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BIOLOGY OF TWO SPECIES OF LAKE ERIE MAYFLIES, EPHORON ALBUM (SAY) AND EPHEMERA SIMULANS WALKER

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BIOLOGY OF TWO SPECIES OF LAKE ERIE MAYFLIES, EPHORON ALBUM (SAY) AND EPHEMERA SIMULANS WALKER

INTRODUCTION

The Great Lakes have long been known for their high productivity of commercially important fresh water fishes. Lake Erie is the most productive of the five lakes constituting the Great Lakes System. Its shallow western end yields the major proportion of the commercial catch from this lake. The factors involved in this high productivity are rather complex. One obvious factor is the abundance of food available to the fishes in this part of the lake. The shallow western end has numerous streams (Fig. 1) which supply abundant nutrients for the production of phytoplankton and algae, which in turn becomes food for zooplankers, insects, and small fishes.

Very few of the commercially important fishes are able to utilize the basic plant materials directly, but must obtain them through some inter-

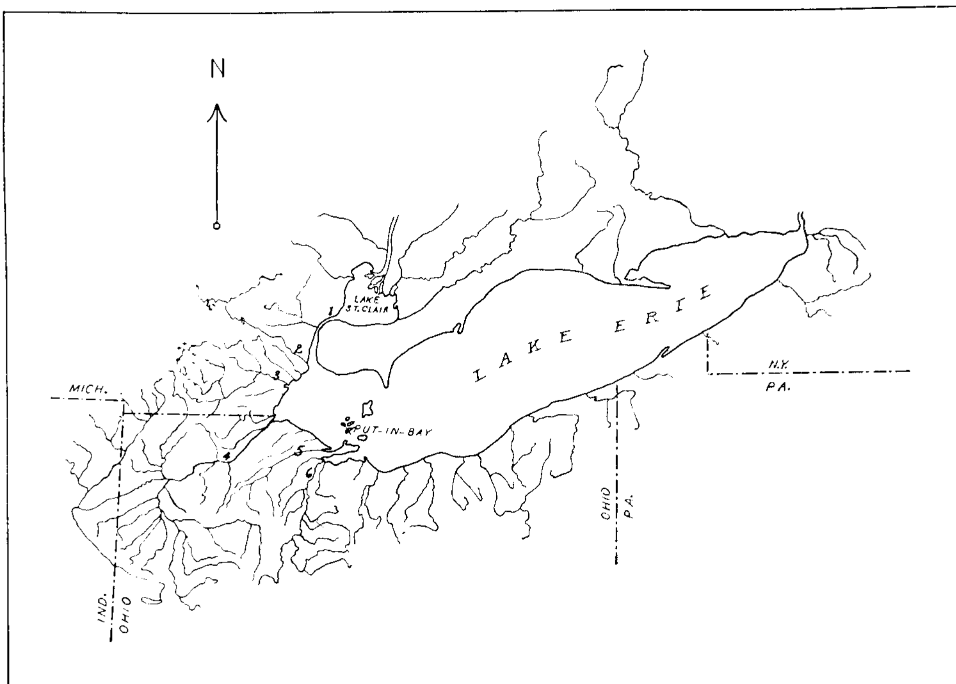

FIG. 1—Map of Lake Erie showing river systems. (1) Detroit River, (2) Huron River, (3) Raisin River, (4) Maumee River, (5) Portage River, (6) Sandusky River.

mediate source. The microcrustacea, insects, and small herbivorous fishes provide the necessary link in this food chain. In this respect the most important orders of insects in Lake Erie are Trichoptera (caddis flies), Diptera (flies), and Ephemeroptera (mayflies).

Studies of the food of fishes have shown that mayflies constitute an important part of the diet of many fishes. In some instances during the mayfly emergence seasons, the food of some fishes may consist of nothing but mayflies. The nymphs are probably more important than the adults in this respect. It is quite common to find large quantities of nymphs in the stomachs of perch (*Perca flavescens*), yellow pikeperch (*Stizostedion v. vitreum*), blue pikeperch (*Stizostedion vitreum glaucum*), sauger (*Stizostedion c. canadense*), channel catfish (*Ictalurus l. lacustris*), carp (*Cyprinus carpio*), sturgeon (*Acipenser fulvescens*), and other smaller fishes that feed on or near the bottom. Forbes (1888:484) states that nearly a fifth of the food consumed by all the adult fishes that he studied consisted of aquatic larvae of the Linnaean order Neuroptera, the greater part of which was nymphs of Ephemeroptera. In a study on the biology of the trout perch (*Percopsis omiscomaycus*) in western Lake Erie, Kinney (unpublished thesis, 1950:45–52) found that in any one collection, the stomach contents of different specimens were similar. More than half of the adult stomachs examined from twenty-two collections contained only Ephemeroptera nymphs. In another case where 162 adult stomachs were examined, Ephemeroptera nymphs constituted 96% of the total volume.

Since the completion of most of the material for this paper, a significant change in conditions in western Lake Erie beginning in 1953 has drastically altered the bottom fauna resulting in a great reduction in the mayfly population (principally *Hexagenia*) in the deeper water (Britt, 1955a, 1955b). In a recent study of the foods of some Lake Erie fishes, Price (In a Report to The Natural Resources Institute of The Ohio State Universtiy, 1959) showed that mayflies were important as food for several species of Lake Erie fishes in spite of the fact that the mayfly (*Hexagenia*) population in Lake Erie at the time of the study was far below normal.

Needham, Traver, and Hsu (1935:221) express the belief that although mayflies are very important as a primary food of fishes they may be even more important as a secondary food supply.

Besides their value as food for fishes, the mayflies are also a source of food for birds and other animals. Eaton 1879:268) reported that around Nyassa Lake in Africa the natives consider *Caenis Kungo* and *Caenis cibaria* as edible and make them into cakes. The mayflies may also be of some value as scavengers by helping clean up decaying material on the bottom. Bragina (1931:350) states that mayflies are probably very important in the control of mosquitoes, and Enderlein (1931:506) mentioned mayfly larvae as helping in the control of Simuliidae.

In resort areas and around cities near the lakes, some species of mayflies may become a nuisance. In western Lake Erie some species, principally of the genus *Hexagenia*, collect around lights making streets and walks slippery and dangerous. Along the lake shores thousands of the dead bodies drift onto the beaches. If they are not removed, the odor becomes very disagreeable. Another thing which may have contributed to the unpopularity of mayflies is the hypersensitivity of some people to them.

Figley (1940:377) showed that in 1284 cases of seasonal hay fever 95 (7.4%) were sensitive to mayflies.

Aside from the indirect observations made on mayflies as the result of their economic importance, they have long been subjects of interest and study. As early as 1737 Swammerdam (Needham et al, 1935:6) published an account of the structures, habits, and life history of *Ephoron virgo* (Oliver) of Europe. Since then many workers have contributed valuable information on this order. Among some of the more important publications are those of John Lubbock (1864-1866), Reaumur (1742), Pictet (1843), Hagen (1861), Eaton (1883-1888), Vayssiere (1882), Ulmer (1920), and Needham, Traver, and Hsu (1935).

In 1947 studies were started on the life history and ecology of some of the species of mayflies inhabiting the Bass Island region of Lake Erie. This paper is part of the results. The part of this study dealing with the life history of *Ephoron album* was submitted as a dissertation in partial fulfillment of the requirements for the degree Doctor of Philosophy in 1950. The abstract of the dissertation was published in 1953 (Britt, 1953a).

In this study, the first specimens of *Ephoron album* (Say) to be found were a few dried and shriveled individuals found tangled in spider webs along the walls of Stone Laboratory in the summer of 1948. Since the individuals of this species have a very short adult life and are relatively poor fliers, it was obvious that the nymphs had developed in the vicinity. There was only one record of the nymphs having been collected in this area. Wright, Tiffany, and Tidd (1955:258), using a Helgoland Trawl in the island region of Lake Erie in 1929-1930, collected a few of the nymphs along with other shoal forms. The method used in collecting, however, yielded practically no information concerning the habitat of the nymphs. No one appeared to know where the nymphs lived. The curiosity aroused by this situation led to a search for the nymphs and eventually resulted in the present study of this species.

At about the same time this study was being made, Edmunds, Nielsen, and Larsen (1956) were making a similar study of *Ephoron album* in Utah. Each of these studies was made independently of the other with each worker being unaware that the other was working with the same species. Apparently Edmunds, Nielsen, and Larsen had not seen the abstract of the work done on Lake Erie (Britt, 1953a) when they published the results of their study in 1956.

In many cases the results obtained by Edmunds, Nielsen, and Larsen were identical or similar to those obtained in the Lake Erie study; however, in some cases quite different results were obtained. In addition, the Lake Erie study covered some aspects not covered in the Utah study.

In the course of the study on *Ephoron album* nymphs, it was discovered that the same area supported large populations of water mites, amphipods, decapods, ostracods, cladocerans, copepods, small fishes, mollusks, worms, midges, caddis flies, and other species of mayflies. There were large populations of the mayfly genera *Caenis, Stenonema,* and *Ephemera. Ephoron album* and *Ephemera simulans* belong to the same family and each is potentially capable of producing large populations. In order to better understand the ecological relationships between these two species, a parallel study of the biology of *Ephemera simulans* was undertaken. Various phases of these studies continued from 1948 until 1953.

In this investigation the facilities of the Franz Theodore Stone Laboratory of The Ohio State University were used. Dr. T. H. Langlois, the director of the laboratory at the time of this study, arranged for financial aid in the form of an assistantship from funds provided by the Ohio Division of Wildlife to cover part of this investigation. Appreciation is expressed to Dr. B. D. Burks for checking the identification of the *Ephoron album* specimens. Thanks are due also to Dr. Earle Lyman, Dr. David C. Chandler, Dr. M. W. Boesel, Dr. T. H. Langlois, Dr. Jacob Verduin, Dr. M. T. Trautman, the librarian, Mrs. E. C. Kinney, and others who assisted in various ways throughout the course of this study.

