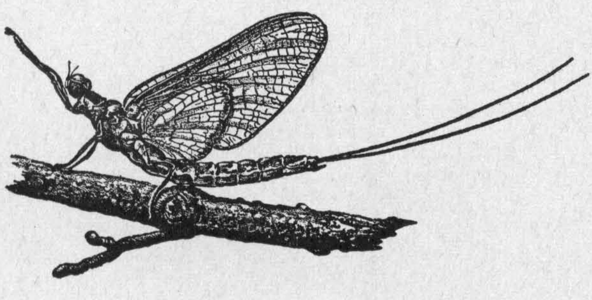
BULLETIN OF THE INSTITUTE FOR FISHERIES RESEARCH NO. 4

The Life History and Economic Importance of A Burrowing Mayfly, *Hexagenia limbata*, In Southern Michigan Lakes

By

Burton P. Hunt



MICHIGAN DEPARTMENT OF CONSERVATION

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THE LIFE HISTORY AND ECONOMIC IMPORTANCE OF A BURROWING MAYFLY, *HEXAGENIA LIMBATA*, IN SOUTHERN MICHIGAN LAKES

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INSTITUTE FOR FISHERIES RESEARCH
(Michigan Department of Conservation)

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ANNOUNCEMENT

The Institute for Fisheries Research is the technical and research agency of the Fish Division of the State Conservation Department operating in cooperation with the University of Michigan. The Department furnishes the funds and the University provides the office and laboratory facilities. The Director and most of the staff are permanent employees of the Conservation Department, but are assisted by special investigators and candidates for advanced college degrees.

The problems under investigation by the Institute as requested by the Department include: inventory of the lakes and streams to determine suitable management methods; studies of the life histories and requirements of the principal game and forage fishes; intensive studies of the food supply and means for its improvement; determination of fish yield by creel censuses conducted by Conservation Officers and by other Department employees—the latter on experimental lakes and streams where changes in regulations and other management procedures are being tested; experiments in fish population control; continued appraisal of the value of various methods of fish planting; and studies of fish parasites and diseases both in hatcheries and in natural waters.

Bulletin No. 4 of the Institute reports on the investigation of the burrowing mayfly, several species of which are of great economic importance to fishermen and bait dealers. The aquatic stages of these insects are extensively eaten by various species of fish, and they form one of the most popular baits used by anglers, especially in winter. The winged, adult stages stimulate feeding orgies of game fish at the surface of lakes and streams and are therefore of special interest to the fly fisherman. The mass emergence, mating flights, and subsequent death struggle on the water are eagerly awaited by trout fishermen in the north each summer, and many fine catches are made during these erroneously termed "caddis hatches." The need for proper conservation of burrowing mayflies to permit maximum harvest for bait and still not rob the natural fish food supply led to the studies reported in this bulletin. The findings recorded here will aid in establishing intelligent regulations to protect this resource and should also lay the groundwork for attempts to increase the supply throughout the state.

ALBERT S. HAZZARD
Director of the Institute for
Fisheries Research

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THE LIFE HISTORY AND ECONOMIC IMPORTANCE OF A BURROWING MAYFLY, *HEXAGENIA LIMBATA*, IN SOUTHERN MICHIGAN LAKES[1]

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INTRODUCTION

BURROWING mayflies of the genus *Hexagenia* (order Ephemeroptera) are widely distributed in lakes and streams throughout much of eastern and northern North America. Their great abundance in many localities is attested by huge flights of adults which occur in late spring and early summer. Throughout Michigan these insects are of general occurrence in many lakes and probably in all major river systems. Although they constitute a conspicuous element of the aquatic insect fauna in many places, comparatively little knowledge has existed on their habits, life history and ecological requirements.

Like all mayflies, members of *Hexagenia* hatch from eggs laid in the water, and spend the greatest part of their life span as aquatic nymphs. When mature, they transform to the winged stage and leave the water. Their life as aerial insects, lasting at most for only a few days, has reproduction as its sole objective. Common names of these insects in the winged stages in Michigan are: fish fly, Canadian soldier, June fly, sand fly, shad fly, "caddis" and "Michigan caddis." The two latter names, in general use by anglers on the principal trout streams of the Lower Peninsula, are particularly unfortunate since they attach to these mayflies the common name of a very different group of aquatic insects, the true caddis flies (Trichoptera). However, the term "caddis hatch" is in wide local use to designate not only the emergence but also the mating flights of these burrowing mayflies. The aquatic nymph is almost universally called "wiggler" by bait dealers and fishermen.

Because confusion often arises from the improper use of names, both common and scientific, it is well at this point to give some attention to the name applicable to the particular burrowing mayfly which is the subject of this study. The forms encountered in this investigation which were originally described as species and which have subsequently been considered by various workers as good species, subspecies or varieties, are *Hexagenia limbata* (Serville), *H. viridescens* (Walker), *H. occulta* (Walker), and *H. venusta* Eaton (Eaton, 1871, 1883; Ulmer, 1921; McDunnough, 1924, 1927; Ide, 1930; Neave, 1932; Needham, Traver, Hsu, 1935; Spieth, 1941; Lyman (MS); and others). In a survey of the genus, Spieth (1941) placed all of these forms as subspecies of a single species, *Hexagenia limbata* (Serville). The present writer found that adults in

[1]From a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan, 1950.

a single mating flight at the lakes studied exhibited the coloration and color patterns described for *occulta, viridescens* and *venusta,* and intergrades between the three. Since the populations seem to be completely heterogeneous in their color characteristics and display no discernible differences in life history or ecology, the author has chosen (Hunt, 1951) to regard the burrowing mayfly considered in this study as *Hexagenia limbata* (Serville). The description in Needham, Traver and Hsu (1935) which best fits the Michigan forms of *limbata* is that given for *H. occulta* (Walker).

Hexagenia limbata is the only representative of the genus found in the lakes investigated, although in the Great Lakes and in some inland lakes and streams it often occurs in company with other species. Collection of adults and nymphs from many localities in Michigan has led the writer to conclude that *limbata,* which is encountered in both lakes and streams, is the most common and widely distributed *Hexagenia* in the state.

Although the value of burrowing mayflies in the diet of fishes has long been known, it is only recently that the nymphs have been elevated to the status of a commercialized natural resource. For several years large *Hexagenia* nymphs have been important as bait for winter fishing in Michigan. Fishermen's demand for the nymphs has resulted in ever-increasing efforts by commercial bait collectors to obtain these immature insects for the market. Since nymphs are obtainable in quantities sufficient to be commercially profitable only from certain lakes and streams, concentrated bait collecting in such waters has increased greatly. Several problems have arisen as a result of this exploitation. Removal of nymphs and the concurrent disturbance of lake and stream bottom have met with considerable public opposition, based on assumed physical damage to lakes and streams and removal or destruction of fish-food organisms. Thus far the real effects of dredging and screening operations incidental to nymph collection on the *Hexagenia* populations and on the waters involved have been largely conjectural.

In order to obtain information which would facilitate intelligent handling of the problems involved and to form a basis for proper management of a valuable resource, an investigation of the biology and economics of burrowing mayflies in Michigan was undertaken. This study, begun in 1946, was supported by an Institute research fellowship in the University of Michigan.

Early in the investigation it became apparent that, although nymphs of several species of burrowing mayflies were used for bait, *Hexagenia limbata* (Serville) was by far the most important commercially; and, therefore, intensive research was restricted to this one species. Objectives of the study were to determine: (1) the length of life cycle and other pertinent facts concerning the life history, (2) ecological factors influencing distribution and abundance of nymphs, (3) density of nymphal populations, (4) importance of the species in the diet of fishes in the waters investigated, and (5) effects of removal of nymphs for bait. Much of the commercial collecting of nymphs for bait has been centered in southern Michigan. Pine Lake in Barry County and Gun Lake in Barry and Allegan counties were selected for study, since both have been important in the production of "wigglers" for bait (Fig. 1). Big Silver Lake in Washtenaw and Livingston counties was chosen because of its proximity to the Ann Arbor laboratory.

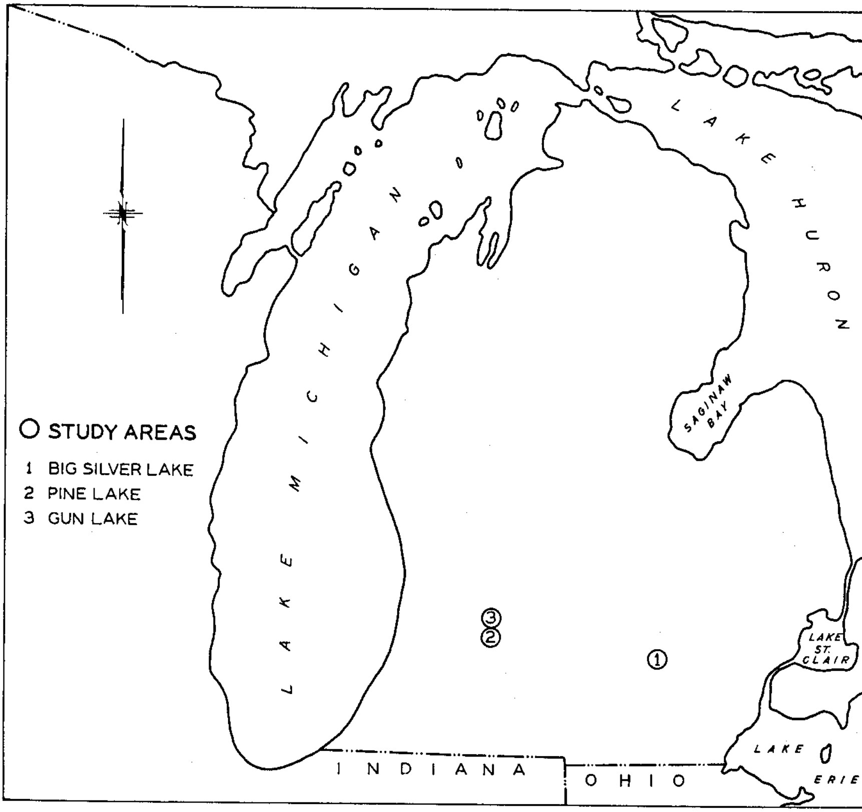


Figure 1. Map of part of Michigan showing the locations of study areas.

METHODS AND EQUIPMENT

Water temperatures were obtained by the use of pocket, maximum-minimum, and Negretti and Zambra reversing thermometers. Chemical analyses of water were made according to directions in *Standard Methods for the Examination of Water and Sewage* (1936); pH readings were obtained with a Hellige colorimeter.

To obtain the large number of quantitative samples of lake bottom mud necessary to study nymphal populations, an Ekman dredge with a sampling area of 0.25 square foot (Fig. 2), and a Petersen dredge with a sampling area of 0.82 square foot, were employed. Quantitative samples were washed in screens of 35 mesh-per-inch size, and organisms were sorted from the debris while still alive whenever possible (Fig. 3). When immediate sorting was not possible, samples were placed in 2-quart jars and preserved with 10 percent formalin for later examination. A "salting-out" technique similar to that used by Lyman (1943a) proved to be so effective in floating *Hexagenia* nymphs of all sizes that virtually all specimens in preserved samples were recovered. This procedure also worked well with fresh samples, provided the residues were relatively

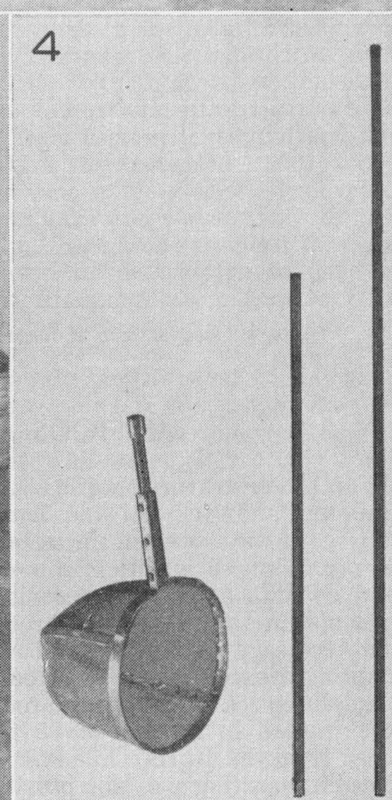


Figure 2. Taking bottom samples with Ekman dredge through ice on Gun Lake.

Figure 3. Sorting bottom samples on Gun Lake in winter.

Figure 4. Long-handled scoop used in reconnaissance sampling.

heavier than the nymphs. Specimens retained for study were killed in weak alcohol to prevent undue distortion, and preserved in 80 percent alcohol. Results of dredge sampling were recorded in terms of numbers of organisms per square foot of bottom.

It was impossible to collect all nymphs less than 4 mm. in length since they could pass through the 35-mesh screen. However, practically all specimens 5 mm. or more in length were retained in the screens. Specimens obtained by quantitative sampling were considered to be representative of the size composition of the entire nymphal population, within the limits of the methods employed.

Qualitative bottom samples were secured by means of scoops of various kinds (Fig. 4), to aid in reconnaissance work and to secure many nymphs quickly.

Measurements were made on large numbers of nymphs to ascertain average body lengths and the size composition of the populations. The body length of the nymph, as used in this study, is the length from the tip of the frontal projection of the head to the tip of the abdomen, excluding the caudal filaments. Individuals which were broken or in an obviously unnatural position due to excessive contraction or extension were rejected. Length measurements of large nymphs were made, usually to the nearest millimeter, with a micrometer caliper accurate to 0.1 mm. Very small specimens were measured with a Whipple ocular micrometer. In order to compare body lengths of live and preserved nymphs, 88 specimens of different sizes were placed in weak alcohol until swimming motions had ceased, were then measured to the nearest 0.1 mm., and preserved in 80 percent alcohol. After approximately six months the specimens were remeasured. The results indicated that, although some shrinkage accompanied preservation, the average amount was less than 0.5 mm. For the purpose of this study, it is considered that preserved length is equal to live length.

To determine sex of nymphs, two characters were used—genitalia of males, very obvious in large nymphs and visible in most specimens 10–12 mm. in length; and difference in size and shape of the eye. The eye characters, first employed and described by Neave (1932), allowed separation of the sexes in individuals as small as 4–5 mm., with some degree of confidence. The eye of the male is proportionately larger than that of the female and its median posterior margin is sharply angled, while that of the female is rounded.

Sex determination was made mostly on preserved nymphs, but it was also attempted on a sample of live nymphs as a check on the accuracy of the latter method. When 323 live nymphs, 8–16 mm. in length, were separated according to sex, divided into six groups, and reared to a larger size, the error was found to be from 0.0 to 4.4 percent (average 3.5). It seems quite certain that sexing of preserved material was accomplished with much less error than this.

Volumetric measurements of preserved material (and of live nymphs, for a conversion factor) formed the basis for comparing and computing the quantity of organisms present in bottom samples. The volumes of live and preserved organisms were determined in centrifuge tubes by displacement of water and alcohol, respectively. Weight of this material was secured by placing specimens on filter paper to remove excess liquid and then weighing them immediately on an analytical balance. Live volume and live weight measurements were obtained for each of 19 samples of nymphs containing from 7 to 103 specimens. After the samples had been in preservative for six months, volume and weight measurements were repeated. From these data a conversion factor of 0.95 was derived for changing preserved volume in cubic centimeters to an equivalent live weight in grams. By a similar procedure it was found that the factor for converting preserved volume in cubic centimeters of representative invertebrates, excluding *H. limbata* nymphs, into an equivalent live weight in grams is 0.97. (Using similar methods, Ball, 1948, found the conversion factor to be 0.98.) Since the factor is close to unity, 1 cc.

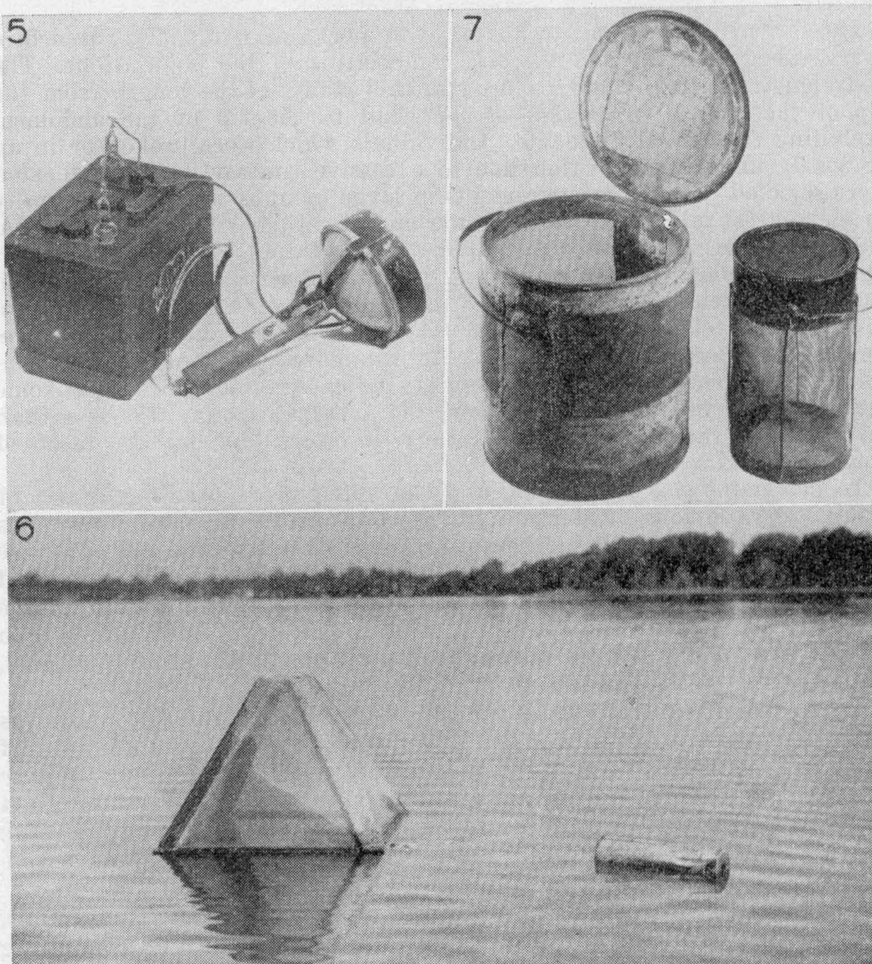


Figure 5. Sealed-beam spotlight and wet-cell storage battery.

Figure 6. Floating trap in operation.

Figure 7. Rearing cage, on left, and cage used to hold subimagoes, on right.

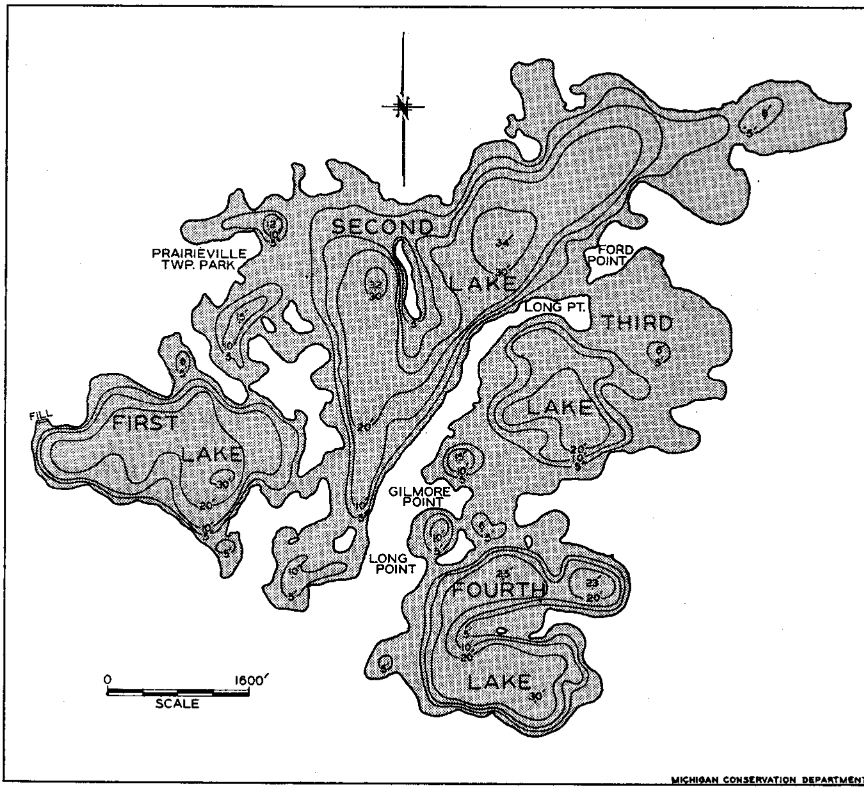


Figure 8. Outline map of Pine Lake.

of preserved volume of nymphs and other invertebrates is considered to be equivalent to 1 gram live weight.

Because emergence and mating activities of burrowing mayflies usually occur at dusk or later, a great deal of time was spent on the lakes at night. A gasoline lantern was employed for night collecting since the winged stages are attracted to light. A spotlight (Fig. 5), consisting of a sealed-beam automobile headlight connected to a 6-volt wet-cell storage battery proved very successful for general reconnaissance and observation. This light also could be used under water. During winter, underwater observations were made at night by using a small battery-powered light suspended through a hole cut in the ice. In order to supplement observations on the time and extent of emergence, pyramidal floating cages (Fig. 6), patterned after those employed by Scott and Opdyke (1941), were employed to trap insects as they left the water.

Rearing of nymphs to observe rate of growth and to obtain winged stages was an important part of the work. Specimens raised in natural waters or in artificial ponds at fish hatcheries were retained in tubs or screened cages of various kinds (Fig. 7). Indoors, aquaria of various sizes were used; some nymphs were reared individually in 1–gallon pickle jars. A layer of finely screened marl-mud 2–6 inches deep was placed in aerated aquaria, and depth of the layer was adjusted to the size of nymphs inhabiting it. Occasionally the old layer was removed and replaced by finely screened, fresh mud from Big Silver Lake, and water added when needed. High, screened covers placed on aquaria retained newly emerged subimagoes.

WATERS INVESTIGATED

Pine, Gun and Big Silver lakes differ greatly in shape, size and depth, but are very similar in their chemical, temperature and biological features, and are classified as "warm-water" lakes. All have numerous cottages on their shores, and are frequented by many people during both summer and winter.

Pine Lake (area 660 acres) has no inlet or outlet. It is divided into four basins—known locally as First, Second, Third and Fourth lakes—connected by channels of various widths (Fig. 8). Hereafter, these basins will be referred to by the numerical designations. Because most of the commercial bait collecting has been centered on Third Lake, the investigation of Pine Lake was confined largely to this basin.

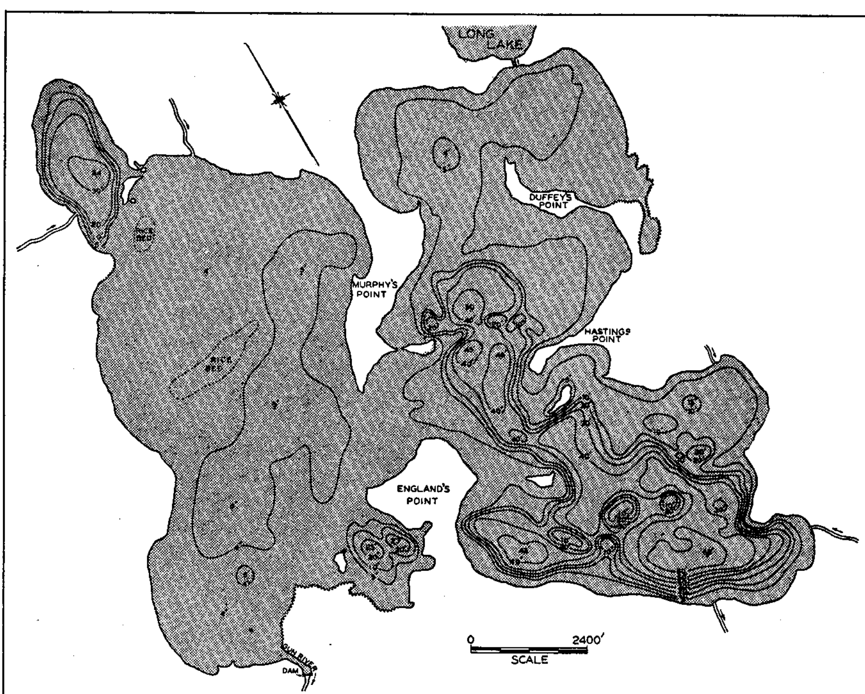


Figure 9. Outline map of Gun Lake.

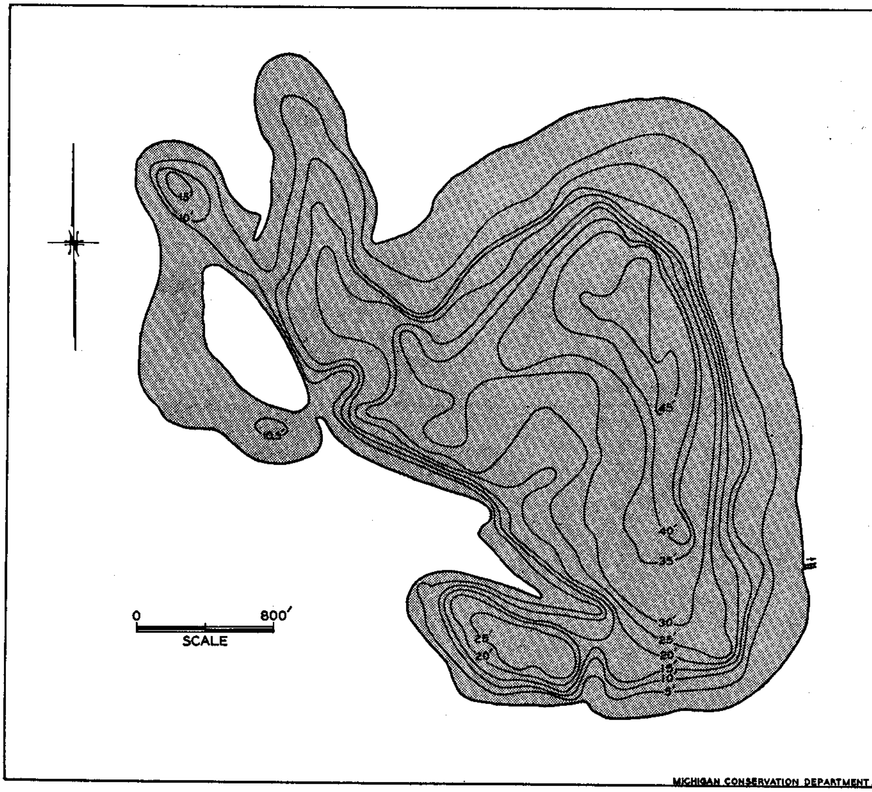


Figure 10. Outline map of Big Silver Lake.

Gun Lake, situated about 10 miles north of Pine Lake, is divided into two basins known locally as East Gun Lake and West Gun Lake (Fig. 9). It has an area of 2,680 acres. Inlets enter the north end of each basin; and the outlet, Gun River, is at the south end of the west basin. Most of the work in this study was done on West Gun Lake.

Big Silver Lake (area 217 acres) has a single basin with no inlet and one small outlet which enters the Huron River drainage (Fig. 10). Data for this study were secured from the entire basin.

Physico-Chemical Features

In all basins of Pine Lake the bottom in shoal areas is predominantly marl, grayish or whitish in Third and Fourth lakes, and considerably darker in First and Second lakes because of intermixed organic debris. Pulpy peat forms the bottom in the deep regions of all basins. Sand and gravel occur only in a few restricted areas around the lake margin. In Third Lake marl and pulpy peat are the principal bottom types (Fig. 11). Much of Third Lake is shallow, the depth being less than 3 feet in 45 acres (35 percent), less than 5 feet in 82 acres (63 percent), and under 10 feet in 98 acres (76 percent).

The main body of West Gun Lake has a maximum depth of 5 feet and much of the area is no more than 3 feet deep. The bottom is composed principally of sand, marl, muck and mixtures of the three (Fig. 12). Extensive sand shoals are situated along the entire eastern border of the basin and in two small areas on the western side. Most of the lake bottom is composed of fine mud, designated as marl in this report. The chief ingredient appears to be finely divided marl, but a sufficient amount of partly decomposed organic matter is present to give it a very dark color. In the two depressions and at the outlet the bottom is composed of very fine black mud, classed as muck for purposes of this study.

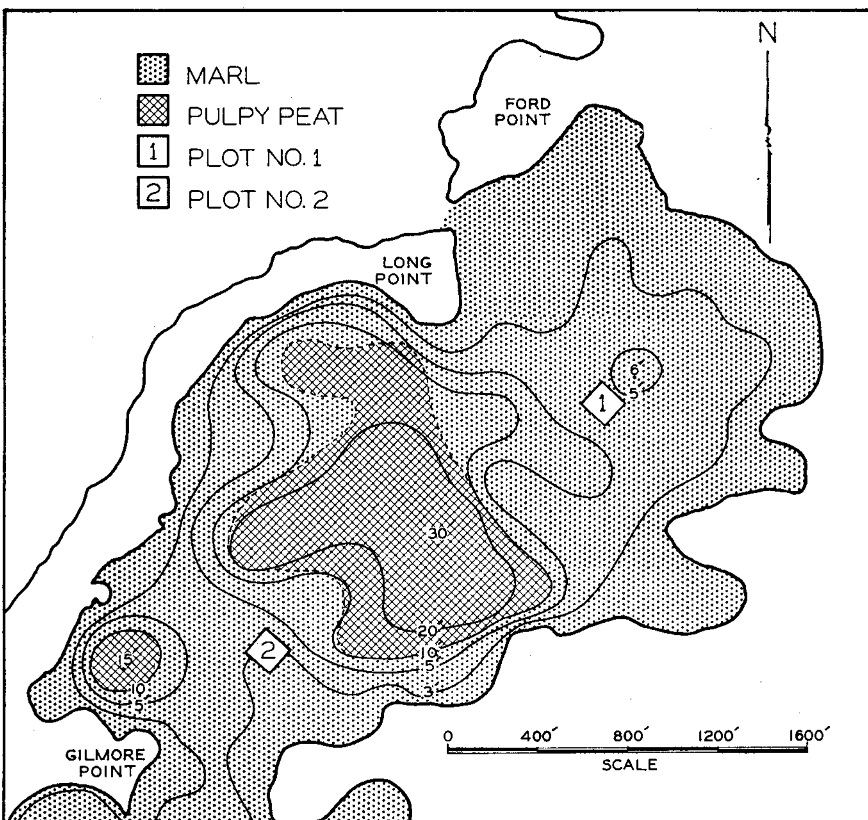


Figure 11. Bottom types in Third Lake (part of Pine Lake).

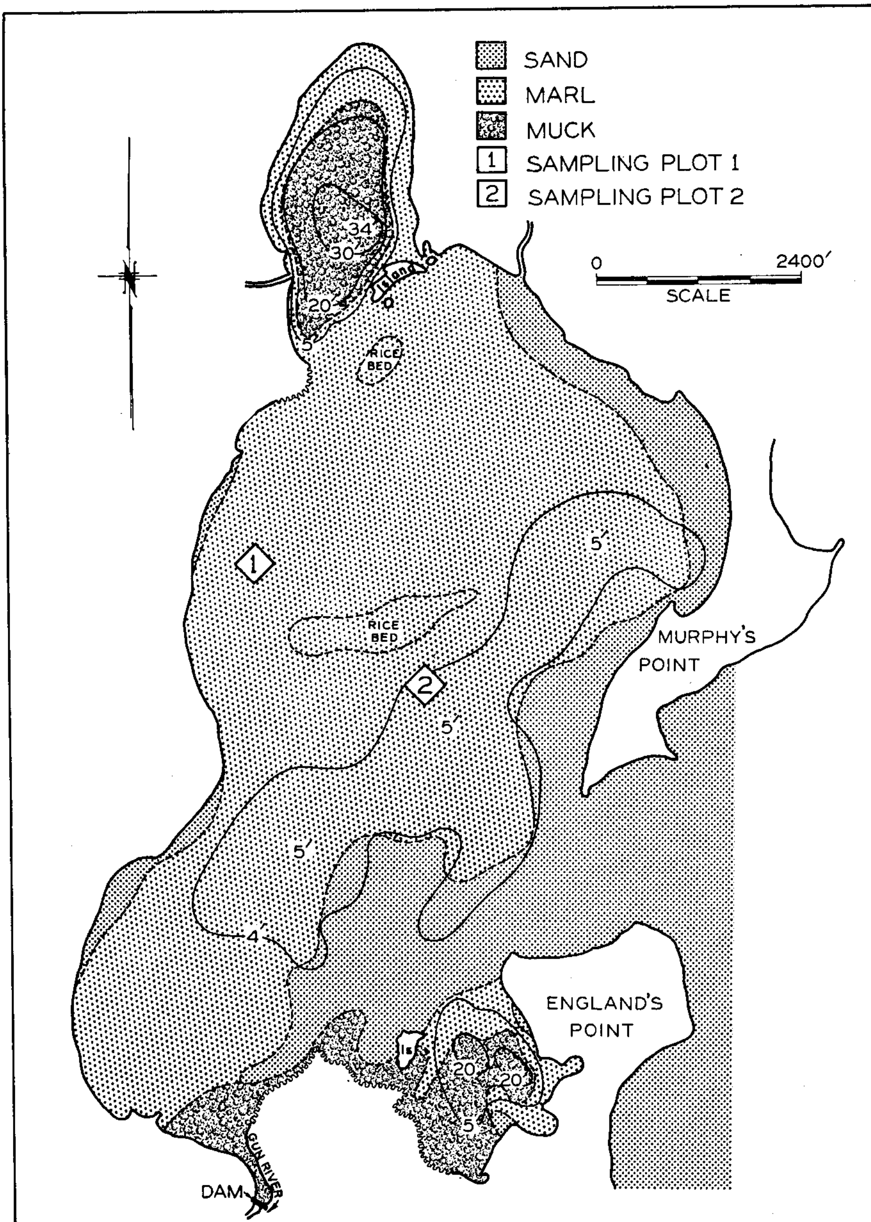


Figure 12. Bottom types in West Gun Lake.

The various bottom types in Big Silver Lake are depicted in Figure 13. Sand and gravel occur around the periphery of the basin, and marl bottom is so distributed as to form a band extending around the lake bordering the pulpy peat which makes up the bottom in deeper water. About 44 percent of the lake is less than 10 feet in depth.

Seasonal water temperatures were quite similar in the three lakes, although the summer maximum in West Gun Lake was usually about 3°F. higher than in the other two. Maximum-minimum thermometers were kept in Gun and Big Silver lakes for varying periods (Tables 1 and 2). In 1949, Big Silver Lake had maximum water temperatures, in degrees Fahrenheit, as follows: June 12, 77; July 2, 90; July 3, 91; July 4, 89. No continuous record was obtained for Pine Lake, but records made throughout the study period showed that seasonal temperatures were similar to those of Big Silver Lake. The lakes are ice-covered from late December to late March in most years. Surface temperature ordinarily rises to 50°F early in April and reaches 70° or higher by early June. Until September the temperature ranges from 70° to 90° F. or higher. By mid-October the

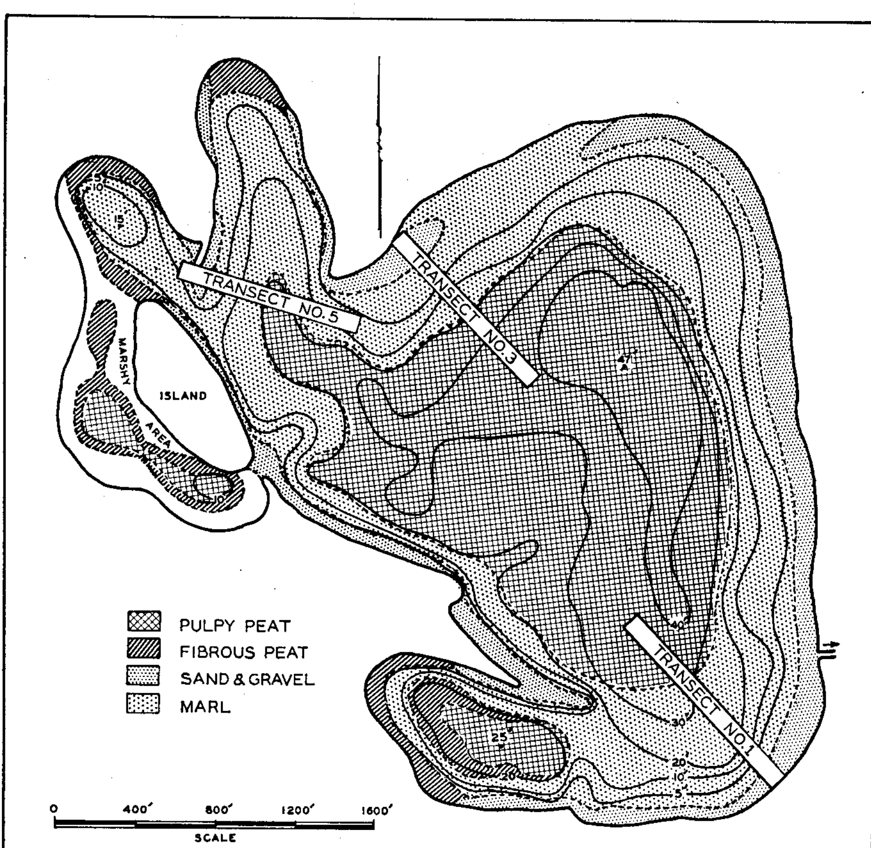


Figure 13. Bottom types in Big Silver Lake.

Table 1. Surface water temperatures of West Gun Lake

Period	Temperature °F.	
	Maximum	Minimum
1947		
May 19–21	66	60
May 21–22	68	63
May 22–June 3	70	54
June 3– 4	70	62
June 4– 6	71	67
June 6–July 1	85	68
July 1– 2	84	67
July 2– 3	84	74
July 3–Aug. 14	93	73
Aug. 14–15	89	81
Aug. 15–16	88	75
Aug. 16–Sept. 11	92	75
Sept. 11–12	81	76
Sept. 12–13	79	73
Sept. 13–Dec. 9	80	33
1948		
April 6–7	51	47
April 7–May 5	67	46
May 5–June 4	78	62
June 4–July 11	88	69
July 11–Aug. 26	91	74

temperature usually drops to 50° F. or lower and continues to decline until the freeze-up occurs. The lakes warmed up rapidly in the spring of 1946, 1948 and 1949, but the cold weather during spring and early summer of 1947 is reflected in the lower lake temperatures recorded during that period. Thermal stratification occurs in the depressions of the lakes in summer.

Chemical characteristics of the various lakes are shown in Table 3. In Third Lake dissolved oxygen was never entirely absent from the 25-foot depth but was reduced in late summer to less than 1.0 ppm. Oxygen ranged between 2.6 and 3.4 ppm. at the 20-foot level during the summer and winter stagnation periods. Chemical stratification was very marked in Big Silver Lake. However, during stagnation periods at least 1.0 ppm. of oxygen remained at 25 feet in summer and at 37 feet in winter.

Biological Features

Aquatic vegetation is, with few exceptions, similar in composition and distribution in each of the three lakes. In general, the marl and sand shoals of Pine and Big Silver lakes are rather barren and support a sparse growth of vegetation, principally *Scirpus* and *Chara*. Large areas in Third Lake support a moderate growth of *Najas*, evident only in late summer. In these two lakes a rather thick belt of vegetation extends around the perimeter of the depressions, located approximately between the 8- and 14-foot contours. *Anacharis, Ceratophyllum, Myriophyllum,* *Utricularia* and various species of *Potamogeton* are the most abundant plants in this belt. Heavy growths of dense *Chara* and *Nitella* occur from about the 14- to 18-foot contours, but no vegetation is found in water deeper than 18–20 feet. Because of its shallowness the western portion of Gun Lake supports a sparse to moderate growth of *Chara* and *Scirpus* over much of its basin. Various species of *Potamogeton* and other common aquatic plants occur in varying degrees of density over much of the shallow (2–3 feet) areas. Wild rice *(Zizania aquatica)* forms two rather dense beds, with a total area of about 25 acres.

The invertebrate bottom fauna in the lakes is similar and includes much the same assemblage of organisms. Snails, and fingernail clams (Sphaeriidae) were abundant. Large mussels, occasionally taken in samples, were not included in the counts of bottom organisms. Water mites (Hydracarina) usually occurred in limited numbers. Leeches were common in local areas in all lakes. Crustacea were represented by scuds *(Hyalella)*, abundant in all sampling areas, and crayfish *(Cambarus)* which were abundant in Gun Lake, common in Big Silver Lake and quite

Table 2. Surface water temperatures of Big Silver Lake

Period	Temperature °F.	
	Maximum	Minimum
1947		
May 3– 8	56	46
May 16–27	68	57
May 27–30	62	54
May 30–June 7	68	53
June 7– 9	74	65
June 9–11	74	68
June 11–16	74	63
June 16–19	74	64
June 19–27	76	70
June 27–29	80	73
June 29–July 6	81	74
July 6–Aug. 9	86	73
Aug. 9–10	81	78
Aug. 10–28	88	78
Aug. 28–Sept. 3	83	75
Sept. 3– 8	80	74
Sept. 8–30	80	60
Sept. 30–Oct. 6	64	60
Oct. 6–10	66	61
1948		
April 15–22	55	47
April 22–May 21	64	51
May 21–June 6	75	53
June 6–10	76	65
June 10–July 4	79	72
July 4–22	83	75
July 22–25	77	73
July 25–Aug. 1	76	74
Aug. 1–29	85	75
Aug. 29–Sept. 5	85	74
Sept. 5–12	76	70

Table 3. Physical and chemical features of Pine, Gun and Big Silver lakes.

Lake	Area in acres	Area of bottom types in acres				
		Sand, gravel	Marl	Pulpy peat	Fibrous peat	Muck
Pine	660	....	....	....	....	....
First	94	....	....	....	....	....
Second	323	....	....	....	....	....
Third	129	0.0	98	31	0.0	0.0
Fourth	113	....	....	....	....	....
Gun	2,680	....	....	....	....	....
East	1,457	....	....	....	....	....
West	1,223	243	865	0.0	0.0	115
Big Silver	217	34	95	75	13	0.0

Lake	Chemical features of surface waters Range throughout investigation			
	Free carbon dioxide, ppm.	Phenolphthalein alkalinity, ppm.	Methyl-orange alkalinity, ppm.	pH
Pine	0.0–1.5	0.0–16	104–135	7.7–8.3
First	0.0–0.0	4.0–14	102–133	7.9–8.2
Second	0.0–1.5	0.0–16	103–134	7.7–8.3
Third	0.0–1.0	0.0–14	104–135	7.8–8.2
Fourth	0.0–0.0	6.0–14	104–135	8.0–8.2
Gun	0.0–4.5	0.0–16	92–169	7.5–8.4
East	0.0–3.0	0.0–16	98–164	7.7–8.4
West	0.0–4.5	0.0–16	92–169	7.5–8.4
Big Silver	0.0–0.0	4.0–12	115–143	8.0–8.3

rare in Pine Lake. Aquatic insects constituted the most conspicuous element of the macroscopic bottom fauna. Mayflies (Ephemeroptera), caddis flies (Trichoptera), dragonflies (Odonata), and midges (Diptera) were the most important insect groups present. *Sialis* (Neuroptera) larvae, which frequently appeared in samples from all lakes, are burrowing forms frequently associated with *Hexagenia* nymphs.

Mayflies were represented by a number of species, the dominant form in all lakes being *H. limbata*. This species occupied most of the basin of West Gun Lake and the marl shoals of Big Silver and Pine lakes. In the latter body of water, comparatively few *limbata* nymphs were encountered in First and Second lakes but large numbers were found in Third and Fourth lakes. A smaller burrowing mayfly, *Ephemera simulans,* was abundant in sandy-mud in Big Silver and Gun lakes but was encountered infrequently in Pine Lake.

All three lakes contain large fish populations and are popular fishing areas. Those species captured for stomach analysis are listed in Table 4. Data concerning the number of fish caught and their food are presented in a later section.

Table 4. Fishes collected for stomach analyses

Common name	Scientific name	Pine Lake	Gun Lake	Big Silver Lake
Longnose gar	*Lepisosteus osseus*	....	+	....
White sucker	*Catostomus commersoni*	....	+	....
Lake chubsucker	*Erimyzon succetta*	....	+	....
Carp	*Cyprinus carpio*	....	+	....
Yellow bullhead	*Ameiurus natalis*	+	+	+
Brown bullhead	*Ameiurus nebulosus*	....	+	....
Black bullhead	*Ameiurus melas*	....	+	....
Northern Pike	*Esox lucius*	+	+	+
Yellow perch	*Perca flavescens*	+	+	+
Smallmouth bass	*Micropterus dolomieui*	....	+	....
Largemouth bass	*Micropterus salmoides*	+	+	+
Bluegill	*Lepomis macrochirus*	+	+	+
Pumpkinseed	*Lepomis gibbosus*	+	+	+
Warmouth	*Chaenobryttus coronarius*	....	+	+
Rock bass	*Ambloplites rupestris*	+	+	+
Black crappie	*Pomoxis nigromaculatus*	+	+	+

History of Bait Collection

Commercial bait dealers have been collecting large nymphs of *H. limbata* from Pine Lake for more than a decade. Initially, bait collecting (known among bait collectors as "wiggler digging") was largely confined to Second Lake, particularly the shoal area near Prairieville Township Park. From about 1944 to 1949, Third Lake received most of the attention of bait gatherers. Only a small amount of bait collecting has taken place in Fourth Lake in recent years.

For several years Gun Lake was the most important lake in the region as a source of nymphs for the bait trade. Most collecting was done in the west basin, but some digging occurred in the north end of the eastern basin. In 1946, a special act of the State Legislature prohibited the removal of nymphs from Gun Lake for commercial purposes. No collecting of nymphs, except for local use, has occurred since March, 1945.

