat during development but careful comparison enables one to separate the sexes with some degree of confidence down to the smallest nymphs included in plotting length frequencies, *i.e.*, 6 or 7 mm. (figures 7 and 8, E-H). The somewhat laborious process of separating this species from *H. rigida* and of sexing the nymphs of both correctly has kept the number of measurements within modest limits. Nevertheless it is felt that they are sufficient to establish certain facts relative to the life-history. For the July population, length frequencies of 144 males and 172 females collected at or just before the swarming time, show (figure 2), particularly in the case of the males, two peaks, indicating the presence of two size groups. One of these groups represents nymphs about to transform, the other consists of one-year-old nymphs which will not swarm until the following year. The distinction is usually evident not only by size of body but also by the degree of development of the wing pads. For August length frequencies are given of the nymphal population (267 males, 289 females) after the emergence of the current year (figure 3). As might be expected, they tend to form a single main peak, lying between the two peaks of the previous graph and indicating the further growth of the year-old nymphs. For June length frequencies(figure 4) of 497 males and 617 females, do not conform so obviously to this view, and it will be noted that in all three cases there are a number of peaks, of varying size, which remain to be explained.

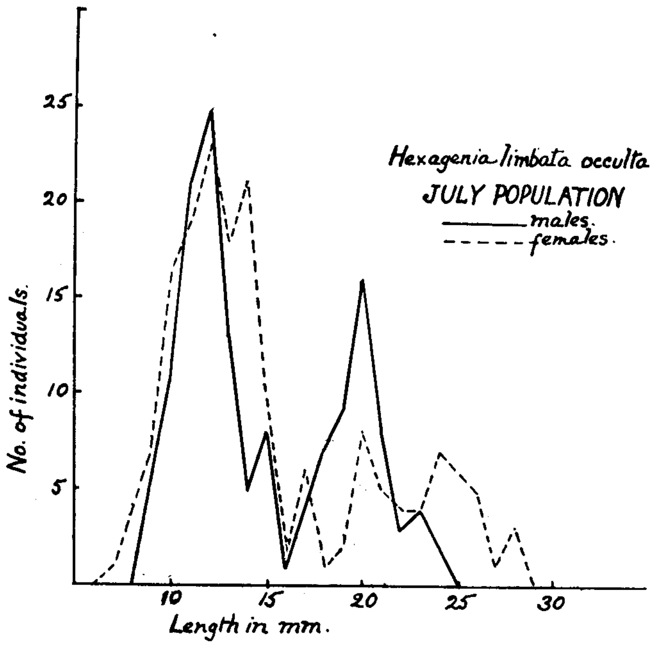

FIGURE 2. Length frequencies of July population.

At first it was thought that some of the smaller maxima might represent the product of the smaller swarms which occur after the main flight is over, or that they might be due to differences in dates of swarming in different parts of the lake. The whole egg-laying season, however, is so short that one would scarcely expect such definite groupings to be maintained throughout the nymphal life. Moreover, an examination of the graphs shows that, whatever the season, the peaks always tend to lie at certain points, though they vary in height. Thus, in the males, the maxima tend to lie at 13, 18 and 20 mm. The females are most numerous at or about 14, 17, 20, 23 and 28 mm. The conclusion is that the peaks represent sizes at which moults take place. The growth of *Hexagenia*, like other arthropods, is not a continuous process but takes place mainly immediately following ecdysis, before the new cuticle hardens. The depressions between the peaks indicate the comparative scarcity of nymphs captured during these short growth periods. In order to check, if possible, the accuracy of these conclusions, shed nymphal skins were collected and measured as opportunity offered. In view of the considerable degree to which they can be stretched or telescoped, these skins leave something to be desired as objects for exact measurement. They were, however, arranged in what was considered to be a normally extended condition. Out of 26 skins examined, 13 (including both sexes) were between 11 mm. and 14.5 mm. in length. The remainder were as follows: males, 18 (2), 22 (2), and 26 mm.; females, 17.5, 26, 27 (3), 28, 29, and 30 mm. These meas-