DESCRIPTIONS OF STATIONS

Ephoron album nymphs may be found in numerous places along the shores of South Bass Island. Each year, for example, there is a large population in the shallow water just off the shore at Oak Point between Squaw Harbor and Hatchery Bay. The map (Fig. 2) shows the depth of water in Hatchery Bay and Squaw Harbor from May 22 to June 6, 1936. Since the lake level is always changing, these depths can be used only as an index of the relative depths of this area. During the same period in 1949 the average lake level was approximately one and a half feet above that

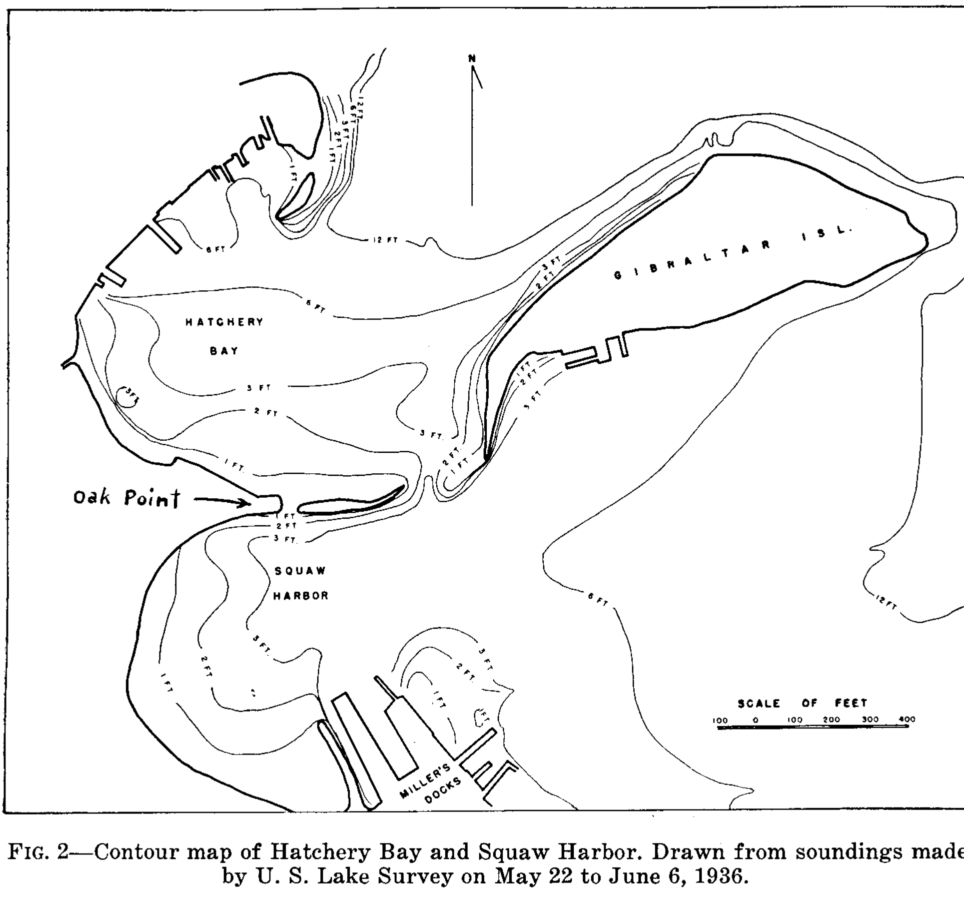

FIG. 2—Contour map of Hatchery Bay and Squaw Harbor. Drawn from soundings made by U. S. Lake Survey on May 22 to June 6, 1936.

of 1936. This amount of water was sufficient to completely cover the gravel bar shown between Oak Point and Gibraltar Island (Fig. 2). The annual high water level usually occurs in May and June. Then there is a gradual decline until January or February when the low level for the year is reached. The lake level around the islands is temporarily influenced by the direction and velocity of the winds. These winds may cause seiches which result in temporary changes in the water level of as much as five feet.

During strong southwest storms, the area between Oak Point and Gibraltar Island may be completely exposed (Fig. 3).

Krecker (1928) showed that water currents change direction periodically in the mouth of Terwilliger's Pond. There are similar oscillations in the water around the concrete wall at Oak Point. These alternating currents have formed a small basin which is shown in Fig. 3. This photograph of the area was made during a seiche.

Linduska (1942) has shown that the type of bottom is an important factor influencing the distribution of mayfly nymphs. Some species were found most often on mud bottom while others were found only on rubble, gravel, or sand bottom. The bottom in the area where the samples were taken consists chiefly of coarse gravel and a few scattered boulders with

FIG. 3—Photograph of Oak Point Bar during a period of low water.

sand and detritus intermixed. From 3 to 18 inches below the surface of this gravel and sand there is a tough, white, clay subsoil.

Since this area is directly connected with the open lake, the chemical and physical conditions are much the same as those found in the open lake. Studies made by Chandler (1940) from September 1938 to November 1939, and by others since then, indicated that under normal conditions there are always large quantities of oxygen in this shallow water. The pH value of the water may vary from about 7.5 to 8.4. Since the waters in Hatchery Bay and Squaw Harbor are shallow and relatively protected from wind, small changes in temperature may occur more quickly than in the open lake.

The oscillations in the lake level provide an almost continual movement of water past Oak Point. The current produced in this way provides a suitable habitat for those forms that require a current, and it may bring in food for those that are present.

During the winter when the water level is low, a strong southwest wind may temporarily force the water from this area, thus exposing the bottom. If the temperature is below 0° C., this exposed area freezes. Any aquatic forms not capable of migrating or burrowing into the bottom are, therefore, exposed to the freezing temperatures.

MATERIALS AND METHODS FOR COLLECTING AND PRESERVING

EGGS

Several methods were used for collecting the eggs of *Ephoron album.* Some of the eggs used for hatching experiments were obtained by quickly scooping up in an insect net those females which settled on the water surface. This method required precise timing since the females ejected their eggs almost instantly on striking the water. Even at this rapid rate of operation, eggs were obtained from only a part of the females thus collected. Sometimes the mass of eggs released by the female was caught in the net. While the above method was not very efficient, it appeared to offer a good chance of obtaining fertilized eggs. It was sometimes possible to capture a copulating female and remove the eggs.

Another method of obtaining large quantities of eggs was by collecting many of the females from the mating flight without regard to their having mated. These females, along with several males, were put into dry bottles (wet bottles caused the females to expel their eggs) and taken to the laboratory where the eggs were removed and placed in depression slides containing Hobson's Ringer Solution (Barnes, 1937:26). Male reproductive organs were then crushed in the depression slides with the eggs. Observations of these slides under a compound microscope revealed millions of spermatozoa actively swimming among the eggs.

The eggs collected by the above methods were divided and placed into a series of two-ounce bottles of lake water. The bottles were connected to a small aerating pump and left at room temperature until needed for hatching experiments.

An attempt was made to determine the number of slowly sinking eggs in the water by using a plankton net, but this was abandoned after one trial. It was found that the egg masses remain intact and sink rapidly until the water has time to dissolve the adhesive and set the individual eggs free. In the shallow water where the collections were made, the eggs were near the bottom before they had time to disperse. Another factor unfavorable to this method of collecting was the large amount of plankton collected. This made the counting of the eggs almost impossible.

To estimate the quantity of eggs per unit area the following method was used: A battery jar having an inside diameter of 14.8 cm. was placed on the bottom about six feet from the concrete wall at the end of Oak Point. This jar was held in place by a loop of strong wire driven into the lake bottom. The depth of water above the top varied from 12 to 18 inches during the evenings that collections were made. On evenings when these collections were made, the jars were removed after all the mayflies in the evening's flight were dead. The eggs in the jar were then counted and the number per unit area determined.

Another method, useful in studying the development of the eggs in their natural habitat, was that of taking eggs directly from samples of gravel and sand brought in from the area studied. This method was used at intervals of 2 to 4 weeks throughout the winter of 1948 and spring of 1949.

The gravel and sand samples were brought into the laboratory where they were thoroughly agitated and washed in U. S. Standard Sieves numbers 5, 18, and 35, having openings of 4, 1, and 0.5 mm., respectively. After all dirt had been flushed away, small samples of sand from sieves numbered 18 and 35 were examined under a binocular microscope. Large masses of eggs were often found clinging to the pieces of sand too large to pass through the openings of the sieves. In general, sieve number 18 appeared to give the best results. Eggs collected in this manner were used for hatching experiments and for obtaining quickly large numbers of young nymphs for study.

Eggs of *Ephemera simulans* were obtained by capturing copulating females and removing the fertilized eggs. Eggs of this species were also taken from females without regard to their having mated. These were mixed with sperm in ringer solution as mentioned above. The mating flight of this species differs from that of *Ephoron album*, and the females distribute the eggs over a larger area; therefore, no attempt was made to estimate the number of eggs falling on a unit area of the bottom. The eggs of this species have an adhesive covering which quickly becomes covered with fine particles of sand and silt. This makes it almost impossible to distinguish them from particles of sand. Thus, no *Ephemera simulans* eggs were collected from the bottom.

Ethyl alcohol (70% to 95%) was quite satisfactory for preserving the eggs.

Nymphs

Previous studies of the nymphs of *Ephoron album* and *Ephemera simulans* have been inadequate, probably because of the difficulty involved in collecting them. Dredges, which are successful in collecting *Hexagenia* nymphs from the soft mud bottom, are useless on the coarse gravel and boulder-strewn bottoms inhabited by these nymphs. Methods used for collecting *Stenonema* and other sprawlers which cling to stones are also useless, as these nymphs do not cling to the stones.