So far as is known to the writer, commercial nymph collecting in Big Silver Lake has been on a very small scale and restricted to the activities of one man who operated in the bay on the northwest side of the lake. Some digging occurred during January and February of 1946 and 1947.

Sampling Stations

Widespread reconnaissance sampling, using both Ekman and Petersen dredges and screen scoops, was employed to determine the distribution and abundance of *H. limbata* nymphs in the four basins of Pine Lake. Extensive quantitative bottom sampling was conducted only in Third Lake and on the shoal at Prairieville Township Park in Second Lake. In the latter, bottom samples were taken at random over the shoal at irregular intervals. Sampling in Third Lake was confined, for the most part, to two specific areas and was conducted at regular intervals. Not all parts of Third Lake were dug by bait collectors; therefore, two square plots of 1 acre each were marked off and intensive sampling was carried out only in these designated areas. Plot 1 was located in a section used extensively by bait collectors, and Plot 2 in an area where they seldom operated (Fig. 11). The corners of each plot were initially marked in January, 1947 by poles driven into the lake bottom. During the summer these corners were marked by buoys. The major difference between the two plots was that the water depth in Plot 1 ranged from 5–6 feet, while in Plot 2 it was much shallower (2–4 feet). The marl bottom was similar in appearance in both areas but was more firmly packed where the water was 3 feet or less in depth. Vegetation, principally *Chara* and *Scirpus,* was scanty in both locations.

At the beginning of the investigation on Gun Lake, bottom samples, using both screen scoops and an Ekman dredge, were obtained throughout the entire lake to determine the distribution of nymphs. In January, 1947, square-foot samples were taken at 200-foot intervals along a transect extending across the lake from the tip of Murphy's Point northwestward through the wild rice bed to the western shore. Subsequent sampling was confined largely to two square plots of 2 acres each, designated as Plot 1 and Plot 2 (Fig. 12). The corners of each plot were marked during the winter by poles thrust into the lake bottom and in the summer by small buoys.

At Big Silver Lake, 9 transects, 50 feet wide, were established, each beginning at a marked point on the shore and extending outward at right angles into the deeper portions of the lake. Bottom samples were taken at marked stations along these transects. Subsequently, intensive sampling was restricted to Transects 1, 3 and 5 (Fig. 13). Reconnaissance sampling, conducted over the entire lake during the course of the investigation, disclosed the general distribution of burrowing mayfly nymphs.

LIFE HISTORY

In brief, the life history of all species of *Hexagenia,* in so far as it has been made known by the observations of many investigators, is as follows: Eggs, which hatch on the bottom of lake or stream, produce an aquatic larval form known as a *nymph,* the first of 3 different life history stages in the life cycle of each individual mayfly. Immediately the young nymph enters soft mud and begins a burrowing existence which continues for a year or more until it is mature. The nymph then leaves the bottom mud and swims to the surface where its outer skin splits and the winged *subimago* emerges. The subimago flies at once toward the nearest land, where it seeks shelter on trees, shrubs, boat houses, or other suitable resting places. It remains rather quiet for a day or two, then molts to become a sexually perfect adult or *imago.* On the evening following the final molt, the imagoes mate at dusk in swarms high above the edge of the lake or stream. The females then fly out over the water and deposit their eggs on the surface. Both male and female imagoes die within a few hours or days after mating. The eggs at once sink to the bottom, and in a few weeks a new generation of nymphs hatches out to renew the cycle. Various phases of the life history of *H. limbata* in southern Michigan lakes will be discussed in the following pages.

Nymph

The nymphal stage is a very important one since it is in this form that the insect lives for all but about 3–5 days of its entire life cycle. Too, it is only as a nymph that the insect feeds and grows, for in the winged stages the mouth parts are vestigial and no food is taken. It is important to know something of the habits and requirements of the nymphs because so large a proportion of the life span is spent in this stage.

Newly hatched nymphs, measuring 0.83–0.88 mm. in body length, become active immediately upon leaving the eggs and make their way into the mud bottom of lake or stream, where they begin to feed and grow. Nymphs increase in size by going through a process of molting whereby the old skins or exuviae are shed, followed immediately by a sudden increase in body size before the new skin or exoskeleton hardens. Body proportions and size of various parts such as tusks, eyes, gills, caudal filaments and wing pads change somewhat with each succeeding molt. The form of the nymph between molts is known as an instar, and the period of time between molts is a stadium. Although the number of nymphal instars of *H. limbata* is not certainly known, it probably is near the 30 estimated for *Ephemera simulans* (Ide, 1935a) and 27 found for *Baetis vagans* (Murphy, 1922).

In two observed instances the time required for completion of a nymphal molt was 3 and 5 minutes. Just where the molts occur in nature is not known; but it is presumed that they take place within the burrow, since nymphs were never seen on the mud surface by either day or night under aquarium conditions. Occasionally, exuviae were found on the surface of the mud in rearing containers, but it is likely these were washed out of the burrows by water currents. Examination of many specimens of all sizes indicated that the first 3 or 4 molts, easily recognized by the changes in gills and mouthparts, occurred within a week after hatching. Likewise, the last 4 instars, in which wing pads are developing rapidly and genitalia of the males show marked changes, are not difficult to distinguish. The last nymphal instar is characterized by the large size of the wing pads which nearly double in length after the next to last molt. The wing pads become progressively darker, to the point where they appear black by the time the nymph is ready to transform to the winged stage (Fig. 14). Information obtained by rearing nymphs and examining specimens in the field indicates that duration of the last stadium is 3 to 4 weeks. Size attained by full-grown nymphs varies with the sexes and with individuals of the same sex. In the waters studied, males reached the last instar, or maximum size for the individual, at length of 17–27 mm., while females arrived at this stage of development at lengths ranging from 23–35 mm. Average size of grown nymphs from Pine, Gun and Big Silver lakes was 22.0, 22.3, 21.7 mm. for males and 27.5, 27.8, and 27.8 mm. for females, respectively. The most noticeable diagnostic features of the nymphs of *limbata,* as well as those of other *Hexagenia,* are: the long, curved tusks extending beyond the head; the dome-shaped prominence on the front of the head; the broad, flanged digging legs; the wing pads, which are conspicuous only in large specimens; the long, bushy or feathery gills attached to the abdomen; the dark color pattern on the dorsum of the abdomen; and the three hair-fringed caudal filaments (Fig. 14).

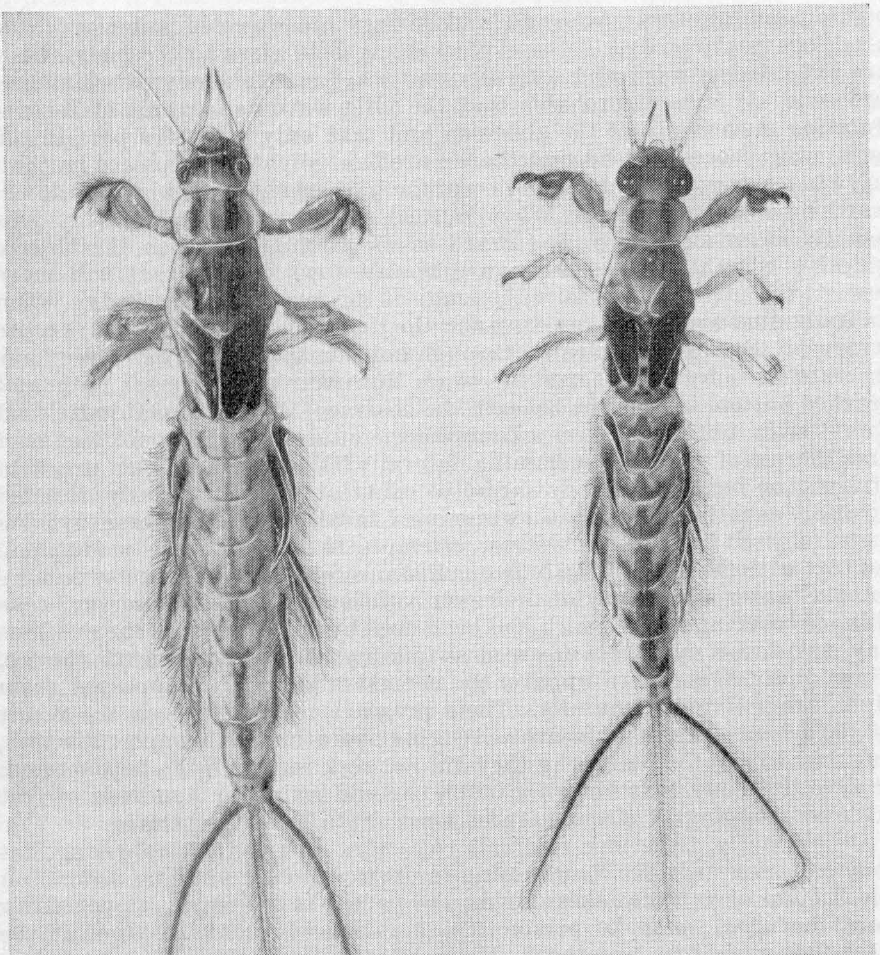


Figure 14. Female (left) and male (right), last instar nymphs of Hexagenia limbata. Wing pads are black.

Swimming and Burrowing

Swimming and burrowing activities of *Hexagenia* nymphs have been described by Lyman (1943b). The writer's observations of the movements of *limbata* nymphs confirm the findings previously reported; therefore, only a brief description of them will be given here.

Swimming is accomplished by dorso-ventral undulations of the body, chiefly of the abdomen. The caudal filaments are directed backward and overlap one another; fore and middle legs are directed anteriorly, the hind legs posteriorily, all three pairs being held close to the body. Gills are extended upward and laterally and wave continuously as swimming proceeds. It is most probable that the gills wave as a result of the undulating movements of the abdomen and take only a passive part in the swimming process. Head and thorax are bent slightly downward so that, in swimming with the dorsal side up, the path of the nymph angles downward toward the bottom. When released at the water surface, nymphs usually swim vigorously downward in an attempt to reach the bottom quickly. Should the specimen turn upside down, however, it will move toward the surface because of the angle of the forepart of the body. When an individual swims for any distance, the line of movement is always quite irregular. Specimens, released through holes in the ice on Big Silver Lake in water 3–6 feet deep, usually swam downward in a spiral path and reached bottom in the area beneath the observer. An occasional individual would swim out of sight on a course horizontal to the bottom. The head and thorax of nymphs swimming laterally through the water are held straight or bent slightly upwards, in contrast to the ventrally directed position usually assumed in swimming. In all instances where nymphs were released in natural waters, attempts to burrow were made upon contact with the bottom. In only one instance were nymphs seen swimming in open water apparently of their own volition. When the observer broke thin ice covering a hole which had been used by bait collectors the previous day, two large nymphs were seen swimming about just beneath the ice. These individuals were apparently normal and soon disappeared from sight, travelling horizontally. Their presence may have been the result of disturbance caused by nearby dredging operations by numph collectors, but this does not explain why they did not seek refuge in the bottom mud. It is quite likely that large individuals could swim for hundreds of feet without stopping, if circumstances necessitated such movement.

Occasionally, fishermen and bait collectors reported to the writer that they had seen "wigglers" swimming in open water or crawling around on the bottom of various lakes during the period of ice cover. Opportunity never occurred to make personal observation of such activities at the time they were seen by others. However, a considerable amount of time was devoted to observing lake bottoms both in daytime and at night, winter and summer. Several winter nights were spent on Big Silver Lake in making observations, through holes cut in the ice, in water 3–6 feet in depth, and over bottom containing many nymphs. The small light with reflector, previously described, was suspended beneath the surface of the water and turned on for a few minutes at intervals of 30–45 minutes. No *H. limbata* nymphs were ever seen either crawling on the bottom or swimming. Both large and small nymphs of *Blasturus nebulosus* and *Ephemerella* sp. frequently swam through the area under observation, some immediately beneath the ice, others at lower levels. Twenty-two summer nights of slow cruising with an underwater light over shoals pitted with nymphal burrows failed to reveal nymphs either on the mud surface or swimming, although many fishes and invertebrates were clearly visible.

Burrowing into soft mud is usually accomplished in a matter of seconds. Often, nymphs swimming to the bottom reach it with the head tilted slightly downward, the fore legs extended anteriorly, and the abdomen at a slight angle to the mud surface; and they begin to dig at the point of contact. At other times, nymphs will come to rest on the bottom for a short time before beginning to burrow, or may crawl or swim along it for some distance before entering the mud. Entrance is gained by powerful digging movements of the fore legs, pushing by the hind legs, and occasional strong, undulating movements of the abdomen and gills. Once the head and legs are beneath the surface of the mud, the remainder of the body quickly disappears from sight. After completely burying itself, the nymph may rest quietly for a few seconds before gill movement begins. A small plume of mud particles rising from the entrance hole signifies that clearing of the burrow by means of gill-induced water currents has begun. After a few minutes the anterior portion of the burrow is cleared as mud is drawn into the burrow by currents resulting from vigorous waving of the gills. Particles are drawn past the nymph and carried to the mud surface at the entrance hole. The anterior portion of the burrow is completed when sufficient mud is drawn inward to establish an opening to the surface in front of the nymph. Burrow openings remain small for a few hours but are gradually enlarged by the continual passage of water currents. It is clear that burrowing is accomplished by actions of four parts of the body working together, namely: digging of the fore legs; pushing of the middle and hind legs; undulating movements of the abdomen, which propel the body forward; and action of the gills. As pointed out by Morgan and Grierson (1932) and Lyman (1943b), gills of burrowing mayflies are not only true respiratory structures but are necessary in clearing and maintaining a burrow. Nymphs with gills removed made little or no attempt to burrow and soon came to the surface after entrance to the mud was made. Presence of nymphs in marl bottom or mud banks could usually be detected by inspection of the surface for burrow openings. The mud surface usually was thickly beset with openings wherever nymphs were abundant. Entrances to burrows are shown in Figure 15.

Size and depth of burrows depend on the size of the nymphs constructing them. Diameter of the tunnel is such that the nymph can move backward and forward and turn around in it, and is estimated to be one-third or more wider than the individual inhabiting it. A typical burrow is shaped like a shallow U with the two arms inclined about 45 degrees from the perpendicular, each opening to the surface. A number of burrows constructed parallel to the glass sides of aquaria were measured. The largest one observed, made by a large female, measured 7.5 inches between the two openings and had a maximum depth of 5 inches. Many others, smaller in size but of similar proportions, were constructed by smaller nymphs. Small individuals did not ordinarily penetrate more than 3 inches beneath the surface. Where the layer of suitable mud was shallow, burrows were usually proportionately longer and shallower than the one just described. In some instances large nymphs constructed and maintained burrows in closely packed marl-mud only 1.5 inches deep. In the latter case, some burrows were 8 inches between the two openings.

Very young nymphs were seen to clamber around in the interstices of the bottom material and did not remain in one place all of the time. Observations suggested that typical burrows are constructed by nymphs that have attained a length of 2–3 mm. Subsequent nymphal life appears to be lived exclusively in burrows.

Side or branch burrows were frequently constructed. Individual nymphs placed in gallon jars containing mud first constructed a U-shaped burrow as evidenced by the two openings. On subsequent days additional openings were seen. Some nymphs seemed content to remain in one place,

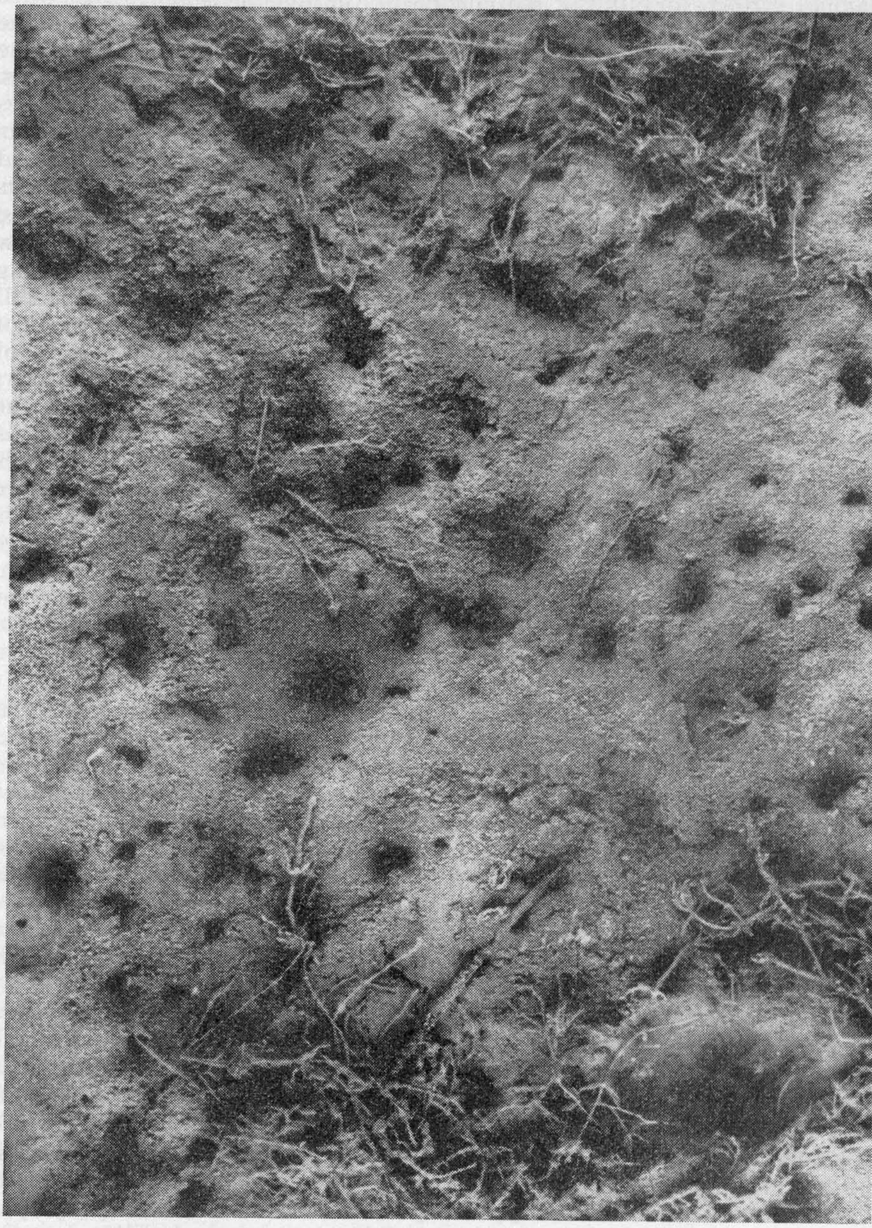


Figure 15. Photograph of mud surface in bottom on Big Silver Lake showing numerous burrow openings. Largest holes are about one-half inch in diameter.

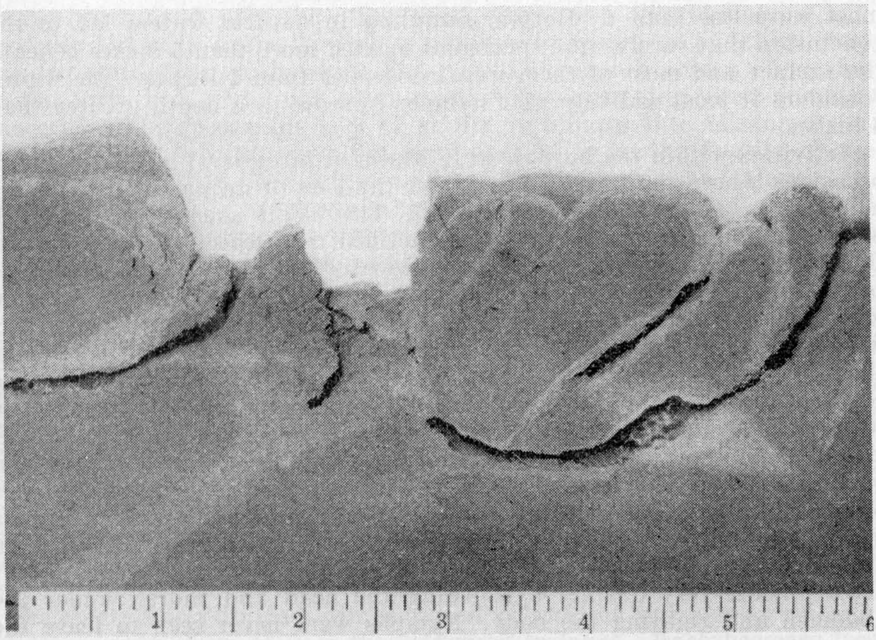


Figure 16. View of nymphs inside burrows. Photograph taken through side of very narrow aquarium. Scale is in inches.

while others dug a number of branch burrows. One nymph created only one additional opening in three weeks. The largest number of openings produced by a single nymph in addition to the original two was eight, which appeared in a period of two weeks. It was never determined with certainty whether the nymph deserted the original for the side burrows or made continued use of all tunnels constructed.

It was noted early in the investigation that surprising numbers of nymphs were taken from very small areas. Interpreted in terms of cubic inches of habitat, it meant that several nymphs were living in the same burrow or that burrows were maintained at several different levels. Nymphs seen to come in contact in aquaria appeared to repel each other; hence it was assumed that no more than one nymph occupied a burrow at a time. Placing a large number of nymphs of assorted sizes in a small aquarium and later draining off the water and carefully cutting away sections of the mud revealed that nymphs were living in separate burrows formed at several different levels. Usually the small nymphs were near the surface and the larger ones toward the bottom. Specimens placed in a very narrow aquarium (½ inch wide, sides covered with removable black paper) showed the same arrangement of burrows. In one instance 3 nymphs were situated in the same vertical line but at different depths. Position of nymphs in burrows and burrow formation are shown in Figure 16.

The maximum depth to which nymphs may burrow in the natural habitat is not known with certainty and may well vary with circumstances. No burrows deeper than 5 inches were observed in the laboratory and most were less than 4. Bottom sampling in natural waters led to the conclusion that rarely were specimens located more than 5 inches beneath the surface and most of them were no deeper than 4 inches. The writer considers it most unlikely that nymphs burrow to a depth greater than 6 inches.

Activities within the burrow were observed for several minutes on two occasions where the burrow paralleled the side of an aquarium and the nymph was partially exposed to view. The insect usually lay near the bottom of the burrow facing up the inclined tube leading to the surface. Occasionally it moved forward or backward a half inch or less, then came to rest again. Rhythmical waving of the gills, which varied in duration and intensity, was the only movement occurring most of the time. Gills were seen to wave at a rate of about 1 beat per second for 15 to 70 seconds, then increase in tempo to 2 or 3 times the former speed. Rapid waving continued for 6 to 15 seconds, then all movement ceased for 10 to 30 seconds. After the rest period, gills began to wave slowly again. Sometimes after a quiet period gill movement began at a rapid rate and gradually slowed down until it ceased altogether. Whenever small pieces of mud fell from the burrow roof, gills beat rapidly for a few seconds until the particles had been washed away. Individuals were seen to turn around and take up a resting position facing the opposite opening, a shift accomplished very quickly by turning the head and thorax under the abdomen and righting the body. Nymphs were never seen to leave the burrow except to transform or to escape conditions resulting from water stagnation. Frequently at night and sometimes during the day, individuals were seen with their heads near or at the mouth of the burrow. Upon being disturbed they immediately retreated out of sight.

Type of bottom into which nymphs can or cannot burrow deserves considerable attention. For aquarium use in these studies the writer chose a soft, gray, marl-mud taken from Big Silver Lake. Both screened and unscreened mud seemed to be ideal for burrowing since nymphs could easily construct and maintain burrows in it. Most of this material passed through screening of 100 meshes to the inch. Although finely divided, it consolidated into a firm, soft layer upon being allowed to settle for a day or two. Burrows in this material often remained open for several days or weeks after nymphs had deserted them. Assuming the marl-mud described above to be an optimum medium for burrowing, the ease with which nymphs entered it and constructed burrows was used as an index in evaluating other types of bottom. Various kinds of mud from Big Silver Lake were brought into the laboratory and used for burrowing experiments. Marl-sand combinations, found in many places in the lake, were simulated by artificial mixtures containing varying proportions of the two materials. Five to ten nymphs of medium size were placed in aquaria containing the various types of bottom and their burrowing activities observed. Nymphs could not burrow into sand no matter how fine, because the grains continually tumbled back into the excavation made by the fore feet and specimens could not force their way into it by undulating movements of the body. Entrance into mixtures of marl and sand of any grade in which the sand made up one-third or less of the total volume was effected with ease. A mixture of one-half coarse beach sand and one-half marl was penetrated with great difficulty. Nymphs could not enter a mixture containing two-thirds coarse beach sand. On the other hand, they were able to burrow successfully but with difficulty into a mixture composed of one-third marl and two-thirds fine sand, which had passed through a screen 65 meshes to the inch, but could not enter a mixture containing three-quarters fine sand. The reason for lack of ability to burrow into mixtures containing a high percentage of fine sand seemed to be the density of the mixture rather than the caving-in effect observed with sand alone. Individuals were able to excavate small openings but became exhausted before significant progress was made. It was noted that while some nymphs were present in marl-sand mixtures in the lake, they were always fewer in number per unit area than in marl-mud alone.

Pulpy peat from the depression in Big Silver Lake proved to be quite unsatisfactory for burrowing because of its flocculent nature. Nymphs were able to swim into it but could not make or keep a tunnel open and soon came to the surface. Mud containing marl and a large amount of organic debris, present in some areas of Big Silver Lake, contained few or no nymphs. Samples of this mud were brought into the laboratory for burrowing experiments. Once it had settled, and lost most of the decomposition gases in the process, nymphs were able to inhabit it satisfactorily. Since a considerable amount of decomposition was occurring in this type of lake bottom, it was concluded that possibly the accumulation of gases rendered the habitat unsuitable for nymphs.

Seemingly finely-divided, compact mud in streams provides as suitable a burrowing medium as does the soft marl in lakes. Each becomes less suitable in proportion to the amount of undesirable material, such as sand, organic debris, woody debris, detritus, gravel, etc., mixed with it. A great deal of additional information is needed before an exact measure of the suitability of bottom types for burrowing of the nymphs can be secured. Since water soils vary greatly in composition and are not well classified or described, it is a problem in itself to properly determine the relationships between various types of bottom and the burrowing nymphs. Therefore, a general definition of a suitable bottom type must suffice at the present. To be satisfactory as a burrowing medium, mud must be soft, but not so flocculent that a burrow cannot be maintained; firm enough for a burrow to be constructed, but not so dense that nymphs cannot burrow readily; contain comparatively little sand and detritus; and be free from quantities of decomposition gases. Although nymphs often were found in all kinds of bottom ranging from near flocculent material to almost pure sand, concentrations of nymphs were encountered only in mud the nature of which approached that of the optimum burrowing medium described above.

Food and feeding activities

All feeding by *H. limbata* is confined to the aquatic stages, for like all mayflies, mouthparts are atrophied in the winged condition and energy stored while in the nymphal stage must supply the needs of their aerial existence. Most mayfly nymphs are vegetarians, feeding upon algae and plant debris. Nymphs of *limbata* appear to be mud eaters, deriving nourishment from organic material and perhaps bacteria which are ingested along with the mud. Intestinal tracts have the appearance of long, mud-filled tubes. Examination of 43 alimentary tracts revealed little except material closely resembling the mud from which they were collected. Fragments of higher plants, filamentous algae, and various diatoms were found along with the usual large quantity of marl-mud or silt. Diatoms identified were *Navicula, Gomphonema, Synedra, Cocconema, Stephanodiscus, Fragilaria, Tabellaria* and *Cymbella*. Fragments of entomostracans were found in a few specimens. Grains of sand occurred in the intestinal tract of most nymphs taken from streams. Although alimentary tracts of both large and small individuals collected at all times of the year were examined, no significant difference was discernable in the amount or composition of material eaten by specimens of different sizes or in different seasons. Analyses of intestinal contents of burrowing nymphs have been reported by other authors. Morgan (1911) described material from the intestine of 2 specimens of *H. variabilis* (= *H. limbata*) as ooze and diatoms. Neave (1932) examined the alimentary tract of 23 nymphs and found diatoms and other algae, fragments of entomostraca and large quantities of mud. Since contents of alimentary tracts of nymphs always contain large amounts of mud, it must be concluded that some nutritional benefit is derived from it as well as from the identifiable organic components of the diet. It is probable that nymphs are not carnivorous in any sense but that they do consume animal fragments encountered while feeding.

On several occasions in the laboratory, nymphs were seen at the mouths of burrows in the daytime, apparently feeding. Small pieces of mud, pulled down from the edge of the burrow by the fore legs, landed between the tusks, and the maxillary and labial palps were seen manipulating the material. Occasionally small fragments of plant were seen to disappear, presumably taken between the mandibles. No details could be ascertained with the naked eye and at each attempt to employ a hand lens the nymph hastily retreated into its burrow. At night, with the aid of a dim flashlight, nymphs frequently were observed at the mouth of the burrows apparently feeding. Increase of light intensity invariably resulted in the nymphs retreating into the burrow. Although heads of nymphs were often observed at the rim of the burrow opening, no individuals were seen to leave their tunnels. Observations, conducted on a number of nights at different hours, certainly should have led to the discovery of nymphs on the mud surface if they habitually leave the burrow to forage.

Growth and length of life cycle

Comparatively little attention has been given to growth of *Hexagenia*. Neave (1932) stated that nymphs of *H. l. occulta* in Lake Winnipeg undergo no appreciable growth during winter and that August was the period of greatest increase in size. Curves (*op. cit.*) show that nymphs living through a 2-year cycle are about half grown at the end of their first year of life and have nearly reached maximum size upon entering the second winter of their existence. Some growth occurs in the spring preceding maturity and transformation.

Growth curves constructed by Lyman (1940) for *H. viridescens* in Douglas Lake, Michigan, show that newly hatched nymphs, which appear in August, are three-fourths grown by late the following summer (one year old) and transform in June and July of their second year of life. Spieth (1938) checked the growth rate of newly hatched *H. occulta* under controlled conditions in northern Indiana and found that specimens hatched on July 8 reached an average length of 11.3 mm. (nearly half grown) by October 15 (88 days after hatching), some individuals being 16 mm. long on this date. Lyman (1943a) gives no length measurements but indicates that young *H. bilineata* nymphs in Tennessee grew very rapidly from August to October, 1941, trebling their size in 2 months.

Rate of growth is closely linked with length of life cycle and apparently largely determines the time required for the insect to reach maturity. In order to interpret correctly the size-frequency distribution of nymphal populations at various times of year, and the length of life cycle in the localities under consideration, it was necessary to establish the rate of growth in natural waters and under various experimental conditions. Growth rate in the natural state was determined from length measurements of nymphs collected at various times of year and substantiated by noting increase in length of specimens of known age under experimental control in natural waters. Growth experiments, carried out in laboratory aquaria, gave additional information of value in evaluating life cycle data.

Collections of large male and female nymphs from several localities were brought into the laboratory in Ann Arbor on dates ranging from September 19 to February 1 to be reared for identification purposes. Water temperature in the laboratory during the rearing periods ranged from 62° to 86°F. (usually between 69° and 75°F.), while in the natural habitats from which the nymphs were taken it was near freezing. In all instances these nymphs began to emerge within 31 to 46 days after they were transferred from the cold water of the natural environment to the warm water of the aquaria. The interval during which nymphs emerged varied from 3 to 6 weeks. The significant fact is that these specimens normally would have emerged during the following June and July. Consequently the life cycle was reduced by approximately 4 to 9 months in the instances cited. Shortening of the nymphal life of mayflies under laboratory conditions has been demonstrated by other investigators (Morgan, 1911; Neave, 1932). It is evident that these large nymphs were nearly full grown when collected and that the comparatively short period spent in the warm water of the laboratory was sufficient for them to complete normal nymphal development. It also demonstrates the fact that little or no growth and development occurs under the low temperatures in effect in winter. Imagoes secured from these groups of nymphs were normal in all respects. The females carried a normal egg load and were fertile, as demonstrated by artificial insemination experiments.

Entire life cycles were successfully completed in the laboratory. Both naturally fertilized and artificially inseminated eggs from 6 different sources were hatched, and the nymphs reared to the imaginal stage. The growth history of three of these lots, one from each of the lakes studied, was followed. Since the results secured by rearing specimens through a complete life cycle were similar in all instances, the progress of only one of these, Artificial Insemination Experiment No. 11, will be discussed in detail. On June 2, 1947, eggs and sperm from a female and a male imago, both of which had been reared from nymphs collected from Big Silver Lake, were mixed. The artificially inseminated eggs were incubated in a finger bowl in the laboratory. Nymphs which hatched on June 24, 1947, were placed in an aquarium and examined periodically to determine rate of growth. The mud in the aquarium was changed four times in the course of the experiment. From June 24, 1947, to June 13, 1948, the nymphs were measured on ten occasions. Prior to December 3, 1947, only small samples of specimens were removed, preserved and measured each time, but on December 3 and thereafter all specimens were measured, and returned to the aquarium alive. The results are given in Table 5. At the time of hatching the young nymphs measured between 0.8 and 0.9 mm. in total length. By March 18, 1948, the average length was 21.1 mm., and 37.8 percent were in the last instar. On June 13, 1948, the remaining nymphs were very large (average length, males, 24.2 mm.; females, 29.7 mm.) and 47.4 percent were mature. On March 4, 1948 (8 months and 8 days after fertilization), 3 abnormally small male subimagoes emerged (body length 13.0–14.8 mm.; wing 11.7–12.7 mm.). On March 10, 4 male nymphs transformed

Table 5. Growth of nymphs in artificial insemination experiment No. 11

Sex and date	Number measured	Length in mm.		
		Minimum	Maximum	Average
Males				
8/25/47	6	3.0	5.3	4.0
9/ 4/47	6	3.0	5.3	4.6
9/25/47	6	4.3	6.4	5.2
10/ 8/47	14	5.6	13.3	8.9
11/ 5/47	7	6.6	12.2	8.8
12/ 3/47	99	8.0	20.0	12.4
3/18/48*	41	14.0	23.0	19.2
6/13/48†	16	22.0	26.0	24.2
Females				
8/25/47	11	2.7	5.6	4.2
9/ 4/47	4	4.0	6.4	4.9
9/25/47	6	5.0	12.0	8.3
10/ 8/47	8	5.7	16.7	9.6
11/ 5/47	8	7.2	16.0	10.6
12/ 3/47	76	7.0	21.0	13.0
3/18/48*	33	18.0	28.0	23.6
6/13/48†	22	26.0	33.0	29.7
Both Sexes				
6/24/47‡	6	....	....	0.9
7/21/47‡	15	....	....	2.4
8/11/47‡	11	....	....	2.8
8/25/47	17	....	....	4.1
9/ 4/47	10	....	....	4.8
9/25/47	12	....	....	6.7
10/ 8/47	22	....	....	9.4
11/ 5/47	15	....	....	9.8
12/ 3/47	175	....	....	12.7
3/18/48*	74	....	....	21.1
6/13/48†	38	....	....	27.3

*15 males, 13 females in last instar.
†14 males, 4 females in last instar.
‡Sex not determined.

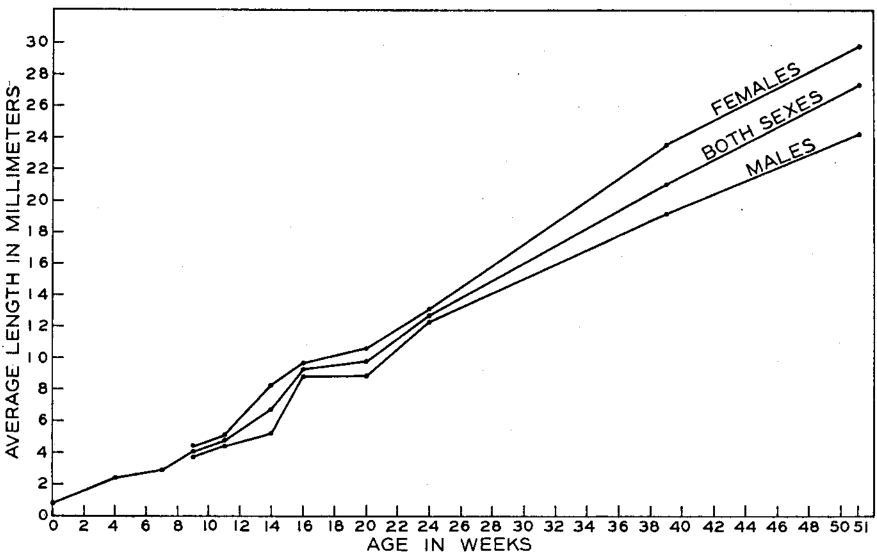


Figure 17. Growth of nymphs in Artificial Insemination Experiment No. 11.

and successfully completed the subimaginal molt. Again these were abnormally small (body length 13.2–14.8 mm.; wing length 12.5–13 mm.). From March 16 to May 23, 17 male nymphs transformed, all of which became imagoes of normal size (body length 16–21 mm.; wing length 16.4–20.6 mm.). From June 1 to July 18, 1948, 24 male and 36 female subimagoes emerged, all of normal size. The last emergence occurred 12 months and 24 days after fertilization of the eggs and the over-all period during which emergences occurred was 4 months and 16 days. To test the fertility of adults obtained during this experiment, 2 males and 3 females were used as parents in artificial insemination experiments. In all cases fertilized eggs were obtained.

It was obvious immediately that some nymphs were growing much faster than others. Not only were females increasing in size more rapidly than the males, but individuals of each sex showed rather great differences in length at any age. Differentiation between the sexes was first accomplished on August 25, 1947; thereafter individuals of each sex were measured separately. Growth of the nymphs by weeks is shown in Figure 17. It is apparent from the curve that the dimorphic size difference between the two sexes exists at a very early age and becomes greater with increase in length. Whether the larger size attained by females is the result of slightly greater increase in length at each instar or the inclusion of more molts during their growth period is not known. The average growth curve appears to be a straight line. Some divergence occurred in the early stages (Fig. 17) but may have been due to the small samples measured rather than to a slower growth rate during this phase of development. The size-frequency distribution of the nymphs, without taking size differences of the two sexes into consideration, is shown in Figure 18.

Probably both overcrowding and a food shortage existed at times during the course of the experiments. Although conditions in the aquaria were suitable for nymphal growth, it is likely that in most cases they were inferior in all respects other than temperature to those existing in the natural environment and that the growth rate was slower than it would have been under natural conditions at similar temperatures.

Another group of 20 newly hatched nymphs, secured on October 15, 1947 from Gun Lake stock, was reared in a large aquarium, in which mud was

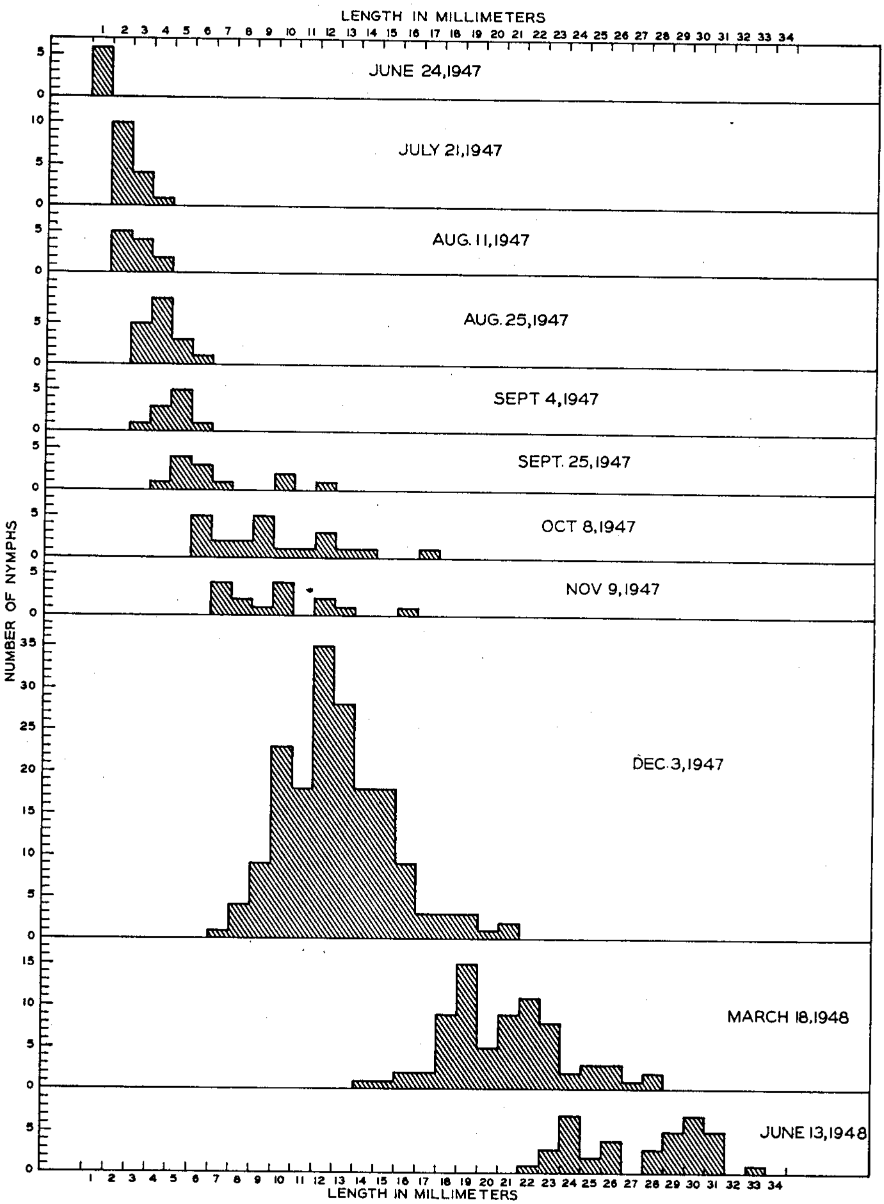


Figure 18. Size-frequency distribution of nymphs in Artificial Insemination Experiment No. 11.

changed frequently. Only one specimen (a large male subimago, normal in all respects) lived to reach maturity, transforming on March 30, 1948. Elapsed time from hatching to emergence was 5 months and 15 days, by far the shortest individual life cycle encountered during the experimental work begun in 1947. The 5.5-month period of growth and development would have corresponded to a normal one year's growth in Gun Lake providing little or no growth had occurred during the winter months. It is believed that the history of this individual contributes strong evidence that a life cycle could be completed in 1 year in a natural environment under favorable conditions.

Newly hatched nymphs (0.8–1.0 mm. in length) secured on June 22–24, 1948 from hatching jars containing eggs obtained from ovipositing females at Pine Lake the night of June 2, 1948 were reared in aquaria. Water temperatures in individual containers were recorded by maximum-minimum thermometers. All nymphs were examined and measured on August 13 and again on September 10, when the experiment was terminated, and all surviving specimens preserved. Food deficiencies, noted or suspected in previous experiments, were apparently remedied by maintaining a "bloom" of plankton algae in the aquaria. All were seeded from an algal culture and small amounts of commercial plant fertilizer were added to the water from time to time. A heavy bloom was maintained in aquaria near a large window, but it was impossible to maintain a good culture in aquaria removed some distance from this light and heat source. No noticeable amount of algae was ever present in the stock aquarium. Examination of the intestinal tract of nymphs from aquaria containing large quantities of algae showed that considerable amounts of these plants were consumed along with the large amount of marl-mud always present. Since a considerable amount of mud was always found in the intestinal tract of nymphs from any aquarium, it was thought that the additional food material from the algae crop was of considerable importance in maintaining the extremely rapid growth rate.

Nymphs in aquaria were designated by groups and the progress of each was followed throughout the experiment. Growth data obtained during this experiment are shown in Table 6. It is seen at once that the growth rate differed considerably among the various groups, depending upon the temperature and food supply. In all cases the nymphs appeared healthy and vigorous when examined. Group 1 was located near a large window where the sunlight heated the water (70°–95°F.) considerably higher than room temperature (65°–80°F.). This group, last measured on August 13, showed very rapid growth and development (Table 6). On this date, 52 days after hatching, specimens averaged 18 mm. in length (males 17.2, females 19.1 mm.). Four (length 18–20 mm.) of the 11 males had reached the last instar and one of the 7 surviving females had reached this developmental stage at a length of 23 mm. This rapid growth is credited to the high temperature and abundant food in the aquarium during the entire growth period. Just when the first transformation would have occurred is not known since this group of nymphs was lost shortly after August 15 due to a broken air hose. Considering that the last nymphal instar was reached by some individuals in less than 72 days from the time the eggs were fertilized, it is quite possible that some of them would have transformed within 3 months from the time

Table 6. Growth of nymphs in aquaria, 1948, under different conditions of temperature and food

Group and date	Males				Females				Average length in mm., all nymphs	Temperature range during preceding period, °F.	Plankton algae
	Number measured	Length in mm.			Number measured	Length in mm.					
		Min.	Max.	Avg.		Min.	Max.	Avg.			
Group 1											
June 22–24	15	0.8	1	0.9	15	0.8	1	0.9	0.9	.....	....
Aug. 13	11	14	20	17.2	7	15	23	19.1	18.0	70–95	Abundant
Group 2											
June 22–24*	..	..	..	0.9	..	..	..	0.9	0.9	.....	....
Aug. 13**	10	5	10	5.9	12	5	13	8.7	7.4	65–80	Scarce
Sept. 10	39	12	20	16.2	34	14	24	20.2	17.9	70–95	Abundant
Group 3											
June 22–24*	..	..	..	0.9	..	..	..	0.9	0.9	.....	....
Aug. 13**	20	3	8	4.5	28	4	9	5.4	5.1	65–80	Scarce
Sept. 10	16	13	19	15.9	50	14	23	18.8	17.4	70–95	Abundant
Group 4											
June 22–24*	..	..	..	0.9	..	..	..	0.9	0.9	.....	....
Aug. 13	20	3	8	4.5	28	4	9	5.4	5.1	65–80	Scarce
Sept. 10	35	6	14	9.3	64	6	20	10.6	10.0	65–80	Scarce

*Sex not determined.
**Aquaria moved near window on this date.

the eggs were secured. Certainly the abbreviated life cycle evidenced in this instance indicates that the potentiality for a very short life cycle exists within the species.