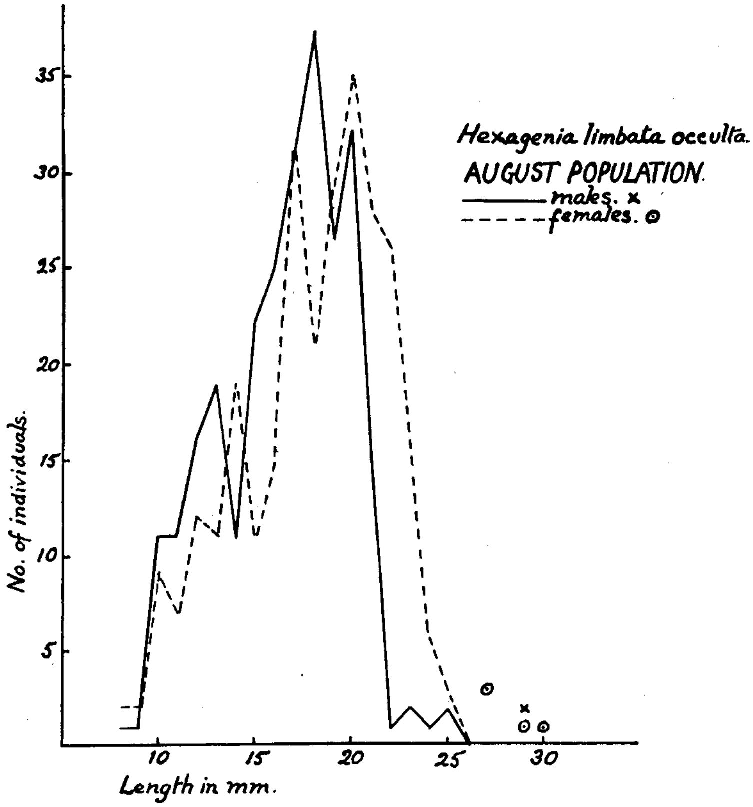

FIGURE 3. Length frequencies of August population.

urements, even allowing for slight inaccuracies, bear out the view that a moult normally occurs at about 12 to 14 mm., as indicated by the constant peak in the graphs. The female skins show another group from 26 to 30 mm., also corresponding approximately to a peak. The remaining scattered measurements are not inconsistent with the curves. The rapidity with which the nymphs grow to their new size after a moult is indicated by the size of two nymphs which still had their previous skins attached at the tip of the abdomen. One (a male) measured 21.5 mm., the attached skin only 18 mm. The other (a female) measured 16 mm., the skin 12 mm.

It seems that the female attains its larger size by undergoing about two more moults than the male. As to the number of moults which take place before the 13 to 14 mm. ecdysis, the writer is unable to hazard an opinion, due to lack of material as explained on page 17, last paragraph. From the evidence of these graphs and especially on the strength of a hundred nymphs collected in October,

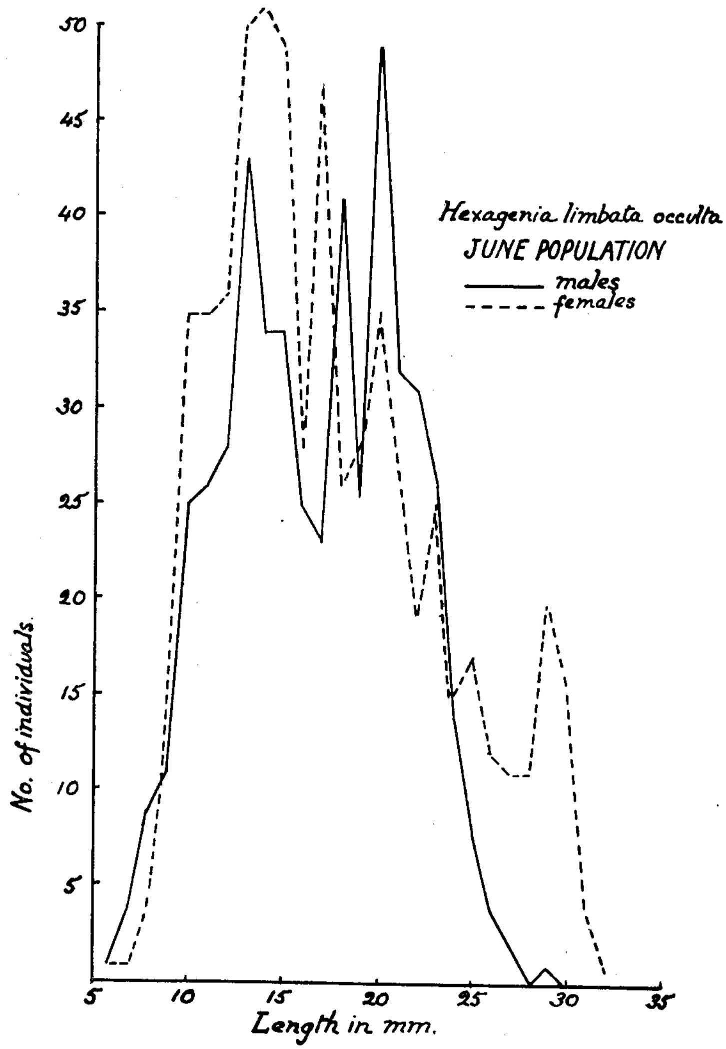

FIGURE 4. Length frequencies of June population.

the writer is inclined to think that there is a moult at about 10 mm. Not many nymphs, however, are in this instar during the summer months.