Percival and Whitehead (1926:137) described a special shovel which they used for taking quantitative samples of sand and small gravel. The variable sizes of the bottom particles at the Oak Point collecting station made reliable quantitative sampling by this method almost impossible. For most collections of both *Ephoron album* and *Ephemera simulans*, a rounded or pointed shovel was used for securing the gravel and sand containing the nymphs. This was then agitated and the water containing the swimming or suspended nymphs was poured through the set of standard sieves previously described in connection with egg collecting. The use of a shovel of this type limits to about three feet the depth to which samples can be taken.

When it was desirable to make a rough estimate of the population, a number 10 metal can, 10.5 cm. in diameter, open at one end and with a small hole in the other, was used. The open end of the can was pushed into the bottom until it was embedded in the clay subsoil. The small hole in the top permitted trapped air and water to escape. The shovel blade was forced under the open end of the can. Then with the small hole in the top closed, by placing a thumb or finger over the opening, the can and its contents were easily lifted and placed in a bucket of water for washing and sieving.

At first, nymphs obtained by these methods were placed in bottles of 95% ethyl alcohol. When examined at a later date, the preservative was found to be unsatisfactory because many of the nymphs had become soft thus making it difficult to study their structural details. In order to get more satisfactory specimens, the nymphs from all subsequent collections were killed and fixed in KAAD.[1] Then they were transferred to 95% alcohol.

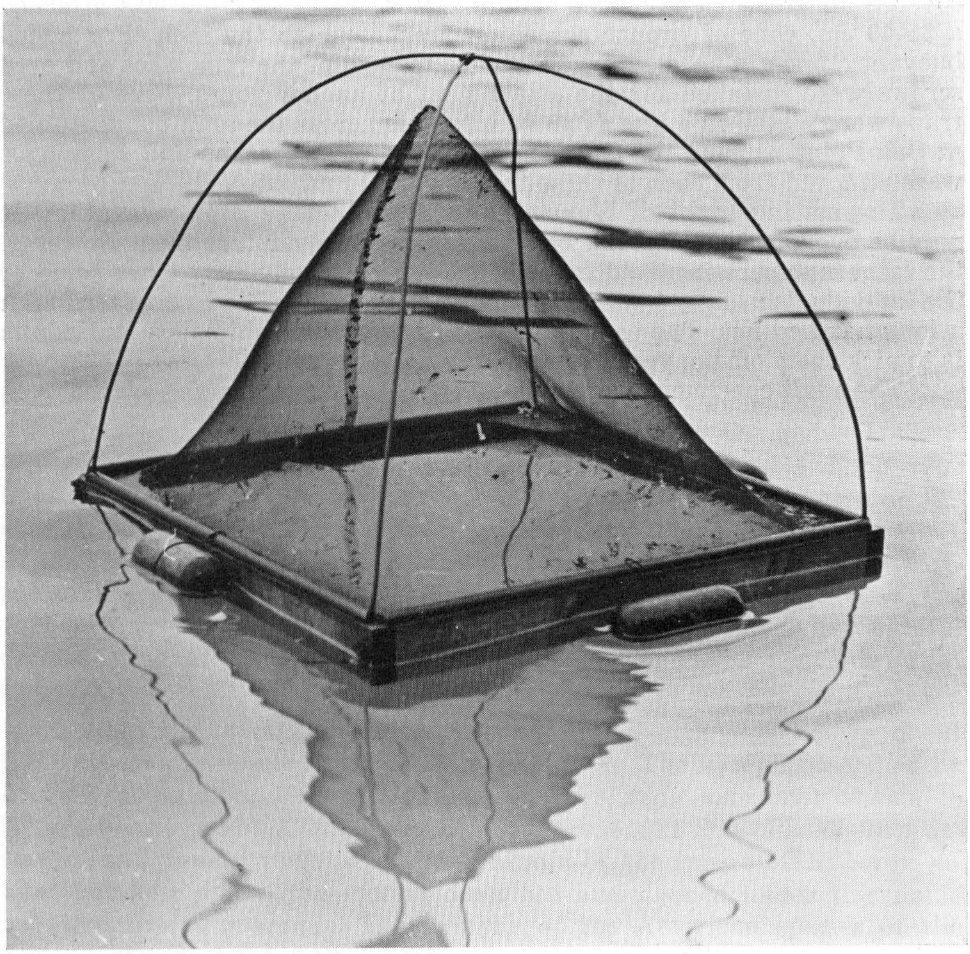

FIG. 4—Tent trap used for collecting emerging *Ephoron album subimagos.*

ADULTS

The adults of *Ephoron album* were easily collected during the short period of emergence and mating flight with an insect net swept about a foot above the surface of the water. The insects collected in this manner were stored in bottles of 95% alcohol. Since these insects were extremely

[1] Formula for KAAD (Peterson, 1948:6–8)
10 parts 95% grain alcohol
2 parts glacial acetic acid
1 part kerosene
1 part dioxane

fragile, only a few specimens could be placed in each bottle without damaging the whole collection.

For the study of the period of maximum daily emergence and the number emerging per unit area, tent traps were used similar to those used by Scott and Opdyke (1941) on Indiana lakes and by Adamstone and Harkness (1923) and Miller (1941) in Canada. Each of these tent traps (Fig. 4) consisted of a square wood frame of 50 cm. inside measurement and covered an area of one-fourth square meter. To this frame was attached a 35-40 cm. cone of bronze screen, sixteen mesh to the inch. For added buoyancy, one gill net float was attached to each of the four sides and eyed screws were installed for the attachment of anchor ropes. Five of these traps were placed in a line at 10 ft. intervals across the area being studied at Oak Point. During the periods of emergence all imagos and subimagos were removed from each of these traps every 15 minutes.

The mating flight of *Ephemera simulans* occurs over vegetation. It may be over a lawn, a group of shrubs, or even over tree tops. However, the large numbers involved make collecting relatively easy since some of the individuals usually come near enough to the ground to be captured with a long handled net. The easiest way to capture the subimagos and adults is to pick them off the vegetation during the daytime.

The adult specimens were satisfactorily preserved in 95% alcohol.

EPHORON ALBUM (SAY)

LITERARURE REVIEW

The first Nearctic species of the mayflies to be described was *Ephoron leukon* (Williamson, 1802:71–73). *Ephoron album*, another species of this genus, was described by Thomas Say in 1824 (Keating, 1824:305) under the name *Baetes alba*. Hagen (Walsh, 1863a:170) considered *Baetes alba* Say to be a synonym of *Ephoron leukon* Williamson. Eaton (1868:84) erected the genus *Polymitarcys* using *Ephemera virgo* Oliver as genotype. Later (1883–1888:47) he included *Baetes alba* Say under this genus as *Polymitarcys albus* and considered *Ephoron leukon* Williamson as a synonym. McDunnough (1926:184) showed that the name *Ephoron leukon* was valid and that *Baetes alba* Say, although belonging to the same genus, was not a synonym of *Ephoron leukon*. Ulmer (1932:208; 1933:197) retained both *Ephoron* and *Polymitarcys* as valid genera, with *Ephoron leukon* Williamson as the genotype for the American genus *Ephoron* and with *Polymitarcys virgo* (Oliver) as the genotype for the genus *Polymitarcys*. Needham, Traver, and Hsu (1935:241) considered *Polymitarcys* to be a synonym of *Ephoron*. Lestage (1938) studied the literature on the subject, but was unable to arrive at any definite conclusion. Spieth (1940a) reviewed all available literature on this subject. He also made a comparison of the wings, legs, eyes, genitalia, cerci, size, and coloration of the various species of the genera *Ephoron* and *Polymitarcys*. After careful consideration of the various aspects of the problem, he concluded that *Polymitarcys* is a synonym of *Ephoron*.

Except for taxonomic studies on the adults, little was known about the American species of this genus before 1935. The nymph described by Howard (Needham, 1905:60) as *Polymitarcys albus* was later shown to belong to the genus *Potamanthus*. Needham (1921:285, Pl. 77–78) described and figured the wings and genitalia of the imago of *Ephoron album*, but here again, the nymph described and figured under this name was that of *Potamanthus*. The nymphs of the American species of the genus *Ephoron* were first reported by Needham and Christenson from Utah in 1927, and by Argo from the Potomac River in 1927. Spieth (1933), in discussing the phylogeny of mayflies, gave some figures of structures of the imago and nymph of *Ephoron* under the genus name *Polymitarcys*. Ide (1935a) figured the first, second, and last instars of the nymphs of *Ephoron leukon*. In this paper he described the habitat in which the nymphs were found. Since the nymphs lived among stones and gravel, but did not cling to the stones when lifted, they had escaped notice for many years. Edmunds (1948:12) described the nymphs of *Ephoron album*. The most recent taxonomic study of this genus is that of Burks (1953:32–35). In this study he redescribed *Ephoron album* and *Ephoron leukon* imagos and figured the male genitalia of each species.

IDENTIFICATION

Adults

The adults of *Ephoron album* were described by Needham, Traver, and Hsu (1935:243) and by Burks (1953:34–35). In general the adults of this species collected in Lake Erie appeared to agree in most details with the descriptions given by the above workers. However, some differences were observed in the size of the individuals and in the genitalia. In the descriptions, the body length was given as 12 mm. Body length of males taken on Lake Erie varied from 11.2 mm. to 15.2 mm., while that of the females usually exceeded this length. Since they usually expel their eggs and contract in length as soon as they are put into preservative, it is difficult to determine the length from preserved specimens. It was estimated that the average body length of the males was between 13 and 14 mm. Measurements were made of the length of the caudal and lateral filaments of subimago and imago males and also those of the adult females. The lateral filaments of the male subimagos averagèd about 25 mm. in length and the median filament about 0.5 mm. The lateral filaments of the male imago was about 45 mm. or almost twice that of the subimago, while the median filament remained about the same size as that in the subimago stage. The lateral filaments of the subimaginal females were about 14 mm., while the median filament of the subimaginal females were about 14 mm., while the median filament was about 8 mm. in length. The females of this species do not molt after reaching the flying subimaginal stage.