Group 2 was maintained well back from the window under room temperature conditions (65°–80°F.) and with little algae in the aquarium from June 24 to August 13. On the latter date the aquarium was moved to the window, where the temperature was much higher and an algal bloom was maintained until September 10. Growth rate of nymphs, slow under the first set of conditions, increased greatly in the more favorable environment. From August 13 to September 10 (28 days), the average length of the nymphs rose from 7.4 to 17.9 mm., an increase of 10.5 mm. None had attained the last instar, but a number of individuals had reached the size range at which maturity could be expected to occur. Group 3, comprising a number of specimens taken from Group 4 on August 13, was placed in the window in order to determine the effect of the higher temperature there. A marked increase in growth rate occurred during the ensuing period; from August 13 to September 10 the average length increased from 5.1 to 17.4 mm., a gain of 12.3 mm. None of the specimens attained the last instar. Group 4, kept in the stock aquarium, remained in the back of the room, where water temperatures ranged from 65° to 80°F. during the entire period. These specimens were somewhat crowded and the food supply was presumed to be low because of the lack of visible plankton algae in the water. Growth rate was very slow. On August 13 the average length was 5.1 mm. and on September 10 was 10.0 mm., an increase of only 4.9 mm. The comparatively slow rate of growth of this group was apparently due to the lower temperature and scantier food supply available. Growth curves for the four groups are shown in Figure 19. The sudden increase in growth rate exhibited by Groups 2 and 3 after they were subjected to higher temperatures and a more abundant food supply is very evident. Also the difference in size of individuals of the same age was very marked. Lengths of the largest and smallest individuals in the

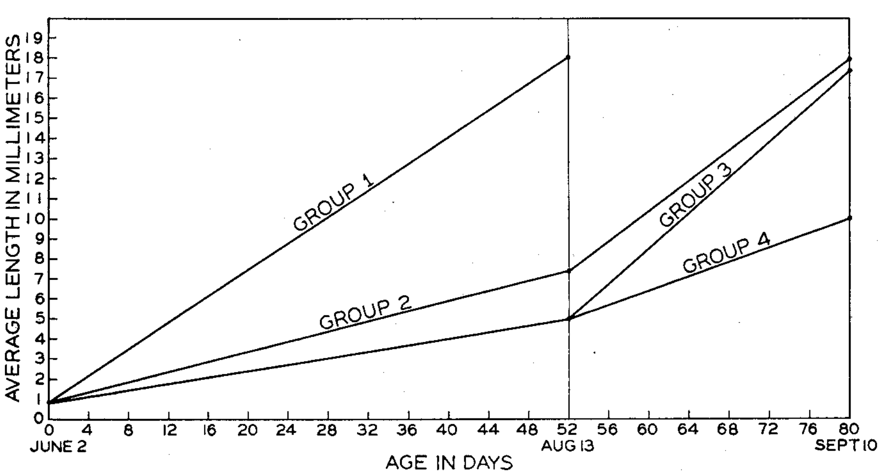


Figure 19. Growth of nymphs in aquaria under different conditions of temperature and food, 1948.

various groups are shown in Figure 20. This difference in growth rate of individuals of the same age was noticed in every instance in which development was followed, and occurred irrespective of the particular environment involved.

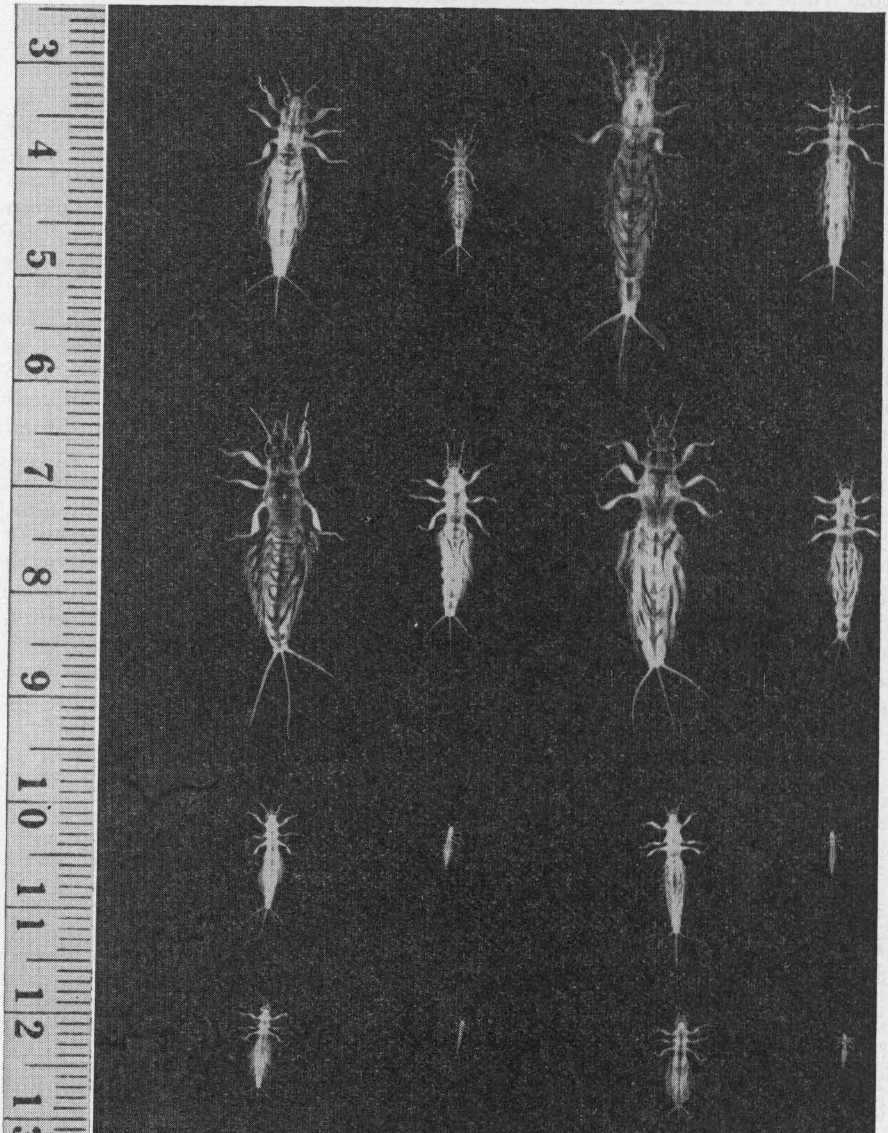


Figure 20. Comparison of size of nymphs reared in aquaria under different conditions of temperature and food, 1948. Scale is in centimeters. Nymphs in columns reading from left to right are: largest male, smallest male, largest female, smallest female. Top row: Group 2, age 80 days; second row: Group 1, age 52 days; third row: Group 2, age 52 days; Bottom row: Group 4, age 52 days.

It was recognized that growth in aquaria might not correspond to that found in nature. Certainly it was obvious from experiments conducted in 1947 that the time required for nymphs to reach maturity under continuously favorable temperature conditions represented far more than a year of growth in the lakes studied. Too, it was evident from the extremely rapid growth exhibited in the 1948 experiments that, if such a rate were realized in nature, some nymphs would undoubtedly mature in the same summer they were hatched; and no evidence to support this conjecture was secured. In order to obtain information on the growth rate of known-age nymphs under natural conditions, experimental groups of specimens were placed in containers in certain natural waters and were examined and measured periodically. In three instances nymphs were successfully reared over a sufficiently long period to obtain valuable data. Each of these three experiments will be discussed separately.

Transplantation Experiment No. 1 was begun on June 11, 1947, when 80 small nymphs were collected in Big Silver Lake, measured, sexed and transported to the Hunt Creek Fisheries Experiment Station, Montmorency County, Michigan. After making certain that all nymphs had survived the trip in good condition, they were put in a previously prepared rearing cage placed in Fuller Creek, which flows through the station grounds.

The cage (Fig. 7) was constructed of a 5-gallon paint can. Two sections were cut out of the sides and one from the lid; these openings were covered with brass screen, 16 meshes to the inch, soldered to the can. The bottom section was left intact to contain mud. Finely screened marly-mud from Big Silver Lake was poured into the can to the height of the screen and allowed to settle until a compact layer 4 inches deep was formed. After the nymphs were put into the can it was placed in a pool so that water covered its top to a depth of 10 inches. The cage was anchored in position by attachment to posts deeply driven into the bottom A log, placed 5 feet upstream from the container, diverted part of the slow current to one side. The cage operated efficiently, the screen sides remaining clean, so that water circulated continuously through it. Siltation within the cage was at a minimum.

Fuller Creek (tributary to Hunt Creek, which empties into Thunder Bay River) has its origin in, and flows for a considerable portion of its length through, spruce-cedar swamps. Spring seepage adds to the volume along its entire length and insures a rather constant flow of cold, clear water. In the area selected for the cage site, Fuller Creek has spread out into an area formerly flooded by a beaver dam. The bottom is composed of sand and fine silt mixed with woody debris. In most places the creek is about ten feet wide with an average depth of about one foot. The pH of the water ranges from 7.8 to 8.3; phenolphthalein alkalinity varies from 4 to 8 ppm., and methyl-orange alkalinity ranges from 162 to 167 ppm. Volume of flow fluctuates little and the temperature remains low in the summer (50°–63°F.) and comparatively high in the winter (32°–38°F.). A recording thermograph, located about 200 feet upstream from the site selected for the cage, provided a continuous record of water and air temperatures.

Fuller Creek contains a sizeable population of *Hexagenia recurvata* but no *H. limbata* nymphs have been found in it, although they occur in the lower reaches of Hunt Creek.

When the nymphs were placed in the cage in Fuller Creek (June 13, 1947), the average length of all specimens was 12.3 mm. (range 10–16 mm.). At the time the nymphs were collected the seasonal emergence on Big Silver Lake had just begun, consequently the specimens selected must have been hatched the preceding summer (i.e., 1946) and would normally have reached maturity and transformed by mid or late summer, 1947. In the changed environment they continued to grow through the summer until about October 15, 1947 (Table 7). At that time the males had nearly reached their maximum size but the females showed a considerable amount of growth after that date. Very little increase in length occurred from October 15, 1947 to May 11, 1948. From then to June 15, 1948, there was a slight increase in average length as the nymphs reached the last instar. After having been in the creek a year, all males (20) and 9 of the 12 females had reached the last instar and 40 percent of the original number survived. When the experiment was terminated on August 8, 1948, 14 months after its inception, only 2 nymphs—immature females—were left. Remains of 2 subimaginal females indicated that the nymphs had matured and transformed, as expected, during July and August but had drowned and disintegrated in the submerged cage. Since the nymphs must have been 1 year old or

Table 7. Growth of nymphs transplanted from Big Silver Lake to Fuller Creek

Sex and date	Number of nymphs	Average length, in mm.	Average increase in length, in mm.	Percentage of nymphs surviving
Males				
6/13/47	54	11.2	...	100.0
8/ 6/47*	24	15.5	4.3	....
10/15/47	25	20.4	4.9	46.3
3/ 8/48	22	21.1	0.7	40.7
5/11/48	20	21.2	0.1	37.1
6/15/48	20	21.7	0.5	37.1
Females				
6/13/47	26	14.4	...	100.0
8/ 6/47*	12	18.7	4.3	....
10/15/47	18	23.5	4.8	69.2
3/ 8/48	15	24.1	0.7	57.7
5/11/48	14	24.1	0.0	53.8
6/15/48	12	25.6	1.5	46.2
8/ 8/48	2	26.4	0.8	7.7
Both sexes				
6/13/47	80	12.3	...	100.0
8/ 6/47*	36	16.6	4.3	....
10/15/47	43	21.4	4.8	53.8
3/ 8/48	37	22.1	0.7	46.3
5/11/48	34	22.2	0.1	42.5
6/15/48	32	23.0	0.8	40.0
8/ 8/48	2	26.4	3.4	2.5

*Only some of the nymphs examined.

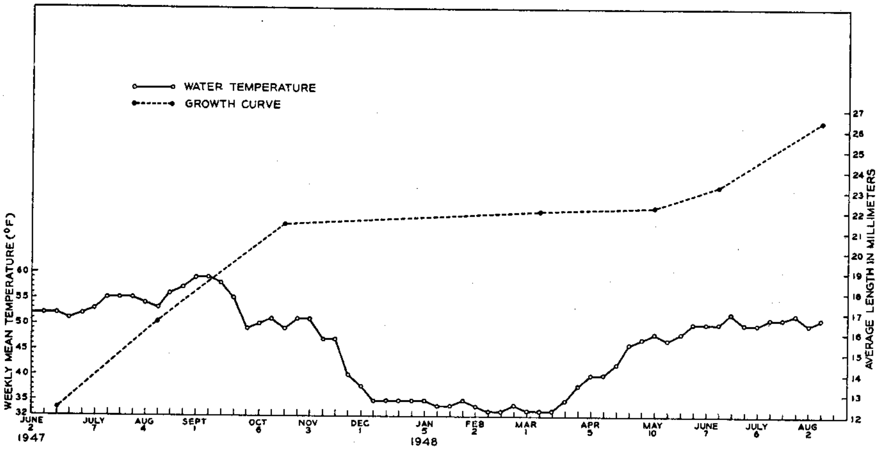


Figure 21. Growth of nymphs transplanted from Big Silver Lake to Fuller Creek, correlated with temperature of the stream.

nearly so when collected and lived through parts of 2 summers and 1 winter in Fuller Creek, it can be concluded that this experimental group lived for 2 full years and successfully reached maturity at the end of that time.

Low temperature is believed to have been the cause of the slow growth and retarded development of the transplanted nymphs since it alone of the environmental factors was greatly different from those of the lake from which the specimens were originally taken. A correlation between growth curve and stream temperature is shown in Figure 21. In this figure time is given in weeks with the date of the ending of the week used as the reference point on the abscissa. Mean weekly temperature was determined by inspection of thermograph recordings, which covered the entire period and are considered accurate. Temperature of the stream was very constant. The greatest difference found between the maximum and minimum readings in any week was only 11°F.; usually it was not more than 8°F.

Inspection of the figure shows that nymphal growth occurred during the summer of 1947 until the stream temperature began to fall rapidly in November from the average of 50°F. maintained in late October. During the winter little increase in size was discernible. After May 10, 1948, when the mean weekly temperature ranged between 48° and 50°F., growth was resumed and continued through the summer. It can be concluded, since other factors remained nearly constant, that temperature alone was the controlling factor influencing growth of *limbata* in Fuller Creek. It is clear also that these insects are able to increase in size at temperatures as low as 48°F., but that growth is greatly retarded or ceases entirely at lower temperatures. Other experiments have shown that the growth rate is greatly accelerated at high temperatures (80°–90°F.).

In Transplantation Experiment No. 2, eggs secured from ovipositing imagoes at Gun Lake on June 2, 1948, were incubated in glass jars in the laboratory. Nymphs which hatched during the period June 22–27 were placed in aquaria containing mud and allowed to grow. On July 11, approximately 1,000 nymphs were taken to the State fish hatchery at Hastings, Michigan, and reared in one of the ponds. *Hexagenia* were not present in the hatchery ponds. Following previously described methods for rearing *Hexagenia* nymphs (Spieth, 1938), a quantity of finely screened marl-mud was placed in a large tub and allowed to settle into a compact layer 5 inches deep. The young nymphs were introducced into the tub and allowed to establish themselves overnight. The following day the tub was placed near the outlet of the display pond at the hatchery so that water covered it to a depth of 1.5 feet. A maximum-minimum thermometer was placed near the tub but was not read until August 26, 1948. During that interval the minimum water temperature was 64°, the maximum 81°F. Filamentous algae and rooted plant growth was very abundant in the pond during late summer. Chemical analyses showed pH values in the range 8.0–8.4, phenolphthalein alkalinity 6–8 ppm., and methyl-orange 142–154 ppm.

On August 26, 1948, all surviving nymphs (males 130, females 26) were removed, measured, and their sex determined. In the interval they had grown enormously. No obvious explanation existed to account for the great disparity in the number of each sex. However, it was noted that the marl-mud had packed down in the interim until it was only 2–3 inches in depth. Shallowness of the mud may have caused some females to leave the tub since they were much larger than the males and presumably needed to burrow more deeply. Fifty-five males and 11 females were preserved. A total of 90 nymphs (75 males and 15 females) was replaced in the tub for further observation.

On November 8, 1948, Mr. K. G. Fukano emptied the tub and preserved all remaining nymphs. A total of 77 survived (62 males and 15 females), a loss of 14.4 percent of the population (14 specimens, all males) occurring in the interim.

Growth was very rapid (Table 8) and by November 8, 1948, most individuals had reached the size range at which maturity occurs. Examination of the wing pads and genitalia of males indicated that many of them were lacking only two or three molts of reaching the last instar. There is no doubt that they would have matured and emerged early in 1949 if left to continue development. Again a great disparity in length

Table 8. Growth of known-age nymphs in tub in pond at Hastings State Fish Hatchery

Sex and date	Number of nymphs measured	Length in mm.			Age in days
		Minimum	Maximum	Average	
Males					
6/22/48	..*	..	..	1.0	...
8/26/48	96	7	20	16.4	63
11/ 8/48	62	16	25	20.6	106
Females					
6/22/48	..*	..	..	1.0	...
8/26/48	26	16	24	20.4	63
11/ 8/48	15	14	29	25.1	106

*Approximately 1,000 nymphs placed in tub on this date. Sex of nymphs not determined.

Table 9. Size-frequency distribution of known-age nymphs reared in a tub in a pond at the Hastings State Fish Hatchery, 1948

Sex and date	Length in millimeters														Total
	1	2–6	7–8	9–10	11–12	13–14	15–16	17–18	19–20	21–22	23–24	25–26	27–28	29	
Males															
June 22*	10	..	..	..	..	..	..	..	..	..	..	..	..	..	10
Aug. 26	..	..	1	2	4	4	32	44	9	..	..	..	..	..	96
Nov. 8	..	..	..	..	..	..	2	4	19	29	6	2	..	..	62
Females															
June 22*	10	..	..	..	..	..	..	..	..	..	..	..	..	..	10
Aug. 26	..	..	..	..	..	..	1	5	7	9	4	..	..	..	26
Nov. 8	..	..	..	..	..	..	..	1	1	1	1	4	5	2	15

*Nymphs hatched on this date.

of individual nymphs of the same sex was noted. On November 8, males of the same age ranged in length from 16 to 25 mm., and females varied from 17 to 29 mm. The size-frequency distribution of the nymphs for each date on which they were examined is given in Table 9.

Since the hatchery pond simulated natural conditions, growth exhibited by nymphs reared in it is considered to be representative of growth in Pine and Gun lakes, which are in the near vicinity. A close correlation was found to exist between growth rate and size-frequency distribution of known-age nymphs in the hatchery pond and those of Pine Lake during the summer and fall of 1948.

In Transplantation Experiment No. 3, a number of young-of-the-year nymphs were collected in Big Silver Lake on July 22, 1948, measured, separated into two groups, and the sex of the larger individuals determined. Lengths of specimens in Group 1 ranged from 4 to 10 mm., in Group 2 from 11 to 16 mm. Each group was placed in a tub containing screened marl-mud and the containers submerged in Third Sister Lake so that water covered them to a depth of 6 inches. This lake, located near Ann Arbor, contains no burrowing mayflies. The nymphs were measured on August 27 and again on September 10, 1948, when all survivors were preserved. Water temperature during this period ranged between 71° and 83°F.

Growth of these individuals was very rapid, particularly nymphs in Group 1 (Table 10), which nearly trebled in average length in the 50 days they were in the tub. The average size (males 15.3 mm., females 17.8 mm.) compared very favorably with that of smaller nymphs collected in Big Silver Lake in September. Components of Group 2 showed a slower growth rate than those of Group 1, but by September 10 had reached a size comparable to that of larger individuals found in the lake in late fall and winter. Growth of these nymphs paralleled that of the lake population in August and September, 1948, and demonstrated that the increase in size apparent in size-frequency curves of the natural population represented real growth. While many of these nymphs were less than half grown at the end of the first summer of life, others were nearly full grown. Thus it may be inferred that growth necessary in the spring before a given individual reaches maturity depends on size attained the preceding fall. Large individuals grow but little, whereas small specimens entering the spring and summer growth period must increase their size by 50 percent or more before maturity is reached.

These rearing experiments revealed that *H. limbata,* under different environmental conditions, may complete its life cycle in a few months, or may require as much as 2 years. Maximum potential length of life has not been determined, but is probably less than 3 years. Data obtained from rearing nymphs under field conditions in the vicinity of the lakes covered by this report support the conclusion that a 1-year life cycle is in effect in these southern Michigan lakes.

As shown by experiment, rapidity with which maturity is reached is dependent upon growth rate. Since it has been shown that temperature is an exceedingly important factor, it follows that amount of growth during a season is determined in large part by temperature and the span of its duration at various levels. Thus in nature the time at which eggs are deposited, the rate at which newly-hatched nymphs will increase in size during the summer, and duration of fall growth are governed by the prevailing temperature. Since weather conditions largely determine the temperature of lakes and since water temperature in turn has a profound effect on rate of nymphal growth and time of year at which emergence of *limbata* occurs, they must be taken into consideration in dealing with the life cycle of this insect. Perusal of air temperatures recorded by the University of Michigan weather station at Ann Arbor and the weather station at Hastings (near Pine and Gun lakes) shows that the spring and summer of 1945, 1946, 1948 and 1949 were warm but that the same period in 1947 was comparatively cold. Lake temperatures showed a direct relationship to the air temperatures for the same years. Observations indicate that an early ice break-up, combined with a warm spring and early summer, results in rapid maturing of the nymphs and their early transformation to the winged stage. Under these conditions eggs are deposited early in the season and the new generation has a long summer period in which to hatch and grow. On the other hand, a late ice break-up followed by a cold spring and

Table 10. Growth of nymphs transplanted from Big Silver Lake to Third Sister Lake, July 22, 1948

Date	Males				Females			
	Number examined	Length in mm.			Number examined	Length in mm.		
		Min.	Max.	Avg.		Min.	Max.	Avg.
Group 1								
7/22/48*....	..	4	10	6.2	..	4	10	6.2
8/27/48.....	6	12	16	14.7	7	12	20	16.0
9/10/48.....	21	14	17	15.3	11	13	21	17.8
Group 2								
7/22/48.....	17	11	16	13.1	17	10	16	13.2
8/27/48.....	15	15	20	17.9	10	19	22	20.6
9/10/48.....	13	15	21	18.6	8	18	25	21.7

*Sex not determined for nymphs 4–10 mm. in length.

summer will result in slow maturing of the nymphs, and a belated and prolonged emergence period. Thus the length of time available for growth and development of the new generation is considerably shortened. Since emergence, egg deposition and hatching take place in these southern Michigan lakes to some extent during the entire summer, it is obvious that nymphs of different ages and sizes, produced during a single summer, are present during the following seasons. Success in effectively discriminating between various year-classes of nymphs depends entirely on their difference in size, which in turn is largely determined by the rate of growth as influenced by climatic factors. An early and compact emergence results in a well defined group, while a prolonged emergence results in a poorly defined group of nymphs in which the size of individuals produced in the same summer varies greatly. The expected characteristics of a nymphal population which should be evident if a 1-year life cycle is in effect are: (1) presence of one size and age group of nymphs in the fall, winter and spring; (2) evidence of the transformation of the entire group during the early summer; (3) a paucity of large individuals in late summer; and (4) the appearance of large numbers of newly hatched young in mid- or late summer. The distinctness of these population characteristics is markedly influenced by weather, not only in a given year but also over a sequence of years.

Periodic analysis of the size composition of nymphal populations in the various lakes supplied facts basic to determination of growth rate and the length of life cycle. For this purpose it was assumed that specimens from a given collection formed a sample representative of the size composition of the total population in the study area. Nymphs secured from each sampling station were preserved, measured, and their sex determined. These data for each sampling area were then assembled in the form of size-frequency tables which, when considered along with observations of emergence and growth rates of the nymphs, allowed definite conclusions to be drawn regarding length of life cycle in the waters investigated.

Study of *H. limbata* in Pine, Gun and Big Silver lakes from June, 1946, to June, 1949, has resulted in the conclusion that on the whole a 1-year life cycle is in effect in these waters. Data concerning emergence periods, size composition of the nymphal population at various times of year, and the maturing of nymphs and their abundance, when considered along with water temperature and general climatic conditions occurring during and prior to the period of investigation, have offered convincing evidence that the life cycle is completed in one year. The criteria for a 1-year cycle are met in that a single age and size group of nymphs is present throughout most of the year, and the evidence indicates an emergence of the entire group during the summer following hatching. Also, the expected hiatus between the old and new generation of nymphs during and following emergence is present although somewhat obscured by the prolonged period of emergence and mating activities which occurs even in very favorable seasons.

Although in these lakes the life cycle of the population as a whole is completed in one year, there is evidence to show that in certain years or a succession of years in which low temperatures prevail, a small percentage of slow-growing nymphs, hatched in late summer, does not mature in one year but carries over into the second winter and presumably survives to transform early the following summer at an approximate age of 20–22 months. This percentage is small, however, and does not refute the generalization which applies to the species in these lakes. It does, nevertheless, indicate that the ability of the species to live for longer or shorter periods, as evidenced by experiments, allows for a considerable amount of flexibility in nature in completing the life cycle.

Data obtained from Pine, Gun and Big Silver lakes are similar in most respects and support the conclusions previously stated. Although the same events occurred in the development of the nymphal populations in the two full years covered by sampling (1947, 1948), there was a definite difference in the seasonal pattern resulting from the difference in weather. In 1947, low temperatures prevailed in spring and early summer, resulting in a late (June 3–10) and prolonged transformation period and a considerable overlap of the two generations of nymphs in the lakes. The warmer weather in 1948 resulted in a much earlier (May 5–18) and shorter main transformation period and very little overlap of the two generations of nymphs. A similar condition existed in 1946 and 1949. The percentage of nymphs in the last instar—never encountered during late fall or winter—during the investigation (Appendix Tables 1–5) showed that transformation ordinarily occurred over a period of nearly 3 months but was heaviest during the first 4–6 weeks of the emergence period. Although few last-instar nymphs were obtained in August and September, a few individuals were observed transforming as late as the first week in September.

The size-frequency distribution of all nymphs found in bottom samples taken from the lakes over several seasons is shown in Appendix Tables 6–10. These tables show definite trends and shifts as the seasons progressed, the changes being similar for both sexes when dimorphic size differences are taken into consideration. Significant features of seasonal trends in the size composition of the nymphal population are discussed in the following paragraphs.

Collections made in late May and early June, 1946, revealed few nymphs in the lakes. All specimens were quite large. The nymphal population in January, 1947, showed a very considerable range in length for both sexes and a semblance of a bimodal size-frequency curve. In late May and early June, 1947, the range in size was still very apparent but a definite shift was noticeable in the frequency distribution toward the mature size range (males 17–27; females 23–35 mm.). By July, the bulk of the population had shifted into the mature size range and a high percentage of the individuals were reaching maturity. By August, two age and size groups were present with a rather definite break between them. At this time the population consisted of a few 1-year-old nymphs which had not yet transformed and large numbers of young of the year, already showing rapid growth as indicated by the range in size. By mid-September, a single size-frequency mode was in evidence. Large-size nymphs present on this date could have been either immature 1-year-olds or fast-growing individuals hatched early in the season. By November, 1947, the single mode persisted but a shift towards the mature size range was very pronounced. The same size-frequency curve apparent in November was continued with little change through the winter to April, 1948. From early May to mid-July, 1948, the shift of the population towards maturity and transformation was very marked. On the latter date only a few large nymphs remained and these were obviously maturing rapidly.

In late July, 1948, numerous young-of-the-year nymphs, 2–4 mm. in length, appeared in the samples. This group was readily separable, on the basis of size, from nymphs still remaining from the previous year-class. By August, 1948, essentially only one group of nymphs was present in the lakes. These had grown rapidly, many of them reaching the mature size range. No collections were made during the winter of 1948 and spring of 1949; however, collections secured at Pine Lake on June 13, 1949, after the main period of emergence had passed, revealed few nymphs present, most of them in the mature size range. The size-frequency distribution at that time showed definitely that the individuals remaining were remnants of the large population present the previous fall. It should be noted particularly that a marked break occurred between the old and new generations in collections taken in July, 1948. A similar but much less pronounced hiatus appeared in late summer of 1947. These characteristics of the nymphal populations were clearly evident in Pine and Gun lakes but somewhat obscured in Big Silver Lake because of a slightly later and more prolonged emergence period and greater overlap of the two generations of nymphs.

The size-frequency distribution data show a semblance of a bimodal curve which appeared to be characteristic of the nymphal populations in the winter of 1947-48. It was suspected that these two modes represented young produced by adults emerging in large concentrations at least twice during the summer. Some light was shed on this matter by close and continual observation of emergence on Big Silver Lake. Large numbers of imagoes were observed during the last 2 weeks of June and the first 2 weeks of July, 1947. A noticeable decline in the intensity of emergence followed, only a few adults being observed on various nights during the latter part of July and the first part of August. During the middle of August a noticeable number of subimagoes was seen by cottagers at the lake. Observations by means of a spotlight on the nights of August 10, 11 and 13 indicated that the emergence was general over the lake and was quite intensive although individuals were not as abundant as during June and July. This period of activity lasted about 10 days. Since emergence is promptly followed by oviposition, it is to be expected that these two peaks of emergence about 3 weeks apart would produce two large broods of nymphs which would be recognizable later in the size-frequency distribution of the nymphal population. The actual appearance of two such broods is evident in the nymphal population in Plot 1, Gun Lake on July 11, August 26, and November 9, 1948 (Appendix, Table 8). The logical explanation of the bimodality shown here is that it represents two main periods of egg deposition in this plot, separated by a time interval of 2 or 3 weeks. Certainly the two modes in the size-frequency curve are due to size differences of a single year-class rather than to two groups of nymphs hatched in different years. This conclusion is further substantiated by the single mode displayed by the nymphal populations in May and June in all lakes, and in Pine and Big Silver lakes in the late summer and fall of 1948.

It should be noted that a few very small nymphs, 3–8 mm. in length, were found in samples taken during April, May and June, 1948. These individuals apparently passed through the winter in the first few instars or as embryos which hatched in the spring. This group can still be identified in the size-frequency distribution tables for July, 1948. By late August these individuals had either matured and emerged or had lost their identity among the rapidly growing individuals hatched during the summer of 1948. Whether they were able to complete their growth and emerge during 1948 or were able to live through the winter and emerge during the following summer could not be determined. It is not illogical to believe that these slow-maturing nymphs would have lived through the winter and transformed the following year, thereby completing their life cycle in approximately 20–22 months.

If the life cycle is to be completed in one year, when development of nymphs essentially ceases during winter, growth must be very rapid during the summer in which the nymphs are hatched. That this occurs is apparent from the average lengths of the entire nymphal populations in the three lakes at various times of year, as shown in Figure 22 and Appendix Tables 11–14.

Some hesitancy was felt at first in accepting as real the apparent intial rapid increase in length of young nymphs in the lake and the size attained in the first summer of life. A comparison of growth rate and size-frequency distribution of the population in Pine Lake in July, August and November, 1948, with that of known-age nymphs reared in a hatchery pond during the same period dispelled any doubts concerning the validity of the interpretation of data secured from the natural population. A comparison of the size-frequency distribution of male nymphs from the two sources (Table 11) shows that growth was similar in both instances. A parallel correlation was noted for the females. While the average length of nymphs reared in the tub in the hatchery pond was slightly greater than that of specimens in the natural population, it is quite evident that many individuals in the lakes are nearly full grown at the end of their first summer of life.

A summarization of the growth of nymphs in these lakes and the length of time necessary to complete nymphal life—essentially the length of the life cycle of the insect—is as follows: At temperatures prevailing in Pine,

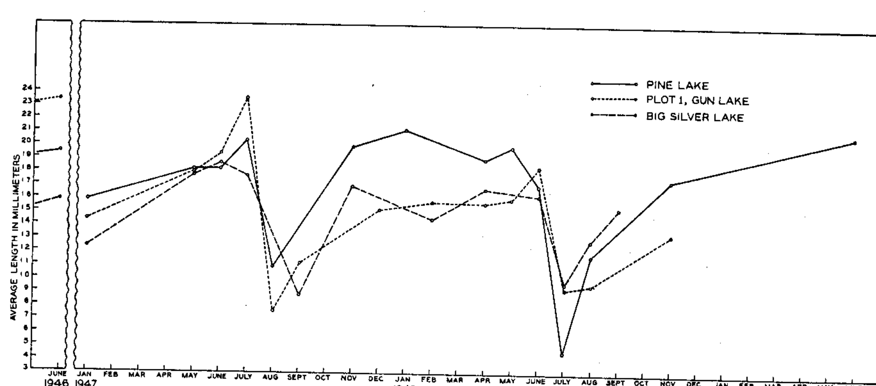


Figure 22. Average length of nymphs collected on various dates from Pine Lake, Gun Lake (Plot 1), and Big Silver Lake.

Table 11. Comparison of size-frequency distribution of male nymphs hatched in 1948 from Plot 1 at Pine Lake and from rearing tub in pond at Hastings State Fish Hatchery

Locality and date	Lengths in millimeters													Total
	1–2	3–4	5–6	7–8	9–10	11–12	13–14	15–16	17–18	19–20	21–22	23–24	25	
Pine Lake														
July 12.....	110	36	..	..	..	..	..	..	..	..	..	..	..	146
Aug. 25.....	...	3	18	13	12	14	21	23	5	1	..	..	..	110
Nov. 10.....	...	..	2	4	4	..	6	4	12	32	10	1	..	75
Hatchery pond														
June 22.....	10	..	..	..	..	..	..	..	..	..	..	..	..	10
Aug. 26.....	...	..	..	1	2	4	4	32	44	9	..	..	..	96
Nov. 8.....	...	..	..	..	..	..	..	2	4	19	29	6	2	62

Gun and Big Silver lakes during the summer, eggs hatch in 14 to 20 days. Growth of nymphs is rapid during the remainder of the summer and continues until the water temperature drops below approximately 48°F. Growth, virtually nonexistent during the winter, is resumed in spring, when water temperatures again rise above 48°F., and within 4 to 6 weeks thereafter many nymphs are mature and ready to emerge. A growth history of the various generations of nymphs present in Pine Lake from January, 1947, to June, 1949, is shown in Figure 23. Development of each year-class was similar in that rapid initial growth began after hatching and a slowing down or cessation occurred during the winter. A further increase in size took place during early spring, but after transformation began the growth curves are quite irregular. In each case the nymphal stage of development was completed in one year.

In contrast to the 1-year life cycle in effect in these southern Michigan lakes, it has been found that the life cycle of various species of *Hexagenia* is 2 years in the following localities: *Hexagenia* sp., Shakespeare Island Lake, Ontario, (Cronk, 1932); *Hexagenia* sp., Connecticut lakes (Deevy and Bishop, 1941); *H. viridescens,* Douglas Lake, Michigan (Lyman,

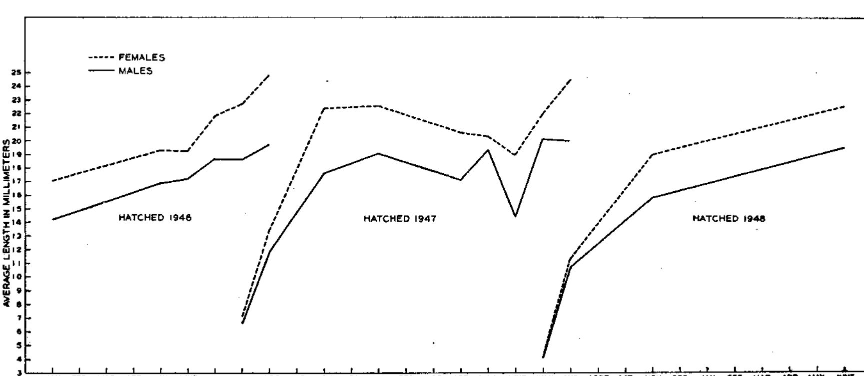


Figure 23. Growth of nymphs hatched in different years in Pine Lake (a 1–year life cycle).

1940); *H. variabilis* Etn. (=*H. limbata*), streams in New York State (Morgan, 1913); *H. limbata occulta* and *H. rigida,* Lake Winnipeg, Manitoba (Neave, 1932); *H. bilineata,* northern part of Mississippi River drainage (Needham, 1920); *Hexagenia* sp., Ontario streams (Ricker, 1934); *H. occulta,* northern Indiana lakes (Spieth, 1941); *H. occulta* and *H. rigida,* western Lake Erie (Dr. David C. Chandler, personal communication). Also the author has concluded that the life cycle of *H. limbata* in the Au Sable River, Michigan, is 2 years. Although many authors have concluded that a 2-year cycle is the rule for *Hexagenia,* Lyman (1943a) found in a pre-impoundment study of the Watts Bar Reservoir area in Tennessee that *H. bilincata* completes its life cycle in 1 year in that area.

A comparison of temperature conditions in Pine, Gun and Big Silver lakes with published reports of those of other bodies of water in which the length of life cycle of *Hexagenia* is known, reveals some interesting and significant facts. It has been concluded that *Hexagenia* has a life cycle of 2 years in the following lakes: western Lake Erie, Douglas Lake and Lake Winnipeg. It has been found (Chandler, 1940, 1942, 1944; Chandler and Weeks, 1945) that from June to September the temperature of surface waters of western Lake Erie range from 17.2° to 27.4°C. (63.0°–81.3°F.). Usually the temperature is about 70°–73°F. in the summer. Published records of the temperature of surface waters of Douglas Lake recorded for the period 1911 to 1933 (Welch, 1927; Welch and Eggleton, 1932; Welch and Eggleton, 1935; Eggleton, 1935) show that the range during June, July and August was from 17.2° to 29.4°C. (63.0°–86.7°F.)—the usual summer temperature range being 19°–23°C. (66.2°–73.4°F.). Neave (1932; 1934) found the temperature of surface waters of Lake Winnipeg to be 13.8°C. (56.8°F.) in June and to range from 18° to 23°C. (64.4°–73.4°F.) in late July and August. Water temperatures in the Au Sable River range from 50° to 78°F. during the summer.

It is quite evident that summer water temperatures of the lakes mentioned above are far below those recorded for the southern Michigan lakes covered by this report, in which *limbata* has a 1-year life cycle. On the other hand, summer temperatures of the lakes just discussed are very similar to those recorded in the Au Sable River, where 2 years are required to complete the life cycle of *limbata.* Lyman (1943a) gives no temperature records for the Tennessee River in which *H. bilineata* has a 1-year life cycle but it is not unlikely that water temperature, especially in summer, approaches that of Pine, Gun and Big Silver lakes. Published accounts of *H. bilineata* (Needham, 1920; Lyman, 1943a) show that this species may complete its life cycle in either 1 or 2 years depending upon the geographical location and the influence of different environmental factors. Since this observation has been made for one species of *Hexagenia,* others with an extended north-south distribution range can be expected to show the same variation. Since *limbata* is widely distributed in North America from north to south and from east to west, it is obvious that the species lives in a great variety of situations where temperature and other factors would be expected to vary widely. It is only logical to assume that in different ecological situations the period required for hatching of eggs, the growth rate of nymphs, and the time of year at which emergence and mating take place would vary. These variations in different phases of the life cycle might be expected to be reflected in the total time required for a generation to be born, mature, and reproduce itself.

Factors influencing distribution of nymphs

The investigations of many authors, too numerous to mention here, have indicated that the type of bottom exerts a profound influence on the distribution of a great many aquatic insects in streams. Lyman (1943b) stated that character of bottom was one of the most important environmental factors influencing the distribution of *Hexagenia* nymphs. The writer has concluded that although other limiting factors may be operating at times, in general the nature of the bottom is the most important factor influencing local distribution of *limbata* nymphs in both lakes and streams. Since this fossorial insect is by adaptation and necessity an inhabitant of a soft substratum, it is restricted to areas in which suitable materials occur. Bottoms composed of sand, gravel, rubble or peat are entirely unsatisfactory as nymphal habitat, while those consisting chiefly of soft marl, soft clay, firm muck or stream mud are admirably adapted to the burrowing requirements of these insects.

Within a lake harboring them, the local distribution of nymphs is not usually cosmopolitan but rather irregular, depending upon the location and extent of a satisfactory burrowing medium. In waters such as Pine, Gun and Big Silver lakes, nymphs are largely confined to soft marl-mud and are not found in numbers on adjoining sand, sand-gravel, or peat bottoms. In such bodies of water these insects occur wherever suitable bottom exists providing that other environmental factors, such as the amount of dissolved oxygen, are favorable, and are lacking in areas having an unsuitable bottom although the environment is otherwise satisfactory. The maximum depth at which nymphs are found in Pine and Big Silver lakes is determined chiefly by the bottom type rather than by other factors since marl-mud begins to be displaced by peat at about 10–15 feet, a depth at which few nymphs ordinarily occur. Since dissolved oxygen was present in deeper water in sufficient quantities to sustain them, it seems certain that change in character of bottom from marl to peat is a deciding factor in restricting nymphs to the shallower areas.

Evidence of limited migrations of individuals in which the movement appeared to be definitely related to the character of the substratum was secured at Transect 1, Big Silver Lake. Imagoes were seen to oviposit on the sand shoal and later rather large numbers of young nymphs were taken in bottom samples from this area. A thin layer, no more than one-half inch thick, of very fine sand, silt and organic debris lay on top of hard packed sand and provided a habitat for these very small individuals. As the summer progressed, a definite decrease in numbers of nymphs, correlated with increase in size, was noted. By early fall few specimens, none of them more than about 15 mm. in length, could be found on the sand shoal. A logical explanation of the disappearance of nymphs is that as they grew larger a deeper soft substratum was needed and individuals moved from the shoal into deeper water adjoining it, where deep mud was available.

Samples of bottom mud from the waters studied were washed through a set of 6 Tyler screens to determine size and nature of the included materials. Analyses of lake mud from areas of nymph concentration in the three lakes (Appendix Tables 15, 16, 17) showed greater similarity and revealed that the chief constituent was finely divided marl, most of which easily passed through screen 100 meshes to the inch. Furthermore, water comprised 66.5–84.0 percent of the weight of the mud. Samples of marl and sand mixtures secured in Big Silver Lake from an area where sand and marl adjoin (Appendix Table 18) show that sand, fine gravel and coarse marl flakes made up more than half of the material. Sufficient fine marl was present, however, to render the bottom habitable by nymphs. In these samples water made up only 28.4–38.9 percent of the total weight. It is clearly indicated that the bottom consisting principally of very fine marl and having a high percentage of water was more suitable as a habitat than the more dense and heterogeneous bottom.

Chemical analyses showed a considerable variation in properties of mud from different waters as well as from different parts of the same lake (Appendix, Table 19). Nymphs were known to occupy the bottom from which all these samples were taken, therefore it cannot be inferred from the limited data that chemical conditions in one area were more or less suitable as a nymphal habitat than those in another. The data serve only to indicate in part the chemical composition of the mud in the various waters.

Normal seasonal variations in the chemical features of waters investigated are well within the toleration range of *H. limbata*. Experiments have shown that nymphs are not adversely affected by pH ranging from 7.4 to 9.6. It is not known if they are able to tolerate acid conditions since no opportunity was presented to observe the reactions of specimens in natural acid waters. Nymphs suffered no ill effects after living several days in water with ph-th alkalinity as high as 32 ppm. and M. O. alkalinity as low as 14 ppm.

It is known that when the amount of dissolved oxygen becomes reduced, a condition usually accompanied and complicated by an increase in free carbon dioxide, nymphs are adversely affected. Several times specimens reared in aquaria died under conditions resulting from failure of aerators. In all such cases, water analyses revealed that dissolved oxygen was less than 1.0 ppm. and that free carbon dioxide ranged from 1.4–5.5 ppm. To obtain more exact information on the lethal effects of stagnation, 8 bottom samples, including vegetation, washed debris and at least 10 nymphs each, were placed individually in 2-quart jars filled with lake water. After 48–52 hours of observation the water of each was analyzed and the nymphs examined. In 7 jars more than one-half the nymphs were dead and the others in poor condition. Analysis gave the following results: dissolved oxygen 0.0–0.3 ppm., free carbon dioxide 0.7–2.35 ppm., pH 7.2–7.5, and methyl-orange alkalinity 142–163 ppm. A few individuals were still alive in each jar although two of them contained no oxygen and three others contained less than 0.1 ppm. In the eighth jar, with 1.0 ppm. of oxygen and 0.6 ppm. of carbon dioxide, 4 of 19 nymphs were dead.

In order to observe the reaction of nymphs in natural waters under conditions of summer stagnation, specimens were placed individually in 250 cc. bottles containing water of known chemical properties secured at various depths in Big Silver Lake in late summer. Observations indicated that nymphs apparently suffered some discomfort when the dissolved oxygen content dropped to 1.5 ppm. and the carbon dioxide content rose to 2.0 ppm. Distress became more evident as the amount of oxygen decreased and free carbon dioxide increased. Initial symptoms of distress were continual swimming and violent and continuous waving of the gills. After several hours, specimens became very weak, and periods of crawling and gill-waving were interspersed with long intervals in which no movement at all was discernible. Some individuals were seemingly dead by the time the oxygen content of the water was reduced to 0.7–0.5 ppm., while others were comparatively lively. Upon removal to fresh water, nymphs which had appeared lifeless for as long as 2–4 hours rapidly recovered from their torpor.