Roughly, the life-history can be summed up as follows. The eggs, laid in July, hatch in August and by the following June most of the nymphs are in the 12 to 14 mm. instar. Some have not yet reached this stage and, on the other hand, a few have probably attained the 17 to 18 mm. instar. In August most of them reach the latter phase or the 20 mm. halting point. Little or no growth takes place during the winter. In June of the second year the males are mostly in the 20 mm. instar, but many of the females have undergone one or more additional moults. The conditions under which the nymphs live vary widely in different places. Type of bottom, availability of food supplies, number of competitors of the same and other species must all affect the growth, and it is probable that by June there is a slight overlapping in size of the largest first-year individuals and the smallest second-year specimens. This overlapping is probably represented by the 17 to 18 mm. peak in the June graphs. The graphs also indicate the variations in the size of the "crop" from year to year. It will be seen that in the June graph the number of second-year nymphs is about equal to the number of first-year nymphs, although they have been exposed to the depredations of enemies for a year longer. This is due to the inclusion of a large number of dredgings made in June, 1930. The 1930 flight of imagines was a very heavy one and is correctly forecast by the graphs. A graph based on collections made in June 1929 only, shows a preponderance of first-year nymphs, which were estimated to form 61 per cent. of the material collected (see also the July graph, which is based mainly on 1929 material). The 1931 flight promises to be considerably smaller than that of 1930. Owing to these large fluctuations from year to year, and also to the probability that the methods of collection did not secure quite all of the first year group, it is impossible to estimate accurately the mortality which takes place during the second year of nymphal life, but the inference is that less than half of the nymphs which reach an age of one year are killed during their second year. This seems a low death rate, but it must be remembered that few animals prey on these large nymphs except certain of the larger fishes, some of which are depleted in numbers due to extensive fishing. Indications are that *Hexagenia* could provide food for many more fishes than exist in lake Winnipeg to-day. The mortality among the eggs and during the first year of nymphal life, of course, must be enormous.

FOOD.

The growth being intimately connected with the food supply, it is of interest to note the chief constituents of the latter. The contents of the alimentary canals of 23 nymphs were examined. These were taken at various localities in the northern and southern portions of the lake at various depths down to 15 metres, and ranged in size from 8 to 28 mm. They were collected during the months of February, July, August and October. The nature of the food was very similar in all cases, showing no appreciable differences according to age of nymphs or season of the year, though the quantity present in the February specimens was much less than in the others, one in fact being quite empty. The following organisms occurred most constantly: *Stephanodiscus niagarae, Melosira varians, M. granulata, Asterionella formosa.* Other algae included *Pediastrum* spp., *Synedra, Fragilaria crotonensis, Tabellaria, Navicula, Nitzchia, Oocystis,* and other minute forms of plant life. Animal fragments were found in 10 cases but they formed an insignificant part of the total quantity of food. The following forms were represented: *Daphnia, Diaptomus, Cyclops,* ostracod(?), also a rhizopod and the chaeta of an oligochaete worm. In addition to the food items, a quantity of mud, etc., was constantly present.

It is evident, therefore, that the nymphs subsist largely on phytoplankton, with an occasional *Daphnia* or copepod. The quantity of this phytoplankton is at a low ebb during the winter months. The nymphs feed less and undergo no appreciable growth during this season. A close relationship between the development of the nymphs and the quantity of plankton available is seen by comparing the nymphal growth with the seasonal variations in the amount of plankton (figure 5). The great abundance of plankton in August coincides with the period of greatest growth. Moreover, this increase in plankton, as explained by Bajkov

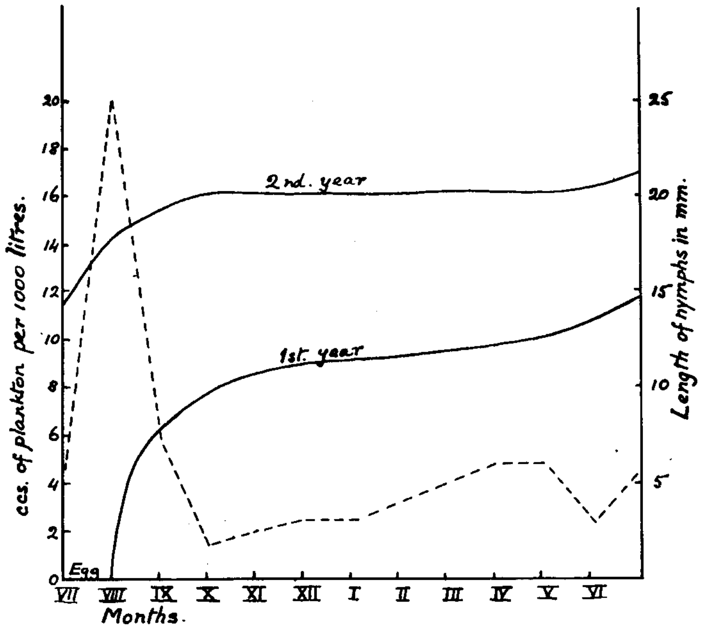

FIGURE 5. Growth of nymphs of *Hexagenia limbata occulta* over a two-year period. The broken line indicates seasonal variations in the amount of plankton present (after Bajkov).