In mounts of the genitalia made by the author from preserved specimens, the lateral angles of the penis lobes did not appear as acute as those figured by Burks (1953:34, Fig. 67), but they followed his description in being slightly upcurved at the tips. The forceps also differed slightly from those figured by Burks.

Specimens tentatively identified as *Ephoron album* (Say) were sent to Dr. B. D. Burks. He verified the identification and added the specimens to the collection at the U. S. National Museum in Washington, D. C.

Nymphs

Ephoron album appears to be the only member of this genus to have been reported from Lake Erie. Since thousands of eggs were hatched in the laboratory and many mature nymphs were observed at the time of emergence, there was never any question as to the identity of the nymphs. In the field, where careful study could not be made, the small nymphs might be confused with small *Hexagenia* or *Ephemera* nymphs, but once seen through a microscope, they are easily distinguished from all other forms found in the island region of Lake Erie.

In general, the nymphs from Lake Erie agree with those described by Edmunds (1948:13–14) from Utah. A detailed description of mature nymphs of *Ephoron album* is given below.

Maximum length of males 17.4 mm., exclusive of caudal filaments and mandibular tusks. Lateral filaments about 12 mm., median 8.9 mm. Maximum length of females up to 20.5 mm., exclusive of caudal filaments and tusks. Lateral filaments about 6 mm., median 10 mm.

The head is concave where it joins the thorax. On the front is a sharply rounded frontal process or rostrum similar to that in *Hexagenia*. Across the front of the head and extending above the posterior end of the rostrum is a dense row of stiff, plumose hairs. On either side of the ends of this row of hairs is an antenna. Each antenna is composed of two relatively large basal joints and a slender, whitish, almost hairless flagellum of about 5 mm. in length. At the base of each antenna is a chitinous projection or "post-antennal" spine. The eyes and ocelli are jet black. The compound eyes of the males are much larger than those of the females (Fig. 5). The pigmented area of each member of the pair of ocelli form a crescent, while that of the median ocellus varies in shape from a straight bar to a half circle. The strong down-curving mandibular tusks

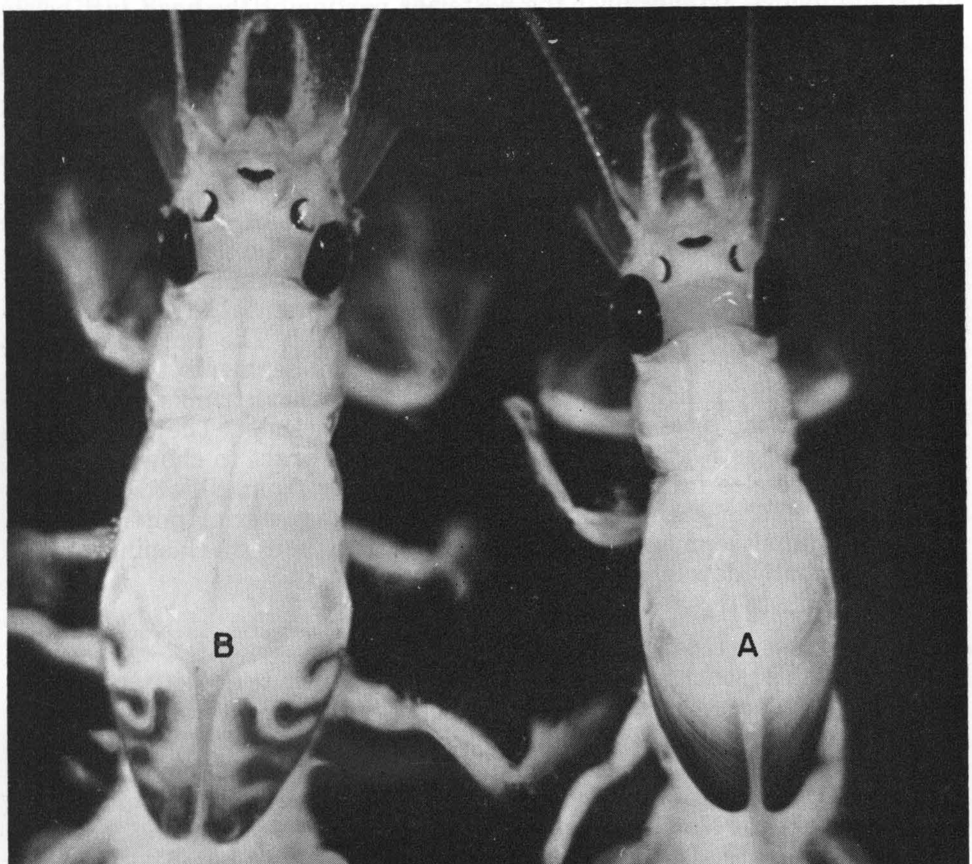

FIG. 5—Photograph showing the contrast between the size of the eyes of (A) male and (B) female *Ephoron album* nymphs. Convolutions in wing pad are shown in B.

have denticles and long hairs on their outer surfaces. The number of denticles on each tusk varies from 15 to 26 in males and from 18 to 31 in females. On the base of each of these tusks there are long plumose hairs arranged in the form of an oval and extending obliquely forward. There is also a small tuft of plumose hairs on the dorsal part of the tusk just in front of each antenna. In large specimens, the length from the molar surface to the tip of the tusk may exceed three millimeters. The comb-like structures on the galea-lacinia and the maxillary and labial palps consist of dense groups of plumose hairs with some smooth ones intermixed.

The forelegs are strong and well adapted to digging. There are two groups of long plumose hairs on the tibia and one on the femur. The hairs in each group are arranged in the form of an oval. Long, smooth hairs fill the spaces between the groups. There is a row of tubercles on the ventral surface of the basal half of the femur. The hind legs are weaker than the forelegs while the middle legs are much smaller and weaker than either of the other pairs. The middle and hind legs are less densely covered with hairs, but none are of the plumose type.

On each side at the anterior end of the prothorax there is a pointed projection which extends over the posterior portion of the head just below the eye. The pronotum appears to have a translucent yellowish-white color. The mesonotum is slightly more yellowish than the pronotum and shows faint bands of different color intensities, apparently the result of the muscles showing through the covering. The mesothoracic wing pads, during the stage prior to emergence, exhibit a pattern of convolutions due to the rapid growth and crowding of the wing inside the wing pad (Fig. 5).

The terga of the first six or seven segments of the abdomen are almost transparent, often permitting a view of the muscles and intestines in the males or of eggs in the females. Segments eight, nine, and ten usually have a light brownish-gray color obscuring the internal structures. Segments one to seven each posses a pair of lateral gills. The pair on segment one is very small and without branches. Those on segments two to seven have large double lamellae, but only the main tracheal trunks of each are pigmented. At the base of each gill is a dense black dot. The ventral side of the abdomen is whitish, allowing the digestive tract to show as a dark line. There are also faint lines extending obliquely from gill attachment to the anterior end of each segment. On the ventral posterior portion of the ninth abdominal segment of the male there is a pair of clasping organs and the partially developed divided penis.

Geographical Distribution

If Spieth's conclusion (Spieth, 1940a:111) that *Polymitarcys* is a synonym of *Ephoron* is accepted, this genus is then Holarctic in distribution. The distribution of *Ephoron album* is not well known due to the short life of the adults and the elusive habits of the nymphs. Entomologists and fisheries investigators have occasionally observed the adult of this species in various parts of North America. It has been reported from the following localities which are also shown on the distribution map (Fig. 6).

Manitoba, Winnipeg River, observed by Say in 1823 (Keating, 1824: 114, 305), North Red River (Hagen, 1861:40), Lake of the Woods on United States-Canadian border (Needham, 1921:286), Manitoba, several places (McDunnough, 1926:184), Lake Winnipeg (Neave, 1932:54; 1923: 186), Aweme (Daggy, unpublished thesis, 1941:56) ; *Ontario*, Rainy River (Keating, 1824:114), Credit River (Ide, 1935a:113), Pelee Island (Jenkins, unpublished thesis, 1939:10).

Idaho, Lewiston (Daggy, unpublished thesis, 1941:56) ; *Illinois*, northern Illinois (McDunnough, 1926:184), Ottawa (Needham, 1921:287), Foster, Kankakee, Momence, Prophetstown, St. Charles, Wilmington (Burks, 1953:35), Rock Island (Thew, 1958:9) ; *Iowa*, Fairport, Keokuk (Needham, 1921:286), Mt. Pleasant (Daggy, unpublished thesis, 1941:56) ; *Kan-*

sas (Banks, 1894:179); *Maryland*[2], Potomac River (Argo, 1927:321); *Minnesota,* Minneapolis, St. Paul, Coon Rapids on Mississippi River at Fridley, Anoka, Blue Earth River at Rapidan, Crookston, Browns Valley, Root River at Chatfield (Daggy, unpublished thesis, 1941:56); *Nebraska,* Parks (Needham, Traver, and Hsu, 1935:244); *New York*[2], Corning, Ithaca, Susquehanna River (Needham, 1921:286); *Ohio,* Cincinnati (McDunnough, 1926:184), Lake Erie (Wright et al, 1955:258), Gibraltar Island, Catawba Point, Sandusky (Jenkins, unpublished thesis, 1939:10); *Utah,* Jordan River, Bear River, Logan River (Needham and Christenson, 1927:16), Sandy (Edmunds, 1948:12); *Washington,* Pullman (McDunnough, 1926:184).