Observation indicated that a few individuals succumbed under stagnation conditions when dissolved oxygen was reduced to about 1.0 ppm., that most specimens did not become motionless until oxygen was less than 0.5 ppm., and that a few nymphs were still active when analysis showed no oxygen present. Some individuals survived conditions of water stagnation in which little or no oxygen was present for as long as 6 hours. Although some specimens proved to be very resistant to low concentrations, the writer has concluded that exposure to conditions in which only 1.0 ppm. of dissolved oxygen is present will result in the death of most individuals within 30–48 hours.

A situation which unquestionably has a counterpart in nature was created by removing the aerator from an aquarium containing a marl-mud bottom and a large number of nymphs. On the following day distress was evident, for several nymphs had left the burrows and were lying on the mud surface, the gills waving continuously. Later all individuals left the burrows and most of them attempted to remain at the water surface by hanging on to the sides of the aquarium in the corners while others climbed on to thin wood chips floating on the surface. Analysis of water secured midway between top and bottom revealed 1.2 ppm. of oxygen and 1.6 ppm. of carbon dioxide. The reaction of nymphs to the lowering oxygen content of water under stagnation conditions appeared to be one of escape to a better aerated environment. Introduction of fresh water and compressed air into the aquarium soon resulted in return of the nymphs to the bottom and a burrowing existence.

That nymphs are sometimes driven from the bottom mud and even die in large numbers in winter due to oxygen depletion in ice-covered waters appears to be a fact although such a situation has never been witnessed by the writer. While conducting an investigation on fish mortality resulting from winterkill in certain lakes near Ann Arbor, Dr. Gerald P. Cooper and Mr. George N. Washburn saw dead and dying *Hexagenia* nymphs on the bottom of several lakes and later informed the writer of their observations. Reports were received from several anglers and bait collectors that they had seen, at various times in the past, large numbers of nymphs swimming in the open water during late winter. As one angler put it, "I saw hundreds of 'wigglers', like schools of minnows, swimming past my fishing hole, just beneath the ice, and all were going in the same direction. The procession lasted about 20 minutes." A bait collector whose observations should be fairly reliable reported seeing great numbers of large nymphs congregated about holes cut in the ice in West Gun Lake in 1945. In his words, "They seemed to be trying to get air. I scooped up four or five thousand and (after placing them in large cans filled with lake water) carted them home, but next day most of them were dead." The finding of these nymphs and their subsequent death strongly indicate an oxygen deficiency in Gun Lake at that time.

Since winter stagnation conditions are comparable to those of an unaerated aquarium, there is little doubt that in some waters nymphs are occasionally adversely affected by water stagnation causing low oxygen concentrations and other chemical changes which result in forced migrations and even death.

Lyman (1943b) concluded that lack of oxygen was a limiting factor in the depth distribution of *Hexagenia* nymphs in Douglas Lake, Michigan, since the lower limits of their range there (15 meters or just under 50 feet) coincided with a rapid decrease in dissolved oxygen, and the character of the bottom was similar both above and below that depth. However, it seems quite unlikely that lack of oxygen is a factor limiting the depth distribution of nymphs in Pine, Gun and Big Silver lakes since sufficient amounts to sustain them were always found in the depressions at depths greater than their normal range

It has been determined that temperature is the most important factor influencing the geographical range of many aquatic insects, and that within the limits set by it a number of other factors determine the local distribution of each species (Ide, 1935b; Sprules, 1947). The annual temperature range of Pine, Gun and Big Silver lakes is well within the thermal toleration limits of *limbata* and is of no significant importance in determining local distribution of nymphs in these waters. A temperature range of 32°–93°F. normally occurs in these lakes during the year.

Depth of water in itself does not appear to be a factor limiting the downward distribution of nymphs in the lakes considered here. Although the maximum depth reached in Pine and Big Silver lakes was about 16 and 20 feet, respectively, *Hexagenia* nymphs are known to occur at depths as great as 69 feet in other lakes (Lyman, 1943b; Neave, 1934; Rawson, 1930). Other factors previously discussed, rather than depth alone, apparently operate to prevent them from existing in deeper water.

Wave action in lakes apparently does not influence distribution of nymphs directly, but rather indirectly, through its effect on the lake bottom. In Gun and Big Silver lakes extensive shoal areas are uninhabitable because of wave action which keeps the sand bottom well washed and prevents accumulation of sediment on top of the sand. In other parts of the same lakes soft marl bottom and nymphs are found within 3–4 feet of the water line in sections well protected from waves. Although much of the third basin of Pine Lake is only 3 feet deep and subject to disturbance by water movements, comparatively little of the firmly packed marl-mud is loosened by wave action and nymphs apparently are not displaced. There is a possibility, however, that in large, shallow lakes with soft bottom violent wave action might dislodge nymphs from their burrows.

Light probably has little or no influence on the lateral or vertical distribution of nymphs. It is known that except for a short period during transformation nymphs of all sizes and ages exhibit a strong negative phototropic response which results in their lying deep in the burrows, where light is at a minimum, during daytime hours. As mentioned previously, during hours of darkness nymphs were frequently seen at the mouths of the burrows but always retreated when the beam of a small flashlight was turned full upon them.

Simple experiments conducted with newly hatched individuals in which light was directed from various angles toward Petri dishes used in incubating eggs resulted in all specimens moving away from the light and congregating in shaded areas. The negative response and resultant concentration in a small area made it possible to remove them from hatching vessels without disturbing the remaining eggs.

During periods of ice cover on the lakes nymphs are not adversely affected except when unfavorable chemical conditions develop. In a few small areas where nymphs were located within a few feet of shore in shallow water, it appeared that they were driven out or destroyed when water froze to the bottom. Since few individuals and small areas were involved, the effect on the population as a whole was negligible.

Extent of aquatic vegetation apparently is a factor which influences both the distribution and density of a nymphal population. Early in the study routine lake bottom sampling where varying quantities of plants were encountered suggested that fewer nymphs existed in thickly vegetated bottom than in barren or sparsely vegetated sections. Subsequently vegetation (principally *Chara*) in each of a large series of square-foot bottom samples was drained and weighed. Results showed that no difference existed in the average number of nymphs per unit area of bottom where the wet weight of plants ranged from 0 to about 85 gm. per square foot. When it increased to about 85–170 gm. per square foot, a definite decrease in number of nymphs was evident, the density being 50–75 percent lower than in adjacent areas supporting little vegetation. That this reduction was not due to malfunctioning of the dredges was shown by the comparatively few nymphs secured in samples taken with scoops in dense vegetation. In certain localities where *Chara* was particularly thick and blanketed the bottom, no nymphs were ever located. Few specimens were encountered in the belt of heavy vegetation situated on the drop-off in the lakes. Their near absence in these areas may have been due to the density of vegetation coupled with the changing character of the bottom. Since in some instances the underlying mud was not noticeably different from barren bottom nearby, it seems likely that the density of the vegetation itself created a condition unfavorable for the nymphs.

An experiment indicated that dense vegetation interfered with burrowing and possibly adversely affected the flow of water through the burrow. A layer of firm marl-mud 3 inches deep was placed in an aquarium and one-half of it covered with a dense mat of short *Chara*. Several nymphs were released so that they reached bottom in the half covered by plants. None of the specimens attempted to penetrate the *Chara;* instead all eventually moved to the exposed mud and burrowed there. In several other instances nymphs were allowed to become established in a burrow, then a dense mat of short *Chara* was placed over the mud surface so that the burrow openings were covered. After a day or two all specimens moved so that the new burrow openings were not obstructed by the *Chara*.

Emergence

Transformation of mature nymphs to the winged subimaginal stage (emergence) ordinarily began in May and continued throughout the summer in the waters studied. Usually most of the nymphs emerged during the 3- to 6-week period following the first appearance of the winged stages. However, stragglers continued to appear as late as September. Warm weather in spring and early summer of 1946, 1948 and 1949 resulted in an early and concentrated emergence of *limbata*. The cold season experienced in 1947 caused the emergence to be late and prolonged without the usual concentration of subimagoes evident in more favorable years. Emergence periods on the lakes studied are shown in Table 12.

Table 12. Emergence period on certain Michigan lakes from 1946 to 1949 (from records of author and others)

Locality	Year	Approximate date of first emergence	Approximate period of heavy emergence	Date of last observed emergence
Pine Lake	1946	May 7	Before May 31	Unknown
	1947	June 6	June 15–Aug. 16	Sept. 12
	1948	May 8	May 25–July 11	Aug. 25
	1949	May 5	May 17–June 7	Unknown
Gun Lake	1946	May 7	Before May 30	Unknown
	1947	June 3	June 18–Aug. 1	Sept. 10
	1948	May 5	May 20–June 30	Aug. 26
	1949	May 3	May 15–June 5	Unknown
Big Silver Lake	1946	May 19	June 1–July 5	Sept. 2
	1947	June 10	June 20–Aug. 25	Sept. 15
	1948	May 18	May 28–July 30	Sept. 5
	1949	May 15	May 18–June 15	Unknown

Data accumulated by the author from observations made during evening and night on 52 different occasions on Pine, Gun, and Big Silver lakes, showed that emergence of *limbata* always occurred in the forepart of the night. Despite the fact that various authors have reported transformation of *Hexagenia* in early morning and afternoon (Needham and Betten, 1901; Morgan, 1911; Neave, 1932; Lyman, 1940), the writer has never seen subimagoes emerging during the day or early morning from the waters studied. The earliest observed emergence occurred at 7:40 p.m., E.S.T., July 21, 1948. In all instances, few subimagoes appeared before the onset of darkness. Emergence, always at its height from 1 to 2 hours after darkness set in, was usually over by 11:00 p.m., E.S.T. In few cases were subimagoes seen to emerge as late as midnight. The emergence on Big Silver Lake the night of June 18, 1947, was typical of all those observed on the three lakes and will be described. Subimagoes first appeared at 8:45 p.m., E.S.T., just as darkness was falling. By 9:15 large numbers were on the water; at 9:30 the peak of emergence was reached; and by 10:30 it was virtually completed. Only scattered individuals appeared from 10:30 to midnight. Four floating traps (total collecting area 27 sq. ft.) operating the same night caught a total of 45 subimagoes from 8:00 to 10:00 p.m., and only 1 between 10:00 p.m.

and 7:00 a.m. the next morning. On three other occasions traps were cleared of specimens at 10:00 p.m. and caught few or no subimagoes during the remainder of the night. In several instances it was determined that specimens emerging in the laboratory always did so between the onset of darkness and midnight. While subimagoes usually emerged only after dark in the lakes studied, the writer observed that on three occasions a few nymphs transformed an hour before sunset on East Fish Lake, Montmorency County.

Transformation was frequently observed at close range on the lakes at night. Mature nymphs, as well as subimagoes, show a strong positive phototropic response and the former frequently came to and congregated around a partly submerged sealed-beam spotlight hung over the side of the boat. The journey from the lake bottom to the water surface was usually accomplished rather quickly, but on four occasions an individual was seen to swim about for several minutes, never quite reaching the surface, until, becoming exhausted, it sank back to the bottom and was eaten by a fish. Usually nymphs were seen to move almost directly upward until the surface was reached and then to swim erratically about for from 10 seconds to a minute or more. Several individuals were observed to swim from bottom to surface, a distance of about 6 feet, in 10–15 seconds. Very shortly after reaching the surface, the nymph's swimming movements slow and eventually stop so that the insect is floating with thorax exposed and legs extended out from the body. With cessation of swimming movements, the nymphal skin splits down the top of the head and thorax, and the body of the subimago immediately begins to protrude. Movement of the body is upward and forward. Until the appendages are released, the nymph is perfectly still, the only visible movement being the rapid and steady protrusion of the subimaginal body through the dorsal thoracic rent in the nymphal skin. Head and thorax are first freed from the nymphal skin, followed by the legs and wings. Once, the wings are free, they instantly unfold and are ready for use. The abdomen is cleared of the nymphal skin by one or two lateral undulations of the body, aided by a flap of the wings. Almost at once the newly emerged subimago tries to fly away. Often the first attempts result in flights covering a distance of no more than a few feet before the insect strikes the water, but after further trials it becomes airborne and flies heavily and erratically to shore. The cast nymphal skin (exuviae) remains floating on the surface. After extensive emergencies these exuviae carpet the water and later form windrows on the lake shore when cast up by wave action.

The interval between cessation of nymphal swimming motions and completion of emergence was recorded for 18 individuals, the shortest period being 10 seconds, the longest 95. Usually the process of transformation was completed within 15–30 seconds. Five nymphs, watched from the time they reached the surface, were not able to transform. Transported to the laboratory in a bucket of water, these individuals continued to swim and struggle until they died. Very frequently a few dead mature nymphs were found on the lake among drifting masses of exuviae. No evidence that mature nymphs crawl around on the bottom for a time before swimming to the surface was secured either in the field or laboratory. It is most probable that this insect, once it is motivated to transform, travels directly from its burrow to the water surface.

In most instances, calm water prevailed at the time of emergence. However, observations on windy nights showed that transformation occurred without hindrance and that most subimagoes were able to fly from the water. On one occasion a very strong wind, causing waves about 2 feet high, did not prevent transformation but did prevent subimagoes from getting into the air. Instead, they were blown along with the waves like so many tiny sailboats. Although they were frequently blown over on their sides, none was seen to become soaked and drown. Transformation to the winged stage was observed to take place during light rain storms and on both dark and moonlight nights. Heaviest emergences always occurred on warm nights when air and water temperatures were above 70°F. On cold nights, the number of nymphs transforming was invariably small.

The effect of air movement on distribution of subimagoes around a lake is very pronounced. Even a very slight breeze is sufficient to cause all emerging individuals to fly down wind and become concentrated on the side of the lake toward which the wind is blowing, resulting in subsequent mating flights being heaviest in that area.

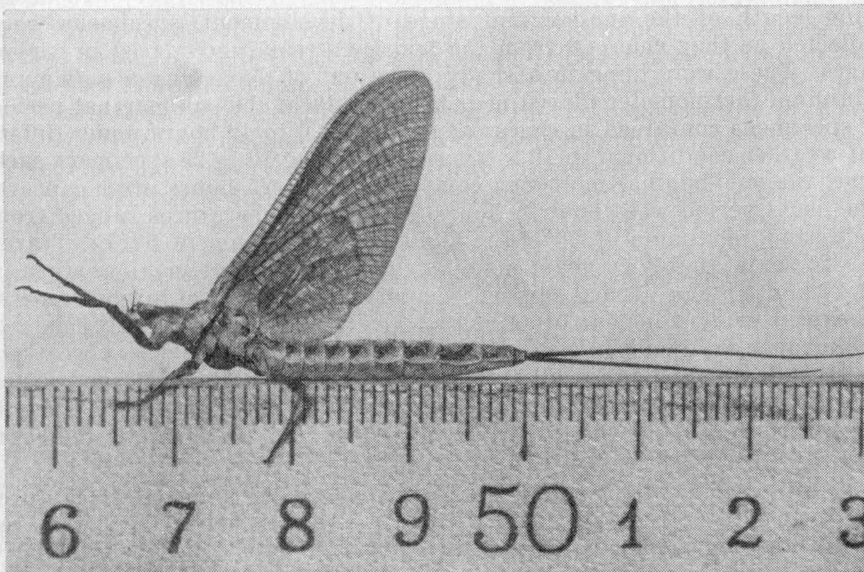
Although it was not possible to obtain a season-long check on the number of subimagoes emerging per unit area of water surface, a limited amount of trapping did give an indication of the number emerging in a short period. One large floating trap was located on Transect 5, and 1 large and 2 small ones on Transect 3 in Big Silver Lake. From the afternoon of June 11 to the morning of June 19, 1947, a total of 104 subimagoes was caught. The average number emerging from 1 square foot of water surface during that period was 3.8.

Subimago

After emerging and flying to land, subimagoes come to rest on ground, trees, shrubs, cottages, and other objects near the water's edge. Here they pass the remainder of the night. With rising of the sun, shifting of position occurs as the mayflies seek shade and shelter in vegetation. Short flights carry the insects from place to place. At this time birds were often seen catching them on the wing. As the morning progresses, subimagoes become dispersed from the water's edge. Usually most individuals remain within 100–200 yards of the shore, but often scatter much farther, as shown by collection in the afternoon of a few specimens a quarter-mile from the edge of Gun Lake. After the initial morning dispersal to find suitable shady resting places, subimagoes remain quiet during the balance of the day. Although thousands of individuals may be present in a small area, they are inconspicuous and are not noticeable until search for them is made. Favored resting places appear to be trunks and limbs of trees and the underside of leaves. Under ordinary circumstances, they are not usually found on the ground or in grass during the latter part of the day.

Subimagoes differ considerably from imagoes in appearance and are frequently considered by fishermen to be a different kind of insect. Opaque wings, short caudal filaments and dull colored body are typical of this stage (Figure 24).

Time spent in the subimaginal stage varies considerably and is apparently largely controlled by conditions of temperature and humidity. Measurements of the latter were not made, but some authors have con-



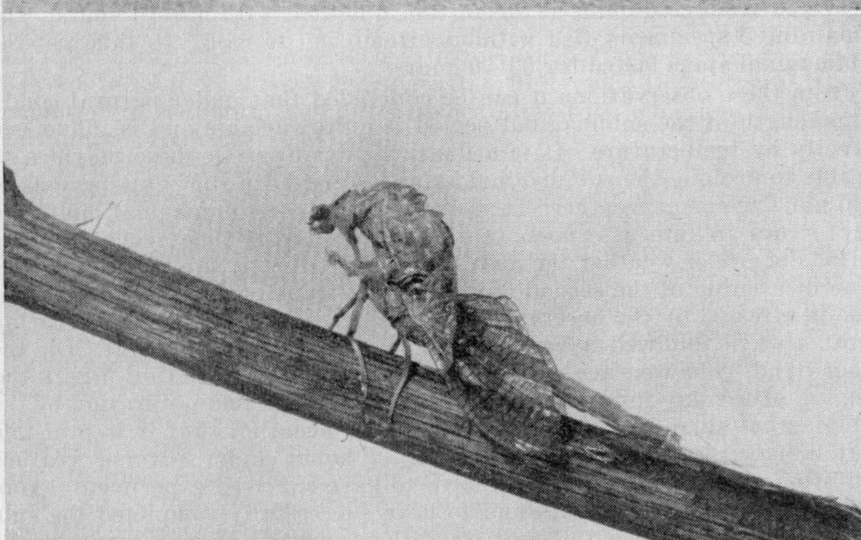


Figure 24. (Upper photo.) Large female subimago reared in an aquarium. Scale is in centimeters.

Figure 25. (Lower photo.) Female imago partially emerged from subimaginal skin.

sidered it of minor importance (Clemens, 1913; Lyman, 1944). To determine length of the subimaginal stage of development, specimens were collected as they emerged from the lake or stream and placed in screen cages. These were hung in a shady place out of doors and a maximum-minimum thermometer placed near by. Length of the subimaginal period of specimens contained in cages ranged from 20 to 49 hours under different weather conditions. In 10 instances, involving 10 to 26 specimens each time, the subimaginal molt was completed in 20–25 hours after capture. The usual period was about 22 hours when air temperatures ranged from a daytime maximum of 90° to a night time minimum of 59°F. Traver (1932) found that *Hexagenia carolina* completed the subimaginal stage in 22–27 hours under normal summer temperatures. Effect of lower temperatures was evident in four other cases in which from 13–18 newly-emerged subimagoes were held in cages during periods of cold, inclement weather. In these instances, subimaginal molts occurred from 36 to 49 hours after capture. Most specimens completed the molt in 40–44 hours. Maximum temperatures during the day were 65°–71°F., minimum night temperatures 49°–54°F.

As an experiment, 11 subimagoes were placed, 12 hours after capture, in a refrigerator regulated at 38°–40°F. After 48 hours, they were removed and left at room temperature (74°F.). Most specimens rapidly recovered from cold-induced torpor and 6 molted within 9–10 hours. The remaining 5 specimens died without attempting to molt. In this test the subimaginal stage lasted for 69–70 hours.

From these observations it can be concluded that under natural conditions length of the subimaginal period is quite variable and is influenced directly by temperature. It is a distinct advantage to these mayflies to be able to prolong the subimaginal stage, as an aid in surviving periods of cold and inclement weather. In warm weather the subimaginal molt usually occurs in late afternoon of the day following emergence. During periods of colder weather the molt takes place during late morning, afternoon or evening of the second day following transformation. That this is true is attested by the observation that in warm weather a heavy mating flight always followed a heavy emergence the preceding night. On the other hand, cold weather resulted in no or very light mating flights the evening of the day following heavy emergence. Maximum duration of the subimaginal stage was not determined with accuracy, but it is probable that in nature it may last as long as 72 hours under adverse weather conditions. Other mayflies are known to have survived experimental conditions of cold for 130 hours and to have successfully completed the subimaginal molt at the end of that time when normal summer temperatures were restored (Lyman, 1944). The usual length of the subimaginal stage was 24 hours (*op. cit.*).

The subimaginal molt is usually completed in 2–4 minutes. Before the molt begins, the subimago secures a firm grip on the surface on which it is resting. Initiation of the process is marked by a slight flutter of the wings, followed by splitting of the dorsal thoracic skin. Immediately the imaginal thorax and head begin to protrude and the wings to gradually lower backwards and sidewards. As the body continues to protrude forward and upward, the wings and legs are freed by pulling and wrenching movements of the body. Once the appendages are free, the imago walks forward and pulls the abdomen and caudal filaments from the subimaginal skin. The position of a specimen about midway through the subimaginal molt is shown in Figure 25. Many caged individuals were unable to free themselves from the subimaginal skin at various stages of the molt and eventually died. This inability to complete the molt successfully probably resulted from injuries sustained during previous handling, for rarely was an abortive molt observed in the natural environment.

The attraction to lights of the subimagoes of all species of *Hexagenia* is too well known to be discussed here except to mention that advantage was taken of this trait to capture the insects at night. Accounts of tremendous concentrations of burrowing mayflies around lights in towns located near lakes and rivers have appeared from time to time in the popular press as well as in scientific literature.

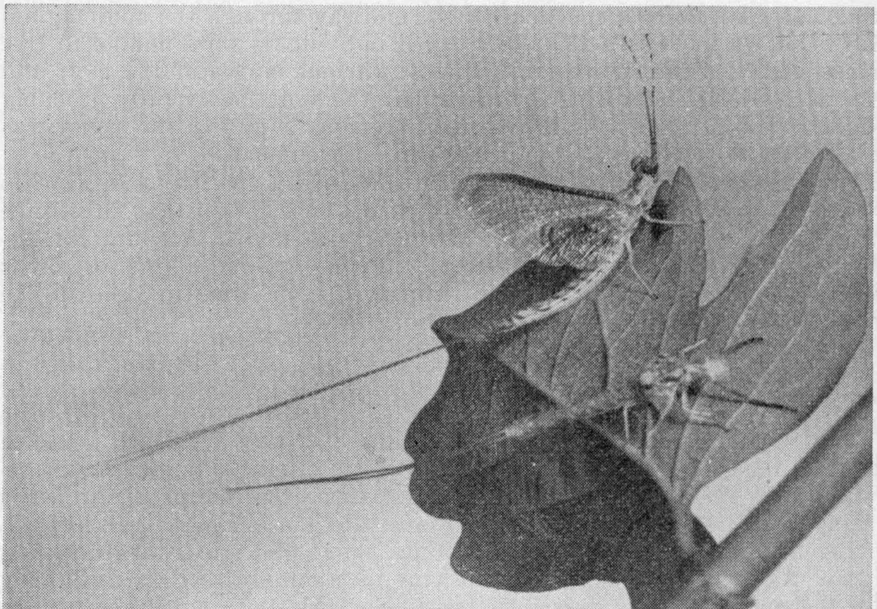
Imago

Upon completion of the subimaginal molt, the fully developed adult or imago is ready to mate. Those which emerge during daylight hours remain quietly resting in various shady places awaiting the proper time for mating activities to begin. Little movement of the imagoes is discernible during the day except for an occasional short flight to change resting places. As dusk approaches they become increasingly restless until they join the mating flights described later. Several times subimagoes were observed to molt at dusk when a mating flight was in progress. Upon completion of the molt, the adults immediately took wing and joined the swarming mayflies overhead.

In superficial appearance imagoes differ from subimagoes in that wings are hyaline, body colors are bright and forelegs and caudal filaments are long (Figs. 24, 26 and 27). With shedding of the subimaginal skin the insects are much more active and capable of better flight. Average size of males is much smaller than that of females. In addition, males have much longer tails, longer forelegs, and are considerably darker in color than females, and the male claspers are quite conspicuous.

Duration of the imaginal stage varies considerably and differs with the two sexes. Males were observed to live approximately 12–57 hours. Those which survived longest—more than 30 hours—were individuals captured while undergoing the subimaginal molt and which had no opportunity to mate. In some cases, males, collected during a mating flight, lived only 12–16 hours after capture, although others survived as long as 34 hours. How long these specimens had lived as imagoes before capture is not known. In any case, it is quite certain that most males exist long enough to be able to engage in mating flights on at least two successive days.

Females still retaining eggs lived from 31 to at least 58 hours. Specimens collected at Gun Lake the night of July 1, 1947, were kept in captivity until they died 58 hours later. These individuals must have existed as imagoes for more than 60 hours. It is certain that female imagoes, providing they retain their eggs, can live for more than 30 hours and are capable of mating on either of two successive days. Spent females were known to live only 4–26 hours after releasing their eggs. Most spent females, collected at night during ovipositing flights, died before noon of the following day. Death of imagoes is apparently caused by gradual



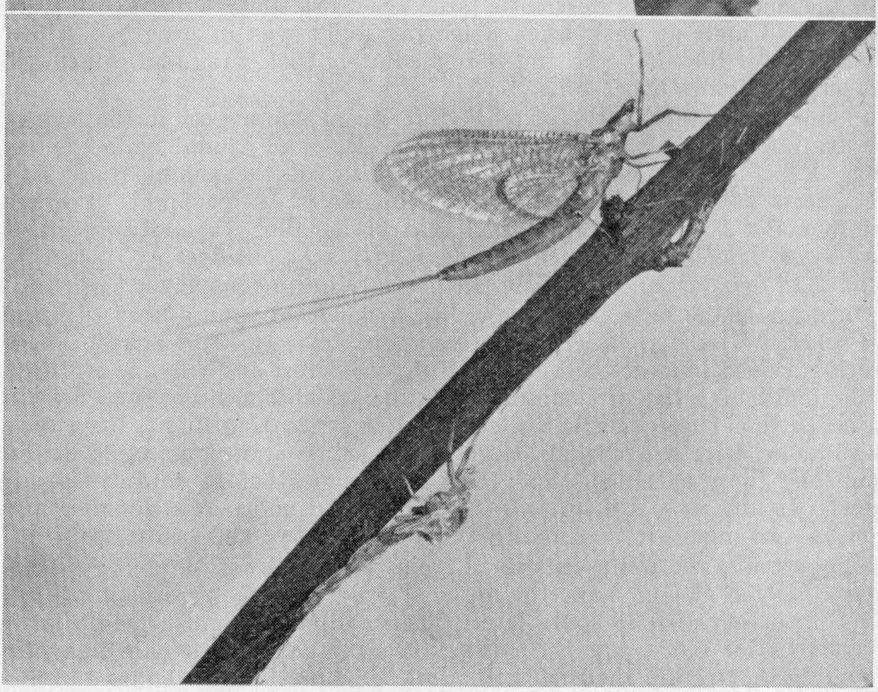


Figure 26. (Upper photo.) Male imago, with cast subimaginal skin nearby.
Figure 27. (Lower photo.) Female imago, with cast subimaginal skin nearby.

desiccation, and in most instances individuals which lived for long periods became quite incapable of active flight some hours before death.

The ability of both males and females to live for two days or more is of great value to the species in partially circumventing the effect of high winds and storms which might prevent mating and ovipositing flights during an evening. It is quite certain that individuals prevented from mating one evening can do so the next.

Imagoes exhibit size differences similar to those of full-grown nymphs discussed previously. A series of males and females collected at intervals during the emergence period from each lake included in this study were measured (Table 13). Size of imagoes was essentially the same in all waters.

Table 13. Size of imagoes, in millimeters

Locality	Males				Females			
	Body length		Wing length		Body length		Wing length	
	Range	Average	Range	Average	Range	Average	Range	Average
Pine Lake.......	18–24	20	17–22	18	20–28	24	19–26	22
Gun Lake.......	17–25	21	15–22	19	21–30	25	18–27	23
Big Silver Lake..	17–24	20	15–22	18	20–29	24	18–26	22

Measurements of imagoes collected in different months of the summer showed that specimens which emerged early were larger than those which appeared later in the season. This difference is well illustrated in Big Silver Lake. In 1947 the average body length of males was as follows: June, 23 mm.; July, 21 mm.; August, 19 mm. A similar difference in average length of females is shown by the following measurements: June, 26 mm.; July, 24 mm.; August, 23 mm. It was also noted that imagoes appearing early in the season at Pine and Gun lakes were slightly larger in average size than those in evidence during late summer. These seasonal size differences apparent in the adults are also suggested by the average lengths of last instar nymphs collected at intervals throughout the summer.

Ide (1935b) found seasonal size differences in individuals of *Iron pleuralis* and *Epeorus humeralis*. In these instances individuals appearing early in the season were larger than those occurring at the height of emergence. However, specimens appearing toward the end of the season approached the size of early season adults, a fact which is at variance with findings relating to *H. limbata* in certain Michigan waters.

It is suspected that individuals of *H. limbata* may occasionally reach a larger size than any collected. The largest specimen obtained was reared to the subimaginal stage but did not complete the subimaginal molt (Fig. 24). Since the body length of this specimen measured 35 mm.—about 1⅜ inches—it is quite certain the imago would have been larger than any collected in the field.

Difficulties were encountered in capturing male imagoes at night on both lakes and streams. As previously mentioned, subimagoes of both sexes are readily attracted to a strong light at night. The trait is still well defined in female imagoes and made collecting them a comparatively easy matter. Male imagoes, on the other hand, were rarely attracted to collecting lights even though at times the latter were situated on high banks near the level of the mating dance. The difference in behavior of subimaginal and imaginal males has led the writer to conclude that in the adult stage males are no longer positively phototropic.

Mating Activities

Mating activities of mayflies have attracted a good deal of attention from biologists and are well known for many species. Morgan (1913), Needham (1927), Neave (1932), Needham, Traver and Hsu (1935) Spieth (1940), and others have described in detail the mating activities of *Hexagenia* and other mayfly species. The swarming of *Hexagenia* is a spectacular affair although the activities are usually shrouded in gathering darkness and not easily seen.

Since swarming of *Hexagenia* is well known, only a brief resumé will be given of the mating activities of *limbata* as they invariably occurred at the lakes studied. Just at dusk, male imagoes begin to leave their resting places and congregate alongside and above the trees on the lake shore. It was noted particularly that the dance took place along the margin of the lake above vegetation and that most participants were flying at tree top level, some 30–60 feet above the ground. Immediately upon reaching the area, each individual begins the up-and-down flight generally characteristic of male mayflies. In a matter of 5–10 minutes most males in the vicinity have joined the dance, each one flying rapidly upward for several feet and then with motionless wings planing downward to repeat the upward flight. A few minutes later, females join the swarm and fly horizontally through the dancing males. A male seizes the female from underneath, his elongated forelegs clasping her thorax, and immediately copulation takes place. The copulatory position and act have been adequately described by Spieth (1940). Individuals *in copulo* continue flying, but slowly lose altitude. Within a few seconds to perhaps a half minute the members of a pair separate. The female almost always leaves the swarm and flies directly out over the lake; males usually return at once to the dance, which continues until just after darkness has set in, when males gradually leave the area to return to resting places in vegetation where they eventually die. Since females leave the swarm after copulation, the dance ends with only males present, as was the case when it began.

Upon leaving the swarm, females invariably flew out over the lake. It appeared that some individuals plunged immediately into the water while others flew rapidly back and forth 10–20 feet above the surface for several minutes. Usually within 30 minutes after the first female appeared over the lake, almost all those taking part in the mating flight had dropped to the water surface, deposited their eggs and been eaten by fish, so that nothing remained to indicate the event had taken place. On nights when very extensive swarming occurred, a few female imagoes, usually spent, were still flying about an hour or more after the first ovipositing females appeared. It was observed repeatedly on Big Silver Lake at Transect 3 that females remained over the shoal area, very few being seen over deep water. There appeared to be a definite attempt to remain in the proximity of the shoal, for the ovipositing imagoes are strong and rapid fliers and could easily have flown across the entire lake if they had been so inclined. It was frequently observed while cruising in deep water that only an occasional female fell to the water near the boat, although nearer shore the surface was in a turmoil from struggling insects and splashing fish. In Pine Lake ovipositing females were seen to fall into the water over most of the lake but were concentrated near shore. In Gun Lake very few females landed nearer than 100 feet from shore. Most individuals reached the water surface 100–1,000 feet from the lake margin although during big flights females could be found in the middle of the lake. The tendency, however, appeared to be to deposit eggs in shoal water comparatively near shore. On one occasion 2 females were seen to dip down and deposit eggs within 10 feet of a sandy beach.

Eggs were deposited in the water in three different ways. Most females simply plummeted erratically into the water from heights of 10–20 feet. As they lay on the surface with fluttering wings outspread, the last two abdominal segments were raised sharply upward and the two egg packets very quickly extruded by rhythmical contractions of the abdomen. Upon contact with the water, the eggs separated and began to sink immediately. Females which had "crash landed" were seldom observed to right themselves and fly from the water. Usually within a minute or two their struggles attracted a fish which consumed them. The second method, used by comparatively few individuals, was to land upright upon the surface, remain quiet for a few seconds, discharge a few eggs, then fly up again to repeat the performance. Examination of females which flew to a light in the boat showed that some had lost only a portion of their eggs. Since these individuals easily discharged the remaining eggs when placed in contact with water, it was assumed they had been merely dipping to the surface. The third method was observed only four times. In these instances the female extruded her eggs while flying above the water and dropped the packets from an altitude of 10–15 feet. On several other occasions females were seen carrying partly extruded egg packets as they plunged to the water surface.

It was noticed that when females left the swarm and came directly to a collecting light, many of them began to extrude the egg packets within a few seconds after landing on a hard surface. This may indicate a tendency to begin to oviposit very shortly after mating. On several occasions unmated female imagoes extruded their eggs in the laboratory while being held by the wings.

In only one instance on the many days spent on the lakes was it seen definitely that the weather prevented oviposition. At Gun Lake on July 1, 1947, a very strong wind, accompanied by light rain, sprang up just at dusk and continued for 2 hours. Later that night a large number of female imagoes, a few with egg packets partly extruded, were found in the grass along the lake shore. About 50 were induced to lay their eggs in a 2-quart jar filled with water. A very high percentage of these eggs eventually hatched, indicating that the sudden wind had broken up a mating flight after copulation had been effected and before oviposition could be completed. Next morning many imagoes, both male and female, were seen in the vicinity, all alive and active. Presumably these individuals completed their reproductive activities the following evening.

In the lakes studied, fishes usually devoured all spent females soon after they landed on the water. Only during very heavy flights were individuals found floating on the lake the next day. On many larger lakes, however, sizeable windrows of dead females and nymphal exuviae often accumulate as drift on the beaches. Anglers regard the short interval of oviposition as a profitable time to cast artificial flies for lake fishes which are drawn to shoal areas by the mating activities of *limbata*.

Dancing male mayflies will occasionally seize and attempt to mate with subimaginal females, caddis flies and other insects which fly through the swarm (Spieth, 1940). The author witnessed only one such incident. A male *limbata* seized a large male *Stenonema* and struggled with it until both fell low enough to be collected with a hand net.

Reproduction

The percentage of male and female nymphs collected during the investigation is shown in Table 14. Only those specimens whose sex could

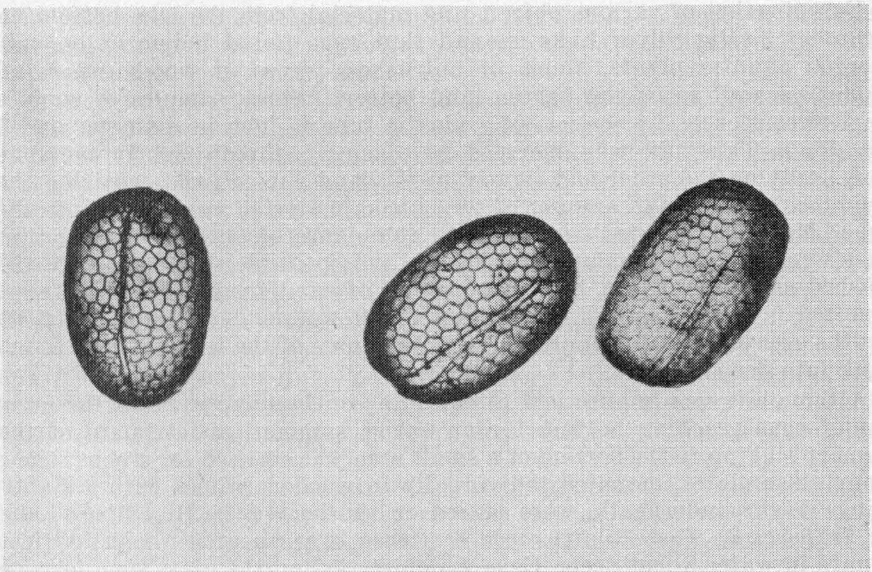
Table 14. Number and sex of nymphs

Locality	Number of nymphs	Number of males	Number of females	Percent males	Percent females
Pine Lake........	4,561	2,103	2,458	46	54
Gun Lake........	5,181	2,492	2,689	48	52
Big Silver Lake...	3,294	1,622	1,672	49	51
Total......	13,036	6,217	6,819	48	52

be determined with some degree of certainty were considered, most individuals over 6 mm. in length being included. The data show that in all cases females were more numerous than males although the difference was not great except in Pine Lake (9 percent). Neave (1932) determined the sex of 2,513 nymphs of *Hexagenia l. occulta* and found that 45 percent were males and 55 percent females. In the present study 48 percent of the total number of nymphs were males and 52 percent females. Even this small difference is probably of advantage to the species since males apparently mate more than once. The number of male and female nymphs in individual bottom samples was usually nearly the same, but in some collections nymphs of one or the other sex predominated. The basic reason for a higher percentage of females is not known.

Number of eggs produced by individual females is of considerable importance in evaluating the probable success of reproduction of the species. Needham (1920) estimated the number of eggs carried by *Hexagenia* females to be upwards of 8,000. Neave (1932) counted the eggs of two *H. l. occulta* imagoes; one contained 3,631 eggs, the other 3,388. Size of these females was not recorded. In order to ascertain more exactly the number produced, actual counts were made of the eggs carried by 24 female imagoes (Hunt, 1951). Total numbers of eggs varied between 2,260 and 7,684. An average size female produces about 4,000 eggs. The mature eggs are ellipsoid and measure 0.16–0.19 by 0.28–0.32 mm. (Fig. 28).

Observations of ovipositing females revealed that eggs began to sink immediately upon contact with water. Laboratory experiments showed



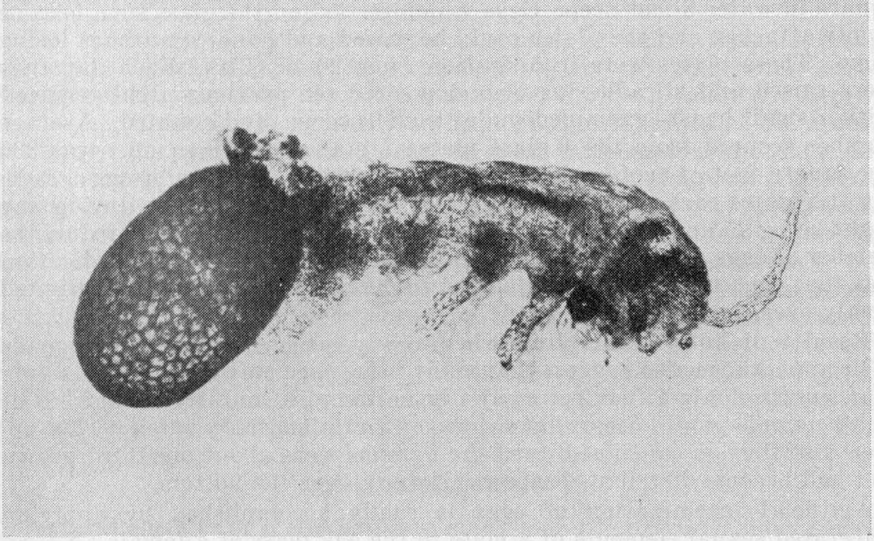


Figure 28. (Upper). Photomicrograph of hatched eggs showing fissure through which nymphs escaped. Egg size, 0.16-0.19 mm. wide by 0.28-0.32 mm. long.

Figure 29. (Lower). Photomicrograph of nymph near completion of hatching process.

that in still water individual eggs sank at an average rate of 1 foot in 80 seconds, and small clumps of eggs settled 1 foot in about 60 seconds. Two to 3 minutes were required for eggs to settle 1 foot when the water was agitated. Application of these results to natural waters indicates that more than 6 minutes would be required for eggs to reach bottom in still water 5 feet deep. It is quite probable that at times wave action and currents serve to distribute eggs widely before they eventually come to rest.

Examination of various objects and material from the lake bottom on Transect 3, Big Silver Lake showed that eggs found lodgment on submerged aquatic plants, stems of bulrushes, pieces of wood and small stones, as well as on the barren mud bottom. Small samples of surface mud were secured by the use of a plastic tube ½-inch in diameter and 5 feet long. This tube was operated by placing a thumb tightly over one end, applying the other end lightly to the mud surface and releasing the thumb so that a small amount of the bottom material was drawn into the tube. Mud thus secured contained an abundance of eggs, indicating that they were spread over the entire shoal. It is possible that some eggs are washed ashore and lost, but examination of sand from the water's edge resulted in finding only 2 eggs. No attempt was made to obtain eggs at depths greater than 5 feet and nothing is known of the fate of those which sank into deep water.

Although it was impractical to obtain a continuous record of the number of eggs reaching bottom for an entire summer, an estimate of the number sinking to the bottom of a small area was secured for a short time. Four glass plates, mounted individually in wooden frames with a stabilizing weight underneath, were placed on the bottom in Big Silver Lake at Transect 3. These plates were scattered over an area about 100 feet square in water 3 feet deep. Eggs which settled on the glass soon became firmly attached and the plates could be raised and handled without losing them. These plates were in operation June 20–27, 1947. Each day they were raised and all adhering eggs deposited the previous night removed with a small brush, examined under a microscope, and counted. Average number secured from the 4 glass plates (total area 370 sq. in.) was 336 per square foot of surface for the 8-night period. Quantity of eggs reaching the plates each night varied greatly, the smallest number during any night being 25 and the largest 310. Great variation was also noted in the number of eggs adhering to individual plates on any night. The indication was that eggs tended to reach bottom in clumps and were not distributed evenly over the bottom.

Results of bottom sampling when newly-hatched nymphs first made their appearance also suggest that many more eggs may reach a given area than another only a few feet away. Some samples contained hundreds of small nymphs while others taken nearby contained only a few. This uneven distribution continued until the nymphs were about one-third grown and had become distributed more uniformly over the bottom.

Artificial insemination of eggs is easily accomplished by applying macerated sexual elements of a male to the egg mass of a female (Neave, 1932; Needham, Traver, Hsu, 1935). The author resorted to artificial insemination 27 different times to secure fertilized eggs for various purposes. Macerated male sexual organs were mixed with eggs stripped or dissected from a female. After 1–2 minutes the eggs were placed in water, and about 45 seconds later they became sticky and began to adhere to the glass of the container. At the end of about 3 minutes all were firmly attached and remained so during incubation and hatching. This adhesive property made it very convenient to handle them since they remained in place at all times. Imagoes and subimagoes proved to be equally fertile, showing that ova and spermatozoa are fully mature when the winged fly first emerges. Unfertilized eggs obtained from 7 reared female imagoes were incubated for a long period but did not hatch. Results of artificial insemination and incubation varied greatly: the percentage of eggs which hatched ranged between 2.7 and 88.6.

Eggs obtained from 110 female imagoes captured during ovipositing flights were separated into 15 lots and incubated in aerated jars to determine the efficiency of natural fertilization (Hunt, 1951). A count made after hatching had been completed showed that in all cases more than 91 percent of the eggs hatched (average 96.3 percent). Since some embryos died during incubation, the initial fertilization rate was slightly higher. The high fertility and the large number of eggs produced by individual females point to a high reproductive potential. In nature, however, the loss of eggs and very young nymphs must be enormous.

The shorter the incubation period, the longer the growth period for newly-hatched nymphs during the remainder of the summer. Again, temperature is an important factor influencing the rate of embryonic development. In the laboratory, the incubation period as related to water temperature was as follows: 75°–95°F., 11–14 days; 67°–81°F., 18–22 days; 62°–73°F., 20–26 days. At summer water temperatures obtained in the lakes studied, nymphs began to hatch from the eggs after about two weeks of incubation. Experiments proved that fertilized eggs were killed by freezing, and by air-drying for 4 hours.

The hatching process was observed a number of times. Nymphs escape through a ventral fissure which extends along one side and nearly across one end of the egg (Fig. 28). When hatching begins, a small slit appears in the egg immediately beneath the head of the embryo and the frontal portion of the nymphal head appears to exert force against the shell. The slit increases in length as the head thrusts forward and downward accompanied by pushing and wriggling movements of the body. At intervals all motion ceases, followed by renewed efforts to gain freedom. Once the head and thorax are free, a few seconds of violent wriggling serves to pull the remainder of the body through the slit (Fig. 29). Nymphs become active immediately upon emergence from the egg and usually swim rapidly away. Swimming is accomplished by violent lashings of the entire body in a lateral plane which propel the nymph erratically forward. Time required for completion of hatching after appearance of the initial slit in the egg shell varied from 10 to 21 minutes in 6 cases observed.