(1930a), consists chiefly of the phytoplanktonic elements on which *Hexagenia* is especially dependent. It is possible to note also a coincidence between the August growth and the maximum temperature of the water. This, while doubtless a prime factor in causing the above-mentioned development of the phytoplankton, probably does not directly influence the nymphs to any great extent. As noted previously, imagines from Limestone bay are of smaller average size than elsewhere in the lake Winnipeg area. On account of its northern latitude, very shallow condition and remoteness from the influence of rivers, this bay is undoubtedly ice-bound for a very long season, leaving a shorter period for the development of the proper sequence of the plankton, and probably limiting the amount or the duration of the food supply for the nymphs.

DISTRIBUTION

The nymphs of *Hexagenia limbata occulta* occur from Warrens landing and Limestone bay, at the extreme northern end of lake Winnipeg to the southern limit of the lake and also in the larger tributary rivers, *e.g.*, the Assiniboine, Red and Pigeon. Within this area, however, distribution is not uniform and is affected by several factors in addition to the somewhat fortuitous manner in which the eggs are deposited.

The type of bottom is, naturally, of considerable importance. The favourite habitat is soft mud, which, according to Bajkov (1930a), constitutes 85 per cent. of the bottom of lake Winnipeg. The associated fauna of these mud areas consists chiefly of the crustaceans *Pontoporeia* and *Estheria*, various small molluscs (especially *Pisidium*, *Sphaerium* and *Amnicola*) and, among insects the larvae of *Phryganea* and *Chironomus*. *Chironomus*, however, not infrequently shows a sort of reciprocal relationship with *Hexagenia*, one or other being dominant in a particular "patch," though both inhabit the same type of bottom.

The nymphs also live to some extent, however, on clayey, gravelly and sandy areas, sometimes sharing the latter with the larvae of *Molanna*, and, in shallow bays, overlapping the habitats of *Ephemera*.

Depth, in itself, does not appear to have a great influence over distribution in this comparatively shallow lake, nymphs being found from quite shallow water down to 17.5 metres, which is almost the maximum depth of the lake. While it is true that *Hexagenia* is scarce over a large area in the northern portion of the lake where the depth is about 16 to 18 metres, it is possible that this scarcity is due rather to distance from land (over which the mating flights always take place) and to the character of the bottom mud which in many places is of a peculiar stringy character, favourable for oligochaete worms but ill-suited to the fossorial operations of May-fly nymphs. Rawson (1930), however, finds that in lake Simcoe *Hexagenia* fails at about 18 metres, so it may be that all these factors are at work.

Hydrogen-ion concentration within the limits recorded from this lake does not appear to influence distribution. The pH values in the lake itself vary from 7.9 (east shore) to 8.4, but are lower in some of the rivers inhabited by *Hexagenia*.

It is, of course, impossible to make any estimate of the numbers of eggs or very young nymphs in any locality, but some idea of the older nymphal population has been obtained by an extensive use of the Ekman dredge and careful counts of the resultant material. A 9-in. (23.16 cm.) dredge was employed and the organisms were extracted by means of sieves of 0.05 in. (1.16 mm.) mesh. This mesh undoubtedly allows very small nymphs to slip through and is perhaps not strictly accurate even up to 10 mm. or 11 mm. specimens. The proportion of individuals of smaller size than this, however, is not great during the summer months, when most of the dredging was done. Further, the time which is necessary to wash the tenacious mud of lake Winnipeg through a finer screen than the above without injuring the organisms, would preclude the taking of a large number of samples. In any case, it is necessary to draw the line somewhere, as the newly-hatched nymphs could pass through no. 6 bolting silk. The usual inaccuracies incidental to the use of the dredge are involved, namely, that it works much better on certain types of bottom than on others, and that it is sometimes difficult to avoid covering the same spot twice. Owing to these sources of error and the loss of a certain number of small individuals, as already explained, it is evident that the figures obtained represent minimum, not average, numbers.