These records indicate that this species is most likely to be found between forty and fifty degrees north latitude. More intensive study of streams and lakes may broaden the known range of the species. As will be

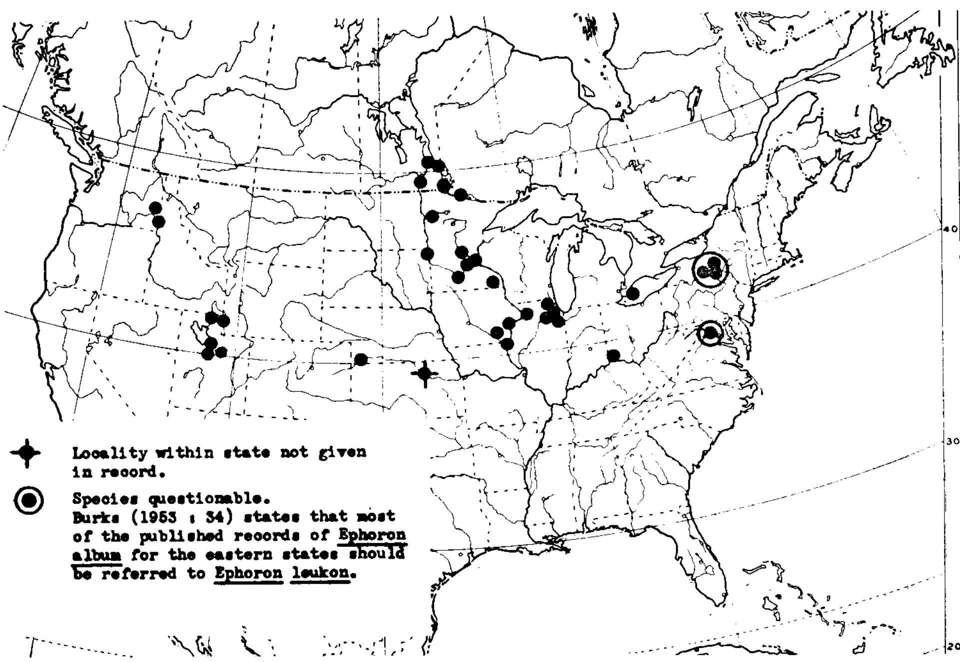

FIG. 6—Map showing reported geographical distribution of *Ephoron album.* Based on Goode Base Map No. 102, Copyright 1937 by the University of Chicago. Used by permission of the University of Chicago Press.

shown later, the eggs of *Ephoron album,* unlike those of most species of mayflies, require a period of cold weather to promote hatching. After the period of dormancy and cold weather, they require temperatures about 10° C. for hatching, and relatively high temperatures during a growing season of two and a half to four months. These temperature requirements may be responsible for holding the species within its narrow range, usually between forty and fifty degrees north latitude. South of this range where the

[2] Species questionable. Burks (1953:34) states that most of the published records of *Ephoron album* for the eastern states should be referred to *Ephoron leukon.*

winters are relatively mild, the eggs may not receive sufficient cold to promote their hatching. North of this range the water temperature may not rise above 10° C. thus preventing the hatching of the eggs. Even if the temperature does rise sufficiently to allow the eggs to hatch, the growing season may not be long enough to permit the nymphs to reach maturity and emerge.

Ecological Distribution

Argo (1927:321) dug the nymphs of *Ephoron* out of the sand and silt on the soft bottom of a slow-moving portion of the Potomac River. Ide (1935a:113) found the nymphs of *Ephoron leukon* in the Credit River. They were found in tubular burrows associated with stones in the rapids. He could find no nymphs under the loose stones in the rapids, but large stones, partially embedded in fine gray silt, when turned over often revealed nymphs clinging to the bottom and sides in the remnants of their tubular burrows. He also found that it was easier to collect the nymphs in the evening than during the day when the light was strong. He concluded that the nymphs are nocturnal and that they go deep into their burrows under the stones during the day and come to the upper part to feed when the light diminishes with the approach of night. Edmunds et al (1956:153) drew similar conclusions.

Ephoron album nymphs for this study were collected from the area in the vicinity of Oak Point (Fig. 2). This area has a heavy clay subsoil topped with three to eighteen inches of gravel and sand. There are a few boulders and the area has some fine detritus and silt intermixed with the gravel and sand. The nymphs were found about two to four inches below the surface of the gravel.

From observations made on the live nymphs placed in an aquarium containing gravel and sand, it was concluded that the nymphs made their burrows between the larger gravel particles by utilizing the small particles of sand and silt to fill in the spaces. On many occasions while collecting where the layer of gravel and sand was shallow, nymphs were removed from shallow burrows in the clay subsoil. No nymphs of this species were ever found in the soft bottom mud which is commonly inhabited by *Hexagenia* nymphs. Ide and Edmunds, et al. found the nymphs more difficult to collect during the day than at night. In this study nymphs were collected with equal ease at any time during the day or night. This was probably due to the different method of sampling which took bottom material to a greater depth. In aquaria the nymphs displayed a negative reaction to light during the day. By quietly approaching the aquarium at night and suddenly flashing on a light, it was often possible to catch the nymphs either partially or completely out of their burrows, apparently feeding on the detritus along the bottom. It is not known, however, whether this behavior occurs in the natural habitat or is a reaction to the conditions in the aquarium.

Having found the large population of *Ephoron album* nymphs inhabing the Oak Point shoal area, observations were made at other similar habitats around South Bass Island. The results indicated that this species can be found in this locality wherever there are suitable habitats.

It is not known to what depth the nymphs of this species may be found, but from the nymph collections and from emergence observations it is believed that the majority of the nymphs inhabit the bottom in water less than five feet in depth. They, like *Stenonema* and other stream forms found in the lake, always appear to be found where there are currents produced either by wave action or by seiches. Perhaps this distribution may be due to bottom types rather than to currents since this type bottom is found only where currents and waves come into contact with the bottom.

THE EGG

The average size of the egg of *Ephoron album* is about 0.37 by 0.21 mm. The eggs have a rather hard outer shell which is able to withstand much of the molar action of the sand in which they are found. The most striking characteristic, though, is the adhesive disc located at one end of the egg. If the egg comes to rest on a solid surface shortly after it is set free by the female, it becomes attached to this surface where it remains until it hatches or until it is scraped off by molar action or some other disturbance. Figure 14 is a photograph of a group of *Ephoron album* eggs showing the eyes of the fully developed embryos inside.

From some preliminary experiments started in September, 1948, enough information was obtained to suggest that the eggs of *Ephoron album* required a long development period associated with special temperature conditions. Eggs were removed from females captured during the evening mating flight, put into petri dishes containing lake water, and left on a table at room temperature. The water was changed every day for the first two months. About two weeks after the eggs were collected, the developing eyes of the embryos became visible. At the end of a month, the embryos appeared to be fully developed, and the collections were carefully examined each day for the expected hatching. After many weeks had passed with no apparent change in the eggs, they were neglected and the water allowed to evaporate from all except two of the collections, thus destroying most of the eggs. On February 12, 1949, after washing the eggs of the two remaining collections in very cold water, one nymph was observed about halfway out of the egg. No more observations were made until March 4, when it was discovered that a few eggs had hatched since the last observation, but all the nymphs were dead. Since these eggs had apparently been fully developed for many weeks, it appeared that the cold water used in washing the eggs on February 12 may have been sufficient stimulus to cause a few to hatch.

Other workers have experienced difficulty in hatching the eggs of this and other species of this genus. Joly (1876a:484) in his study of the embryology of *Ephoron virgo* (Oliver) mentioned the difficulty involved in getting the eggs to hatch. He found that from six to seven months were necessary for the hatching of eggs of this species. Ide (1935a:115) was unsuccessful in getting the eggs of *Ephoron leukon* to hatch until he exposed them to low temperatures. He concluded that low temperatures probably were a necessary stimulus for the hatching of the eggs. Edmunds, Nielsen, and Larsen (1956:148) did some hatching experiments on eggs of *Ephoron album*. They found that low temperatures had a stimulating effect on the eggs.

In the Lake Erie study another indication that either a long period of time or low temperatures were required for hatching is shown in the graph (Fig. 7). Eggs collected from the Oak Point habitat at intervals from January to July, 1949, showed a progressive decrease in the length of time required for hatching at room temperature (average room temperature, about 20° C.). The eggs collected on January 28 required eleven days to hatch while those which remained in the natural habitat until March or April required only about half as much time at room temperature. Those collected on June 10 showed very few hatches. Of the hundreds of eggs collected on June 29, only two hatched. This occurred on July 1. Collections made on July 5 and July 13 showed no hatching, thus the latest date at which eggs are likely to hatch in the Lake Erie region is about the middle of June.