Natural Enemies

Natural enemies of *H. limbata* are many and differ with various periods of the life cycle. The winged stages are known to be preyed upon by many fishes and birds. Bats, often seen sweeping over the lake during emerggences, were almost certainly feeding on the subimagoes. The writer has been told by Dr. J. W. Leonard that the winged stages are captured and eaten by dragonflies and damselflies. It is during nymphal life, however, that various predators have the greatest opportunity to reduce the population. Little is known about the activities of predators in natural waters except those of fishes, to be discussed later. By analogy, however, one can conclude that the numerous invertebrate carnivores prey upon the nymphs. Laboratory experiments showed that crayfish, and dragonfly nymphs (*Aeschna* and *Tetragoneuria*), avidly seized and devoured *limbata* nymphs placed in containers with them. Newly hatched specimens placed in a culture of *Hydra* were quickly caught and eaten. It is quite probable that most carnivorous animals in the water take a toll of younger individuals. Rapid decrease in numbers of small nymphs late in the summer and fall suggests enormous losses to predators. Among populations of large-sized nymphs, fishes are probably the only predator capable of causing large-scale losses.

A rather comprehensive list of parasites known to infest various may-flies is given by Needham, Traver, and Hsu (1935, p. 218). In addition, Neave (1932) reports that many of the nymphs of *Hexagenia l. occulta* and *H. rigida* collected in Lake Winnipeg carried cysts of a trematode, *Crepidostomum cornutum.* The writer has found no parasites inhabiting either nymphal or winged stages of *H. limbata* except a larval trematode which appeared to be *Crepidostomum cornutum.** These larvae are usually found encysted in the muscles of the abdomen, less frequently in the thorax and attached to the gills of nymphs. The parasite, acquired by the nymph, remains in the body of the insect throughout its life. Cysts in the nymph appear as small, darkly colored circular or oval bodies easily seen with the naked eye. Infected nymphs were found in abundance in all waters included in this study as well as in most collections from other localities in Michigan. In various collections from 1.9 to 100.0 percent of the nymphs were parasitized. The usual number of cysts per nymph was 3 or 4 although as many as 241 have been found in one individual. Nymphs smaller than 15 mm. seldom carried cysts, while a high percentage of large specimens were infected. Whether the parasites are harmful to the nymphs is not known. It is probable that a heavy infestation does have a deleterious effect on the well-being of the nymph.

POPULATIONS

Pine Lake

Distribution

Distribution of *limbata* nymphs in Third Lake is shown in Figure 30. Nymphs are found as near the water's edge as 2 to 5 feet, there being no appreciable sand or gravel beach along most of the shore of this basin; and they range downward to a depth of 16 feet. Although nymphs were abundant from near shore to a depth of about 9 feet, the greatest number per unit area was found at depths between 3 and 7 feet. With increasing depth the number of individuals decreased markedly. In general, it can be stated that the significant population is limited to bottom above the 10-foot contour and is best represented in the rather barren marl shoals. This statement also holds true for the other basins of Pine Lake.

Total area in Third Lake occupied by nymphs in significant numbers is about 91 acres, some 71 percent of the total, and the concentration area (10 or more nymphs per square foot during most of the year) comprises about 52 acres or 40 percent of the total basin.

Comparison of the distribution in Third Lake with that of *Hexagenia* in other lakes shows a definite similarity in all instances. In Lake Nipi-

*Tentative identification by Dr. George R. LaRue, University of Michigan.

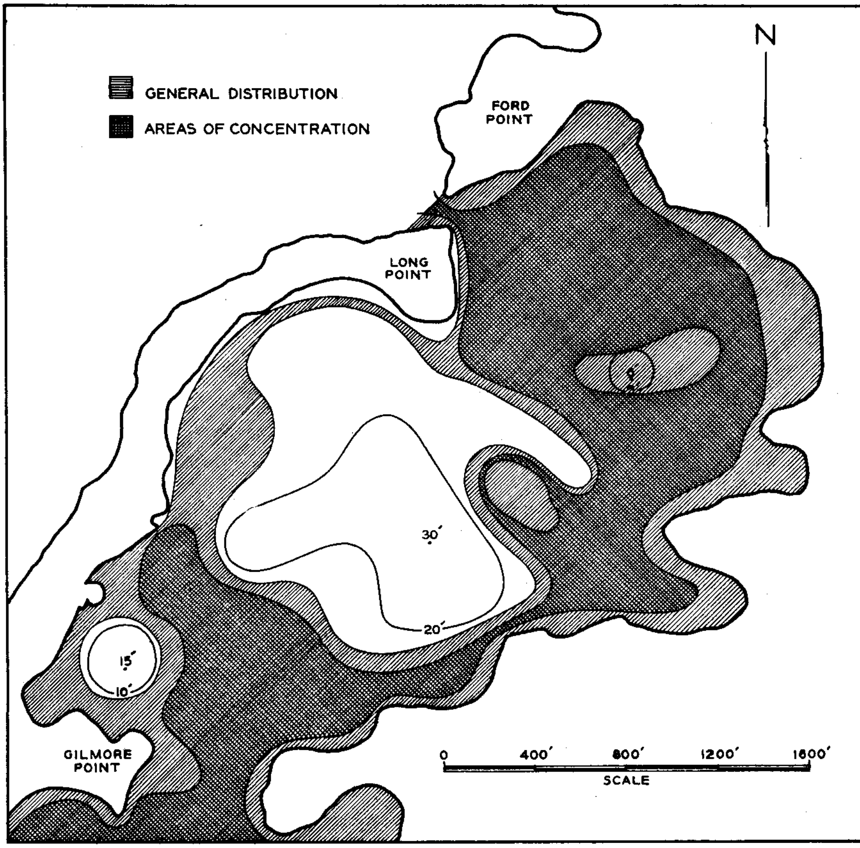


Figure 30. Map of Third Lake (part of Pine Lake) showing general distribution of nymphs and areas of concentration. Compare with bottom soil types in Figure 11.

gon, nymphs of *H. bilineata* were found to be quite abundant at depths ranging from 0 to 30 feet, with a maximum between 9 and 15 feet (Adamstone, 1923, 1924; Adamstone and Harkness, 1923). In Shakespeare Island Lake, Ontario, Cronk (1932) found that nymphs were abundant at depths ranging from 8 to 13 feet. Miller (1938), in a study of the bottom fauna of 5 Algonquin Park lakes, found that the depth range of *Hexagenia* nymphs began at about 3 feet and extended downward to various depths, a maximum of 70 feet being recorded for Lake Opeongo. In Lake Simcoe the range of *Hexagenia* extended down to 21 feet (Rawson, 1930). In all waters cited above, these insects were largely restricted to soft mud bottom.

Density of population

Number of nymphs per unit area of bottom varied greatly throughout the year. It was lowest immediately after emergence, and greatest in late summer and fall when young-of-the-year appeared. In general there was close correspondence between numbers of specimens taken outside and inside the sampling plots. On June 2–3, 1948, few nymphs could be found in either plot in Third Lake. At that time a total of 12 square-foot samples, taken at various points around the lake, indicated a paucity of nymphs in the entire basin. Other samples obtained later in the summer revealed an increase in numbers, corresponding to a similar increase observed in the plots.

Combining the data from both plots for the entire sampling period shows that the average number of nymphs per square foot was 23.5 (212 per sq. yd.; 248 per sq. m.) with an average volume of 1.58 cc., giving a calculated number per acre of 1,023,000 with a wet weight of 152 pounds. These figures are approximations but serve to show the average density of the population in Third Lake.

Production in Third Lake compares favorably with that of other lakes known to have very large populations of *Hexagenia*. For the period January, 1947, to November, 1948, the average number of nymphs per square meter ranged from 72 to 423 and from 83 to 747 in Plots 1 and 2, respectively. In Lake Winnipeg, Neave (1932) encountered the greatest concentration in late August, when the number averaged 743 per square meter. Also density of the population in western Lake Erie in 1929 and 1930 was 283 and 510 per square meter, respectively (Wright and Tidd, 1933). Since there is some difference in the number of nymphs per square foot in the two plots in Third Lake and Second Lake, the three sampling areas will be discussed separately.

It was hoped that sampling in the area designated "Plot 1," known to have been "dug" by bait collectors for a number of years, would show by comparison with Plot 2 the effect of the removal of nymphs and also reveal the number which escaped the dredging. The original supposition, that the two plots were similar, was at fault, for it was soon evident that Plot 1 was the more productive of the two, not only in the

Table 15. Number and volume of nymphs in samples taken in Plot 1, and calculated quantities per acre, in Pine Lake

Date	Number of sq.-ft. samples*	Nymphs per square foot			Nymphs per acre	
		Number		Volume, in cc.	Number	Wet weight, in lbs.
		Average	Range			
6/ 1/46	4	3.5	1– 5	0.39	152,460	38
1/31/47	12	19.6	4–34	2.16	853,776	208
5/20/47	10	22.0	9–36	1.67	958,320	160
6/ 5/47	15	24.0	13–32	1.96	1,045,440	188
7/ 2/47	15	17.3	1–34	2.34	753,588	225
8/15/47	10	39.4	2–63	0.81	1,716,264	78
9/12/47	5	28.0	25–31	1.43	1,219,680	137
11/14/47	10	18.0	9–34	2.13	784,080	205
1/27/48	10	17.5	5–35	2.56	762,300	246
4/ 6/48	10	10.4	3–18	1.25	453,024	120
5/ 6/48	10	12.5	1–22	1.55	544,500	149
6/ 2/48	10	6.8	2–14	0.63	296,208	61
7/12/48	5	31.8	10–68	0.33	1,415,208	32
8/25/48	6	40.1	18–60	1.15	1,746,756	111
11/10/48	7	25.1	12–32	3.42	1,093,356	329
6/13/49	6	7.5	5–13	0.92	326,700	88

*Each square-foot sample obtained by combining four 6″ x 6″ Ekman dredge hauls.

number of *Hexagenia* nymphs but in other elements of the macroscopic invertebrate fauna as well.

Data secured in Plot 1 are presented in Table 15. It can be seen that the average number of nymphs per square foot forms a definite seasonal pattern which is repeated each year. A steady decrease in numbers during the late fall, winter, spring, and early summer is evident as is the sudden increase in mid-summer (July and August), when young-of-the-year nymphs first appear. The isolated samples secured in June, 1946, at the end of the main emergence period gave the lowest average (3.5 per sq. ft.) encountered during the study. Likewise, other low points in the cycle of abundance were reached in July, 1947, June, 1948, and June, 1949. The July, 1947, minimum is correlated with the colder season and delayed emergence occurring that year. The sharp drop in average number of nymphs from January (17.5) to April, 1948 (10.4), was closely correlated with the operations of bait collectors who worked the area after the January collections were made. The decrease represents, in part at least, depletion of the population by bait removal. A considerable natural mortality of young is indicated in late summer, for the average number per square foot dropped from 39.4 in August to 28.0 in September, 1947, and from 40.1 in August to 25.1 in November, 1948.

Volume and weight of nymphs per unit area fluctuated with the season but did not correspond to the variation in numbers (Table 15). Lowest volume and weight occurred in late summer, when number of nymphs was greatest and average size smallest. This was expected since larger specimens had transformed and young-of-the-year, although numerous, had little volume. The decrease in volume evident after January followed the removal of large individuals for bait. A steady increase in volume during spring and early summer, corresponding to the growth period prior to emergence, is particularly well illustrated in figures for 1947.

Calculated wet weight of nymphs, based on volume in cc. per square foot, varied from a minimum of 32 to a maximum of 329 pounds per acre. Average number and weight for the period January, 1947 to November, 1948—22.3 specimens per square foot having a volume of 1.67 cc. (160 lbs. per acre)—is considered to be a reliable estimate of the average population. This figure is considerably higher than the 112.4 lbs. per acre estimated for the total macroscopic bottom fauna in Third Sister Lake, Washtenaw County (Ball, 1948).

Although considerable inroads into the nymphal population were made by bait collectors, it is quite clear that the number, volume and weight of nymphs remaining in this plot after the winter digging operations terminated were still high. Comparison with Plot 2 shows that the average number of individuals per square foot was slightly less, 22.3 to 24.7, but that in terms of pounds per acre the production in Plot 1 (160) exceeded that of Plot 2 (1942) by a considerable margin.

Plot 2, selected to serve as an undisturbed control area, was not touched by bait collectors during the winters of 1945–46 and 1946–47. In 1947–48 a small amount of digging was done along one margin, but is believed to have had no appreciable effect on the nymphal population within the plot. Data obtained by sampling this area are presented in Table 16. In most respects seasonal trends in number, volume and weight of nymphs were similar to those of Plot 1.

Table 16. Number and volume of nymphs in samples taken in Plot 2, and calculated quantities per acre, in Pine Lake

Date	Number of sq.-ft. samples*	Nymphs per square foot			Nymphs per acre	
		Number		Volume, in cc.	Number	Wet weight, in lbs.
		Average	Range			
1/30/47	8	24.9	13–38	1.44	1,084,644	138
5/22/47	7	25.1	16–43	2.40	1,093,356	231
6/ 5/47	15	24.3	14–40	2.78	1,058,508	267
7/ 3/47	15	16.5	10–31	1.73	718,740	166
8/16/47	10	10.9	5–24	0.52	474,804	50
9/12/47	5	19.4	9–27	0.54	845,064	52
11/14/47	10	15.4	6–30	1.62	670,824	156
1/27/48	10	12.9	9–26	1.60	561,924	154
4/ 6/48	10	12.3	9–18	1.59	535,788	152
5/ 6/48	10	9.7	4–16	1.29	422,532	124
6/ 3/48	10	7.9	4–10	0.63	344,124	61
7/13/48	7	69.4	4–207	0.81	3,023,064	78
8/25/48	6	70.7	35–92	2.58	3,079,692	248
11/10/48	7	26.0	19–32	1.26	1,132,560	121
6/13/49	6	8.0	5–13	1.10	364,480	106

*Each square-foot sample obtained by combining four 6″ x 6″ Ekman dredge hauls.

A decrease in number of nymphs after January, 1947, very marked in Plot 1, did not occur in Plot 2 since this area was not appreciably disturbed by bait collectors. Immediately following initial appearance of the new generation, a rapid decline in numbers occurred which was shown particularly well in the fall of 1948, when the average number per square foot dropped from 70.7 on August 25 to 26.0 on November 10. A similar but less spectacular decline was evident in the fall of 1947. This pronounced reduction in number of young nymphs was probably due to natural mortality although a limited amount of migration from this shallow shoal to the softer bottom in deeper water may have occurred.

Evidence of a very uneven distribution of eggs and initial spotty distribution of nymphs is supplied by samples taken from July to November, 1948 (Table 16). When young-of-the-year were first taken on July 13, the number per square foot varied from 4 to 207. On August 25, number of individuals per square foot ranged from 35 to 92 and on November 10 from 19 to 32. The more uniform distribution in late fall appears to be the result of lateral dispersion, from concentration centers, which progressed as the nymphs increased in size. That a similar situation existed in Plot 1 is indicated by samples taken during the same period.

Seasonal fluctuations in the average volume per unit area also followed a pattern very similar to that shown in Plot 1. Calculated wet weight of nymphs in Plot 2 for the period January, 1947 to November, 1948 varied between 50 and 248 pounds per acre. The average for the period given above was 24.7 nymphs per square foot, having a volume of 1.48 cc. (142 lbs. per acre).

As mentioned previously, the marl shoal in Second Lake adjacent to Prairieville Township Park was worked by bait collectors for a number of years prior to 1944. Since that time no commercial collecting has been attempted because of a belief that the area is no longer productive.

Table 17. Number and volume of nymphs in samples taken from shoal at Prairieville Township Park, and calculated quantities per acre, in Second Lake (part of Pine Lake)

Date	Number of sq.-ft. samples*	Nymphs per square foot			Nymphs per acre	
		Number		Volume, in cc.	Number	Wet weight, in lbs.
		Average	Range			
6/ 1/46	7	1.4	1– 4	0.13	60,984	12
9/12/47	3	10.0	4–14	0.38	435,600	36
11/14/47	4	12.0	8–17	0.65	532,720	62
4/ 7/48	2.5	10.8	....	0.62	470,448	59
5/ 7/48	2.5	11.6	3–16	0.70	505,296	67
6/ 3/48	3	7.7	3–10	0.63	335,412	60
7/13/48	2.5	8.8	4–10	0.48	383,328	46
8/25/48	2	36.5	35–38	1.10	1,589,940	105

*Each square-foot sample obtained by combining four 6″ x 6″ Ekman dredge hauls.

Data obtained from bottom samples taken in this area are incorporated in Table 17. Seasonal trends in number, volume and weight of nymphs corresponded very colsely to those evident in Third Lake although density of the population was much less. From September, 1947 to August, 1948, average number of nymphs per square foot in this area was 10.7, while in Plots 1 and 2 it was 20.6 and 27.2, respectively. Thus it appears that the population density is approximately one-half that of Third Lake and substantiates the opinions expressed by bait collectors that comparatively few nymphs occur in this area at present.

Associated organisms

In order to compare the population of *limbata* nymphs with that of other animals in the sampling areas, all macroscopic invertebrates were removed from a limited number of bottom samples secured from Plots 1 and 2 and from Second Lake. Organisms were identified to major taxonomic groups and a count of the numbers of each obtained. Volumetric measurements were made of *limbata* nymphs alone and also of all other animals combined. Although only a small number of samples were handled, the results show consistent seasonal trends in number and volume of organisms and are considered to give a reliable approximation of the composition of the macroscopic bottom fauna. Each sampling area will be treated separately.

Data obtained in Plot 1 from July 2, 1947 to August 25, 1948 (Appendix Table 20) show that the seasonal pattern exhibited by both *limbata* nymphs and other bottom animals is much the same. In both instances an increase in number and volume occurs during the fall, a large population is maintained during winter and spring, and a marked decrease is evident in summer. Emergence of insects accounted for a large part of this decrease, but a reduction in the number of amphipods also occurred. While the number of *limbata* nymphs was very low compared to that of other animals, their volume (59 percent) was greater than that of all others combined (41 percent). A comparison of the volume of the two components of the macroscopic bottom fauna is depicted in Figure 31. Average calculated wet weight of *limbata* nymphs was 184 pounds per acre and of other invertebrates 128 pounds for the period covered. The total macroscopic bottom fauna varied from a minimum of 106 to a maximum of 591 pounds per acre. In most samples the volume of *limbata* nymphs exceeded that of other animals although on occasions the reverse was true. A drop in the number of organisms other than nymphs occurred in January and April but is not easily explained. Since the largest number of samples taken in any month was handled in April, it is logical to conclude that the decline represented a real condition existing at that time. If it resulted from destruction of organisms by the dredging operations of bait collectors, it is difficult to explain why the number present in May was even higher than in the previous November.

Number and volume of *limbata* nymphs and other organisms in Plot 2 (Appendix Table 21) showed the same seasonal trends as displayed in Plot 1. However, a drop in number of organisms other than *limbata* did not occur in January and April, a further indication that the decrease noted in Plot 1 may have been related to activities of bait collectors. Again the largest number of organisms was encountered in May, when an average of 912.7 per square foot was recorded. The average volume of *limbata* nymphs (59 percent) exceeded that of the other organisms (41 percent) by exactly the same margin as in Plot 1, although number and volume of both were consistently less than in the other sampling area (Fig. 32). For the entire sampling period the average weight of *limbata* nymphs in pounds per acre was 154, compared to 108 for all other organisms.

Data secured from the shoal of Second Lake at Prairieville Township Park, April–July, 1948, show that nymphs of *limbata* comprised less than one percent of the total number of macroscopic animals present (Appendix Table 22). Likewise, the volume of nymphs, always less than that of other invertebrates, constituted only 25.6 percent of the total. Average

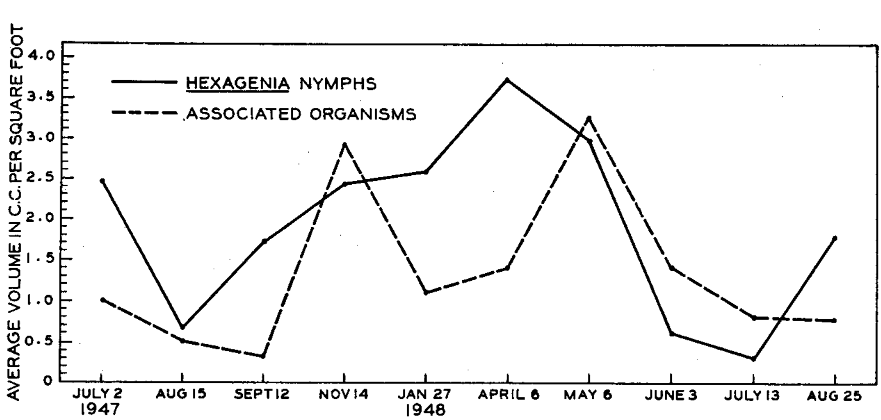


Figure 31. **Comparison of average volume per square foot of *Hexagenia limbata* nymphs and associated organisms in bottom samples from Plot 1, Pine Lake.**

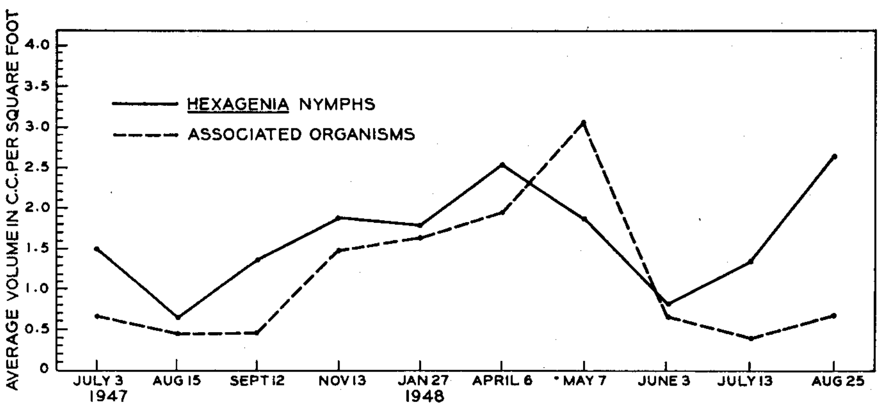


Figure 32. Comparison of average volume per square foot of *Hexagenia limbata* nymphs and associated organisms in bottom samples from Plot 2, Pine Lake.

live weight of all macroscopic animals for the period was 266 pounds per acre, of which nymphs contributed 58 pounds and other animals 208 pounds.

Comparison of this area with Third Lake for the same period shows that the average wet weight of all macroscopic animals was slightly less than in Third Lake, the difference being due to the low production of *limbata* nymphs since the weight of other animals was nearly one-third greater. Although composition of the bottom fauna of the two basins differed principally in the relative abundance of nymphs, the total amounts of potential fish food in each were not greatly different.

Gun Lake

Distribution

West Gun Lake contains a very large nymphal population since, due to its shallowness, a large part of it (70.7 percent) has a soft marl bottom particularly well suited to them. The area occupied, which is essentially the same as that of the marl bottom plus an additional area with a firm muck bottom near the outlet, comprises about 885 acres (72.3 percent) of the total lake bottom (Fig. 33). Distribution is fairly uniform with the exception of the wild rice beds, in which few specimens were found. Nymphs did not occupy the bottom of the depression in the south end of the lake or the larger basin in the north end. A semi-flocculent bottom in both and oxygen depletion below 20 feet in the larger depression rendered the substratum uninhabitable to *Hexagenia* in these two localities. Very few specimens were found on the extensive sand shoals on the western side of the lake. Samples along a transect extending from shore across the sand shoal toward the center of the lake revealed that nymphs, first encountered where sand and marl formed a mixture, became increasingly numerous as the amount of sand decreased and the amount of marl-mud increased. Greatest concentrations of individuals always occurred in marl-mud bottom.

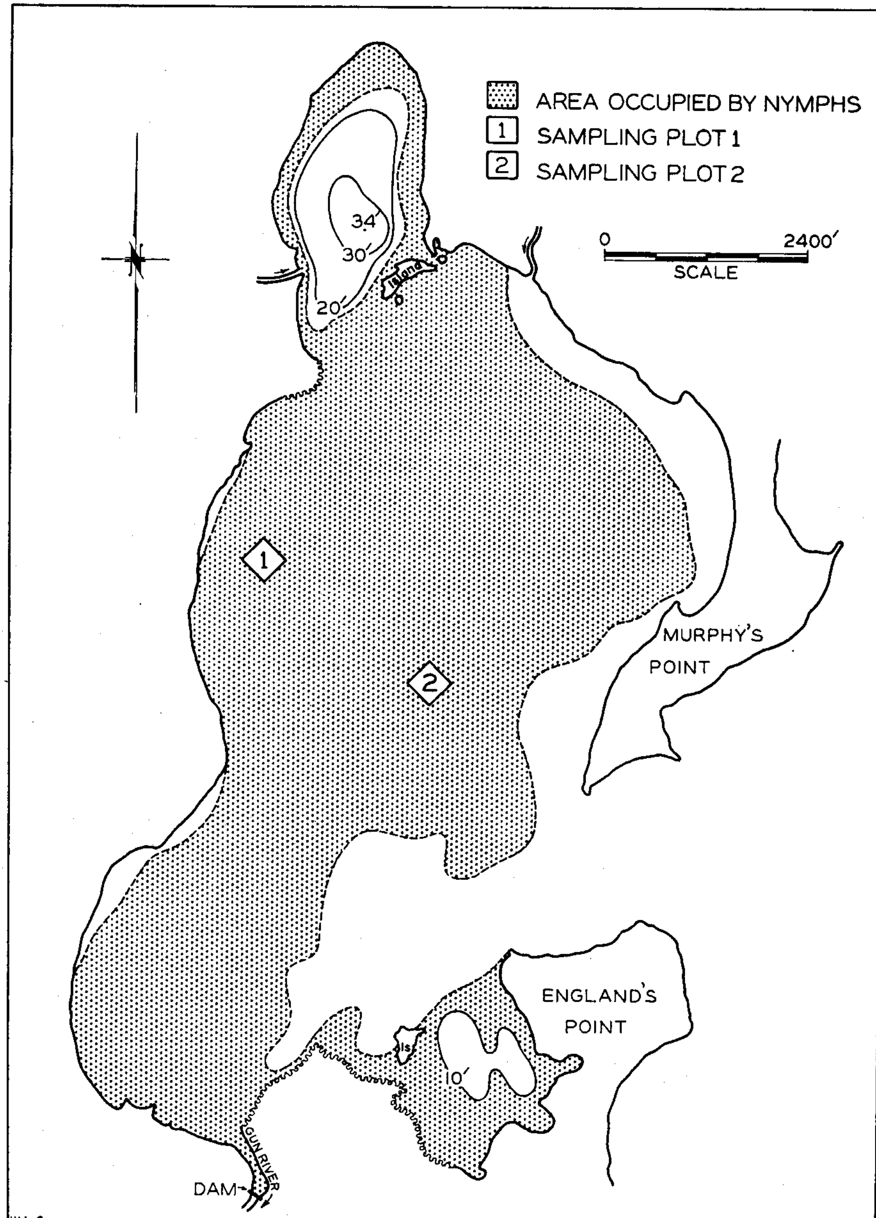


Figure 33. Map of West Gun Lake showing distribution of nymphs. Compare with bottom soil types in Figure 12.

Density of population

As in Pine Lake, the average number of nymphs per unit area in the sampling plots varied with the season, being lowest immediately after the emergence period and greatest after the appearance of young-of-the-year. Occasional collections secured in other parts of the lake showed that seasonal fluctuations apparent within the plots were representative of those in the population as a whole. In combined samples from both plots, nymphs averaged 24.5 per square foot (220 per sq. yd.; 258 per sq. m.) with an average volume of 1.76 cc. These figures are higher than those for Pine Lake. The calculated average number of nymphs per acre for the entire sampling period was 1,067,000 with a wet weight of 169 pounds.

Results of sampling in Plot 1 are presented in Table 18. During the entire period, May 30, 1946 to September 9, 1948, the average number of

Table 18. Number and volume of nymphs in samples taken in Plot 1, and calculated quantities per acre, in Gun Lake

Date	Number of sq.-ft. samples*	Nymphs per square foot			Nymphs per acre	
		Number		Volume, in cc.	Number	Wet weight, in lbs.
		Average	Range			
5/30/46	7	5.3	1- 8	0.83	230,868	80
1/28/47	6	42.0	24–49	2.32	1,829,520	223
5/20/47	6	22.3	11–44	2.41	971,388	232
6/ 4/47	14	19.8	14–30	2.54	862,488	244
7/ 1/47	15	13.2	6–18	2.14	574,992	206
8/14/47	10	8.3	2–18	0.17	361,548	16
9/10/47	5	33.8	21–39	1.14	1,472,328	110
12/ 9/47	7	47.6	33–67	2.51	2,073,456	145
2/ 9/48	10	33.0	23–90	2.63	1,437,480	253
4/ 5/48	10	26.5	13–41	2.45	1,154,340	235
5/ 6/48	12	20.3	9–32	2.70	884,268	260
6/ 4/48	10	15.7	13–25	1.65	683,892	159
7/11/48	9	18.6	5–81	0.70	810,216	67
8/26/48	6	57.0	29–78	1.70	2,482,920	163
11/ 9/48	8	61.7	42–75	3.78	2,687,652	363

*Each square-foot sample obtained by combining four 6″ x 6″ Ekman dredge hauls.

nymphs per square foot varied from 5.3 to 61.7 (48–555 per sq. yd.; 56–652 per sq. m.), a density quite similar to that in Pine and other lakes.

Volume of nymphs in cc. per square foot varied from 0.17 (16 lbs. per acre) to 3.78 (363 lbs. per acre). The average number and volume for the period January, 1947 to November, 1948 was 30 nymphs per square foot with a volume of 2.06 cc. Translated into terms of a calculated average standing crop, nymphs numbered 1,306,800 per acre with a wet weight of 198 pounds. These figures are considerably higher than those obtained in Plot 2.

Data secured in samples taken from Plot 2 are presented in Table 19. Average number of nymphs per square foot varied from 2.8 to 34.9 (25–314 per sq. yd.; 30–368 per sq. m.) with an overall average of 19.1 (831,-

Table 19. Number and volume of nymphs in samples taken in Plot 2, and calculated quantities per acre, in Gun Lake

Date	Number of sq.-ft. samples*	Nymphs per square foot			Nymphs per acre	
		Number		Volume, in cc.	Number	Wet weight, in lbs.
		Average	Range			
1/29/47	7	29.4	14–72	1.54	1,280,664	148
5/20/47	6	26.5	15–37	2.17	1,154,340	208
6/ 4/47	12	22.0	16–29	2.28	958,320	219
7/ 1/47	15	14.0	6–22	1.64	609,840	158
8/13/47	10	2.8	0– 5	0.43	121,968	41
9/10/47	5	8.4	3–13	0.20	365,904	19
12/ 9/47	10	34.9	21–63	1.92	1,520,244	184
2/10/48	9	18.7	5–53	1.06	814,572	102
4/ 5/48	10	21.9	9–40	1.22	953,964	117
5/ 6/48	8	25.4	16–37	2.01	1,106,424	193
6/ 4/48	10	16.7	5–25	2.31	727,452	222
7/12/48	7	7.0	2–10	0.88	304,920	84
8/26/48	7	19.4	4–39	0.47	845,064	45

*Each square-foot sample obtained by combining four 6″ x 6″ Ekman dredge hauls.

996 per acre). In every month in which samples were taken fewer nymphs were encountered in this area than in Plot 1 and this difference is reflected in the average for the 19-month period.

Volume of nymphs varied from 0.20 to 2.31 cc. per square foot (19–222 pounds per acre), the calculated average volume being 1.4 cc. per square foot (135 lbs. per acre). These figures are lower than those for Plot 1 and considerably lower than those for Pine Lake during the same period.

Associated organisms

Although the composition of the macroscopic bottom fauna in both plots was similar, the number and volume was slightly but consistently greater in Plot 1. This difference was largely due to the greater number of scuds, *Hyalella knickerbockeri,* and a greater abundance of *limbata* nymphs. In determining the total yield of macroscopic bottom fauna usually only one square foot sample (4 dredge hauls) was secured from each plot upon each visit to the lake from August, 1947 to August, 1948. Data secured from the combined samples from each plot are presented in Appendix Table 23.

Although the number of bottom samples was small, a seasonal fluctuation in numbers of organisms was evident and followed that previously noted for Pine Lake. Fluctuations in volume during the period were caused chiefly by inclusion in the tabulation of varying numbers of crayfish of different sizes. These crustaceans consistently appeared in samples taken throughout the year and contributed substantially to the total volume.

On a numerical basis, nymphs of *limbata* constituted a relatively small part of the bottom fauna (average number of nymphs per sq. ft. 30, or 11 percent; other organisms 255, or 89 percent), but volumetrically they exceeded all other bottom animals by a wide margin during most of the year. Average volume of the total macroscopic bottom fauna for the entire period was 2.52 cc. per square foot, of which 54 percent (1.36 cc.) was composed of *limbata* nymphs and 46 percent (1.16 cc.) of all other organisms. The average production of bottom organisms, expressed in terms of weight, was 242 pounds per acre for the yearly average, of which *limbata* nymphs comprised 131 pounds and other organisms 111 pounds.

Big Silver Lake

Distribution

Unlike Pine and Gun lakes, in which extensive shallow areas provide a comparatively large amount of habitat, Big Silver Lake has a marl bottom suitable for nymphs only around the margin of the major depression. Thus the distribution pattern (Fig. 34) is essentially that of a comparatively narrow band extending around the lake. In this respect it is very similar to that described for *Hexagenia* in other waters (Adam-

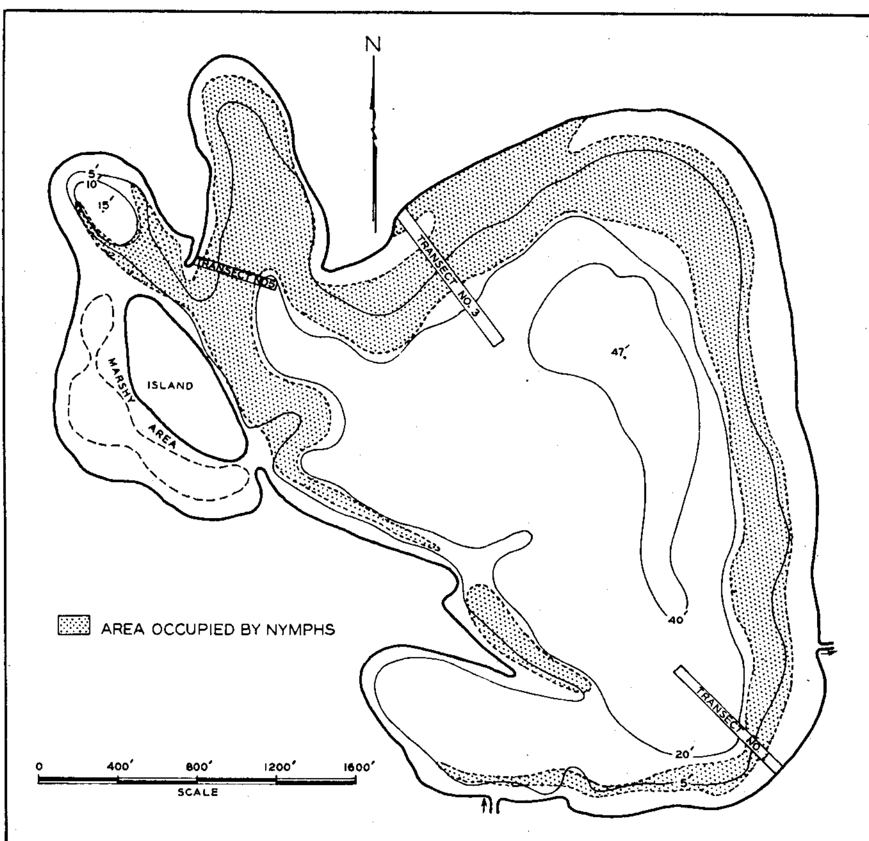


Figure 34. Distribution of nymphs and location of sampling transects in Big Silver Lake. Compare with bottom types in Figure 13.

stone, 1923, 1924; Lyman, 1940). The most extensive area occupied is the shoal on the north side of the basin. Comparison of the distribution of nymphs (Fig. 34) with that of the various bottom types (Fig. 13), shows that nymphs are essentially restricted to the marl substratum and do not occur elsewhere in significant numbers. Sand and gravel bottom near shore exclude the insects from this zone, and their downward distribution is apparently limited by change in bottom type from marl to pulpy peat and by the density of vegetation which occurs at the same depth. Within the area occupied, specimens were most abundant in the middle of the marl belt and decreased toward both shore and deeper water. Distribution along a transect from shore outward is

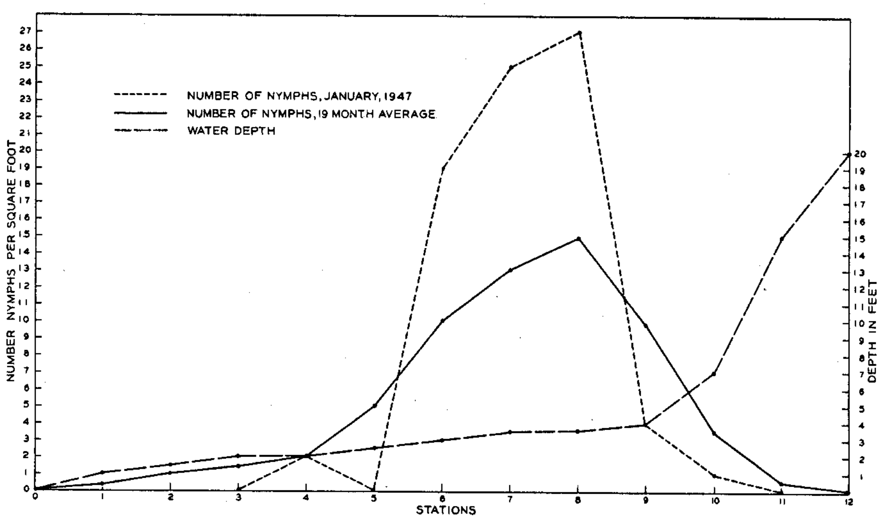


Figure 35. Distribution of nymphs at Transect 3, Big Silver Lake.

shown graphically in Figure 35. The amount of lake bottom providing a habitat for these insects is about 80 acres, or 37 percent of the total area.

Very small specimens, often found on sand shoals in late summer, were obviously young-of-the-year. As the season progressed there was an apparent migration of these individuals into deeper water and softer bottom. That this movement occurred was shown particularly well by collections secured at Transect 1. In that area not only did the number of nymphs on the sand decrease in late fall, but a corresponding increase occurred in water 5–10 feet in depth. Average size of individuals was smallest on the sand shoal and increased toward deeper water and softer bottom, an indication that the sand, overlaid by a thin layer of mud, offered a temporary habitat which was abandoned when the nymphs grew larger.

Density of population

Density of the nymphal population was not everywhere the same and fluctuated to some extent from year to year within a given area. Number per unit of bottom was consistently greater at Transects 3 and 5 than at Transect 1, but nymphs were more abundant at times in other parts of the lake. Throughout the period of sampling specimens were generally more abundant at Transect 5 than at any other. In the most productive portion of this area the average number of nymphs per square foot for the period November, 1946 to August, 1948 was 19 (171 per sq. yd.) with a volume of 0.94 cc. (90 lbs. per acre). By comparison, it is clear that the best yield in Big Silver Lake was considerably lower than the average yield for either Pine or Gun lakes.

Data obtained from bottom samples secured at various depths along Transect 1 are presented in Table 20. The table shows that at Stations 1 and 2 (sand bottom) nymphs were present during late summer and fall but were absent during the remainder of the year. Specimens were always present at Stations 3, 4 and 5 (sand and marl, marl, marl and plant debris bottom, respectively) but few were ever encountered at Station 6 (marl and peat bottom). Average number of nymphs per square foot at this transect for the entire sampling period was 6 (54 per sq. yd.) with a volume of 0.21 cc. (20 lbs. per acre), indicating a very low production in this portion of the lake.

Bottom samples were taken on Transect 3 at 12 stations located approximately 50 feet apart, usually one square foot being secured at each. The lake bottom at Stations 1–5 was composed of hard packed marl, sand or sand-marl-gravel mixtures and supported a considerable growth of *Scirpus*. Stations 6–9 were located in soft, rather barren marl-mud, and 10 and 11 at the drop-off, where marl, plant debris and peaty material occurred. The bottom at Station 12, located just off the shoal in water 20 feet deep, was composed of pulpy peat. Nymphs were never found at this station. Data obtained at this transect are presented in Table 21 and Figure 35.

Although nymphs were found from within a few feet of shore to a depth of 15 feet, they were abundant only between Stations 5 and 10. Average yield of the most productive part of the transect (Stations 6–9) was 12 nymphs per square foot (108 per sq. yd.), having a volume of 0.77 cc. (74 lbs. per acre). Considering the entire shoal area, the number of nymphs per square foot was 6 (54 per sq. yd.) with a volume of 0.36 cc. (35 lbs. per acre).

Bottom sampling at the 8 stations located on Transect 5 (Table 22) revealed a distribution of nymphs similar to that at Transect 3. The bottom at Station 1, situated about 25 feet from shore, was composed of sand and gravel and contained few nymphs, these being very small individuals present only in late summer. A marl-sand mixture formed the bottom at Station 2, while a rather barren, soft marl-mud substratum existed at Stations 3–6. Marl and plant debris constituted the bottom at Station 7; at Station 8 a marl-peat mixture occurred. Comparatively little vegetation was found at depths of 10–15 feet in this area.

A few nymphs occurred here at 20 feet (Station 8), the greatest depth at which they were collected in the lake. Specimens were abundant only between Stations 3–6, the average number per square foot for the entire sampling period (November, 1946 to August, 1948) being 19 (171 per sq. yd.) and having a volume of 0.94 cc. (90 lbs. per acre). Average production for the entire shoal area occupied by nymphs (1–20 ft.)

Table 20. Average number (N) and average volume in cc. (V) of nymphs per square foot of bottom, at Transect 1, Big Silver Lake (tr = trace)

Date	Station number, and depth of water in feet											
	No. 1, 2 ft.		No. 2, 3 ft.		No. 3, 4 ft.		No. 4, 5 ft.		No. 5, 10 ft.		No. 6, 15 ft.	
	N	V	N	V	N	V	N	V	N	V	N	V
10/24/46	1	tr	9	0.05	12	0.20	13	0.20	0	0.00	0	0.00
5/27/47	0	0.00	0	0.00	0	0.00	16	1.35	6	0.75	2	0.30
8/29/47	0	0.00	0	0.00	3	0.25	5	0.50	0	0.00	0	0.00
9/30/47	8	0.08	13	0.10	21	0.15	7	0.50	1	0.05	0	0.00
10/10/47	10	0.05	21	0.10	14	0.25	6	0.30	0	0.00	0	0.00
10/30/47	7	0.05	9	0.05	18	0.15	13	0.37	3	0.25	0	0.00
12/22/47	12	0.10	3	tr	11	0.35	24	1.35	9	0.75	0	0.00
4/15/48	0	0.00	1	tr	2	tr	19	1.95	6	0.70	0	0.00
6/10/48	0	0.00	2	0.05	3	0.20	8	0.65	5	0.60	1	0.10
7/21/48	9	tr	5	tr	7	tr	3	0.40	0	0.00	0	0.00
8/24/48	14	0.05	27	0.10	17	0.15	7	0.50	0	0.00	0	0.00

was 11 nymphs per square foot, with a volume of 0.54 cc. (52 lbs. per acre). These figures are considerably higher than those obtained at Transects 1 and 3.

At this transect it is also evident that young-of-the-year nymphs appeared on the hard bottom at Stations 1 and 2 in mid-summer and moved to a more suitable bottom in deeper water as they grew larger. Average size of specimens, reflected in the volume measurements, was least near shore and greatest in the more favorable bottom at Stations 4–7.

Associated organisms

The macroscopic bottom fauna of Big Silver Lake is similar in composition to that of Pine and Gun lakes, with the nymphs of *limbata* again playing a dominant role. Lack of time prevented a detailed study of the organisms encountered while collecting *limbata* nymphs, but observations indicated that data obtained on three occasions were indicative of conditions existing through the seasons.

Pertinent information obtained at Transect 3 on April 15, 1948 (Appendix, Table 24), before the summer decline of the bottom fauna occurred, showed that *limbata* nymphs comprised 3 percent of the total number of organisms (average number organisms per sq. ft. 185; *limbata* 5, others 180). On a basis of volume, *limbata* contributed 0.63 cc. (31 percent) and other organisms 1.39 cc. (69 percent) to the total average volume of 2.02 cc. per square foot. Average volume expressed in terms of weight amounted to 194 pounds per acre, of which 61 were composed of *limbata* and 133 of other organisms. The presence of *Ephemera simulans* nymphs accounted for the large number of mayflies at Station 5. This species was very abundant from Station 5 shoreward.

All macroscopic organisms were sorted from samples obtained at Transect 5 on April 22, 1948 (Appendix, Table 25). Organisms were somewhat more numerous than at Transect 3, averaging 239 per square foot. *Limbata* nymphs comprised 6 percent of the total number. Total average volume, 1.99 cc. per square foot, was slightly less than that at Transect 3, and *limbata* nymphs composed 48 percent (0.95 cc. per sq. ft.; 91 lbs. per acre) and other organisms 52 per cent (1.04 cc. per sq. ft.; 100 lbs. per acre) of the total. Again nymphs of *Ephemera simulans* were abundant in the sandy bottom near shore and accounted for the large number of mayflies at Station 2. These data can be compared with results obtained in the previous year. On July 22, 1947 all macroscopic animals were collected from samples obtained at Transect 5, Stations 2–7. Average number of organisms per square foot was 161, of which 6 (4 percent) were *limbata* nymphs. These animals comprised 51 percent (0.5 cc. per sq. ft.; 48 lbs. per acre) while other organisms made up 49 percent (0.47 cc.; 45 lbs. per acre) of the total average volume of bottom fauna. The low number and volume present in July and the higher figure obtained in April coincide with the seasonal variation in abundance of bottom fauna shown in Pine and Gun lakes. In Big Silver Lake *limbata* nymphs are the dominant insect of the marl-mud bottom, but in most instances constitute less than one-half the volume of the total macroscopic bottom fauna.