A series of 650 quantitative dredgings made all over the southern part of the lake (*i.e.*, south of the Narrows) mainly in 1929 and 1930, produced 2,108 specimens of the present species. This represents an average of 3.24 per dredge or 62,000,000 per sq. kilometre (over 160,000,000 per sq. mile). This figure, however, is purely theoretical. It so happens that nearly all these dredgings were taken in

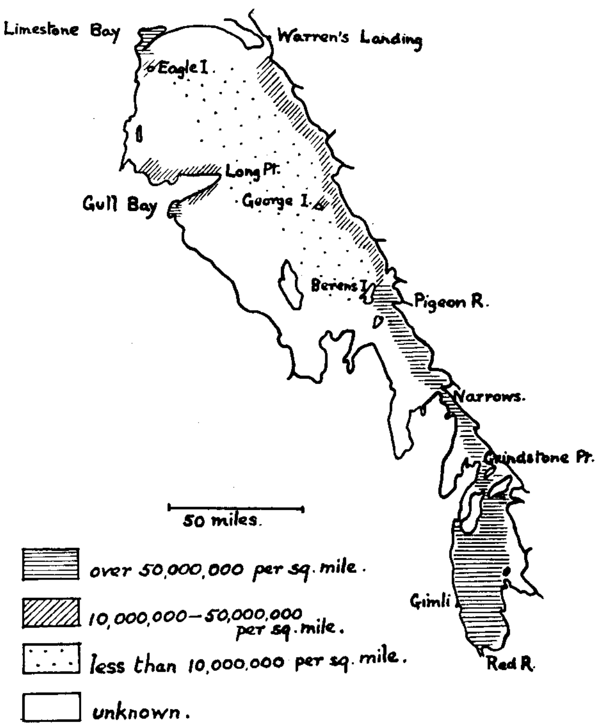

FIGURE 6. Lake Winnipeg, showing distribution of *Hexagenia limbata occulta* (50 miles = 80.5 km.; 50,000,000 per sq. mile = ca. 19,000,000 per km.^{2}).

June or early July just before the season of emergence. Obviously, a census taken in August would show a reduced population. On the other hand there would be countless numbers of unreckoned newly-hatched nymphs in the lake at this time. Bearing these facts in mind, however, the above figures can be used as an indication of the order of abundance of the species. As indicated previously, the distribution is not uniform, crowded spots being interspersed with sparsely inhabited tracts of bottom. From the evidence supplied by this "patchy" distribution and in view of the fact that the inhabitants of a patch frequently show a considerable uniformity in size and appearance, it is surmised that the nymphs usually do not migrate very widely.

In the great northern portion of the lake, a set of dredgings taken during the same periods as those already considered shows a different result. Only 522 nymphs were obtained from 1,000 dredgings, an average of 0.53 per dredge or 10,140,000 per sq. kilometre (25,650,000 per sq. mile). This statement, however, does not give a true picture of the population. In some localities near the shore and in the neighbourhood of islands, the nymphs are found as plentifully as in the southern portion of the lake. On the other hand, there is a very large central area, destitute of islands, over which *Hexagenia* is very scarce (see figure 6).

Sex Ratio

Out of 2,513 nymphs of this species collected at various points in both northern and southern portions, 1.135 were found to be males and 1,378 females, or 45 per cent. and 55 per cent., respectively. As these proportions were found to be roughly true at almost all stations where sufficient collections were made, there is no doubt that the females outnumber the males. Probably the males are capable of fertilising more than one female—at any rate, they nearly always rejoin the mating swarm after copulation.

Parasites

Needham (1920, p. 281) says: "I found a large nematode worm filling the body cavity of one . . . . . . specimen, and most of the nymphs have their gills thickly beset with the cysts of some parasite unknown to me." Many of the lake Winnipeg specimens carry the cysts of a trematode, apparently *Crepidostomum cornutum* Osborn. These cysts occur not only on the gills but also in the tissue of the abdomen and, less frequently, the thorax. The distribution of this parasite is somewhat sporadic, nearly all the specimens from certain localities being infected, while in other places few or none show any cysts. This irregularity in the proportion of parasitised individuals is indicated by the following random counts of nymphal material.

Locality	Date	No. of nymphs	No. parasitised	Percentage
Mouth Red river.............	31.V.29	45	42	93
Manigotagan-Hecla—Sta. I....	4.VI.29	79	0	0
" II...	"	138	0	0
" III..	"	132	0	0
Hecla-Black island...........	21.VI.29	62	2	3
Grindstone Pt................	22-24.VI.29	25	3	12
Hecla-Black island...........	23.VIII.29	358	4	1.1
Gull bay (Long Pt.)..........	7.VII.30	131	99	76

It is evident from these figures that the parasite is abundant in certain localities both in the northern and southern portions of the lake. The abdominal cysts are carried through the subimaginal and imaginal phases.

Seven of the nymphs from Gull bay (see table above) contained a large nematode (family *Mermithidae*) in the body cavity. Only one of these nymphs was also parasitised by *Crepidostomum*.

HEXAGENIA RIGIDA McDUNNOUGH

LIFE HISTORY.