As a check on the date of hatching in the natural habitat, eggs were collected on April 16, 1949, and placed in bottles filled with lake water. These bottles were then attached to an anchor and tossed back to settle on the bottom near the original habitat. The water was changed and the bottles were examined periodically for hatching eggs. The first hatchings

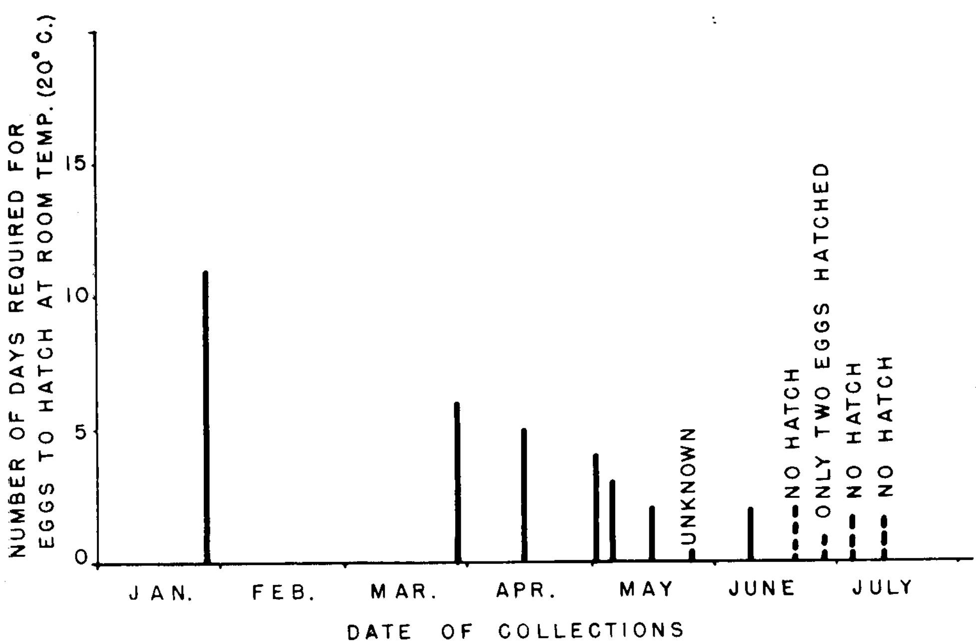

FIG. 7—Graph showing length of time required for the hatching of *Ephoron album* eggs collected at different dates.

occurred on April 30. The water temperature at that time was 13.2° C. Two days later, on May 2, two very small nymphs were found in their natural habitat. This appeared to substantiate the result of the hatching experiment.

In 1950 a similar experiment was performed, but the hatching date for that year was later. This was probably due to the slower rise in water temperature that year. On May 9 two nymphs were found in the bottle while the temperature was only 10° C. On May 10 there were approximately twenty-five nymphs, but the water temperature was still only 10° C. On May 20 the temperature had risen to 13° C. with the result that many eggs had hatched.

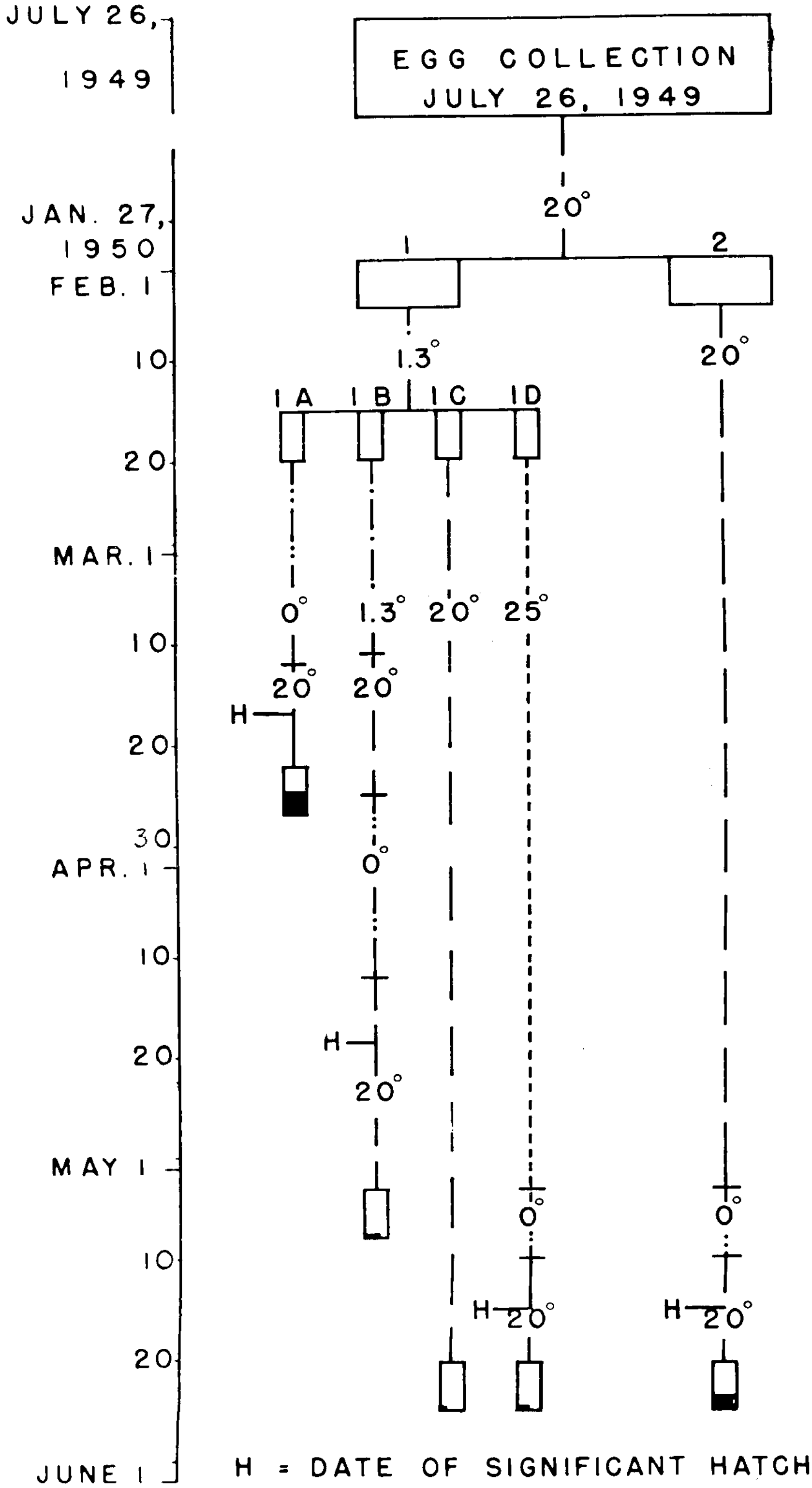

FIG. 8—Experiment 1. Effects of temperature on the hatching of *Ephoron album* eggs. 0° C. represents temperatures from 0°C. to —10° C.

From these experiments it was concluded that in their natural habitat in Lake Erie the eggs of *Ephoron album* begin to hatch when the water reaches a temperature of 10° to 13° C. In the five years in which this study was being conducted this occurred between the last of April and the middle of May. The end of the hatching period was found to be about the middle of June.

Effect of Temperature on the Hatching of Eggs in the Laboratory

The experience of Ide (1935a:115) suggested that a period of cold might be necessary to stimulate *Ephoron leukon* eggs sufficiently to cause them to hatch. The observations on *Ephoron album* also suggested the need for a period of cold during the incubation period. Experiments were conducted in the laboratory in an effort to determine the effects of temperature on the development of the eggs of *Ephoron album*.

Egg collections which had been kept at room temperature for several months and in which the embryos appeared to be fully developed were divided. The portions were subjected to temperatures averaging —6.9° C., 1.3° C., 25° C., 37.5° C., and room temperature (approximately 20° C.) for varying period of time. The samples held at —6.9° C. were held for several weeks in solid blocks of ice. The water in the other samples was either changed or aerated daily in the first part of the experiments; later, aeration was provided every three or four days.

Figs. 8 to 13 give, in condensed form, the complete procedure used and the results obtained. It can be seen in Fig. 8 that there was practically no hatching at any temperature until the various samples of eggs had been treated to a few days of freezing temperatures. Figs. 9, 10, 11, 12, and 13 also indicate that the efficiency of hatching is greatly increased by a period of freezing temperatures. The diagrams also indicate that better results were obtained if the eggs were subjected to the low temperatures relatively early in the experiments. It was shown that the eggs can withstand a wide range of temperature from below —6.9° C. to above 25° C. Temperatures of 37.5° C. seemed to be fatal to the eggs since there were no recorded hatches from any of the samples subjected to this temperature. Edmunds et al (1956:150) got no hatches from eggs immersed in water which was subsequently frozen solid, but they do not state the length of time they were kept at this low temperature.

Although the first four experiments (Figs. 8-11) appeared to indicate that temperatures of 0° C. or lower were necessary to insure the hatching of eggs, experiments 5 and 6 (Figs. 12 and 13) give a slightly different picture. Sample 1B in Figs. 8 and 9 remained at 1.3° C. only until March 11, while in Figs. 10 and 11, sample 1B remained at this temperature until March 24. In Figs. 12 and 13, however, samples 1A and 2, respectively, were allowed to remain at 1.3° C. until April 16, thus making a total of sixty-one days. After this long period of time at 1.3° C. there was a sufficient amount of hatching to modify the earlier indication of need for freezing temperatures.

The later experiments indicate that the near freezing temperatures have a cumulative effect thus giving results over a long period of time similar to those obtained by freezing temperatures for a short period. The number of eggs hatching in the later experiments, however, was significantly lower than in the experiments with freezing temperatures.