Table 21. Average number (N) and average volume in cc. (V) of nymphs per square foot of bottom, at Transect 3, Big Silver Lake (tr = trace)

Date	Station number, and depth of water in feet											
	No. 1, 1 ft.		No. 2, 1.5 ft.		No. 3, 2 ft.		No. 4, 2 ft.		No. 5, 2.5 ft.		No. 6, 3 ft.	
	N	V	N	V	N	V	N	V	N	V	N	V
1/11/47	0	0.00	0	0.00	0	0.00	2	tr	0	0.00	19	0.35
5/16/47	0	0.00	2	0.02	3	0.30	0	0.00	12	0.60	14	0.40
7/30/47	0	0.00	2	0.05	0	0.00	0	0.00	2	0.10	10	0.75
9/ 3/47	1	0.02	2	tr	1	tr	7	0.15	7	0.10	6	0.45
10/10/47	2	0.05	3	0.05	0	0.00	4	0.10	6	0.30	7	0.40
2/16/48	0	0.00	0	0.00	2	tr	0	0.00	2	0.05	7	0.30
4/15/48	0	0.00	0	0.00	5	0.85	3	0.18	7	0.30	3	0.06
7/ 5/48	0	0.00	0	0.00	0	0.00	0	0.00	2	0.10	4	0.05
7/21/48	0	0.00	0	0.00	2	tr	0	0.00	3	0.10	4	0.30
8/23/48	0	0.00	3	0.12	1	tr	4	0.05	10	0.43	27	0.62

Date	Station number, and depth of water in feet									
	No. 7, 3.5 ft.		No. 8, 3.5 ft.		No. 9, 4 ft.		No. 10, 7 ft.		No. 11, 15 ft.	
	N	V	N	V	N	V	N	V	N	V
1/11/47	25	0.80	27	1.10	4	0.40	1	0.05	0	0.00
5/16/47	14	0.45	17	0.65	18	2.10	9	1.30	0	0.00
7/30/47	9	0.45	9	1.20	7	1.00	1	0.30	1	0.15
9/ 3/47	18	1.50	12	0.80	15	0.75	3	0.15	0	0.00
10/10/47	13	0.80	13	0.45	12	1.30	5	0.35	1	0.10
2/16/48	16	1.64	12	1.77	9	0.98	3	0.61	0	0.00
4/15/48	6	0.43	9	2.01	10	1.46	3	0.61	1	0.18
7/ 5/48	5	0.15	2	0.20	3	0.25	2	0.45	0	0.00
7/21/48	12	0.70	22	0.95	2	0.50	1	0.10	0	0.00
8/23/48	13	0.55	25	0.90	18	0.80	7	0.25	2	0.10

Table 22. Average number (N) and average volume in cc. (V) of nymphs per square foot of bottom, at Transect 5, Big Silver Lake (tr = trace)

Date	Station number, and depth of water in feet							
	No. 1, 1 ft.		No. 2, 2 ft.		No. 3, 3 ft.		No. 4, 5 ft.	
	N	V	N	V	N	V	N	V
11/1/46	0	0.00	3	tr	83	1.50	13	2.00
5/29/47	0	0.00	2	0.05	9	0.45	20	1.70
6/24/47	0	0.00	0	0.00	14	1.05	15	1.05
7/22/47	0	0.00	0	0.00	9	0.60	26	1.90
8/29/47	2	tr	45	0.35	93	1.40	60	0.90
10/10/47	0	0.00	3	tr	28	0.60	30	1.65
11/7/47	0	0.00	0	0.00	22	1.85	20	2.35
4/22/48	0	0.00	6	0.30	14	0.65	26	0.55
6/10/48	0	0.00	4	0.25	7	0.75	12	1.35
7/22/48	3	tr	14	0.15	27	0.25	38	0.55
8/24/48	0	0.00	7	0.08	23	1.10	30	1.45

Date	Station number, and depth of water in feet							
	No. 5, 7 ft.		No. 6, 10 ft.		No. 7, 15 ft.		No. 8, 18–20 ft.	
	N	V	N	V	N	V	N	V
11/1/46	11	1.25	2	0.30	0	0.00	0	0.00
5/29/47	5	0.70	3	0.50	1	0.05	0	0.00
6/24/47	16	1.00	4	0.60	0	0.00	0	0.00
7/22/47	11	1.10	3	0.40	1	0.40	0	0.00
8/29/47	23	0.55	0	0.00	0	0.00	2	0.30
10/10/47	21	1.05	3	0.70	2	0.05	0	0.00
11/7/47	7	1.10	1	0.08	0	0.00	0	0.00
4/22/48	17	1.05	12	1.60	9	1.65	1	0.20
6/10/48	6	0.75	7	0.97	0	0.00	0	0.00
8/24/48	46	1.85	2	0.25	0	0.00	0	0.00

ECONOMIC IMPORTANCE

Fish Bait

Use of burrowing mayfly nymphs as a winter fishing bait in Michigan began during the 1930's and has been increasing since that time. Although larvae of corn borers, caddis and various other insects are widely employed as bait for bluegills, perch, rock bass and other pan fish that can be caught legally during the winter, *Hexagenia* nymphs or "wigglers" are the most widely used and most available of all natural baits. Because of the demand created by an ever increasing number of fishermen, many individuals brave the vicissitudes of mid-winter to collect nymphs which are worth at least 75 cents per hundred at wholesale market prices. For several years the minimum retail price has been 20 cents per dozen, although it is often much higher. That collecting these insects is a profitable though rigorous winter occupation is evident when it is considered that a crew of two men working diligently may gather from 3,000 to 6,000 nymphs in a day. However, the hard manual labor involved and the necessity of withstanding exposure on an ice covered lake or stream is sufficient to discourage all but the most hardy individuals from pursuing this occupation.

Once nymphs have been collected, they enter various trade channels and are dispersed alive to retail bait dealers and made available to anglers. These insects may be held during the winter for as long as 3 weeks in wooden holding boxes partially submerged in tanks provided with very cold running water. After that period losses begin to mount although some specimens will survive for a month or more. Nymphs must be kept alive since in that condition they are most effective when impaled upon the angler's hook. Several wholesale and retail bait dealers who handle from 250,000 to 350,000 nymphs during an ordinary 2-months winter fishing season (January and February) are known to the writer. The total number of persons engaged in collecting and selling nymphs each winter in Michigan is not known, but undoubtedly runs into several thousand.

Sources from which these insects may be obtained are, with two exceptions, any accessible lake or stream containing a population sufficiently dense to attract collectors. Commercial collecting of all aquatic insects in trout streams, and in Gun Lake, Barry County, has been prohibited since 1934 and 1945, respectively, by special acts of the State Legislature. Because comparatively few productive waters are known to bait gatherers certain lakes, such as Pine Lake, which have large populations of nymphs, are subject to concentrated bait collecting each winter.

Although collection and use of nymphs as bait is almost exclusively a winter time activity, in a few instances dealers are known to have collected nymphs during the summer for sale. This practice is generally regarded by the public as an unnecessary exploitation of the "wiggler" supply since other natural baits are available in abundance at that time of year. Observations by the writer indicate that during the warm weather of summer large nymphs are generally not abundant, and further that they are more easily injured by rough handling, and harder

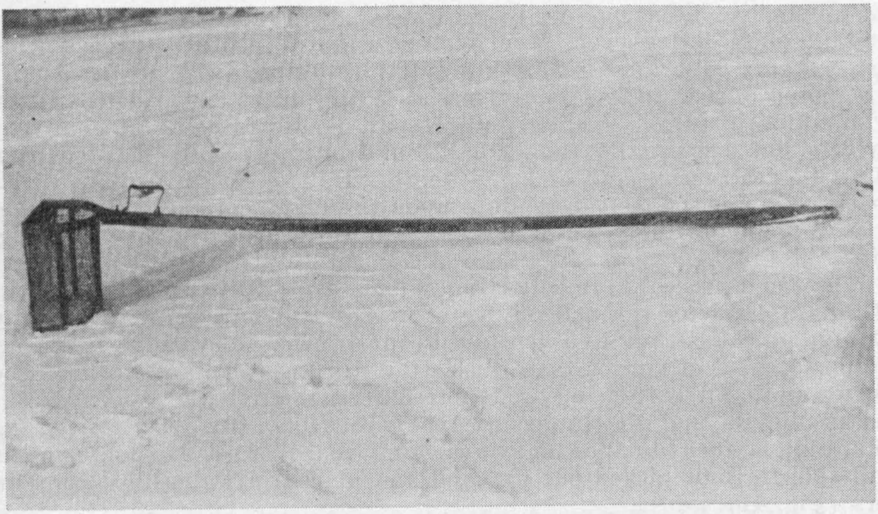


Figure 36. Nymph collector's scoop. Net is half round, 16 inches in greatest diameter, and 18 inches deep. Length of handle 11 feet.

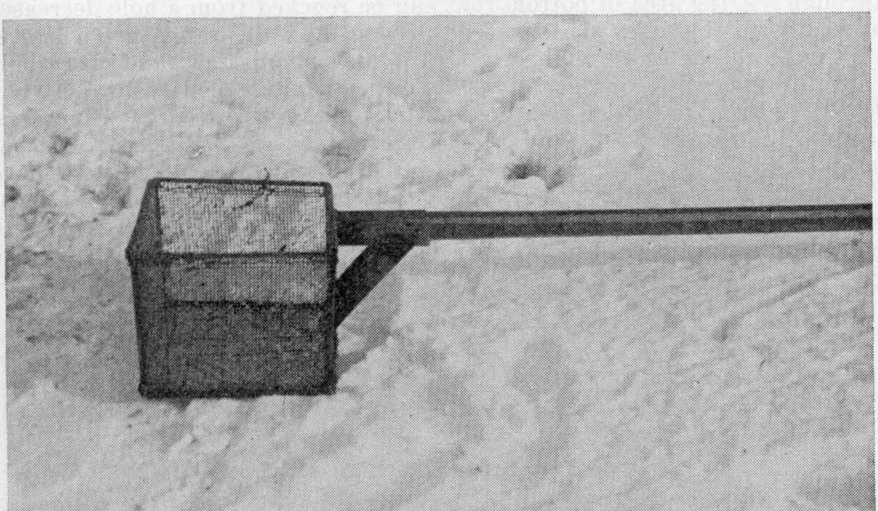


Figure 37. Nymph collector's scoop. Net is 12 inches square and 14 inches deep. Length of handle 13 feet.

to keep alive in the tanks of bait dealers during this season. It appears that the practice of collecting nymphs for commercial bait in the summer time is a misuse of this resource.

Winter collecting methods usually involve manually operated screen scoops of various kinds which are used to separate nymphs from the bottom mud. Brown* was informed that large dredges pulled by a team

*Brown, C. J. D. Supplementary report on the removal of wigglers (mayfly nymphs) from Pine Lake, Prairieville Township, Barry County. Institute for Fisheries Research, Report No. 647. 1941. Unpublished.

of horses had been employed by bait collectors working on Pine Lake but no such devices were seen by the writer. Scoops are constructed by the bait collectors and vary greatly in design. The net is usually composed of grit screen, 4 or 8 meshes to the inch, fastened to an iron rim which in turn is secured to a sturdy handle. Shapes of nets vary widely but are usually round, half-round or square and may be from 1 to 1.5 feet across and of equal depth. Handle length usually varies between 8 and 14 feet, depending upon preference of the collector and the water depth in which he works. Typical scoops are shown in Figures 36 and 37.

The usual procedure in collecting nymphs is to cut a round hole about 3 feet in diameter through the ice (Fig. 38) and then to systematically dredge up the bottom to a depth of about 6 inches, a scoopful at a time. Each scoopful of mud is then washed by jiggling it up and down in the water until all bottom material has passed through the screen except coarse debris and the larger nymphs (Figs. 39, 40). The remaining material is then dumped onto a sorting board or screen and nymphs suitable for bait picked out by hand and placed in water-filled containers (Fig. 41).

Collectors can operate at depths ranging from 3 to 8 feet but digging is most efficient in water 4 to 6 feet deep. Since the operator works through ice, the area of bottom that can be reached from a hole decreases as the water becomes shallower or deeper than the range given above. Cutting large holes through thick ice is an arduous task and every bait collector endeavors to locate his holes as advantageously as possible. For these reasons little collecting is attempted in very shallow situations.

Of primary importance to the bait collector is the average number of nymphs he can obtain per scoopful of mud. Many operators have informed the writer that they consider it necessary to capture at least 8–10 bait-size specimens for each dip of the scoop if the venture is to be financially profitable. A lesser yield results in abandonment of the

Figure 38. Hole being used by nymph collector on Pine Lake. Dark mass in background is washed debris, principally *Chara*.

Figure 39. Bait collector dredging bottom mud in Pine Lake.

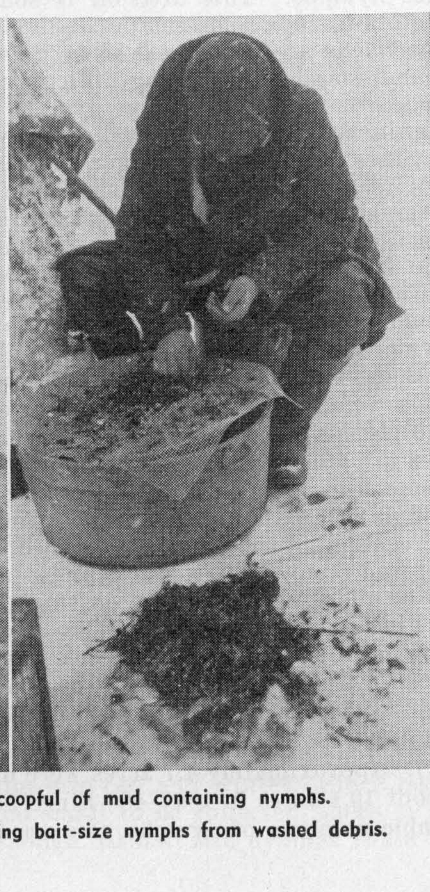


Figure 40. (Left.) Washing a scoopful of mud containing nymphs.
Figure 41. (Right.) Bait collector sorting bait-size nymphs from washed debris.

location and a search for a more productive one; the law of diminishing returns serves to protect areas in which the nymphal population is relatively low. Number of specimens obtained through a single hole varies with density of the population, the proportion of large nymphs in it, and efficiency of the scoop operator. One crew of two bait collectors working on Pine Lake stated that they usually obtained from 2,000 to 3,000 bait-size nymphs from a single hole although occasionally as many as 5,000 were taken. These men usually work over all the bottom within a radius of about 10 feet from the hole, covering a total area of about 380 square feet. Therefore the take was approximately 5–8 nymphs per square foot. These two men estimated that during the winter of 1947–48 they obtained an average of about 4,000 specimens per day and worked approximately 60 days during the winter season. Thus the total take approximated 240,000 bait-sized nymphs. Not all bait collectors work as efficiently as these two men and are satisfied with a smaller catch.

The size of nymphs retained by collectors varies greatly depending upon individual preference, the effect on future sales of included small specimens, and the current supply and demand for bait. Measurement of many specimens kept for bait and others rejected as being a little too small led to the conclusion that a body length of 23 mm. (about 7/8 inches) could be used as a dividing line between bait-size and non-bait-size nymphs. This division is somewhat arbitrary since all bait collectors include some smaller individuals in their catch. However, larger specimens are considered to be better bait and are in much greater demand, smaller ones being difficult to sell. Consequently bait collectors endeavor to obtain as large nymphs as possible and refrain from keeping significant numbers of smaller individuals.

Since females reach larger size than males and many of the latter do not reach a length of 23 mm. even at maturity, it was suspected that nymphs collected for the bait market would show a preponderance of females. Examination of specimens from many bait tanks established the fact that males formed from 5–41 percent of the total nymphs in various lots, usually comprising between 18 and 30 percent. The greatest number of males was always encountered in collections in which all nymphs were of comparatively small size.

Some nymphs are undoubtedly destroyed by dredging, in addition to those removed for bait use. Evidence indicates also that some displaced individuals fall prey to fish. It is probable that subsequent mating activities are affected to some extent by the removal of a portion of the larger nymphs including a disproportionate number of females. In addition, the population is influnced to some extent by the amount of dredging and the percentage of the habitat disturbed. However, the overall effect of dredging and removing bait-size nymphs from the lakes studied does not appear to be unduly harmful to the nymphal populations.

Pine Lake, providing as it does a great deal of bait each winter, was dug quite extensively during the winters of 1946–47 and 1947–48. At the close of the bait collecting season, when the snow had melted and the areas which had been dug were plainly discernible by the outlines of old holes and mud and debris on the ice, the disturbed sections were mapped (Fig. 42). Approximately 4.7 acres were dredged in the winter of 1946–47 and about 10.1 acres in 1947–48. Since 91 acres of this basin produce considerable numbers of nymphs, the amount of productive bottom worked by

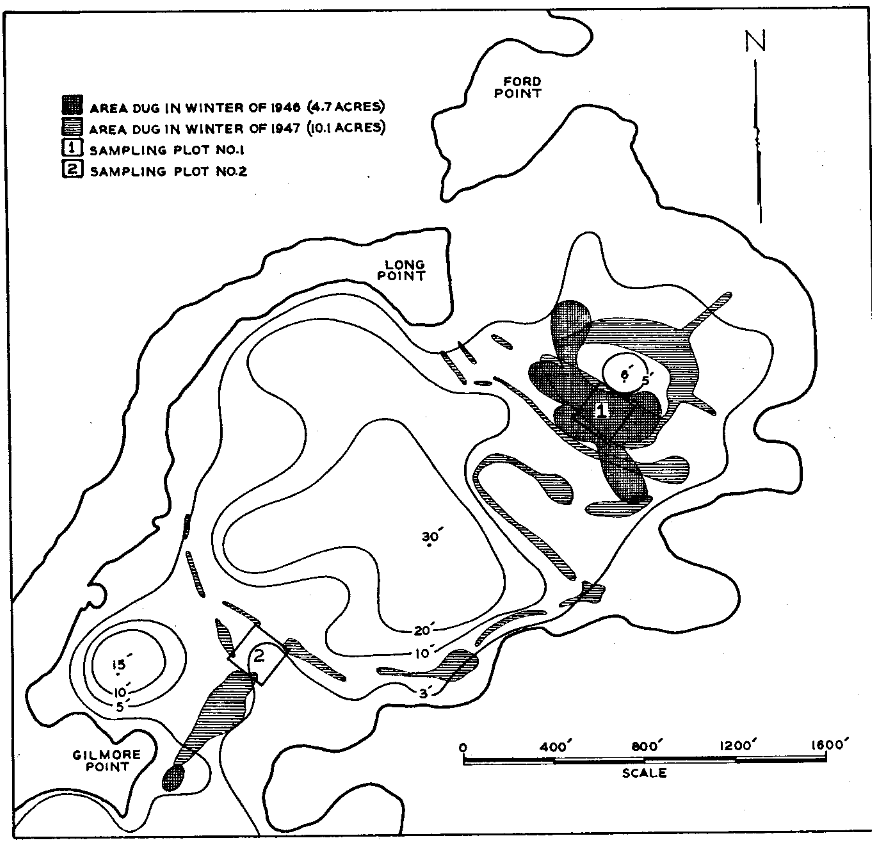


Figure 42. Map of Third Lake (part of Pine Lake) showing areas dug by bait collectors in 1946–47 and 1947–48.

bait collectors during the two winters was 5.2 and 11.1 percent, respectively. Considering the concentration area alone (52 acres) only 9.0 and 19.4 percent of the most productive area was disturbed. On a basis of the area dug, there seems to be no reason for believing that undue exploitation of the population occurred. It was estimated that not more than 1.5 million nymphs were removed in the winter of 1946–47 and that not more than 3.5 million individuals were taken from the lake in 1947–48. These figures are not impressive when it is considered that density of the nymphal population during the winters involved approached one million per acre and that 250,000 to 350,000 of these were of bait size.

The number of bait-size nymphs present in the two plots in Pine Lake at various times of year is shown in Tables 23 and 24. It may be seen that most of the specimens 23 mm. or longer are females and that the number of bait-size individuals per square foot varies greatly in the course of a year. From 31.3 to 47.4 percent of the nymphal population was of large size and available to collectors during late fall and winter. Since more than one-half of the population is too small to be collected, there is no danger of a serious depletion even though all bait-size nymphs could be removed. As previously stated, Plot 1 had been disturbed by bait collectors prior to January 31, 1947, when quantitative samples were first obtained. Even though many specimens had no doubt been removed, the average number remaining per square foot was 18.9, of which 5.9 were of bait size (Table 23). In May and early June, 1947, the average number per square foot was 5.6 and 5.3, respectively, a strong indication that the data obtained in January represented true conditions. The comparatively large population remaining after bait collectors had worked the area shows that not only did many small nymphs survive, but a great many bait-size specimens as well. On January 27, 1948, Plot 1 had been disturbed little, but the area was dredged thoroughly in February. Marked decrease in the average number of bait-size specimens per square foot from January (8.3) to April, 1948 (3.7) indicates that in this interval bait collectors removed an average of about 4.6 large nymphs per square foot. This figure agrees with the minimum number obtained by bait collectors based on their own approximations. In 1948, when bait collecting was much more intense than in the previous year, an average of more than 10 nymphs per square foot remained after the ice break up, nearly 4 of them being of bait size. Even after intensive digging in 1948 the number of large nymphs was reduced only about 56 percent. Samples obtained at the conclusion of field work in November, 1948, contained an average of 10.1 bait-size nymphs per square foot (40.3 percent of all those present), an indication that an ample stock was available for bait collectors the following winter and also that more than half the population was too small to be retained as bait.

It is apparent that fewer large nymphs were present in Plot 2 than in Plot 1, but the seasonal trends are similar. No evidence of a mid-winter loss, such as that shown in Plot 1, is evident in this sampling area. The percentage of the population which had reached bait size was not greatly different than in the other sampling area at various times of year.

Table 23. Average number of bait-size nymphs (23 mm. or longer) per square foot, and its relationship to undersize nymphs, Plot 1, Pine Lake

Date	Number of nymphs, all sizes	Number of bait-size nymphs			Percentage of bait-size nymphs
		Males	Females	Total	
6/ 1/46	3.5	0.0	0.8	0.8	22.8
1/31/47	18.9	1.1	4.8	5.9	31.2
5/20/47	22.0	1.0	4.6	5.6	25.4
6/ 5/47	24.0	1.8	3.5	5.3	22.1
7/ 2/47	17.3	1.2	6.4	7.6	43.9
8/15/47	39.4	0.2	1.9	2.1	5.3
9/12/47	28.0	0.4	1.6	2.0	7.1
11/14/47	18.0	1.5	6.8	8.3	46.1
1/27/48	17.5	0.4	7.9	8.3	47.4
4/ 6/48	10.4	0.4	3.3	3.7	35.6
5/ 6/48	12.5	0.5	2.9	3.4	27.2
6/ 2/48	6.8	0.1	1.8	1.9	27.9
7/12/48	31.8	0.6	0.2	0.8	2.5
8/25/48	40.1	0.0	0.3	0.3	0.7
11/10/48	25.1	0.0	10.1	10.1	40.3
6/13/49	7.5	1.2	2.3	3.5	46.7

Table 24. Average number of bait-size nymphs (23 mm. or longer) per square foot, and its relationship to undersize nymphs, Plot 2, Pine Lake

Date	Number of nymphs, all sizes	Number of bait-size nymphs			Percentage of bait-size nymphs
		Males	Females	Total	
1/31/47.........	24.9	0.4	3.6	4.0	16.1
5/22/47.........	25.1	2.0	4.0	6.0	23.9
6/ 5/47.........	24.3	2.8	6.1	8.9	36.6
7/ 2/47.........	16.5	0.5	3.0	3.5	21.2
8/16/47.........	10.9	0.2	1.4	1.6	14.7
9/12/47.........	19.4	0.2	1.6	1.8	9.3
11/13/47.........	15.4	0.4	3.6	4.0	26.0
1/27/48.........	12.9	0.9	4.0	4.9	38.0
4/ 6/48.........	12.3	0.4	3.3	3.7	30.0
5/ 6/48.........	9.7	1.6	2.5	4.1	42.3
6/ 2/48.........	7.9	0.1	1.5	1.6	20.2
7/13/48.........	62.6	0.3	2.1	1.7	2.7
8/25/48.........	70.7	0.3	0.5	0.8	1.1
11/10/48.........	26.0	0.0	0.6	0.6	2.3
6/13/49.........	8.0	1.0	3.1	4.1	51.3

Second Lake, particularly the shoal at Prairieville Township Park, was a popular collecting area in the past, but in recent years has been unproductive of nymphs. According to reports of bait collectors and members of the staff of the Institute for Fisheries Research, this part of Second Lake produced great numbers of nymphs for the market from about 1939 to 1943. Therefore the population density in years past must have been much greater than at present since there are now not enough nymphs to make collecting them a profitable undertaking. The cause of this unquestioned decline is not known for no data are available for comparing past and present conditions. One might speculate that the decline in the nymphal population may have been due to ecological changes brought about by the continued plowing of the lake bottom incidental to nymph collecting. Examination of bottom material from this shoal reveals that it is brownish and although predominantly marl, contains a high percentage of peaty material and at times large amounts of decomposition gases. Also some areas are densely covered with luxuriant growths of *Chara*. According to reports, vegetation was sparse and the bottom rather barren during the period the shoal harbored a dense population of nymphs. Whether such changes may be expected to occur in other areas as the result of continued dredging over many years is a question which can be answered only by long-term observation. It should be noted that there is no indication of a decline in the nymphal population in Plot 1 after at least 4 years of intensive dredging.

As stated previously, no commercial nymph collecting has occurred in Gun Lake since the winter of 1944–45. Prior to that date it had been a very important source of bait and a considerable amount of intensive digging had taken place each winter, chiefly in the west basin. The area disturbed each year by bait collectors is not definitely known but was estimated at 40 acres in 1944.* At the time the lake was mapped by an Institute for Fisheries Research field party in February, 1945, an estimated 30 acres had been worked. Thus it appears that not more than about 4.5 percent of the bottom inhabited by nymphs (885 acres) was molested in any winter. Although few data exist on the number of nymphs removed or the number remaining after the collecting season was over, it can be safely assumed that efficiency of collecting methods was similar to that at Pine Lake. Hazzard* reported that on May 23, 1944, after emergence had begun, the number of nymphs in 6 square foot bottom samples taken in an area dug the preceding winter ranged from 3 to 12 with an average of 6.5.

The number of nymphs of bait size in Plot 1 (Table 25) was less than in Pine Lake but seasonal patterns were similar. The average number present during late fall and winter was relatively constant. Plot 2 (Table 26) had fewer large nymphs than Plot 1 and the average number per square foot during the fall, winter and early spring showed a much greater variation. Comparison of the two lakes leads to the conclusion that although parts of Pine Lake were disturbed by bait collectors, the number of nymphs remaining was equal to that in Gun Lake, whose population can be considered to be a normal one.

The number and percentage of the nymphal population of bait size at various times of year in Big Silver Lake are shown in Table 27. It should be pointed out that during late fall and winter the percentage of males of bait size ranged from 2.6 to 12.7 and that of females from 5.0 to 17.7.

Commercial collection of nymphs in Big Silver Lake has been on a very small scale and restricted to the bay on the northwest side of the lake. Some digging occurred in both January and February of 1946 and 1947. On March 11, 1947, the writer took a number of bottom samples from the disturbed area to determine the number and size of nymphs and the number of other bottom animals remaining after digging had been terminated for the season. One square foot sample was obtained at a distance of 4–6 feet from the edge of each of 8 abandoned holes previously used by a bait

Table 25. Average number of bait-size nymphs (23 mm. or longer) per square foot, and its relationship to undersize nymphs, Plot 1, Gun Lake

Date	Number of nymphs, all sizes	Number of bait-size nymphs			Percentage of bait-size nymphs
		Males	Females	Total	
5/30/46	5.3	0.3	3.0	3.3	62.2
1/28/47	42.0	0.3	5.7	6.0	14.3
5/20/47	22.3	1.0	5.1	6.1	27.6
6/ 4/47	19.8	1.8	5.6	7.5	37.7
7/ 1/47	13.2	1.8	6.1	7.9	59.6
8/14/47	8.3	0.1	0.4	0.5	6.0
9/10/47	33.8	0.2	1.4	1.6	4.7
12/ 9/47	47.6	1.3	4.3	5.6	11.7
2/ 9/48	33.0	1.6	4.1	5.7	17.3
4/ 5/48	26.5	1.0	4.6	5.6	21.1
5/ 6/48	20.3	0.8	3.5	4.3	21.4
6/ 4/48	6.9	0.7	3.5	4.2	60.9
7/11/48	18.8	0.7	1.2	1.9	10.1
8/26/48	57.0	0.3	1.8	2.1	3.8
11/ 9/48	61.7	0.1	6.6	6.7	10.9

*Hazzard, A. S. Preliminary investigation of the "wiggler" supply in Gun and Pine lakes, Barry County. Institute for Fisheries Research, Report No. 975. 1944. Unpublished.

Table 26. Average number of bait-size nymphs (23 mm. or longer) per square foot, and its relationship to undersize nymphs, Plot 2, Gun Lake

Date	Number of nymphs, all sizes	Number of bait-size nymphs			Percentage of bait-size nymphs
		Males	Females	Total	
1/29/47	29.4	1.2	2.3	3.6	12.1
5/20/47	26.5	1.0	4.0	5.0	18.9
6/ 4/47	22.0	2.6	4.3	6.9	31.4
7/ 1/47	14.0	1.9	3.3	5.2	37.1
8/13/47	2.8	0.3	1.7	2.0	71.4
9/10/47	8.4	0.0	0.6	0.6	7.3
12/ 9/47	34.9	1.0	1.9	2.9	8.3
2/10/48	18.7	0.8	1.9	2.7	14.2
4/ 5/48	21.9	0.7	2.0	2.7	12.3
5/ 6/48	25.4	0.8	3.6	4.4	17.2
6/ 4/48	16.7	1.1	4.5	5.6	33.5
7/12/48	7.0	0.7	2.6	3.3	46.9
8/26/48	19.4	0.3	0.7	1.0	5.1

collector. All macroscopic bottom animals were removed from each sample, counted and measured volumetrically. Number of bait-size nymphs in the 8 samples (Table 28) varied from 1 to 11 with an average of 6.6. Of the males, 11.3 percent were bait size as compared to 32.2 percent of the females. Since this bait collector was known to have worked the area until his efforts were no longer profitable, it is clear that not only did a very substantial number of small nymphs (average 21.4 per square foot) survive the dredging operations but a comparatively large number of bait-size specimens as well (average 6.6 per square foot). Although the density

Table 27. Percentage of bait-size nymphs (23 mm. or longer) in samples from Big Silver Lake

Date	Males		Females		Both sexes
	Number of nymphs, all sizes	Percentage bait-size	Number of nymphs, all sizes	Percentage bait-size	Percentage bait-size
6/16/46	111	6.3	77	11.7	8.5
10/24/46	151	7.3	158	15.2	11.3
1/10/47	168	4.2	172	5.8	5.0
5/16/47	65	16.9	66	9.1	13.0
5/27/47	72	19.4	85	32.9	26.8
6/ 9/47	29	24.1	38	39.5	32.9
6/25/47	96	3.1	97	19.6	11.4
7/30/47	80	5.0	47	36.8	16.6
9/ 3/47	154	0.0	221	5.4	3.2
10/10/47	175	5.1	199	10.1	7.8
11/ 7/47	63	12.7	50	24.0	17.7
2/16/48	76	2.6	84	29.8	16.9
4/22/48	44	11.4	53	45.3	29.9
6/10/48	10	0.0	16	25.0	15.4
7/ 5/48	9	11.1	10	20.0	15.8
7/21/48	156	3.2	136	19.1	10.6
8/24/48	81	1.2	89	11.2	6.5
9/12/48	82	2.4	74	14.9	8.5

Table 28. Number and volume of bait-size nymphs, in relation to undersize nymphs, obtained from 8 square-foot bottom samples taken adjacent to holes abandoned by bait collector, Big Silver Lake, March 11, 1947

Sample No.	Nymphs, all sizes		Number of bait-size nymphs			Percentage of bait-size nymphs, by number
	Number	Volume, in cc.	Males	Females	Total	
1	33	3.40	3	7	10	30.3
2	23	1.65	0	1	1	4.3
3	29	3.30	2	6	8	27.6
4	68	4.30	4	4	8	11.8
5	21	1.65	3	2	5	23.8
6	11	2.60	1	8	9	81.8
7	34	4.50	3	8	11	32.3
8	5	0.80	0	1	1	20.0
Average	28.0	2.77	2.0	4.6	6.6	23.6

and composition of the original population is unknown, it can be concluded from the large number of survivors that dredging did not seriously deplete the stock of nymphs. Data obtained in this instance are similar to and substantiate those secured in Pine Lake.

A precise evaluation of the effect of dredging by bait collectors on the macroscopic bottom fauna other than *limbata* is impossible at this time. There is no doubt, however, that some organisms are destroyed when the lake bottom is torn up and others are killed when the mud is washed through the scoops. Limited data available suggest that the loss of organisms from these activities, in winter at least, is not great and that the bottom fauna as a whole is damaged but little by activities of bait collectors. Since screen 8 meshes to the inch is the finest customarily used on collecting scoops, it is obvious that all but the largest organisms pass through the screen when the mud is washed. Data obtained from Plot 1, Pine Lake (Fig. 31, Appendix Table 20) show that a marked decrease in the number of organisms occurred in samples secured in January and April, 1948. A similar decrease was not evident in Plot 2, Pine Lake (Fig. 32, Appendix Table 21). Since little commercial nymph collecting had occurred in Plot 1 before the bottom samples were taken in January and a reduction in the number of large nymphs did not occur until after that date, it is questionable whether this apparent decrease in number of other organisms could be attributed to dredging operations. Samples taken in May, 1948, indicate that the bottom fauna was abundant in the area disturbed by bait collectors a few months previously. On the basis of these findings it is concluded that no serious destruction of bottom organisms occurred as the result of dredging operations.

No information is available concerning the effect of dredging operations on the bottom fauna of Gun Lake since all commercial bait collecting ceased on that lake prior to the current investigation.

Data secured from an area in Big Silver Lake in which intensive nymph collecting was done in February, 1947 also indicate little or no destruction of bottom organisms. On March 11, 1947, 8 square-foot bottom samples were obtained adjacent to abandoned collecting holes and the results tabulated in Table 29. Nothing is known of the number of organisms present

Table 29. Number and total volume of organisms other than limbata **nymphs obtained from 8 square-foot bottom samples taken adjacent to holes abandoned by bait collector, Big Silver Lake, March 11, 1947**

Kind of organism	Sample number							
	1	2	3	4	5	6	7	8
Gastropoda (snails)	34	73	189	48	104	97	81	169
Pelecypoda (clams)	8	11	14	9	18	32	17	14
Hirudinea (leeches)	0	1	1	0	0	0	0	0
Amphipoda (scuds)	0	3	1	0	2	7	11	21
Ephemeroptera (mayflies)	2	3	2	4	5	18	13	9
Anisoptera (dragonflies)	0	0	1	0	0	0	0	0
Zygoptera (damselflies)	0	0	1	0	1	19	3	6
Neuroptera (alderflies)	4	5	4	2	0	0	2	0
Trichoptera (caddisflies)	4	5	5	4	3	27	22	38
Chironomidae (midges)	78	60	97	87	106	137	91	87
Ceratopogonidae (no-see-ums)	0	0	0	1	0	0	2	0
Total number	130	161	315	155	239	337	242	344
Total volume, in cc.	1.30	1.50	2.80	1.35	2.05	2.10	1.75	3.90

prior to the dredging but the fact that an average of 240.3 organisms other than *limbata,* with a volume of 2.09 cc. per square foot, remained after dredging was concluded is a strong indication that no great loss occurred. A comparison of the number of organisms present in samples from the disturbed area with the number found at Transects 3 and 5 in April, 1948, shows that the bottom fauna surviving the dredging was equal to or greater than that of some undisturbed areas. These results are quite in keeping with those obtained at Pine Lake and support the conclusion that dredging for *Hexagenia* nymphs is not particularly harmful to the bottom fauna as a whole.

Statements have been made that dredging for nymphs during the winter results in enough fine marl being introduced into the water to cause the entire lake to become muddy. No evidence to support this contention was obtained. On the contrary, repeated observations have shown that water is muddied only in the immediate vicinity of dredging activities and that by the following morning it is clear again. Measurements taken with a USGS turbidity rod showed that in 11 instances the initial turbidity, at the time a scoop of washed debris was lifted from a hole, ranged from 200 to 350 ppm. Within 3 minutes the turbidity ranged from 65 to 95 ppm. and at the end of 15 minutes had dropped to 8 to 20 ppm. Within 2–3 hours following the abandonment of a hole through which dredging had been going on for several hours the water was essentially clear. In the above instances scoops with 4 and 8 meshes to the inch were employed. No difference was discernible in the amount of turbidity caused by the use of scoops of these two mesh sizes. The distance that roiled water extended away from the center of disturbance was not great, in several cases not exceeding a distance of 50 feet in any direction even after hours of digging.

That sufficient marl is not left in suspension to muddy the water for a significant period is undoubtedly due to the fact that little of it is broken up into fine particles by the large mesh of the scoops. It is true that in the laboratory much of the marl which had been passed through a screen 100 meshes to the inch remained in suspension for 1–2 weeks. It was noticed, however, that even finely screened marl upon settling to the bottom tended to pack down into a firm layer and was not easily brought up into suspension by water currents. The fear that wave action, following the ice break-up, will bring large amounts of fine marl from the disturbed bottom into suspension is unfounded, for even on windy days comparatively little mud is evident in water on the shoals in Pine Lake.

A few weeks after nymph collecting is over for the season the lake bottom is visibly scarred. However, by early summer it is difficult to determine where dredging occurred since depressions or holes are seldom seen and the bottom presents a rather smooth and level surface. Screened marl apparently fills up the channels left by bait collectors' scoops, and packs into a firm layer. In no case was the bottom so disfigured or disarranged that the marks were permanently visible.

Chemical analyses of water in holes being used by bait collectors showed that pH and total alkalinity rose somewhat and that dissolved oxygen declined slightly but that these effects were local in extent and of temporary duration.

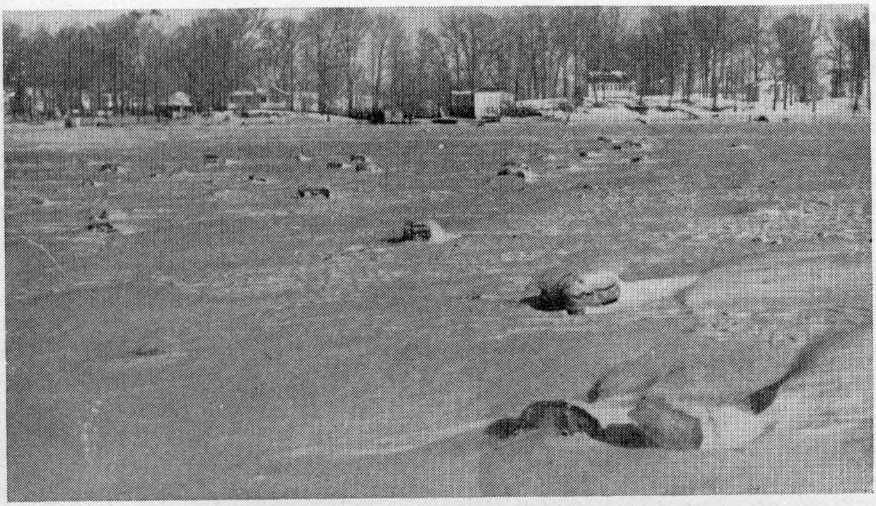


Figure 43. View of Pine Lake in late February showing snow-covered ice blocks left by bait collectors.

One phase of nymph collecting results in an unsightly lake and may justly be criticized. A certain amount of mud and debris is scattered around each of the holes through which nymphs are collected, resulting in mud-stained ice and snow. Piles of debris, including *Chara* and other aquatic plants, clam shells, sticks, etc., are sometimes left on the ice surface instead of being pushed back into the hole. Some small nymphs are inevitably trapped in washed debris and are killed when this material is left to freeze after large specimens are removed. Careful collectors push debris back into the hole once it has been sorted. Various methods are used to mark abandoned holes, which constitute a menace to fishermen until they are frozen over again, but none is entirely satisfactory. Commonly a piece of brush or a pole is placed in the hole and arranged so that it projects above the ice surface and marks the area even though it is covered with snow. In other instances ice blocks, obtained at the time the hole is cut, are upended to mark the location. These methods of marking holes are unsightly and ice blocks, debris, poles, logs, boards and brush are visible on the ice at the time it begins to melt in early spring. Occasionally poles are left protruding from the water surface and constitute a menace to boating later in the summer. Photographs taken at Pine Lake in late winter and early spring, 1948 (Figs. 43, 44, 45) illustrate the visible and objectionable phase of bait collecting just discussed. Although of lesser extent, similar conditions were found to exist on other lakes where bait collecting occurred.

It has been stated by some bait collectors that *Chara* grows more thickly in areas which have been dug repeatedly for several years while others state that less is found after several years disturbance. Observations during the period of investigation have revealed no noticeable changes in the vegetation within the study areas (i.e., Plot 1, Pine Lake). Piles of *Chara,* resulting from the return of debris by bait collectors through former holes in the ice are visible in early spring and summer but are quite inconspicuous in late summer due to the growth of vegetation in adjacent areas. *Chara* appears to be essentially unharmed by dredging if it is returned to the water and it rapidly becomes reestablished in areas scraped bare by collecting scoops. Since practically all collecting is done in areas which support little or no vegetation other than *Chara* and *Najas,* little damage to other aquatic plants (called "grass" by bait collectors) occurs. In Pine Lake it was observed that *Najas,* absent in early spring, became very noticeable in late summer and

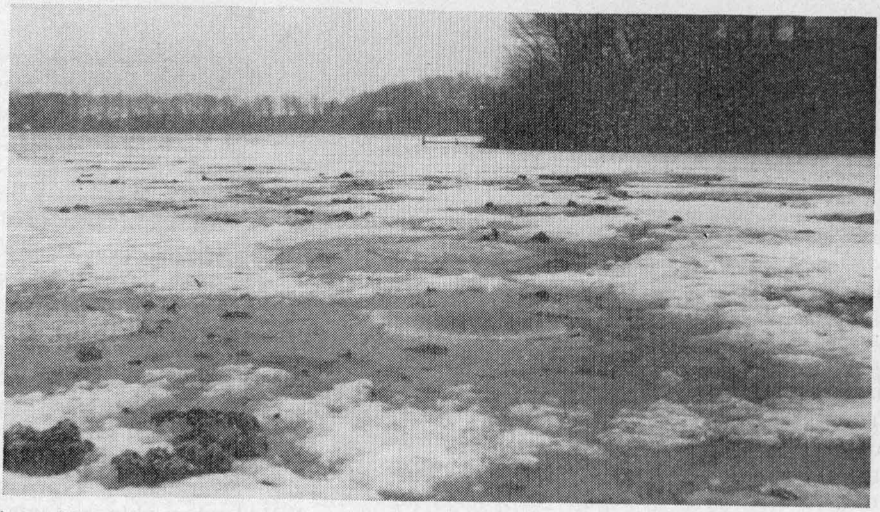


Figure 44. View of Pine Lake in early March showing abandoned holes used by bait collectors. Melting of snow revealed mud and debris on the ice.

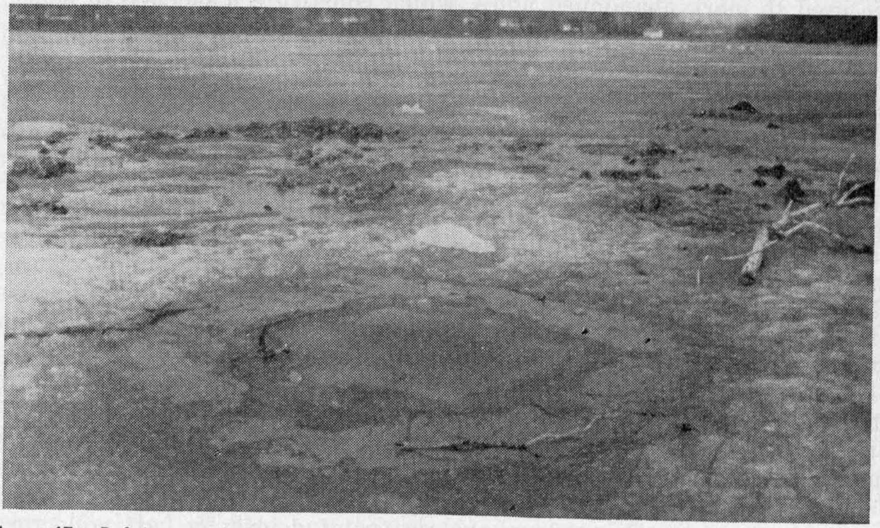


Figure 45. Debris around abandoned holes on Pine Lake in early March after snow had melted. Ice blocks are visible in background.

fall and grew rather profusely on bottom disturbed the previous winter (Plot 1). This plant appeared to be little affected by the dredging operations. Considering the problem in its entirety, the writer has reached the conclusion that bait collecting caused no appreciable damage to aquatic vegetation in Pine or Big Silver Lake during the period of investigation.