Like the preceding species, the winged stages of *H. rigida* appear at the end of June or beginning of July and the imagines of both can frequently be found together during the following month or more. The present species, however,

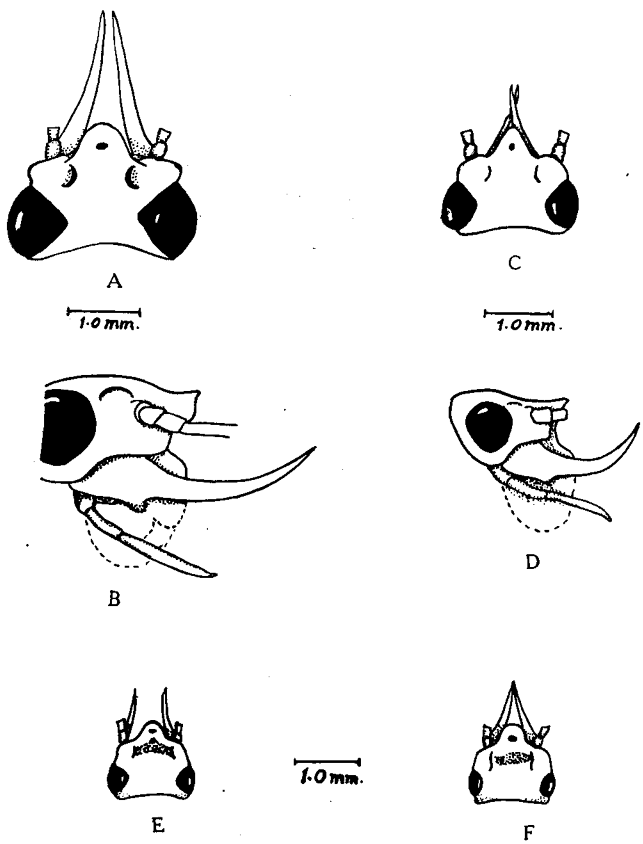

FIGURE 7. A—*Hexagenia limbata occulta*, head of male, 23 mm. long, dorsal view; B—the same, lateral view; C—*Hexagenia rigida*, head of male, 18 mm. long, dorsal view; D—the same, lateral view; E—*Hexagenia limbata occulta*, head of male, 11 mm. long, dorsal view; F—head of female, 11 mm. long, dorsal view.

appears to reach its maximum somewhat earlier than *H. limbata occulta*. At any rate, the only heavy flight of this species which the writer has encountered was on July 7, 1930, a week before *H. limbata occulta* attained its maximum abundance. This was a hot sunny day (temperature 30°C.). The number of imagines over a small area (a sand spit at Gull bay, near Long point) were as impressive as in the case of its congener. The spit is partly covered with willow and balsam poplar, and the stems, branches and under sides of the leaves were packed to capacity. Thousands, in fact, could not find perching room on the bushes and had to settle on the ground underneath. Not one specimen of *occulta* could be found, though a handful of *Ephemera simulans* was scattered among the hosts of *rigida*.

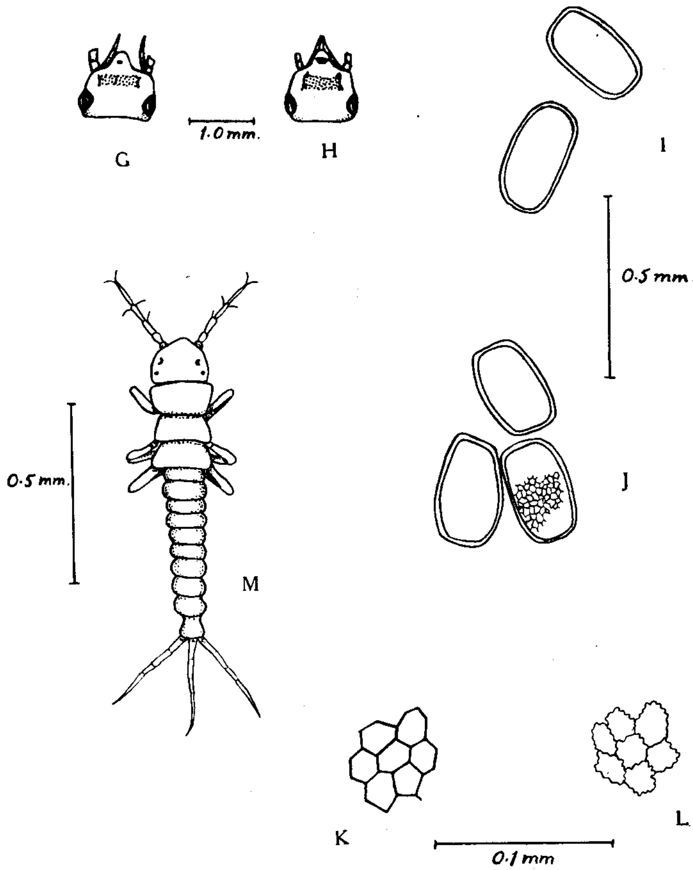

FIGURE 8. G—*Hexagenia rigida*, head of male, 10 mm. long, dorsal view; H—head of female, 10 mm. long, dorsal view; I—eggs (outline only); J—*Hexagenia limbata occulta*, eggs; K—chorionic sculpturing of egg; L—*Hexagenia rigida*, chorionic sculpturing of egg; M—*Hexagenia limbata occulta*, newly hatched nymph.