Since fully developed eggs were used in the above experiments, a question arose as to the effect of freezing temperatures on undeveloped eggs. Eggs removed from females captured on September 28 and September 30, 1950, were mixed with sperm in Hobson's Ringer Solution (Barnes, 1937:26). These were then transferred to lake water and allowed to remain at room temperature for only a few hours. The collections were subjected to freezing temperatures from October 1 until October 26, at which time they were permitted to come to room temperature. By Novem-

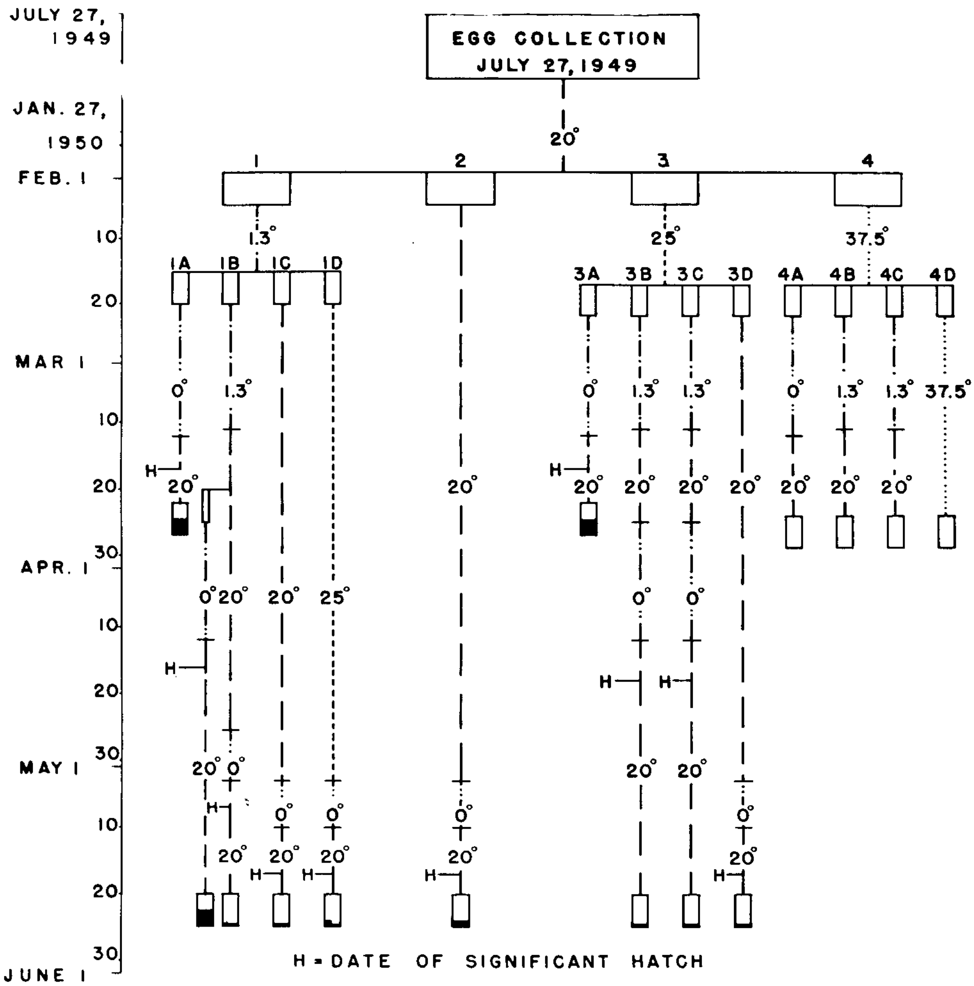

FIG. 9—Experiment 2. Effects of temperature on the hatching of *Ephoron album* eggs. 0° C. represents temperatures from 0° C. to −10° C.

ber 23, eye spots had developed in some of the eggs. By January 17, 1951, the eggs appeared to be fully developed and ready to hatch, but no hatchings occurred. On February 5, they were again subjected to freezing temperatures for several days. A few days after being allowed to come back to room temperature, several eggs hatched in each collection. Thus it appears that, in order to stimulate hatching, the low temperatures must come after the eggs are at least partially developed.

Another experiment was made to see if it would be possible for the eggs to hatch in the autumn of the same year in which they were deposited. Eggs were collected from their natural habitat on the bottom on October 6, 1950. Many of the eggs were fully developed by this time. These eggs

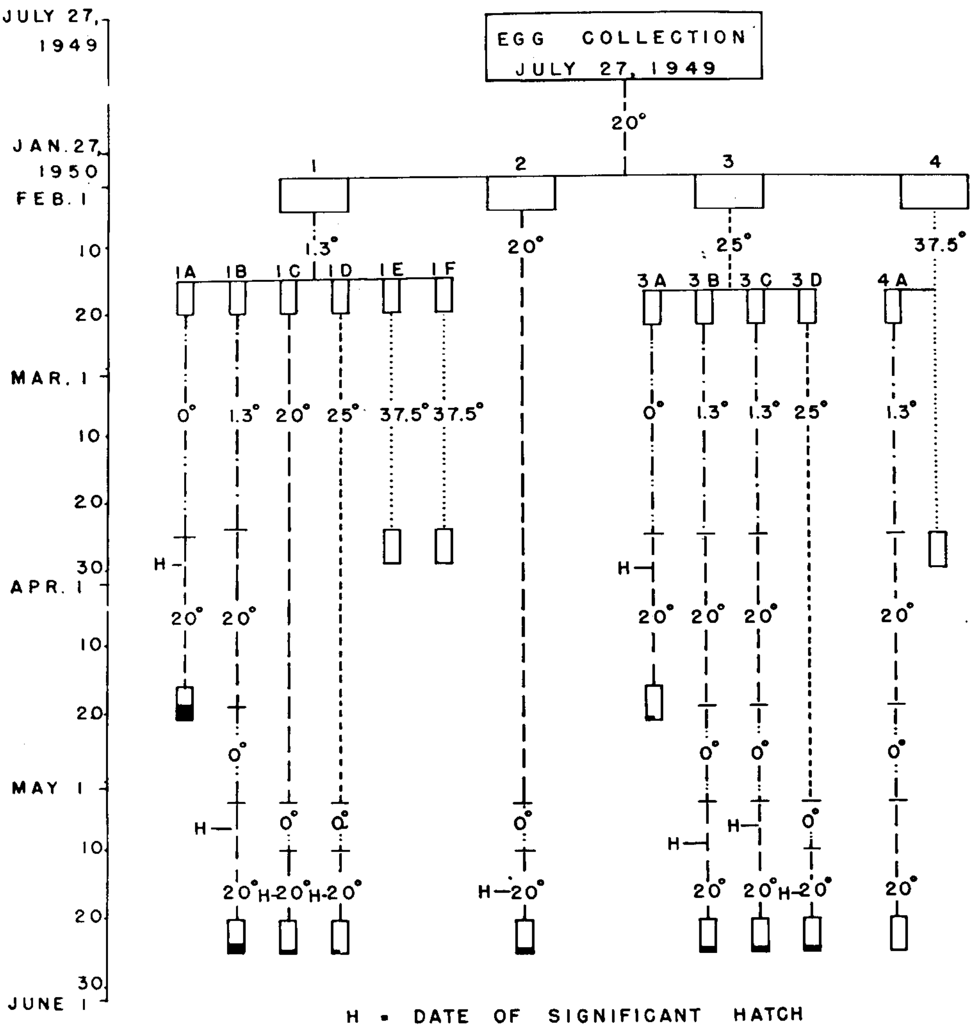

FIG. 10—Experiment 3. Effects of temperature on the hatching of *Ephoron album* eggs. 0° C. represents temperatures from 0° C. to —10° C.

contained in a small bottle of lake water were immediately subjected to freezing temperatures. On November 7, they were brought back to room temperature and by November 14, several hundred had hatched.

Although low temperatures appear to be necessary for the hatching of the eggs, the manner in which the low temperatures bring about hatching is not definitely known. It was thought that the low temperatures might cause a softening of the egg covering, thus permitting the nymph to break out. Several attempts were made to break or soften the coverings by mechanical or chemical means. Eggs which appeared to be ready to hatch were pricked with fine needles and left in water at room temperature, but no nymphs emerged. In other tests, samples of eggs were treated for 5 minutes with HCl and NaOH varying from the concentrated form to a dilution of 10,000 parts per million in lake water. Another sample had carbon dioxide bubbled through it for 10 minutes; then 15 minutes later it was aerated. None of these methods caused the eggs to hatch without the usual low temperature treatment.

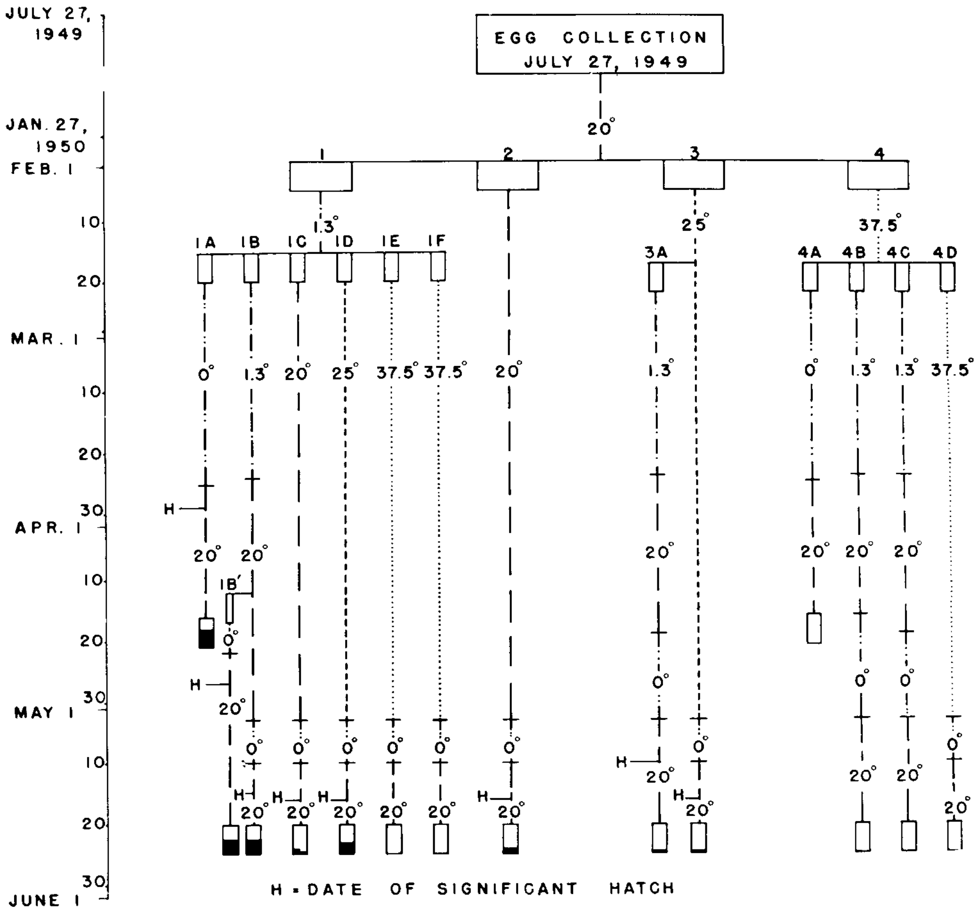

FIG. 11—Experiment 4. Effects of temperature on the hatching of *Ephoron album* eggs. 0° C. represents temperatures from 0° C. to —10° C.