Fish Food

A population of *limbata* nymphs must be considered as an important potential fish food supply and the extent to which it is utilized by the fish is determined largely by the availability of the organism. Since they are fossorial and all indications point to their remaining in the burrows, at least most of the time, the question is raised as to the methods employed by fish to obtain them. It is known from stomach analyses that nymphs are consumed by many species of fish throughout the year; therefore they must be available to some extent, although it might be thought that they would be less available than other invertebrates living on the mud surface or vegetation. The question of how fish get the nymphs has not been settled to the satisfaction of the writer and no feeding experiments were conducted, but the following observations offer a partial explanation: In late summer bluegills and pumpkinseeds were often captured by fly fishing in early morning on very shallow, sandy shoals in Big Silver Lake. Stomachs of many of these fish contained small, recently ingested nymphs of *Hexagenia limbata* and *Ephemera simulans*. On such occasions these fishes sometimes were seen tailing in shallow water—that is, the fish were literally standing on their heads with tails toward the surface, grubbing in the bottom. A considerable amount of fine bottom material was stirred up in what appeared to be an effort to uncover insects located in the mud. That the fish were selective in what they swallowed is shown by the relatively small amount of debris present in the stomachs in addition to food organisms. Yellow perch were observed engaging in similar activities. It is more than likely, therefore, that all fishes which feed on these nymphs actually dig into the mud at times to secure them. This would explain the capture of small nymphs which are not buried deeply but would not satisfactorily account for the capture of larger ones which appear to live, for the most part at least, sufficiently deep in the mud to escape the limited digging abilities of most fishes.

It is obvious that when nymphs leave the burrow they are easy prey to any fishes in the vicinity. During the time mature nymphs are swimming to the surface to transform, they are exposed to the attacks of all predators in the area. Likewise, imagoes and subimagoes which alight on the water are easily captured by surface feeding fishes. It appears also that in winter nymphs may be easily captured at times, since fish caught through the ice often contain large numbers of them, apparently captured within a short period of feeding.

Collections of fish were obtained periodically from Pine, Gun and Big Silver Lakes for stomach analyses. Method of capture varied but gear consisted primarily of gill nets augmented by hook and line fishing. On occasion stomachs were obtained from catches made by other anglers.

Mr. Paul Johnson of Gun Lake kindly collected a number of stomachs of bluegills and yellow perch from that lake during the winter fishing season.

The digestive tract and gills were removed from each specimen soon after capture, labeled, and the viscera preserved in 10 percent formalin. Later, in the laboratory, organisms were removed from stomachs, identified, counted, and their volume measured by water displacement.

Many hundreds of intestines were examined in order to compare the incidence of *limbata* nymphs in the lower intestinal tract with the occurrence of these insects in the stomachs of the same fish. In most cases remains of nymphs were present in each and no significant statistical differences were evident in frequency of occurrence of nymphs in fishes when calculations were based on occurrence in the stomach alone, intestine alone, or in either stomach or intestine.

Uncertainty as to the source of some *limbata* nymphs arose during examination of stomachs secured during the winter fishing season when these insects were being used for bait. In these cases all large individuals (bait size) which showed evidence of having been impaled on a hook or torn apart were considered to have been bait and were discarded. Large undamaged specimens were considered to have been eaten as part of the natural food. In most instances where the origin of a large nymph was questionable, the presence of small specimens offered conclusive evidence that the fish had been feeding on nymphs obtained by its own foraging activities. The presence of an occasional *Sialis* larva in some questionable cases also indicated a natural acquisition of nymphs.

No significant dissimilarity was noticed in food habits of fish of different size in any species except largemouth bass. Small bass (6–10 inches) frequently consumed *limbata* nymphs and other insects but larger ones contained crayfish and fish exclusively.

Stomach contents of various species of bullheads encountered in the lakes were similar and for convenience have been combined in the tabulations. All bullheads were captured in gill nets and because of their habit of regurgitating the stomach contents when trapped, only 57 of the 129 specimens contained food at the time of examination. For this reason stomach analysis is considered to be less reliable in reflecting their food habits than that of other fishes.

Studies of food and feeding habits have shown that in many localities nymphs of *Hexagenia* are an important item in the diet of many species of fish. Adams and Hankinson, 1928; Clemens, 1928; Clemens and Bigelow, 1922; Clemens, Dymond, Bigelow, *et al,* 1923; Clemens, Dymond and Bigelow, 1924; Harkness, 1923; Deevy and Bishop, 1941; Forbes, 1888a, 1888b; Fuller and Cooper, 1946; Needham, 1920; Needham and Betten, 1901; Neave, 1932; Ricker, 1930; Wickliff, 1920; and many other authors have reported the occurrence of *Hexagenia* nymphs and winged stages in stomachs of fishes. That these insects are consumed by fish in both lakes and streams in Michigan is indicated by fish food studies conducted by Hankinson, Needham and Davis (1908), Leonard (1947), and Leonard and Leonard (1949).

The writer has found that *limbata* entered into the diet of many fishes in the waters investigated. A total of 1,569 stomachs, representing 14 species, was obtained from the three lakes and the contents examined. Of these, 370 (23.6 percent) were empty and 1,196 contained food.

A total of 383 fish stomachs obtained from Third Lake (Pine Lake) were examined and 103 (26.9 percent) proved to be empty. Table 30 shows that all fish species except northern pike consistently ate *limbata* nymphs (33.3–75.0 percent of stomachs contained them) but only 4 species—bluegill, pumpkinseed, black crappie, and yellow perch—consumed them in sufficient quantities to comprise more than 30 percent of the total volume of food. These nymphs ranked first in frequency of occurrence in yellow perch and first in percentage of total volume of food in both bluegill and black crappie; it is clear that they are an important item in the food of all fishes which ordinarily utilize bottom organisms. Nymphs of all sizes (5–32 mm.) were consumed by various fishes and often both small and large specimens were found in a single stomach. Usually half-grown nymphs predominated in fish stomachs but most of those eaten by black crappies were very small. Consumption of nymphs at various times of year varied with different species of fish. Bluegills and pumpkinseeds consumed greater numbers during the winter months. Rock bass and largemouth bass (7–12 inches in length) contained more nymphs during spring and early summer, and black crappies consumed them at all seasons but appeared to utilize them most heavily in late summer. Yellow perch consumed nymphs at all seasons but ate them more frequently and in greater number during winter months. The winged stages occurred in stomachs only during early summer at the peak of the emergence season, and only in bluegills and rock bass—probably not a true indication of the predation of fishes generally on the winged stages during emergence and ovipositing flights. At such times crappies, largemouth bass, pumpkinseeds and yellow perch have been seen on the shoals apparently feeding upon adults on the surface. Seasonal occurrence of *limbata* in stomachs of bluegills, by far the most important fish from the angler's standpoint, is shown in Table 31. Nymphs were eaten more frequently and in greater numbers during the winter months than at any other time of year. A completely satisfactory explanation of this fact is lacking. However, it is possible that many nymphs, dislodged during dredging by bait collectors, were eaten to give the high figures found in that season. Spring and early summer were also periods during which many nymphs were consumed, while few appeared in stomachs secured in late summer and fall. As indicated, winged stages are consumed during the short period they are available and often comprise a considerable part of the food during that period. On June 5 and July 2, 1947, imagoes and subimagoes comprised 22.2 and 60.0 percent of the total volume of the stomach contents, respectively, and on June 2, 1948, the winged stages made up 36.0 percent of the total volume of food consumed. Importance of *limbata* in the diet fluctuates widely during the course of a year, but considered on an annual basis, it seems quite certain that these insects are a major item in the diet of bluegills in Pine Lake.

Of the 652 stomachs obtained from Gun Lake, representing 14 species of fish, 108 (16.6 percent) were empty. Examination of the stomach contents (Table 32) showed that while *limbata* nymphs occurred in more than 44.4 percent of the stomachs of 8 species of fish, only 4—bluegill, black crappie, warmouth and yellow perch—consumed them in sufficient quantities to

Table 30. Occurrence of limbata **in stomachs of various species of fish containing food, collected in Pine Lake from January, 1947, to August, 1948**

Species	Number of stomachs	Number of nymphs in stomachs containing nymphs		Percentage of stomachs containing:				Percentage of food volume composed of:			
		Avg.	Max.	Nymphs of *limbata*	Winged *limbata*	Nymphs or winged *limbata*	Other foods	Nymphs of *limbata*	Winged *limbata*	Nymphs or winged *limbata*	Other foods
Bluegill	177	4.1	28	40.7	6.2	46.3	97	50.5	5.3	55.8	44
Pumpkinseed	14	2.5	5	42.8	0.0	42.8	100	31.5	0.0	31.5	68
Rock bass	15	1.0	1	33.3	6.7	40.0	100	6.3	0.1	6.4	94
Black crappie	8	53.1	284	75.0	0.0	75.0	100	56.7	0.0	56.7	43
Largemouth bass	8	1.0	1	37.5	0.0	37.5	100	11.0	0.0	11.0	89
Yellow perch	30	5.3	30	60.0	0.0	60.0	93	41.0	0.0	41.0	59
Bullhead	15	1.0	1	53.3	0.0	53.3	100	1.7	0.0	1.7	98
Northern pike	13	0.0	0	0.0	0.0	0.0	100	0.0	0.0	0.0	100

Table 31. Occurrence of limbata **in stomachs of bluegills collected in Pine Lake (analysis based on stomachs containing food)**

Date	Number of stomachs	Number of nymphs in stomachs containing nymphs		Percentage of stomachs containing *limbata:*			Percentage of total food volume composed of *limbata*
		Average	Maximum	Nymphs	Winged stages	Nymphs or winged stages	
January, 1947	14	4.2	12	85.7	0.0	85.7	81.7
May, 1947	9	2.0	3	33.3	0.0	33.3	36.5
June, 1947	8	3.0	6	50.0	25.0	62.5	77.6
July, 1947	20	3.2	4	20.0	30.0	50.0	81.5
August, 1947	23	3.4	5	21.7	0.0	21.7	2.0
September, 1947	14	9.0	9	7.1	0.0	7.1	6.0
February, 1948	35	5.4	28	85.8	0.0	85.8	84.1
May, 1948	13	1.5	2	30.7	0.0	30.7	18.3
June, 1948	10	4.3	10	30.0	30.0	60.0	81.5
July, 1948	20	2.0	3	15.0	0.0	15.0	35.0
August, 1948	11	1.7	2	27.3	0.0	27.3	5.8
Total	177	4.1	28	40.7	6.2	46.3	55.8

Table 32. Occurrence of limbata **in stomachs of various species of fish containing food, collected in Gun Lake from January, 1947, to July, 1948**

Species	Number of stomachs	Number of nymphs in stomachs containing nymphs		Percentage of stomachs containing:				Percentage of food volume composed of:			
		Avg.	Max.	Nymphs of *limbata*	Winged *limbata*	Nymphs or winged *limbata*	Other foods	Nymphs of *limbata*	Winged *limbata*	Nymphs or winged *limbata*	Other foods
Bluegill	181	2.9	28	54.1	3.3	57.0	88	46.0	9.2	55.2	45
Pumpkinseed	10	0.0	0	0.0	0.0	0.0	100	0.0	0.0	0.0	100
Rock bass	63	5.2	31	44.4	9.5	47.6	87	10.1	3.4	13.5	86
Black crappie	27	12.0	56	51.8	22.2	62.9	92	31.0	19.1	50.1	50
Largemouth bass	27	1.0	1	7.4	0.0	7.4	100	0.2	0.0	0.2	100
Smallmouth bass	2	0.0	0	0.0	0.0	0.0	100	0.0	0.0	0.0	100
Warmouth	28	4.3	16	71.0	7.2	75.0	89	19.6	0.2	19.8	80
Yellow perch	157	3.3	29	49.0	0.0	49.0	81	19.2	0.0	19.2	81
Bullhead	35	4.5	18	57.1	0.0	57.1	97	14.2	0.0	14.2	86
Northern pike	7	0.0	0	0.0	0.0	0.0	100	0.0	0.0	0.0	100
Lake chubsucker	2	0.0	0	0.0	0.0	0.0	100	0.0	0.0	0.0	100
White sucker	2	6.0	6	50.0	0.0	50.0	100	3.2	0.0	3.2	97
Longnose gar	2	0.0	0	0.0	0.0	0.0	100	0.0	0.0	0.0	100
Carp	1	7.0	7	100.0	0.0	100.0	100	1.0	0.0	1.0	99

comprise more than 15 percent of the total volume of food eaten. These insects were of minor importance in terms of volume of food in all other fishes examined. Nymphs ranked first in frequency of occurrence in the bluegill, warmouth bass, yellow perch and bullhead. The comparatively small volumetric percentage of *limbata* in stomachs of many fishes eating them was due to the preponderance of crayfish in the diet. Those fishes eating large numbers of these crustaceans (the dominant item in the diet volumetrically) were rock bass, large- and smallmouth bass, warmouth bass, yellow perch and bullheads. The few suckers and carp obtained had eaten burrowing nymphs and it may be assumed from their bottom feeding habits that they habitually feed upon these insects. This assumption is supported by the fact that one sucker contained 6 *limbata* nymphs, 57 *Ephemera simulans* nymphs and 6 *Sialis* larvae, all of which are burrowing insects. Pumpkinseeds, known to consume burrowing mayfly nymphs in other waters, here had fed almost exclusively upon mollusks. Seasonal differences in the consumption of nymphs, similar to those observed in Pine Lake, were evident in Gun Lake. On the whole, bluegills and yellow perch consumed more of them in mid-winter than at any other time of year although both species utilized them extensively in late spring and early summer. The incidence of nymphs in the stomachs of these species in January and February, however, was not as high as that shown for Pine Lake. Since other species of fish were captured only during the period of open water, it is not known to what extent they fed on these burrowers during the winter. Imagoes and subimagoes were eaten by bluegills, rock bass, black crappie and warmouth bass during the emergence season. It is quite likely that many other fishes also take advantage of this food source when the winged stages are on the water. Evidence shows that many fishes captured nymphs which were mature or nearly so during the early part of the summer, presumably as they left the burrows to transform.

H. limbata nymphs occurred more frequently in the stomachs of bluegills (range in length 4–10 in., average 6.9 in.) and comprised a greater percentage of the volume of food eaten than any other group of organisms. They occurred exclusively in 10.5 percent of the stomachs. Seasonal fluctuations in the consumption of nymphs is shown in Table 33. It is clear that *limbata* is a very important food source for bluegills in Gun Lake during all seasons of the year. It is less important in late summer when few large nymphs are present in the lake.

A series of 157 perch (4.5–12.3 inches in length, average 9.2 inches) containing food was obtained for stomach analysis. Seasonal consumption of *limbata* nymphs is shown in Table 34. Neither imagoes nor subimagoes were found in perch stomachs. Nymphs were eaten more frequently than any other dietary component but ranked third in percentage of total food volume. Small crayfish proved to be the most important food organism. It is of interest that 19 percent of the stomachs contained *limbata* nymphs exclusively and that 28 percent contained crayfish only.

A total of 534 fish from Big Silver Lake was available for stomach analysis, of which 159 (29.7 percent) contained no food. This high percentage reflects the unusually large number of bluegills captured during winter which contained no food. In January and February, 1947, 61 of 86 stomachs and 17 of 56 stomachs, respectively, were empty. In 1948

Table 33. Occurrence of *limbata* in stomachs of bluegills collected in Gun Lake (analysis based on stomachs containing food)

Date	Number of stomachs	Number of nymphs in stomachs containing nymphs		Percentage of stomachs containing *limbata*:			Percentage of total food volume composed of *limbata*
		Average	Maximum	Nymphs	Winged stages	Nymphs or winged stages	
January, 1947	19	1.8	4	57.8	0.0	57.8	89.0
February, 1947	37	2.5	14	51.3	0.0	51.3	26.0
May, 1947	7	1.6	3	71.4	0.0	71.4	29.7
June, 1947	16	1.0	1	18.7	0.0	18.7	17.0
July, 1947	9	3.8	14	66.7	33.1	88.9	83.2
August, 1947	13	1.4	2	38.5	7.7	46.1	18.8
September, 1947	8	1.0	1	12.5	0.0	12.5	2.1
February, 1948	25	2.8	9	88.0	0.0	88.0	72.7
April, 1948	8	2.7	7	87.5	0.0	87.5	49.4
May, 1948	11	10.2	28	26.3	0.0	26.3	74.0
June, 1948	15	1.8	18	66.7	0.0	66.7	67.6
July, 1948	13	1.8	3	38.5	15.4	53.8	43.9
Total	181	2.9	28	54.1	3.3	57.0	55.2

Table 34. Occurrence of limbata **in stomachs of yellow perch collected in Gun Lake (analysis based on stomachs containing food)**

Date	Number of stomachs	Number of nymphs in stomachs containing nymphs		Percentage of stomachs containing *limbata:*			Percentage of total food volume composed of *limbata*
		Average	Maximum	Nymphs	Winged stages	Nymphs or winged stages	
January, 1947	4	1.0	1	25.0	0.0	25.0	2.1
February, 1947	30	2.9	7	56.0	0.0	56.6	7.6
May, 1947	12	7.8	29	83.3	0.0	83.3	62.6
June, 1947	9	1.7	3	66.7	0.0	66.7	17.5
July, 1947	8	3.8	10	75.0	0.0	75.0	50.5
August, 1947	10	0.0	0	0.0	0.0	0.0	0.0
September, 1947	21	0.0	0	0.0	0.0	0.0	0.0
February, 1948	26	2.2	7	80.7	0.0	80.7	28.4
April, 1948	8	2.0	3	50.0	0.0	50.0	13.2
May, 1948	10	2.3	5	60.0	0.0	60.0	19.7
June, 1948	11	2.0	4	45.4	0.0	45.4	14.2
July, 1948	8	1.0	1	12.5	0.0	12.5	3.6
Total	157	3.3	29	49.0	0.0	49.0	19.2

a similar situation existed; 14 of 26 stomachs obtained in January and 23 of 40 stomachs secured in February were empty. During the summer months almost all fish contained food. *H. limbata* nymphs were found in the stomachs of 8 of 9 species of fish caught in sufficient numbers to warrant examination (Table 35). Data show that nymphs are an integral part of the diet of these species but in only 3 did the frequency of occurrence exceed 35 percent. On the other hand, these nymphs comprised less than 15 percent of the total volume of stomach contents of all species except bluegill, rock bass and warmouth. In no instance did *limbata* nymphs rank first in frequency of occurrence in the stomachs and in only one species, the bluegill, did they comprise a greater percentage of the total food volume than any other category of food organism. Comparison of the results of stomach analyses of fish from Big Silver, Pine, and Gun Lakes, show that *limbata* nymphs are of considerably less importance in the diet of fishes in Big Silver Lake than in the other two. By way of comparison, nymphs occurred more frequently in the stomachs of bluegills than any other component of the diet in Pine and Gun Lakes, but ranked third in Big Silver Lake. Also, on a volumetric basis, these insects made up a greater percentage of the total food of bluegills in all three lakes than did any other constituent of the diet. Seasonal fluctuations in feeding on *limbata* nymphs was noticeable in bluegills but could not be detected in other species of fish, for most of them were captured only during the period of open water. Winged *limbata* were found only in stomachs of bluegills and small largemouth bass; however, observations during ovipositing flights indicated that most of the fish listed in Table 35 were present on the shoals and fed upon spent females which landed on the water surface. Samples of bluegills, the most important fish in the lake from the angler's standpoint, were obtained almost every month during a 2-year period. Most of these fish were captured by angling. In all, 332 stomachs were examined, of which 120 (36.1 percent) proved to be empty. The occurrence of *limbata* in bluegill stomachs is shown in Table 36. It is noteworthy that these nymphs were eaten much more frequently and comprised a greater percentage of the food volume during winter months than at any other time of year. Considering the fact that about half the fish were captured during the winter and half during the period of open water, the results of stomach analyses are not unduly influenced in favor of any season. The absence of winged *limbata* from stomachs obtained in early summer, 1948, is indicative of selective sampling methods rather than of no feeding on the winged flies, for bluegills were seen to consume spent females each time an ovipositing flight was observed. It is significant that *limbata* nymphs occurred in only 26 percent of the stomachs but comprised 38.5 percent of the total food volume. The latter figure is about 12 and 8 percent lower than that for bluegills in Pine and Gun Lakes, respectively.

A summary of the position occupied by *limbata* nymphs in the diet of a number of fish has been presented. In order to determine the extent of predation of these fish on the nymphs, it was necessary to compare their position in the macroscopic bottom fauna with that in the invertebrate food of various fishes. This relationship, termed the "forage ratio" (Ball, 1948; Hess and Swartz, 1940), was determined by eliminating vertebrates,

Table 35. Occurrence of limbata **in stomachs of various species of fish containing food, collected in Big Silver Lake from October, 1946, to September, 1948**

Species	Number of stomachs	Number of nymphs in stomachs containing nymphs		Percentage of stomachs containing:				Percentage of food volume composed of:			
		Avg.	Max.	Nymphs of *limbata*	Winged *limbata*	Nymphs or winged *limbata*	Other foods	Nymphs of *limbata*	Winged *limbata*	Nymphs or winged *limbata*	Other foods
Bluegill	212	2.0	7	26.0	0.8	26.0	94	38.5	2.2	40.7	59
Pumpkinseed	34	2.7	8	35.2	0.0	35.2	100	11.6	0.0	11.6	88
Rock bass	24	6.0	16	25.0	0.0	25.0	92	23.3	0.0	23.3	77
Black crappie	15	2.7	8	53.3	0.0	53.3	100	9.7	0.0	9.7	90
Largemouth bass	20	4.7	7	15.0	20.0	20.0	100	2.7	2.9	5.6	94
Warmouth	11	2.5	7	36.4	0.0	36.4	100	18.0	0.0	18.0	82
Yellow perch	31	1.4	5	19.4	0.0	19.4	100	11.2	0.0	11.2	89
Bullhead	7	9.0	9	28.6	0.0	28.6	100	4.6	0.0	4.6	95
Northern pike	21	0.0	0	0.0	0.0	0.0	100	0.0	0.0	0.0	100

Table 36. Occurrence of limbata **in stomachs of bluegills collected in Big Silver Lake (analysis based on stomachs containing food)**

Date	Number of stomachs	Number of nymphs in stomachs containing nymphs		Percentage of stomachs containing *limbata:*			Percentage of total food volume composed of *limbata*
		Average	Maximum	Nymphs	Winged stages	Nymphs or winged stages	
October, 1946	13	1.0	1	7.7	0.0	7.7	8.9
January, 1947	25	1.7	7	40.0	0.0	40.0	61.1
February, 1947	39	2.3	4	61.5	0.0	61.5	57.1
March, 1947	9	1.8	3	55.5	0.0	55.5	56.2
May, 1947	10	1.0	1	20.0	0.0	20.0	33.3
June, 1947	17	1.0	2	28.5	28.5	42.8	33.5
July, 1947	15	0.0	0	0.0	0.0	0.0	0.0
August, 1947	15	0.0	0	0.0	0.0	0.0	0.0
September, 1947	17	0.0	0	0.0	0.0	0.0	0.0
October, 1947	14	0.0	0	0.0	0.0	0.0	0.0
January, 1948	12	0.0	0	0.0	0.0	0.0	0.0
February, 1948	17	1.4	5	35.3	0.0	35.3	58.4
March, 1948	10	1.0	1	10.0	0.0	10.0	23.7
May, 1948	13	1.2	3	23.1	0.0	23.1	22.4
June, 1948	18	3.0	5	33.1	0.0	33.1	37.0
July, 1948	20	0.0	0	0.0	0.0	0.0	0.0
August, 1948	23	1.3	3	30.4	0.0	30.4	10.0
September, 1948	7	0.0	0	0.0	0.0	0.0	0.0
Total	212	1.9	7	26.0	0.8	26.0	40.7

entomostraca, terrestrial insects, and plants from the food volume and recalculating the data on a basis of those fish foods which were obtained by quantitative bottom sampling. Percentage values for the volume of *limbata* nymphs in bottom samples and in fish food, and the forage ratios for certain fishes collected from Pine, Gun and Big Silver Lakes, are presented in Table 37, which shows that bluegills in all three lakes consumed these insects in direct proportion to their volumetric abundance in the bottom fauna. In Pine and Gun Lakes nymphs occupied the same volumetric position in the diet of black crappies as in the bottom fauna of the lakes. In Pine Lake alone did the forage ratio of nymphs eaten by yellow perch reach or exceed 1.0. The volumetric percentage of nymphs in the food of all other fish was much less than that determined for these insects in the macroscopic bottom fauna.

Table 37. Volume of limbata **nymphs in bottom samples and in fish stomachs, and computed forage ratios**

Locality	Species	Percentage in bottom samples	Percentage in stomachs	Forage ratio
Pine Lake	Bluegill	59	64	1.1
	Pumpkinseed	59	32	0.5
	Rock bass	59	25	0.4
	Black crappie	59	61	1.0
	Yellow perch	59	75	1.3
	Bullhead	59	5	0.1
Gun Lake	Bluegill	54	55	1.0
	Rock bass	54	11	0.2
	Warmouth	54	23	0.4
	Black crappie	54	50	0.9
	Yellow perch	54	24	0.4
	Bullhead	54	15	0.3
Big Silver Lake	Bluegill	42	45	1.1
	Pumpkinseed	42	12	0.3
	Rock bass	42	32	0.8
	Warmouth	42	18	0.4
	Black crappie	42	20	0.5
	Yellow perch	42	18	0.4
	Bullhead	42	19	0.4

PRACTICAL CONSIDERATIONS

The practical aspects of this study are many and deserve special mention. Investigations on the biology of *Hexagenia limbata* in Pine, Gun, and Big Silver lakes, have revealed the following facts which must be considered in evaluating the importance of these insects. In addition, these facts provide a basis for devising regulations designed to protect the nymphal populations if such action should be considered necessary.

1. Length of life cycle in these lakes, as established by the examination and measurement of more than 13,000 nymphs and comparison of growth rate in the natural environment with that under different experimental conditions, is one year. Therefore, those nymphs present in winter hatched from eggs deposited the preceding summer.
2. In these lakes nymphs are present in significant numbers only in portions of the shoals (water less than 10 ft. in depth) having a soft marl-mud bottom suitable for burrowing and which supports sparse growths of vegetation. Consequently the amount of habitat is of great importance in determining the size of a nymphal population in any lake.
3. Density of the nymphal population varies greatly during the course of the year. It is greatest in late summer and least during the following emergence season.
4. Nymphs comprised 42–59 percent by volume of the macroscopic bottom fauna in the mud-bottomed shoals of the three lakes studied.
5. Average number of nymphs per square foot in sampling areas of the lakes investigated varied from 19 to 24.5, with a volume of 0.94 cc. (90 lbs. per acre) and 1.76 cc. (169 lbs. per acre), respectively.
6. Reproductive potential of adults is high. The total number of eggs produced by individual females varied from 2,260 to 7,684; an imago of average size produces about 4,000 eggs. Fertility of naturally inseminated eggs averaged 96.3 percent.
7. Examination of 1,569 fish stomachs revealed that nymphs are consumed by all species of fish which feed on the bottom fauna, and are particularly important in the diet of bluegills. Nymphs comprised 38.5–50.5 percent of the total volume of stomach contents of bluegills in the lakes studied. Nymphs were consumed in proportion to their volumetric abundance in the macroscopic bottom fauna by bluegills in all three lakes, black crappies and yellow perch in Pine Lake, black crappies in Gun Lake, and rock bass in Big Silver Lake. They were consumed to a lesser extent by other fishes.
8. The winged stages are an important item in the diet of fishes in lakes during the period of emergence and oviposition.

The above facts clearly demonstrate that *limbata* is able to maintain its nymphal population at a high level in each lake studied and is of considerable importance in the economy of these waters. Certainly these insects are of direct importance to man in that they furnish food for game and pan fishes highly prized by anglers.

The economic value of these insects as bait is considerable. Their use in this way not only furnishes monetary income to the bait collector and dealer but also facilitates harvesting the fish crop in Michigan lakes. Information involving various aspects of the collection of nymphs for fish bait in Pine and Big Silver Lakes is summarized in the following paragraphs.

1. Bait collectors exploit a nymphal population composed of one age group; therefore, the percentage of the population which is of bait size (body length 23 mm. or longer) during the winter months is of great importance. The number reaching large size is dependent upon the rate of growth and the length of growing season in the preceding summer and fall and varies from year to year. In the waters studied, less than one-half of the nymphal population (usually between 11.7 and 38.0 percent; maximum 47.4 percent) was composed of bait-size nymphs in winter.

2. Data obtained from thoroughly dredged areas indicate that less than 60 percent of the bait-size nymphs are removed by bait collectors. Since most small nymphs and about 40 percent of the larger ones survive the dredging operations, a serious reduction of the nymphal population does not occur as the result of bait collectors' activities.

3. Only large nymphs are collected for bait. Because of the size selection, those retained for bait are predominantly females (usually 70–82 percent); comparatively few males reach bait size in winter. Although commercial bait collecting is highly selective in removing large female nymphs, it should be emphasized that less than 30 percent of the total number of females in the nymphal populations were removed from the areas dredged. Thus more than 70 percent of the females remained in the disturbed areas after dredging operations ceased. Since a small percentage of lake bottom containing nymphs is disturbed each winter, reduction in the number of females in such areas does not appear to be depleting the breeding stock sufficiently to cause an appreciable reduction in density of the nymphal populations of the lakes investigated.

4. It is estimated, on the basis of number and size of nymphs in quantitative bottom samples obtained in areas of Pine Lake before and after they had been thoroughly worked by bait collectors, that 5–8 bait-size nymphs were removed per square foot of bottom. Bait collectors state that at least 8–10 saleable nymphs must be secured in each scoopful of mud handled before dredging is profitable. Bait collectors, therefore, operate only in very productive areas, and leave relatively undisturbed those parts of the lake which have comparatively small populations of large nymphs.

5. Efficient dredging by bait collectors working through ice is limited to water depths ranging between about 4 and 8 feet. Effort involved in dredging in water both shallower and deeper than stated above is prohibitive and is an effective check which limits dredging to certain favorable areas and assures certain portions of the lake freedom from disturbance.

6. A small part of the lakes studied was disturbed by bait collectors in any winter. Only 5.2 and 11.1 percent of the productive bottom of the third basin of Pine Lake (91 acres) was dredged by bait collectors in the winters of 1946–47 and 1947–48, respectively. A very small portion of one bay in Big Silver Lake was dredged by bait gatherers. Commercial removal of nymphs has been prohibited in Gun Lake since 1945 but it is estimated that not more than about 4.5 percent of the bottom containing nymphs was dredged in any previous winter.

7. It is doubtful if the loss of potential fish food, represented by the number and volume of nymphs removed for bait, is of serious conse-

quence to the well-being of the fish population. Only a portion of these nymphs would have been eaten by fish if the lakes had not been disturbed and the bulk of the nymphs removed is undoubtedly a small percentage of the total available fish food supply in the lakes.

8. Comparison of the number of animals in quantitative bottom samples from disturbed and undisturbed areas indicates that dredging by bait collectors causes little damage to the macrascopic bottom fauna other than that suffered by the nymphal population of *limbata* due to the removal of a portion of it.

9. Aquatic vegetation is little disturbed by dredging since most of the bait collecting is concentrated in bottom areas which are rather barren of rooted plants. *Chara* and *Najas,* those plants most likely to be disturbed by dredging, are not destroyed if returned to the water and both are soon reestablished in disturbed areas.

10. No evidence was secured to show that sufficient fine silt was left in the water to cause prolonged turbidity. When dredging ceased, the water quickly cleared and fine material, upon settling to the bottom, rapidly packed down to form a firm layer which was not easily brought into suspension by water movements. Scoops used in dredging do not break up marl-mud fine enough for appreciable amounts of it to be suspended in the water.

11. Unsightly conditions which result when mud and debris are left on the ice after dredging has been completed are objectionable features of the practice of collecting nymphs for bait and although undesirable are inseparably a part of the dredging operations.

Data obtained thus far indicate that the present intensity of nymph removal from Pine Lake by bait collectors does not reduce the nymphal population, destroy other fish food organisms, or otherwise affect the lake adversely to an extent which would warrant prohibition of the practice. This conclusion does not rule out the possibility that intensified and continued dredging may in the future alter conditions existing in the lake and ultimately reduce the bottom fauna below the present level. Statements by bait collectors to the effect that certain lakes or parts of lakes which formerly furnished quantities of *Hexagenia* nymphs for the bait market are no longer producing them may have a biological and/or ecological basis in fact. It is possible that effects, undetected in this study, may eventually result in conditions which will reduce populations of *Hexagenia* nymphs far below the original level.

Any current or cumulative damage, and unsightly conditions resulting from the removal of nymphs, must be weighed against the value of these insects for bait for the winter fishermen. There are more than a million fishing licenses sold in Michigan each year, and while the number of anglers engaging in winter fishing is not known, certainly many thousands of sportsmen pursue this pastime. Most natural baits are difficult to obtain in winter and many fishermen depend upon these nymphs ("wigglers") for their bait supply. Natural baits are being supplemented to a limited extent by small spoons and wabblers of various kinds and by artificial flies ("ice flies"), but it is certain that these artificial lures, while useful and effective in the hands of skilled individuals, will not supplant live or natural bait for winter fishing.

Regulations prohibiting the removal of these insects from trout streams are founded upon well established facts and should be continued.

Whether regulations prohibiting their removal from lakes should be placed in effect is questionable in the light of the information obtained in this study. In the opinion of the writer, prohibition of nymph removal from Gun, Pine and Big Silver Lakes is not justified on the basis of information obtained thus far. It is undoubtedly true that in some waters with a limited amount of nymphal habitat, all of which is accessible to bait collectors, serious depletion of the nymphal population may result from intensive and continued dredging. This situation did not obtain in the lakes studied in this investigation.

Adoption of the following suggestions would minimize damage to the macroscopic bottom fauna, reduce the hazard created by open holes through the ice, and limit the concentration of bait collectors on the more productive lakes:

1. Scoops used to collect nymphs for commercial purposes should be equipped with screen no smaller than 8 meshes to the inch. Screen of this size will allow most bottom organisms to escape through the meshes and will reduce the number of small nymphs retained in the scoops. A more stringent requirement would be to limit the mesh size to 4 to the inch, thereby permitting the escape of most bottom organisms including some of the larger nymphs.
2. All debris remaining in the scoops should be immediately returned to the water once bait-size nymphs have been removed, to avoid loss by freezing of small nymphs, other organisms, and vegetation caught in the debris.
3. Bait collectors should at all times attempt to minimize the amount of mud which becomes scattered on the ice as a result of dredging operations.
4. All holes through the ice which are to be abandoned should be marked by placing in the holes small pieces of brush or other material which will sink after the ice breaks up. These markers should project at least 24 inches above the ice surface so they can be seen even though snow obliterates the hole. Poles, which will remain after the ice melts, should not be thrust into the lake bottom to mark the holes. Blocks of ice do not effectively mark the location of a hole when snow is present.
5. Nymphs should not be collected and used for bait except between December 1 and March 15 of any winter. Collection and use of these insects for bait during the summer fishing season is unnecessary since other live baits are available in quantities during that time of year, and constitutes an unnecessary drain on this bait resource, which should be reserved for use only during the winter.
6. Collection of nymphs should be permitted in Gun Lake, Barry and Allegan Counties, and in all other lakes in Michigan which contain warm-water fish populations. Bait collecting should be prohibited only in those waters in which appreciable damage, revealed by thorough investigation, is evident as a result of dredging operations.
7. It is not improbable that circumstances might arise in the future which would intensify commercialization of this bait resource and result in attempts to employ power-driven dredges, suction pumps, etc. to facilitate collection of *Hexagenia* nymphs. While no accurate prediction of effects resulting from use of such devices can be made at present, it is probable that the fauna and flora of lakes would be damaged seriously because of the magnitude of operation possible with mechanization of collecting equipment. Use of such devices should be discouraged.

SUMMARY

1. *Hexagenia limbata,* one of the largest burrowing mayflies, is widely distributed in Michigan and is often abundant in lakes, particularly those with a soft marl bottom. Large populations exist in the three southern Michigan lakes covered in this study.

2. The length of life cycle is normally one year in Pine, Gun and Big Silver Lakes. These conclusions are based on size-frequency data obtained by measuring the length of more than 13,000 nymphs from the natural populations and correlating the information with growth of known-age specimens under controlled conditions.

3. The time required for embryonic development, the growth rate of nymphs, and time of year in which emergence occurs, which together constitute the life cycle and determine its length, are greatly influenced by water temperatures. In the laboratory, under conditions of high temperature, individuals were reared from the egg to maturity in less than 6 months. Specimens reared in natural waters under conditions of low temperature required 2 years to mature.

4. The type of bottom is of great importance in determining the local distribution of nymphs in lakes. Nymphs are usually found in large numbers only in bottom composed of soft marl, mud or clay and are largely restricted to a substratum which is soft, yet firm enough to permit maintenance of a burrow. They do not ordinarily inhabit sand, gravel, rubble, peat or bottom which is flocculent.

5. Nymphs usually live in a U-shaped burrow, both ends of which are open to the mud surface. They maintain a flow of water through the tunnel by rhythmical waving of the gills. These insects are known to burrow to a depth of 5 inches but probably do not penetrate to a depth greater than 6 inches.

6. Nymphs are not able to withstand stagnation conditions in which the dissolved oxygen content of the water falls below about 1.0 ppm. Their distribution in lakes therefore is restricted to areas in which oxygen depletion and other attendant chemical changes do not occur either in summer or winter.

7. Food of nymphs consist of microscopic animal and plant fragments, and large quantities of mud.

8. Average number of nymphs per square foot of suitable bottom in the lakes studied ranged from 6.0, with a volume of 0.21 cc. (20 lbs. per acre) in the least productive part of Big Silver Lake, to 30.0 per square foot with a volume of 2.06 cc. (198 lbs. per acre) in the most productive part of Gun Lake.

9. During the period of investigation the average number of nymphs in Plot 1, Pine Lake (a heavily dredged area) was 22.3 compared to 24.7 in Plot 2, Pine Lake; 30.0 in Plot 1 and 19.1 in Plot 2 of Gun Lake; and 19.0 in Transect 5, the most productive part of Big Silver Lake. These figures show clearly that even though some nymphs were removed by bait collectors the remaining population was comparable to those found in undisturbed portions of Pine, Gun and Big Silver Lakes.

10. In areas in which they occurred, nymphs comprised 59, 54 and 42

percent by volume of the macroscopic bottom fauna in suitable bottom in Pine, Gun and Big Silver Lakes, respectively.

11. In determining density of a nymphal population, it is necessary to take into consideration the seasonal variation in number and volume per unit area during the entire year. Number of nymphs varied as much as 1,200 percent and volume of nymphs fluctuated as much as 2,300 percent.

12. Actual counts showed that female imagoes produced from 2,260 to 7,684 eggs and that an average size specimen produced about 4,000 eggs. An average of 96.3 percent of naturally fertilized eggs hatched when incubated under laboratory conditions.

13. Both the immature and winged stages of *limbata* served as food for many of the lake fishes. Nymphs were eaten by all species of fish which normally consume bottom organisms. Bluegills in all three lakes, yellow perch and black crappies in Pine Lake, black crappies in Gun Lake, and rock bass in Big Silver Lake consumed nymphs in proportion to their volumetric abundance in the macroscopic bottom fauna. Other fishes consumed them in a proportion less than their relative volumetric abundance in the lakes.

14. Large nymphs are collected and sold on the market by bait collectors during the winter months and provide an important source of live bait for winter angling. Because only large nymphs are suitable for bait, those collected by dealers are predominantly females. Comparatively few males reach a size suitable for bait during the winter months.

15. Less than one-half of the nymphal population is composed of bait-size nymphs (body length 23 mm. or longer) in winter. Percentage of bait-size nymphs in the various lakes usually ranged between 11.7 and 38.0 with a maximum of 47.4 percent in winter.

16. Data obtained in areas which had been thoroughly dredged by bait collectors indicated that only about 60 percent of the bait-size nymphs were captured. Therefore the reduction in number of the female nymphs due to wiggler digging is only about 30 percent of the original number present. Only 5.2 and 11.1 percent of the productive bottom of the third basin of Pine Lake was dredged by bait collectors in the winters of 1946–47 and 1947–48, respectively.

17. Efficient manual dredging is limited to water depths between about 4 and 8 feet. Effort involved in dredging in water both shallower and deeper than the range given above is prohibitive and is an effective check which limits dredging to certain suitable areas and assures other regions of freedom from disturbance.

18. Dredging apparently results in little damage to the macroscopic bottom fauna other than that suffered by the removal of a portion of the *limbata* nymphs. Few plants are disturbed by dredging since most of the bait collecting is concentrated in rather barren bottom. *Chara* and *Najas,* those plants most likely to be disturbed, are not destroyed if returned to the water and both soon reestablish themselves when dredging ceases.

19. No evidence was secured to show that enough fine silt was left in the water to cause prolonged turbidity. When dredging ceased, water rapidly cleared up and fine material settling to the bottom rapidly packed down to form a firm layer which was not easily brought into suspension by water movements. Scoops used in bait collecting operations apparently

do not break up the marl fine enough for appreciable amounts of it to remain suspended in the water.

20. Unsightly conditions resulting from mud and debris on the ice after dredging has been completed are one of the chief objections to the practice of collecting nymphs for bait. These conditions are inherent in the methods used in obtaining bait and are not easily corrected.

21. The present intensity of commercial nymph collection in Pine Lake does not appear to be seriously reducing the nymphal population or destroying other fish food organisms and plants on a large scale; neither is it adversely affecting the physical features of the lake to an extent which would warrant prohibition of the practice.

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Literature Cited

Adams, Charles C., and T. L. Hankinson
1928. The ecology and economics of Oneida Lake Fish. Roosevelt Wild Annals, 1: 239–548.

Adamstone, F. B.
1923. The bottom fauna of Lake Nipigon. Univ. Toronto Studies, Biol. 24. Publ. Ont. Fish. Res. Lab., 19: 43–70.
1924. The distribution and economic importance of the bottom fauna of Lake Nipigon with an appendix on the bottom fauna of Lake Ontario. Univ. Toronto Studies, Biol. 25. Publ. Ont. Fish. Res. Lab., 24: 33–100.

Adamstone, F. B., and W. J. K. Harkness
1923. The bottom organisms of Lake Nipigon. Univ. Toronto Studies, Biol. 22. Publ. Ont. Fish. Res. Lab., 15: 121–170.

American Public Health Association
1936. Standard methods for the examination of water and sewage, Eighth Edition. Public Health Assoc., New York, 309 pp.

Ball, Robert C.
1948. Relationship between available fish food, feeding habits of fish and total fish production in a Michigan lake. Techn. Bull. 206, Michigan State College Agr. Exp. Sta., pp. 1–59.

Chandler, David C.
1940. Limnological studies of western Lake Erie. I. Plankton and certain physical-chemical data of the Bass Islands region, from September, 1938 to November, 1939. Ohio Jour. Sci., 40: 291–336.

1942. Limnological studies of western Lake Erie. III. Phytoplankton and physical-chemical data from November, 1939 to November, 1940. Ohio Jour. Sci., 42: 24–44.

1944. Limnological studies of western Lake Erie. IV. Relation of limnological and climatic factors to the phytoplankton of 1941. Trans. Amer. Micro. Soc., 63: 203–236.

CHANDLER, DAVID C., and OWEN B. WEEKS
1945. Limnological studies of western Lake Erie. V. Relation of limnological and meteorological conditions to the production of phytoplankton in 1942. Ecol. Monog., 15: 435–457.

CLEMENS, W. A.
1913. New species and life histories of Ephemeridae or mayflies. Canad. Ent., 45: 246–262.

1928. Food of trout from the streams of Oneida County, New York State. Trans. Am. Fish. Soc., 58: 183–197.

CLEMENS, W. A., and N. K. BIGELOW
1922. The food of ciscoes *(Leucichthys)* in Lake Erie. Univ. Toronto Studies, Biol. 20. Publ. Ont. Fish. Res. Lab., 3: 39–53.

CLEMENS, W. A., J. R. DYMOND, and N. K. BIGELOW
1924. Food studies of Lake Nipigon fishes. Univ. Toronto Studies, Biol. 25. Publ. Ont. Fish. Res. Lab., 25: 103–165.

CLEMENS, W. A., J. R. DYMOND, N. K. BIGELOW, F. B. ADAMSTONE, and W. J. K. HARKNESS
1923. The food of Lake Nipigon fishes. Univ. Toronto Studies, No. 22. Publ. Ont. Fish. Res. Lab., 16: 171–188.

CRONK, MYRA W.
1932. The bottom fauna of Shakespeare Island Lake, Ontario. Univ. Toronto Studies, Biol. 36. Publ. Ont. Fish. Res. Lab., 43: 31–65.

DEEVEY, EDWARD S., JR., and JAMES S. BISHOP
1941. Limnology. Section II. A fisheries survey of important Connecticut lakes. Bull. 63, Conn. Geol. and Nat. Hist. Surv., pp. 69–121.

EATON, A. E.
1871. A monograph on the Ephemeridae. Trans. Entom. Soc. London, 1: 1–164.

1883. A revisional monograph of recent Ephemeridae, Part 1. Trans. Linn. Soc. London, Zoology, 2nd Ser., 3: 1–77.

EGGLETON, FRANK E.
1935. A comparative study of the benthic fauna of four northern Michigan lakes. Pap. Mich. Acad. Sci., Arts and Lett., 1934, 20: 609–644.

FORBES, S. A.
1888a. On the food relations of fresh-water fishes; a summary and discussion. Bull. Ill. State Lab. Nat. Hist., 2: 475–538.

1888b. Studies of the food of fresh-water fishes. Bull. Ill. State Lab. Nat. Hist., 2: 433–473.

FULLER, JOHN L., and GERALD P. COOPER
1946. A biological survey of the lakes and ponds of Mount Desert Island and the Union and Lower Penobscot River drainage systems. Fish. Surv. Rept. No. 7, Maine Dept. Inland Fish. and Game. 221 pp.