The number of eggs laid by each female appears to be somewhat less than in *occulta*. Two females taken from the above-mentioned flight yielded 2,400 and 1,800 eggs respectively. The eggs are similar to those of *occulta* in size and shape but show a characteristic difference in the chorionic sculpturing, as already described (figure 8, K, L). The incubation period is not known nor the stages immediately after hatching, but from 5 mm. onward they closely resemble the previous species, both in structure and habits. Indeed, it seems rather remarkable that the specific distinctions should be so constantly maintained between such closely related forms, living (frequently, at least) under identical conditions of depth, temperature, type of bottom, alkalinity, food, etc. While it sometimes appears that the present species is relatively more plentiful on a substratum containing an admixture of sand or gravel, it is impossible to make a general statement to this effect, as the two species commonly live in association.

Hexagenia rigida, like *H. limbata occulta*, has a life cycle extending over two years. This is particularly well shown in a series of 50 specimens taken in October—a season when size differences between the two sets of nymphs are most pronounced. The material falls into two definite groups, one (nymphs hatched in the current season) averaging about 8 to 9 mm. in length, the other consisting of individuals (more than a year old) about 20 mm. long. There is a complete break between the two groups.

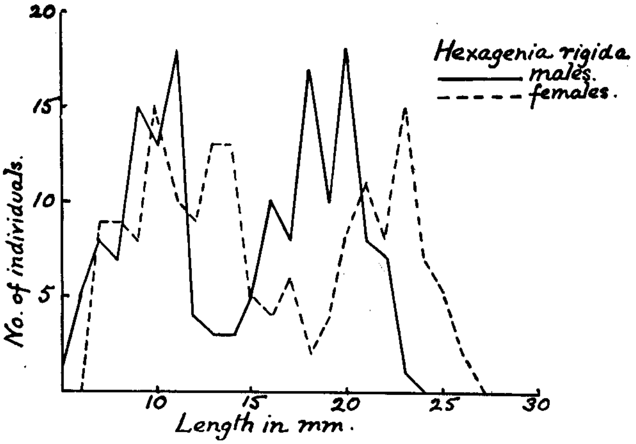

FIGURE 9. Measurements of nymphs, showing sizes at which moults take place.

A series of measurements was made on nymphs of this species, as in the case of *H. limbata occulta*, in order to determine the sizes at which moults take place. In view of the much smaller quantity of available material, it is not broken up into seasons, but the whole of the measurements from various months of the year are incorporated in figure 9. Since the object is merely to show the points at which the growth of the nymph tends to be arrested, the season of the year will not affect the result. The curve indicates moults at about 9, 11, 16, 18, and 20 mm., in the male, and 10, 14, 17, 21, and 23 mm., in the female. It will be noticed, that in both this species and *occulta*, the male shows a great increase in length between two of the early instars.

A number of skins of the last nymphal instar were measured after the escape of the subimago. In the male, these varied from 19 mm. to 23 mm. in length, in the female, 23 mm. to 25 mm.

Growth is sometimes very slow during the first year, nymphs of only 6 or 7 mm. being sometimes found in July, when they must be nearly a year old.

FOOD.

Hexagenia rigida feeds on the same organisms as *occulta*, the most important supplies in both cases being certain diatoms. The alimentary tracts of six nymphs, varying in size from 7 mm. to 24 mm., collected in July and October, yielded the following: *Stephanodiscus niagarae*, *Melosira varians*, *M. granulata*, *Asterionella formosa*, *Epithemia*, *Gomphonema*, *Navicula*, *Nitzchia*, various other diatoms and Chlorophyceae and a few fragments of small crustacea.

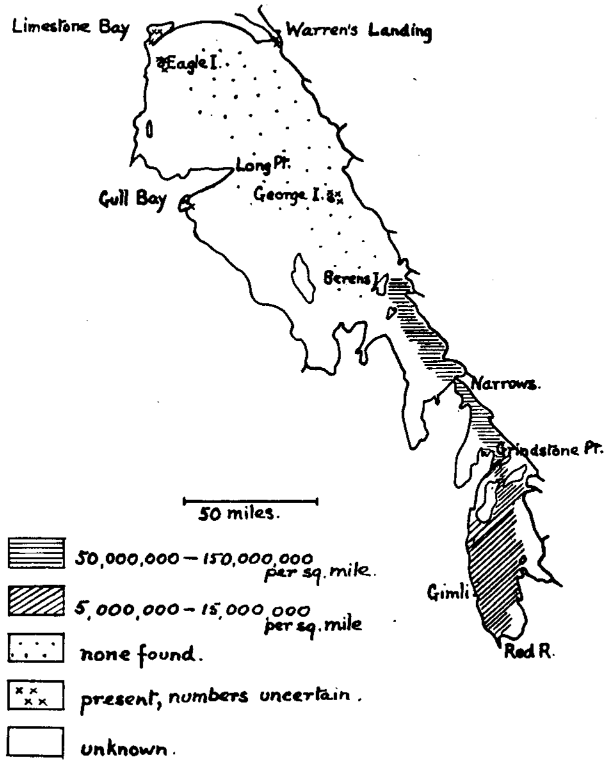

FIGURE 10. Lake Winnipeg, showing distribution of *Hexagenia rigida* (50 miles = 80.5 km.; 50,000,000 per sq. mile = ca. 19,000,000 per km.^{2}).