HANKINSON, T. L., J. G. NEEDHAM, and C. A. DAVIS
1908. A biological survey of Walnut Lake, Michigan. Report of Geological Survey of Michigan for 1907, pp. 230–263.

HARKNESS, W. J. K.
1923. The rate of growth and the food of the lake Sturgeon (*Acipenser rubicundus* Le Sueur). Univ. Toronto Studies, Biol. 24. Publ. Ont. Fish. Res. Lab., 18: 13–42.

HESS, A. D., and SWARTZ, ALBERT
1940. The forage ratio and its use in determining the food grade of streams. Trans. Fifth Wildlife Conf., pp. 162–164.

HUNT, BURTON P.
1951. Reproduction of the burrowing mayfly, *Hexagenia limbata* (Serville), in Michigan. The Florida Ent., 34: 59–70.

IDE, F. P.
1930. Contribution to the biology of Ontario mayflies with descriptions of new species. Canad. Ent., 62: 204–213.
1935a. Post embryological development of Ephemeroptera (mayflies). External characters only. Canad. Jour. Res., 12: 433–478.
1935b. The effect of temperature on the distribution of the mayfly fauna of a stream. Univ. Toronto Studies, Biol. 39. Publ. Ont. Fish. Res. Lab., 50: 3–76.

LEONARD, JUSTIN W.
1947. Differences in the occurrence of nymphs of two species of burrowing mayflies in fish stomachs. Ann. Ent. Soc. Amer., 40: 688–691.

LEONARD, J. W., and F. A. LEONARD
1949. An analysis of the feeding habits of rainbow trout and lake trout in Birch Lake, Cass County, Michigan. Trans. Am. Fish. Soc., 1946, 76: 301–314.

LYMAN, F. EARLE
1940. Limnological investigation of the Ephemeroptera in Douglas Lake, Cheboygan County, Michigan, with special reference to the distribution of immature stages. Unpublished thesis, Univ. of Mich. Library.
1943a. A pre-impoundment bottom-fauna study of Watts Bar Reservoir area (Tennessee). Trans. Am. Fish. Soc., 1942, 72: 52–62.
1943b. Swimming and burrowing activities of mayfly nymphs of the genus Hexagenia. Ann. Ent. Soc. Amer., 36: 250–256.
1944. Effect of temperature on the emergence of mayfly imagoes from the subimago stage. Ent. News, 55: 113–115.

McDUNNOUGH, J.
1924. New Canadian Ephemeridae with notes, II. Canad. Ent., 56: 90–98.
1927. Notes on the species of the genus *Hexagenia* with description of a new species (Ephemeroptera). Canad. Ent., 59: 116–120.

MILLER, RICHARD B.
1938. A preliminary investigation of the bottom fauna of five Algonquin Park lakes. Unpublished thesis, Univ. of Toronto Library.

MOFFETT, JAMES W., and BURTON P. HUNT
1945. Winter feeding habits of bluegills, *Lepomis macrochirus* Rafinesque, and yellow perch, *Perca flavescens* (Mitchill), in Cedar Lake, Washtenaw County, Michigan. Trans. Am. Fish. Soc., 1943, 73: 231–242.

MORGAN, ANN H.
1911. Mayflies of Fall Creek. Ann. Ent. Soc. Amer., 4: 93–119.
1913. A contribution to the biology of mayflies. Ann. Ent. Soc. Amer., 6: 371–413.

MORGAN, ANN H., and MARGARET C. GRIERSON
1932. The functions of the gills in burrowing mayflies (*Hexagenia recurvata*). Physiol. Zool., 5 : 230-245.

MURPHY, HELEN E.
1922. Notes of the biology of some of our North American species of mayflies. Bull. Lloyd Library 22, Ent. Ser. 2: 1–39.

NEAVE, FERRIS
1932. A study of the mayflies (*Hexagenia*) of Lake Winnipeg. Contrib. Canad. Biol. Fish., N. S., 7: 179–201.
1934. A contribution to the aquatic insect fauna of Lake Winnipeg. Inter. Revue der gesamten Hydrobiologie und Hydrographie, 31: 157–170.

NEEDHAM, JAMES G.
1920. Burrowing mayflies of our larger lakes and streams. Bull. U. S. Bur. Fish., 36: 267–292.
1927. The life history and habits of a mayfly from Utah. Canad. Ent., 59: 133–136.

NEEDHAM, JAMES G., and C. B. BETTEN
1901. Aquatic insects in the Adirondacks. Bull. N. Y. State Museum, 47: 383–612.

NEEDHAM, JAMES G., JAY R. TRAVER, and YIN-CHI HSU
1935. The biology of mayflies. Comstock Pub. Co., N. Y., 759 pp.

RAWSON, DONALD S.
1930. The bottom fauna of Lake Simcoe and its role in the ecology of the lake. Univ. Toronto Studies, Biol. 34. Publ. Ont. Fish. Res. Lab., 40: 1–183.

RICKER, WILLIAM E.
1930. Feeding habits of speckled trout in Ontario waters. Trans. Am. Fish. Soc., 60: 1–9.
1934. An ecological classification of certain Ontario streams. Univ. Toronto Studies, Biol. 37, Publ. Ont. Fish. Res. Lab., 49: 1–114.

SCOTT, WILL, and DAVID F. OPDYKE
1941. The emergence of insects from Winona Lake. Inv. Indiana Lakes and Streams, 2: 3–14.

SPIETH, HERMAN T.
1938. A method of rearing Hexagenia nymphs (Ephemerida). Ent. News, 49: 29–32.
1940. Studies on the biology of the Ephemeroptera. II. The nuptial flight. Jour. N. Y. Ent. Soc., 48: 379–390.
1941 Taxonomic studies on the Ephemeroptera. II. The genus *Hexagenia*. Amer. Midl. Nat., 26: 233–280.

SPRULES, WM. M.
1947. An ecological investigation of stream insects in Algonquin Park, Ontario. Univ. Toronto Studies, Biol. 56. Publ. Ont. Fish. Res. Lab., 69: 1–81.

TRAVER, J. R.
1932. Mayflies of North Carolina. Jour. Elisha Mitchell Sci. Soc., 47 : 85–162.

ULMER, GEORGE
1921. Über einige Ephemeropteren-Typen älterer Autoren. Arch. f. Naturg. Abt. A., 87: 229–267.

WELCH, PAUL S.
1927. Limnological investigations on northern Michigan lakes. I. Physical-chemical studies on Douglas Lake. Pap. Mich. Acad. Sci., Arts and Lett., 8: 421–451.

WELCH, PAUL S., and FRANK E. EGGLETON
1932. Limnological investigations on northern Michigan lakes. II. A further study of depression individuality in Douglas Lake. Pap. Mich. Acad. Sci., Arts and Lett., 1931, 15: 491–508.
1935. Additional data on submerged depression individuality in Douglas Lake, Michigan. Pap. Mich. Acad. Sci., Arts and Lett., 1934, 20: 737–750.

WICKLIFF, EDWARD L.
1920. Food of young small-mouth black bass in Lake Erie. Trans. Am. Fish. Soc., 50: 364–371.

WRIGHT, STILLMAN, and WILBUR M. TIDD
1933. Summary of limnological investigations in western Lake Erie in 1929 and 1930. Trans. Am. Fish. Soc., 63: 271–285.

APPENDIX

APPENDIX TABLE 1

Number and size of nymphs in last instar among 1-year-old nymphs, Plot 1, Pine Lake

Date	Males				Females			
	Number of 1-yr.-olds	Nymphs in last instar			Number of 1-yr.-olds	Nymphs in last instar		
		Number	Percent	Average length in mm.		Number	Percent	Average length in mm.
6/ 1/46	11	1	9.1	23.0	13	0	....	....
1/31/47	37	0	....	....	68	0	....	....
5/20/47	57	20	35.1	20.7	69	13	18.8	25.8
6/ 5/47	147	42	28.6	22.9	187	21	11.3	27.7
7/ 2/47	111	39	35.1	21.6	152	42	27.6	26.1
8/15/47*	14	3	21.4	19.0	28	1	3.6	23.0
9/12/47†	5	0	....	....	8	0	....	....
11/14/47‡	79	0	....	....	88	0	....	....
1/27/48	63	0	....	....	112	0	....	....
4/ 6/48	38	0	....	....	62	0	....	....
5/ 6/48	54	29	53.7	21.0	71	26	36.6	28.7
6/ 2/48	28	6	21.4	21.0	39	1	2.6	30.0
7/12/48*	5	1	20.0	22.0	3	1	33.3	25.0
8/25/48†	0	0	....	....	2	0	....	....
11/10/48‡	77	0	....	....	98	0	....	....
6/13/49	23	8	34.8	21.8	22	6	27.3	25.8

*Nymphs more than 12 mm. in length.
†Males more than 22 mm. and females more than 23 mm. in length.
‡All nymphs.

APPENDIX TABLE 2

Number and size of nymphs in last instar among 1-year-old nymphs, Plot 2, Pine Lake

Date	Males				Females			
	Number of 1-yr.-olds	Nymphs in last instar			Number of 1-yr.-olds	Nymphs in last instar		
		Number	Percent	Average length in mm.		Number	Percent	Average length in mm.
1/30/47	92	0	....	....	109	0	....	....
5/22/47	81	27	33.3	22.4	95	14	14.7	29.1
6/ 5/47	187	77	41.5	22.8	168	57	33.9	28.7
7/ 3/47	117	25	21.4	21.1	112	9	8.0	27.1
8/16/47*	12	2	16.7	20.5	17	2	11.8	24.0
9/12/47†	2	0	....	....	10	0	....	....
11/14/47‡	102	0	....	....	79	0	....	....
1/27/48	59	0	....	....	70	0	....	....
4/ 6/48	66	0	....	....	57	0	....	....
5/ 6/48	48	37	77.0	22.5	48	20	41.7	26.8
6/ 3/48	34	2	5.9	19.5	37	1	2.7	28.0
7/13/48*	21	10	47.6	20.3	25	11	44.0	26.8
8/25/48†	2	1	50.0	23.0	6	0	....	....
11/10/48	106	0	....	....	81	0	....	....
6/13/49	23	2	8.7	20.0	25	2	8.0	26.5

*Nymphs more than 12 mm. in length.
†Males more than 22 mm. and females more than 23 mm. in length.
‡All nymphs.

APPENDIX TABLE 3

Number and size of nymphs in last instar among 1-year-old nymphs, Plot 1, Gun Lake

Date	Males				Females			
	Number of 1-yr.-olds	Nymphs in last instar			Number of 1-yr.-olds	Nymphs in last instar		
		Number	Percent	Average length in mm.		Number	Percent	Average length in mm.
5/30/46	9	4	44.4	21.5	28	8	28.6	26.4
1/28/47	116	0	....	....	109	0	....	....
5/20/47	62	10	16.1	22.6	72	11	15.3	29.6
6/ 4/47	97	23	23.7	23.1	93	29	31.2	29.0
7/ 1/47	81	47	58.0	22.8	117	55	47.0	28.0
8/14/47*	4	0	....	....	5	1	20.0	30.0
9/10/47†	8	0	....	....	11	0	....	....
12/ 9/47‡	131	0	....	....	142	0	....	....
2/ 9/48	115	0	....	....	125	0	....	....
4/ 5/48	121	0	....	....	135	0	....	....
5/ 6/48	115	35	30.4	21.6	128	37	28.9	27.2
6/ 4/48	69	11	15.9	21.8	86	15	17.4	28.1
7/11/48*	30	8	26.7	23.8	25	8	32.0	24.0
8/26/48†	5	0	....	....	14	0	....	....
11/ 9/48‡	253	0	....	....	240	0	....	....

*Nymphs more than 12 mm. in length.
†Males more than 18 mm. and females more than 20 mm. in length.
‡All nymphs.

APPENDIX TABLE 4

Number and size of nymphs in last instar among 1-year-old nymphs, Plot 2, Gun Lake

Date	Males				Females			
	Number of 1-yr.-olds	Nymphs in last instar			Number of 1-yr.-olds	Nymphs in last instar		
		Number	Percent	Average length in mm.		Number	Percent	Average length in mm.
1/29/47	97	0	....	....	91	0	....	....
5/20/47	77	15	19.5	22.1	82	13	15.9	29.0
6/ 4/47	101	24	23.8	23.1	95	28	29.5	29.0
7/ 1/47	118	57	48.3	22.1	92	30	32.6	27.4
8/13/47*	5	1	20.0	24.0	17	3	17.6	27.3
9/10/47†	1	0	....	....	4	0	....	....
12/ 9/47‡	151	0	....	....	174	0	....	....
2/10/48	82	0	....	....	86	0	....	....
4/ 5/48	109	0	....	....	110	0	....	....
5/ 6/48	95	13	13.7	22.0	108	17	16.7	26.2
6/ 4/48	82	27	32.9	21.7	83	19	22.9	27.5
7/12/48*	17	2	11.8	21.0	26	11	42.3	26.1
8/26/48†	4	0	....	....	7	0	....	....

*Nymphs more than 12 mm. in length.

†Males more than 18 mm. and females more than 20 mm. in length.

‡All nymphs.

APPENDIX TABLE 5

Number and size of nymphs in last instar among 1-year-old nymphs, Big Silver Lake

Date	Males				Females			
	Number of 1-yr.-olds	Nymphs in last instar			Number of 1-yr.-olds	Nymphs in last instar		
		Number	Percent	Average length in mm.		Number	Percent	Average length in mm.
6/16/46	111	12	10.8	22.4	77	2	2.6	29.5
10/24/46	151	0	....	....	158	0	....	....
1/10/47	168	0	....	....	172	0	....	....
5/16/47	65	2	3.1	22.4	66	1	1.5	28.0
5/27/47	72	29	40.3	22.4	85	18	21.2	29.7
6/ 9/47	29	11	37.9	23.0	38	6	15.8	30.3
6/25/47	96	8	8.3	21.9	97	2	2.1	24.0
7/30/47	80	24	30.0	20.1	47	9	19.1	27.1
9/ 3/47	154	0	....	....	221	0	....	....
9/30/47	175	0	....	....	199	0	....	....
11/ 7/47	63	0	....	....	50	0	....	....
2/16/48	76	0	....	....	84	0	....	....
4/22/48	44	0	....	....	53	0	....	....
6/10/48	10	2	20.0	19.5	16	1	6.3	25.0
7/ 5/48	9	1	10.1	20.0	10	1	10.0	28.0
7/21/48	156	27	17.3	20.1	136	16	11.8	26.3
8/24/48	81	0	....	....	89	0	....	....
9/12/48	82	0	....	....	74	0	....	....

APPENDIX TABLE 6

Length-frequency distribution of nymphs, Plot 1, Pine Lake
(Figures in parentheses indicate number of nymphs in last instar)

Date	Number of individuals by frequency classes of 4 millimeters																	
	Males								Females									
	2–4	5–8	9–12	13–16	17–20	21–24	25–27	Total	2–4	5–8	9–12	13–16	17–20	21–24	25–28	29–32	33–35	Total
6/ 1/46.	..	..	1	1	5	4	..	11	..	..	1	2	5	2	3	..	..	13
1/31/47.	..	5	6	5	18	3	..	37	..	11	12	7	8	9	18	3	..	68
5/20/47.	..	6	12	8	18 (8)	13 (12)	..	57	..	2	10	17	17	12 (2)	9 (9)	2 (2)	..	69
6/ 5/47.	..	12	24	36	31 (4)	35 (29)	9 (9)	147	..	12	44	34	38	19 (1)	32 (13)	8 (7)	..	187
7/ 2/47.	..	1	1	20	35 (9)	46 (30)	2	105	..	..	4	17	21	38 (5)	67 (34)	5 (3)	..	152
8/15/47.	3	51	10	..	9 (3)	4	1	78	2	55	20	3	5	10 (1)	9	1	..	105
9/12/47.	3	6	13	28	4	4	1	59	..	13	21	26	15	4	4	..	..	83
11/14/47.	1	2	4	5	29	35	3	79	..	1	3	6	5	18	35	19	2	89
1/27/48.	..	1	1	6	27	26	2	63	..	5	5	8	9	21	48	16	..	112
4/ 6/48.	..	4	3	6	8	15	2	38	..	1	7	4	14	10	19	6	..	61
5/ 6/48.	..	..	6	7	23 (14)	15 (12)	3 (3)	54	1	6	8	9	14	6 (1)	13 (11)	14 (14)	..	71
6/ 2/48.	..	4	6	2	11 (2)	5 (4)	..	28	..	1	8	8	2	7	12	1 (1)	..	39
7/12/48.	146*	2	3	1	3 (1)	7 (2)	2	164	146*	..	2	..	3	5 (1)	7 (1)	..	..	163
8/25/48.	3	31	26	44	6	..	..	110	6	37	35	27	18	2	2	..	..	127
11/10/48.	..	6	4	10	44	11	..	75	..	2	3	6	9	29	45	4	..	98
6/13/49.	..	..	2	5	5 (2)	6 (5)	5 (1)	23	..	..	3	2	3	4 (1)	9 (4)	1 (1)	..	22

*For nymphs 2–4 mm. inclusive, sex not determined.

APPENDIX TABLE 7

Length-frequency distribution of nymphs, Plot 2, Pine Lake
(Figures in parentheses indicate number of nymphs in last instar)

Date	Number of individuals by frequency classes of 4 millimeters																	
	Males								Females									
	2–4	5–8	9–12	13–16	17–20	21–24	25–27	Total	2–4	5–8	9–12	13–16	17–20	21–24	25–28	29–32	33	Total
1/30/47.	..	17	25	18	23	8	1	92	..	13	24	17	15	22	16	..	..	107
5/22/47.	..	4	11	14	27 (8)	25 (19)	..	81	..	3	10	12	20	21	26 (11)	3 (3)	..	95
6/ 5/47.	..	24	27	26	31 (8)	64 (54)	15 (15)	187	..	8	23	22	16	19 (1)	46 (25)	33 (30)	1 (1)	168
7/ 3/47.	..	..	3	34	52 (9)	32 (16)	..	121	..	..	5	23	21	38	22 (8)	3 (1)	..	112
8/16/47.	2	22	3	3	6 (1)	1 (1)	2	39	1	36	14	1	1	3 (1)	10 (1)	2	..	68
9/12/47.	2	4	5	19	4	1	1	36	4	10	10	13	13	7	3	..	..	60
11/14/47.	..	7	17	12	43	20	3	102	..	4	12	15	9	20	16	3	..	79
1/27/48.	..	2	5	4	18	29	1	59	..	2	7	10	7	8	32	4	..	70
4/ 6/48.	3	9	4	3	23	24	..	66	3	5	4	4	4	18	17	2	....	57
5/ 6/48.	..	4	..	3	16 (14)	20 (18)	5 (5)	48	..	7	1	10	4	5 (4)	17 (12)	4 (4)	..	48
6/ 3/48.	..	6	13	2	7 (2)	6	..	34	..	2	5	9	5	5	7 (1)	4	..	37
7/13/48.	437*	..	3	2	10 (5)	9 (5)	..	461	437*	..	2	3	3	8	9 (9)	2 (2)	..	464
8/25/48.	6	27	44	73	13	2 (1)	1	166	8	34	50	44	32	5	2	..	..	175
11/10/48.	..	5	24	32	44	1	..	106	..	3	27	31	16	3	1	..	..	81
6/13/49.	..	..	3	4	7 (1)	6 (1)	3	23	..	..	1	2	1	6	14 (2)	1	..	25

*For nymphs 2–4 mm. inclusive, sex not determined.

APPENDIX TABLE 8

Length-frequency distribution of nymphs, Plot 1, Gun Lake
(Figures in parentheses indicate number of nymphs in last instar)

Date	Number of individuals by frequency classes of 4 millimeters																	
	Males								Females									
	2–4	5–8	9–12	13–16	17–20	21–24	25–27	Total	2–4	5–8	9–12	13–16	17–20	21–24	25–28	29–32	33	Total
5/30/46.	..	..	1	..	3 (1)	5 (3)	..	9	..	..	..	..	3	12 (2)	8 (5)	5	..	28
1/28/47.	2	25	42	12	18	17	..	116	..	9	40	23	3	11	19	4	..	109
5/20/47.	..	4	15	18	12 (1)	12 (8)	1 (1)	62	..	2	8	14	11	14	15 (4)	7 (6)	1 (1)	72
6/ 4/47.	..	6	14	19	23	28 (19)	6 (4)	96	..	1	8	15	17	16	19 (12)	17 (17)	..	93
7/ 1/47.	..	..	1	9	12	56 (42)	5 (5)	83	..	..	3	10	7	17 (1)	54 (34)	26 (20)	..	117
8/14/47.	6	21	1	..	..	2	1	31	15	24	8	..	1	..	3	1 (1)	..	52
9/10/47.	4	29	17	21	9	3	..	83	3	31	27	5	9	6	2	3	..	86
12 /9/47.	1	19	42	25	22	21	1	131	1	15	28	42	24	10	16	6	..	142
2/ 9/48.	3	22	30	10	20	28	2	115	..	12	31	30	10	11	17	14	..	125
4/ 5/48.	4	23	29	19	25	18	3	121	1	13	22	32	23	14	19	11	..	135
5/ 6/48.	2	24	25	23	14 (9)	24 (23)	3 (3)	115	2	13	27	25	14	11 (4)	24 (21)	12 (12)	..	128
6/ 4/48.	..	4	15	18	18 (3)	13 (8)	1	69	..	1	10	14	15	19	19 (9)	8 (6)	..	86
7/11/48.	98*	8	2	2	16 (6)	8 (1)	4 (1)	138	98*	11	2	4	6	9 (6)	5 (2)	..	..	135
8/26/48.	40	52	19	40	8	2	1	162	24	74	28	23	18	5	8	1	..	181
11/ 9/48.	9	74	51	18	88	13	..	253	3	61	73	29	9	34	29	2	..	240

*For nymphs 2–4 mm. inclusive, sex not determined.

APPENDIX TABLE 9

Length-frequency distribution of nymphs, Plot 2, Gun Lake
(Figures in parentheses indicate number of nymphs in last instar)

Date	Number of individuals by frequency classes of 4 millimeters																	
	Males								Females									
	2–4	5–8	9–12	13–16	17–20	21–24	25–27	Total	3–4	5–8	9–12	13–16	17–20	21–24	25–28	29–32	33–34	Total
1/29/47.	..	7	29	30	20	11	..	97	..	3	30	21	17	9	11	..	..	91
5/20/47.	..	7	22	21	12 (2)	15 (13)	..	77	..	2	13	20	16	11	14 (7)	5 (5)	1 (1)	82
6/ 4/47.	..	3	15	21	25	31 (20)	6 (4)	101	..	1	5	14	16	22	20 (11)	17 (17)	..	95
7/ 1/47.	..	1	8	17	34 (11)	50 (38)	8 (8)	118	..	1	7	7	16	24 (3)	28 (18)	10 (9)	..	93
8/13/47.	1	1	1	..	1	3 (1)	1	8	..	3	..	..	..	4	10 (2)	3 (1)	..	20
9/10/47.	4	12	1	..	..	1	..	18	5	12	1	..	2	2	1	1	..	24
12/ 9/47.	3	25	46	29	23	23	2	151	3	16	38	33	51	18	8	7	..	174
2/10/48.	1	9	29	20	10	12	1	82	1	2	19	24	18	10	8	4	..	86
4/ 5/48.	5	15	35	24	16	13	1	109	..	1	15	31	30	9	11	6	..	103
5 /6/48.	2	9	18	32	21 (3)	12 (10)	1	95	..	10	20	21	23	14 (1)	16 (12)	4 (4)	..	108
6/ 4/48.	..	..	6	16	30 (6)	28 (19)	2 (2)	82	..	1	5	6	13	28 (3)	21 (8)	9 (8)	..	83
7/12/48.	2	1	1	5	4	5 (2)	3	21	2	..	..	1	4	7 (1)	14 (10)	..	..	28
8/26/48.	12	30	10	2	2	..	2	58	19	40	8	3	1	3	4	..	..	78

APPENDIX TABLE 10

Length-frequency distribution of nymphs, Big Silver Lake
(Figures in parentheses indicate number of nymphs in last instar)

Date	Males: 2–4	Males: 5–8	Males: 9–12	Males: 13–16	Males: 17–20	Males: 21–24	Males: 25–27	Males: Total	Females: 2–4	Females: 5–8	Females: 9–12	Females: 13–16	Females: 17–20	Females: 21–24	Females: 25–28	Females: 29–32	Females: 33–35	Females: Total
6/16/46.	..	6	20	39	23 (1)	22 (10)	1 (1)	111	..	2	19	26	17	7	4	2 (2)	..	77
10/24/46.	2	60	33	13	18	21	4	151	2	64	54	9	4	6	8	10	2	159
1/10/47.	1	37	59	32	20	19	..	168	3	46	62	33	16	6	2	3	1	172
5/16/47.	..	11	16	13	6	15 (2)	4	65	..	18	25	12	4	1	5 (1)	1	..	66
5/27/47.	..	7	14	14	14 (7)	19 (18)	4 (4)	72	..	3	20	14	12	16	6 (4)	13 (13)	1 (1)	85
6/ 9/47.	..	1	7	6	5 (1)	7 (7)	3 (3)	29	..	3	2	9	6	7	6 (1)	4 (4)	1 (1)	38
6/25/47.	..	2	23	31	25 (2)	15 (6)	..	96	..	7	13	32	19	13 (1)	13 (1)	..	..	97
7/30/47.	2	1	6	19	39 (14)	13 (10)	..	80	..	3	3	6	13	11	10 (8)	1 (1)	..	47
9/3/47..	18	75	30	2	22	7	..	154	18	126	48	12	3	9	6	..	..	222
9/30/47.	16	48	38	15	36	21	1	175	10	78	51	26	9	7	14	4	..	199
11/ 7/47.	..	8	3	7	18	26	1	63	..	10	12	5	5	9	7	2	..	50
2/16/48.	..	17	23	8	16	12	..	76	..	21	19	13	3	10	16	2	..	84
4/22/48.	3	7	6	9	7	12	1	45	4	8	6	7	2	3	14	6	3	53
6/10/48.	..	2	1	1	5 (2)	1	..	10	..	1	4	4	1	5	1 (1)	..	..	16
7/ 5/48.	..	2	1	3	2 (1)	..	1	9	1	4	1	..	1	1	1	1 (1)	..	10
7/21/48.	110*	62*	33	36	46 (16)	19 (11)	..	306	110*	56*	15	22	24	25 (2)	20 (13)	1 (1)	..	273
8/24/48.	4	17	30	18	5	7	..	81	..	12	28	29	9	5	5	1	..	89
9/12/48.	..	6	14	39	18	4	1	82	..	4	20	12	20	14	2	2	..	74

Number of individuals by frequency classes of 4 millimeters.

*For nymphs 2–5 mm. inclusive, sex not determined.

APPENDIX TABLE 11

Average length of nymphs collected from Pine Lake, Plots 1 and 2 combined

Date	Males		Females		Both sexes	
	Number of nymphs	Average length, in mm.	Number of nymphs	Average length, in mm.	Number of nymphs	Average length, in mm.
6/ 1/46	11	18.5	13	20.1	24	19.4
1/31/47	129	14.2	175	17.1	304	15.9
5/20/47	138	16.9	164	19.3	302	18.2
6/ 5/47	334	17.2	355	19.2	689	18.2
7/ 2/47	226	18.7	264	21.8	490	20.4
8/15/47	117	9.8	173	11.6	290	10.9
9/12/47	95	13.4	143	14.1	238	13.8
11/13/47	181	17.7	168	22.4	349	19.9
1/27/48	122	19.1	182	22.6	304	21.2
4/ 6/48	104	17.1	119	20.7	223	19.0
5/ 6/48	102	19.3	119	20.4	221	19.9
6/ 2/48	62	14.5	76	19.0	138	17.0
7/12/48	...	4.6*	...	4.6*	648*	4.6*
8/25/48	276	11.7	302	11.9	578	11.8
11/10/48	181	15.9	179	19.1	360	17.5
6/13/49	46	19.6	47	22.6	93	20.9

*Sex not determined for these nymphs; average lengths are for both sexes combined.

APPENDIX TABLE 12

Average length of nymphs collected from Plot 1, Gun Lake

Date	Males		Females		Both sexes	
	Number of nymphs	Average length, in mm.	Number of nymphs	Average length, in mm.	Number of nymphs	Average length, in mm.
5/30/46	9	19.6	28	24.7	37	23.4
1/28/47	116	13.0	109	16.0	225	14.4
5/20/47	62	15.8	72	20.0	134	18.1
6/ 4/47	96	17.4	93	21.5	189	19.4
7/ 1/47	83	21.7	117	24.9	200	23.6
8/14/47	31	7.4	52	7.7	83	7.5
9/10/47	83	11.0	86	11.6	169	11.3
12/ 9/47	131	13.9	142	16.2	273	15.1
2/ 9/48	115	14.4	125	17.3	240	15.9
4/ 5/48	121	14.1	135	17.4	256	15.8
5/ 6/48	115	14.2	128	17.6	243	16.0
6/ 4/48	69	15.9	86	20.6	155	18.5
7/11/48	...	9.3*	...	9.3*	169*	9.3
8/26/48	162	8.9	181	10.2	343	9.6
11/ 9/48	253	12.7	240	14.0	493	13.4

*Nymphs not sexed; average of all nymphs.

APPENDIX TABLE 13

Average length of nymphs collected from Plot 2, Gun Lake

Date	Males		Females		Both sexes	
	Number of nymphs	Average length, in mm.	Number of nymphs	Average length, in mm.	Number of nymphs	Average length, in mm.
1/29/47.........	97	14.5	91	15.8	188	15.1
5/20/47.........	77	14.9	82	18.8	159	16.9
6/ 4/47.........	101	17.8	95	22.0	196	19.9
7/ 1/47.........	118	19.5	93	22.1	211	20.6
8/13/47.........	8	17.1	20	23.5	28	21.6
9/10/47.........	18	6.5	24	10.0	42	8.5
12/ 9/47.........	151	13.7	174	15.9	325	14.9
2/10/48.........	82	13.9	86	17.0	168	15.5
4/ 5/48.........	109	13.3	103	17.8	212	15.5
5/ 6/48.........	95	14.8	108	17.5	203	16.3
6/ 4/48.........	82	18.7	83	22.3	165	20.5
7/12/48.........	21	14.7	28	22.1	49	18.9
8/26/48.........	58	7.6	78	8.0	136	7.8

APPENDIX TABLE 14

Average length of nymphs collected from Big Silver Lake

Date	Males		Females		Both sexes	
	Number of nymphs	Average length, in mm.	Number of nymphs	Average length, in mm.	Number of nymphs	Average length, in mm.
6/16/46.........	111	15.9	77	15.9	188	15.9
10/24/46.........	151	12.0	159	12.2	310	12.1
1/10/47.........	168	12.6	172	11.9	340	12.3
5/16/47.........	65	15.1	66	12.5	131	13.8
5/27/47.........	72	16.7	85	18.9	157	17.9
6/ 9/47.........	29	16.8	38	19.9	67	18.7
6/25/47.........	96	15.7	97	16.8	193	16.2
7/30/47.........	80	16.9	47	19.7	127	17.8
9/ 3/47.........	154	9.2	222	8.7	376	8.9
9/30/47.........	175	12.1	199	11.2	374	11.6
11/ 7/47.........	63	17.8	50	16.0	113	17.0
2/16/48.........	76	13.6	84	15.0	160	14.5
4/22/48.........	45	15.1	53	18.5	98	16.9
6/10/48.........	10	15.7	16	16.6	26	16.3
7/ 5/48.........	9	14.4	10	13.4	19	13.9
7/21/48.........	...	9.6*	...	9.6*	419	9.6
8/24/48.........	81	11.6	89	14.0	170	13.0
9/12/48.........	82	14.6	74	16.4	156	15.4

*Average of all nymphs; sex not determined.

APPENDIX TABLE 15

Physical analyses of bottom materials, Pine Lake

Average of three 1,000-gram samples washed through a set of 6 Tyler screens

Measurements of dry weight

Meshes per inch	Size of mesh, in mm.	Materials retained by screen, in grams	Percent of total	Materials
4	4.699	2	0.8	Shells, vegetation
8	2.362	1	0.4	" "
14	1.168	2	0.8	Marl, little organic debris
35	0.417	4	1.7	" " " "
65	0.208	7	2.9	" " " "
100	0.147	7	2.9	" " " "
Pan	.....	213	88.8	" " " "
Loss in washing			1.7	......
Water			72.0	......
Dry matter			28.0	......

APPENDIX TABLE 16

Physical analyses of bottom materials, Gun Lake

Average of three 1,000-gram samples washed through a set of 6 Tyler screens

Measurements of dry weight

Meshes per inch	Size of mesh, in mm.	Materials retained by screen, in grams	Percent of total	Materials
4	4.699	9	3.9	Shells, vegetation
8	2.362	11	4.7	" "
14	1.168	3	1.3	" "
35	0.417	4	1.7	Marl, little organic debris
65	0.208	6	2.6	" " " "
100	0.147	8	3.4	" " " "
Pan	.....	185	79.4	" " " "
Loss in washing			3.0	......
Water			67.7	......
Dry matter			32.3	......

APPENDIX TABLE 17

Physical analyses of bottom materials in area with large nymph population, Transect 3, Big Silver Lake

Four samples (Nos. 1–4) of 1,000 grams each, washed through a set of 6 Tyler screens

Measurements of dry weight

Meshes per inch	Size of mesh, in mm.	Materials retained by screen, in percentage of total sample				Materials
		No. 1	No. 2	No. 3	No. 4	
4	4.699	7.1	5.3	1.3	1.0	Shells, detritus
8	2.362	0.5	0.5	0.3	0.4	" "
14	1.168	1.1	1.5	0.3	0.7	Marl, little organic debris
35	0.417	3.8	5.0	2.4	1.4	" " " "
65	0.208	5.4	6.2	2.1	1.4	" " " "
100	0.147	2.7	5.3	0.8	0.7	" " " "
Pan	.....	74.0	70.4	82.4	85.6	" " " "
Loss in washing		5.4	5.8	10.4	8.8	......
Water		84.0	66.5	69.0	75.6	......
Dry matter		16.0	33.5	31.0	24.4	......

APPENDIX TABLE 18

Physical analyses of bottom materials in area with small nymph population, Transect 3, Big Silver Lake

Samples washed through a set of 6 Tyler screens

Measurements of dry weight

Meshes per inch	Size of mesh, in mm.	Sample 5		Sample 6		Materials
		Materials retained by screen, in grams	Percent of total	Materials retained by screen, in grams	Percent of total	
4	4.699	124	19.3	21	4.1	Gravel, sticks
8	2.362	33	5.1	19	3.7	" "
14	1.168	25	3.9	16	3.1	Fine gravel, little organic debris
35	0.417	86	13.4	55	10.8	Coarse sand, marl, organic debris
65	0.208	158	24.6	105	20.6	Fine sand, marl, organic debris
100	0.147	75	11.7	55	10.8	Sand, marl, organic debris
Pan	.....	125	19.4	229	44.9	Marl, sand, organic debris
Loss in washing			2.6	...	2.0	......
Water			28.4	...	38.9	......
Dry matter			71.6	...	61.1	......

APPENDIX TABLE 19

Chemical analyses of bottom materials by Soils Laboratory, Michigan State College. Sample numbers correspond to those in Appendix Tables 15–18

Locality	Sample No.	pH	Nitrate, in lb. per acre	Phosphoric acid, in lb. per acre	Potash, in lb. per acre
Big Silver Lake (Transect 3)	1	7.35	0	1.30	42
"	2	7.15	0	1.00	32
"	3	6.90	0	1.30	42
"	5	7.30	0	0.48	42
"	6	7.70	0	0.16	32
Pine Lake	1	7.70	0	0.56	36
Gun Lake	1	7.60	0	2.30	46

APPENDIX TABLE 20

Comparison of average number of limbata **nymphs and associated organisms per sq. ft. in Plot 1, Pine Lake, with summary data on average volume in cc. per sq. ft.**

Kind of organism	Date of sample, and (in parentheses) the size of sample in square feet									
	July 2, 1947 (2)	Aug. 15, 1947 (2)	Sept. 12, 1947 (1)	Nov. 14, 1947 (2)	Jan. 27, 1948 (2)	Apr. 6, 1948 (6)	May 6, 1948 (2)	June 3, 1948 (2)	July 13, 1948 (2)	Aug. 25, 1948 (1)
H. limbata nymphs	17	42	30	15	16	28	15	5	31	60
Other organisms	244	215	117	728	460	453	879	309	300	337
Gastropoda	11	13	4	102	94	30	105	136	27	8
Pelecypoda	98	126	56	96	22	37	37	51	74	12
Oligochaeta	2	0	0	10	0	0	0	0	0	0
Hirudinea	1	2	1	10	0	1	3	1	0	1
Amphipoda	24	9	6	182	168	157	265	12	124	114
Hydracarina	3	4	2	8	0	1	4	0	2	3
Ephemeroptera (less *H. limbata*)	2	10	17	82	2	12	37	18	12	14
Anisoptera	1	1	0	3	1	1	0	0	1	0
Zygoptera	3	1	5	14	2	5	5	2	1	7
Neuroptera	1	2	1	1	1	1	1	1	4	12
Trichoptera	17	2	0	12	6	5	20	2	1	6
Diptera	81	45	25	208	164	203	402	86	54	160
Total number	261	257	147	743	476	481	894	314	331	397
Volume, cc. per sq. ft.										
H. limbata nymphs	2.45	0.67	1.70	2.40	2.55	3.73	2.95	0.60	0.30	1.75
Other organisms	1.00	0.50	0.30	2.88	1.14	1.38	3.20	1.37	0.80	0.75
All organisms	3.45	1.17	2.00	5.28	3.69	5.11	6.15	1.97	1.10	2.50

APPENDIX TABLE 21

Comparison of average number of limbata **nymphs and associated organisms per sq. ft. in Plot 2, Pine Lake, with summary data on avearge volume in cc. per sq. ft.**

Kind of organism	Date of sample, and (in parentheses) the size of sample in square feet									
	July 3, 1947 (2)	Aug. 15, 1947 (3)	Sept. 12, 1947 (1)	Nov. 13, 1947 (2)	Jan. 27, 1948 (2)	Apr. 6, 1948 (6)	May 7, 1948 (2)	June 3, 1948 (2)	July 13, 1948 (2)	Aug. 25, 1948 (2)
H. limbata nymphs	16	14	25	19	15	25	11	6	189	68
Other organisms	347	314	136	357	552	520	901	263	239	273
Gastropoda	8	6	13	67	98	100	200	32	5	28
Pelecypoda	21	17	3	27	19	24	15	13	4	11
Oligochaeta	0	3	0	2	2	0	0	0	0	0
Hirudinea	7	12	1	1	4	6	6	1	0	2
Amphipoda	131	162	36	97	176	182	366	54	118	97
Decapoda	0	0	0	0	0	1	0	0	0	0
Hydracarina	8	13	0	5	4	1	3	1	0	0
Ephemeroptera (less *H. limbata*)	22	16	11	5	18	29	38	13	4	9
Anisoptera	0	0	0	1	1	1	1	0	1	0
Zygoptera	6	3	2	9	17	14	33	2	1	4
Neuroptera	0	0	1	1	0	2	0	1	3	2
Trichoptera	12	8	2	7	14	11	24	3	0	4
Diptera	132	74	67	135	199	149	215	143	103	116
Total number	363	328	161	376	567	545	912	269	428	341
Volume, cc. per sq. ft.										
H. limbata nymphs	1.50	0.65	1.35	1.85	1.75	2.48	1.85	0.80	1.28	2.55
Other organisms	0.65	0.45	0.45	1.45	1.60	1.87	3.00	0.65	0.40	0.65
All organisms	2.15	1.10	1.80	3.30	3.35	4.35	4.85	1.45	1.68	3.20

APPENDIX TABLE 22

Comparison of average number of limbata **nymphs and associated organisms per sq. ft. on the shoal at Prairieville Township Park in Second Lake (part of Pine Lake), with summary data on average volume in cc. per sq. ft.**

Kind of organism	Date of sample, and (in parentheses) the size of sample in square feet			
	April 7, 1948 (1)	May 7, 1948 (1)	June 3, 1948 (1)	July 13, 1948 (1)
H. limbata nymphs	11	8	5	4
Other organisms	823	1,115	668	640
Gastropoda	9	14	4	5
Pelecypoda	4	16	7	19
Oligochaeta	0	0	3	9
Hirudinea	0	2	4	1
Amphipoda	324	424	390	427
Hydracarina	6	3	7	4
Ephemeroptera (less *H. limbata*)	23	42	27	5
Anisoptera	0	3	2	0
Zygoptera	5	5	1	0
Neuroptera	2	0	1	1
Trichoptera	27	37	11	5
Diptera	423	569	211	164
Total number	834	1,123	673	644
Volume in cc. per sq. ft.				
H. limbata nymphs	0.70	0.65	0.50	0.55
Other organisms	1.55	3.30	3.00	0.80
All organisms	2.25	3.95	3.50	1.35

APPENDIX TABLE 23

Comparison of average number of limbata **nymphs and associated organisms per sq. ft. based on combined samples from Plots 1 and 2, Gun Lake, with summary data on average volume in cc. per sq. ft.**

Kind of organism	Date of sample, and (in parentheses) the size of sample in square feet								
	Aug. 14, 1947 (2)	Sept. 10, 1947 (2)	Dec. 9, 1947 (2)	Feb. 9, 1948 (4)	Apr. 6, 1948 (2)	May 6, 1948 (2)	June 4, 1948 (2)	July 11, 1948 (2)	Aug. 26, 1948 (2)
H. limbata	3	35	45	31	18	21	18	81	19
Other organisms	162	211	280	289	405	352	254	188	156
Gastropoda	8	6	14	4	11	7	20	25	18
Pelecypoda	2	4	5	12	2	4	3	3	3
Oligochaeta	1	2	4	2	0	2	0	0	0
Hirudinea	2	0	0	0	0	1	4	0	0
Amphipoda	98	66	73	152	198	146	50	70	50
Decapoda	1	2	1	1	1	1	1	1	1
Hydracarina	12	18	9	0	2	6	0	3	0
Ephemeroptera (less *H. limbata*)	1	30	23	5	11	16	8	17	0
Anisoptera	0	0	1	0	0	0	0	0	0
Zygoptera	1	0	0	0	1	3	0	0	2
Neuroptera	1	2	3	3	2	2	1	4	6
Trichoptera	2	1	2	3	1	2	3	0	4
Diptera	33	80	145	107	176	162	164	65	72
Total number	165	246	325	320	423	373	272	269	175
Volume in cc. per sq. ft.									
H. limbata nymphs	0.17	1.50	2.20	1.46	1.79	1.95	2.20	0.50	0.45
Other organisms	0.74	1.00	1.44	1.33	1.25	1.37	0.82	0.75	1.25
All organisms	0.91	2.50	3.64	2.79	3.04	3.32	3.02	1.25	1.70

APPENDIX TABLE 24

Comparison of number of limbata **nymphs and associated organisms in 1-sq.-ft. samples at 8 stations (Nos. 5-12) on Transect 3, Big Silver Lake, April 15, 1948, with summary data on volume in cc.**

Kind of organism	Station number, and water depth in feet							
	No. 5 2.5 ft.	No. 6 3 ft.	No. 7 3.5 ft.	No. 8 3.5 ft.	No. 9 4 ft.	No. 10 7 ft.	No. 11 15 ft.	No. 12 20 ft.
H. limbata nymphs	7	3	6	9	10	3	1	0
Other organisms	218	108	62	91	205	406	220	132
Hirudinea	0	1	0	0	0	0	0	0
Gastropoda	2	1	2	2	12	58	22	7
Pelecypoda	4	3	1	4	0	1	0	0
Amphipoda	41	24	26	13	41	93	23	11
Decapoda	0	0	1	0	0	0	1	0
Ephemeroptera (less *H. limbata*)	65	21	6	6	4	7	9	2
Anisoptera	0	0	0	0	0	1	0	0
Zygoptera	0	1	0	0	5	7	5	0
Neuroptera	0	1	2	2	1	1	0	0
Trichoptera	7	0	0	1	3	10	11	9
Diptera	99	56	24	63	139	228	149	103
Total number	225	111	68	100	215	409	221	132
Volume in cc.								
H. limbata nymphs	0.30	0.06	0.43	2.01	1.46	0.61	•0.18	0.00
Other organisms	2.44	0.55	0.73	0.79	0.95	1.83	2.93	0.91
All organisms	2.74	0.61	1.16	2.80	2.41	2.44	3.11	0.91

APPENDIX TABLE 25

Comparison of number of limbata **nymphs and associated organisms in 1-sq.-ft. samples at 5 stations (Nos. 2-7) on Transect 5, Big Silver Lake, April 22, 1948, with summary data on volume in cc.**

Kind of organism	Station number, and water depth in feet				
	No. 2 2 ft.	No. 3 3 ft.	No. 4 5 ft.	No. 6 10 ft.	No. 7 15 ft.
H. limbata nymphs	6	14	26	12	9
Other organisms	324	250	151	258	146
Oligochaeta	0	0	0	2	0
Hirudinea	1	0	0	3	0
Gastropoda	41	44	6	11	18
Pelecypoda	10	6	2	4	0
Amphipoda	132	98	67	32	7
Decapoda	0	0	1	0	0
Ephemeroptera (less *H. limbata*)	40	4	5	7	2
Anisoptera	1	0	0	0	0
Zygoptera	4	3	0	2	0
Neuroptera	0	3	4	0	0
Trichoptera	4	5	1	9	0
Diptera	91	87	65	188	119
Total number	330	264	177	270	155
Volume in cc.					
H. limbata nymphs	0.30	0.65	0.55	1.60	1.65
Other organisms	1.65	1.10	1.25	0.75	0.45
All organisms	1.95	1.75	1.80	2.35	2.10