DISTRIBUTION

Nymphs of *rigida* have been obtained at depths varying from 2 metres or less to 16 metres, *i.e.*, the same range as *occulta*. Like the latter, the present species occurs from the extreme north end of the lake (Limestone bay and Warrens landing) to the southernmost limit (Red river), but, in general, is considerably less abundant. As indicated previously, the area of maximum abundance is an eighty-mile stretch extending north and south of the Narrows. Ninety-two dredgings in this area produced 211 nymphs of *rigida*, an average of 2.3 per dredge or 44,000,000 per sq. kilometre. During the same operations, 452 nymphs of *occulta* were secured, or 4.9 per dredge (93,700,000 per sq. kilometre). Thus, even in this part of the lake the ratio is 2 to 1 in favour of the latter species.

In the more open part of the south end of the lake the average was only 0.17 per dredge or 3,250,000 per sq. kilometre. For the whole of the southern part of the lake (*i.e.*, south of the Narrows) the average was 0.233 per dredge or 4,500,000 per sq. kilometre. Owing to the greater abundance of this species just north of the Narrows, the ratio for all parts of the lake examined is approximately 7:1 in favour of *occulta*, as mentioned on page 7, last paragraph. In the extensive area north of Berens island, *H. rigida* has been found mainly in sheltered inshore localities such as Limestone bay, Warrens landing, Gull bay (near Long point) and near islands (George island, Eagle island, etc.).

Sex Ratio.

Out of 358 nymphs of all sizes from 5 to 29 mm., which were critically examined, 178 were males and 180 were females. This indicates that the two sexes occur in equal numbers—a point in which this species differs from *occulta* (q.v.).

Parasites

Like its congener, *H. rigida* frequently carries trematode cysts. In the localities where the parasite is plentiful, the nymphs of both species appear to be attacked indiscriminately. The writer has not found nematodes in the present species but this is probably due to the smaller number of specimens which were examined.

COMPARISON OF *H. LIMBATA OCCULTA* AND *H. RIGIDA*

Though both these May flies are abundant in the ordinary sense of the word, it is evident that *H. limbata occulta* is relatively a much more successful species in lake Winnipeg than *H. rigida*. This success is shown chiefly in the utilising of the more open parts of the lake. Whereas *rigida* tends to cling to the narrow portion of the lake and localities not far from the shore, *occulta* has invaded also many feeding grounds in the wider parts of lake Winnipeg. Since these areas are the habitats of the whitefish (*Coregonus clupeaformis*) and other important commercial fishes, it follows that *occulta* is a more important species from the economic standpoint than is indicated by the general ratio of abundance between this species and *rigida*. Similarly, the fishing out of these commercial species will benefit *occulta* more than its congener and should increase the disproportion in numbers between them. This process may be taking place at the present time.

Presumably the great preponderance of *occulta* in the more remote areas is due to some of the females flying farther before depositing their eggs, since evidence has been adduced previously that the nymphs do not migrate extensively. It is perhaps significant that *occulta* appears to produce a greater number of eggs than *rigida* (see page 10, line 2, page 21, line 9). Lastly, the production of a greater number of females than males (see under "Sex Ratio") should be a potent agent in increasing the numerical advantage of *occulta* over its rival (assuming, of course, that the extra females can reproduce). Theoretically, in fact, if a species which has previously exactly maintained its numbers with a 50:50 ratio of males and females should develop a 45:55 ratio, and if the same number survived from each brood as before, it would double its numbers in seven generations. In any case we are probably justified in assuming that a 50:50 ratio is the primitive condition and that *occulta* has departed somewhat from this state. In general it would appear to be a more progressive and adaptable form than *rigida*.

It is noteworthy that, owing to the prolongation of the life cycle over two years in both species there is normally no genetic continuity between the broods of consecutive years. If the length of the nymphal life is unvarying, the May flies of the two lines of descent must be regarded as different "species," in the sense that no interbreeding can take place between them, and it is interesting to speculate on the possibility of mutations or other inheritable characters appearing in one strain and not in the other. It is quite possible, however, that by means of laggards or precociously developing individuals, the gap between the two lines of succession may be bridged to some extent.

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A Study of the May Flies (*Hexagenia*) of Lake Winnipeg

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