Resistance of Eggs to Unfavorable Conditions

About two weeks after the above chemical tests, when it was evident that no hatchings were going to occur, the samples of eggs were given the freezing treatment for 12 days, then they were brought back to room temperature. Hatching was prevented only in the sample treated with concentrated HCl. In this case the embryos appeared to have been dissolved

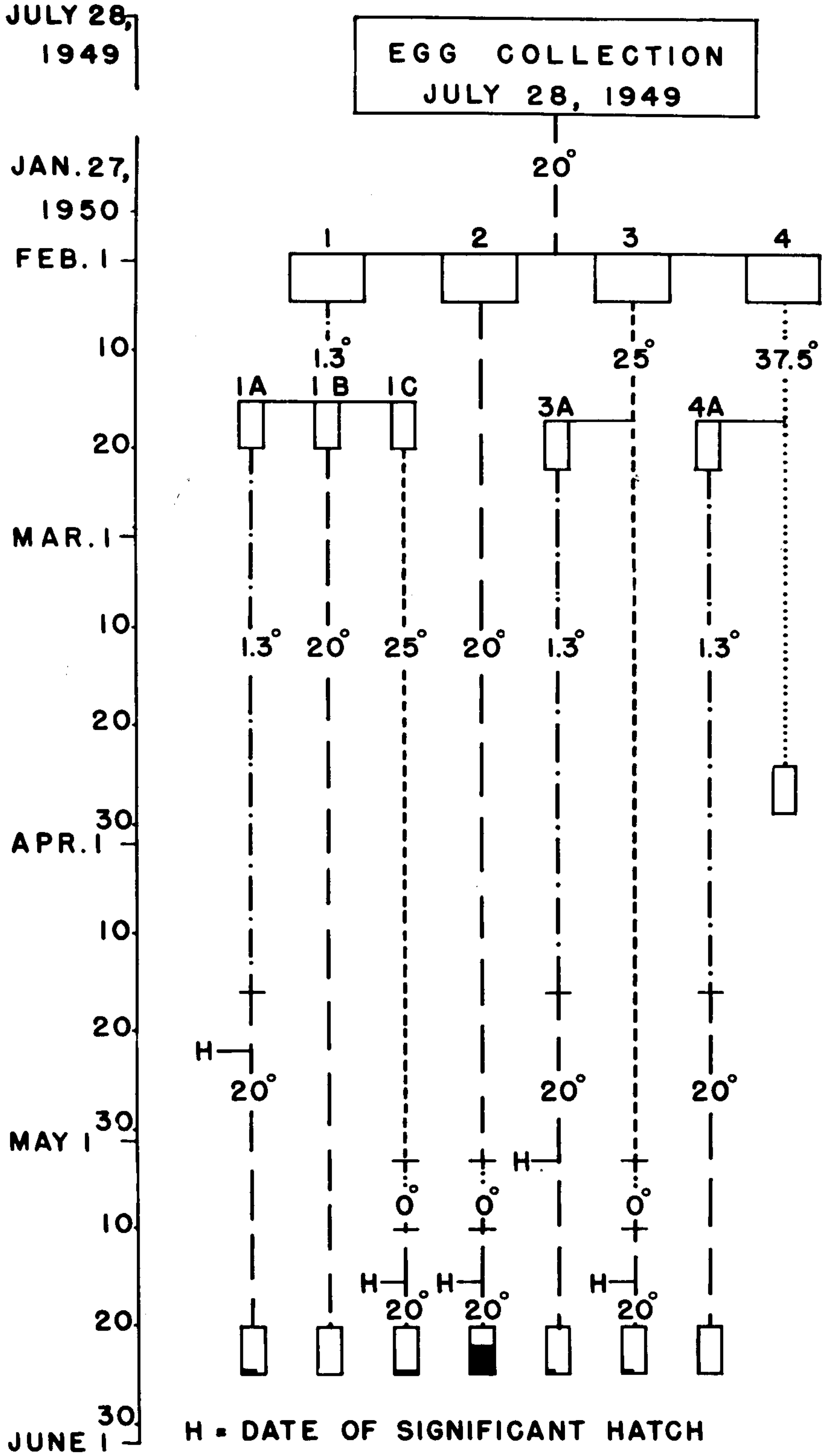

FIG. 12—Experiment 5. Effects of temperature on the hatching of *Ephoron album* eggs. 0° C. represents temperatures from 0° C. to —10° C.

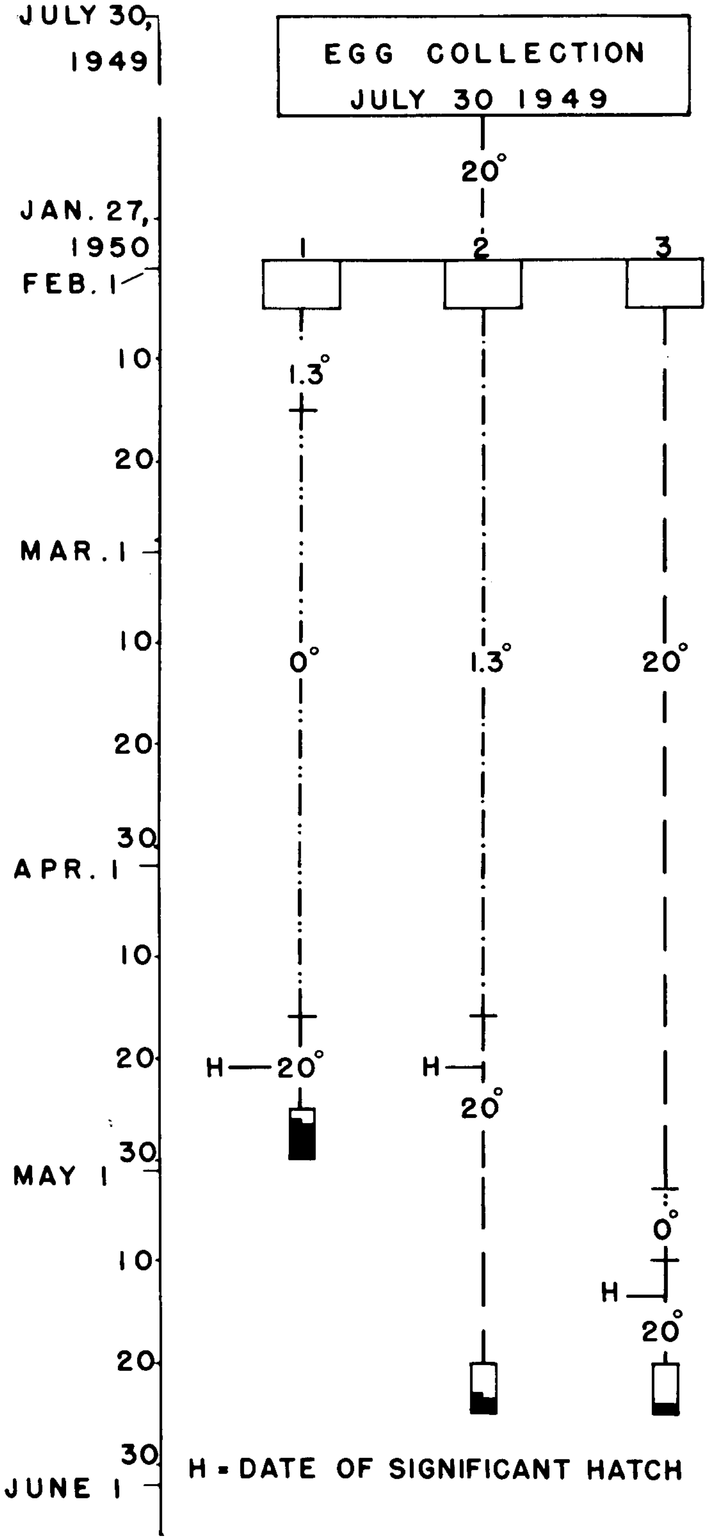

FIG. 13.—Experiment 6. Effects of temperature on the hatching of *Ephoron album* eggs. 0° C. represents temperatures from 0° C. to —10° C.

away, leaving the shell of the egg intact. In the other samples the number of eggs hatching appeared to be roughly proportional to the dilution of the chemicals. In other tests, eggs were removed from water and placed in a dry wide-mouth glass jar. The open jar was placed on a window sill outside the building. After 25.5 hours, the eggs were so dry that they would roll around inside the jar like grains of sand. Water was again added. No hatchings occurred during the following two weeks. The sample was then given the freezing treatment for 12 days. A few days after the sample was brought back to room temperature several eggs hatched.

In further checks on the effects of desiccation, a sample of eggs was kept in a dry, heated room for 25.5 hours. A second sample was kept for 102.5 hours outside a window where wind and sun could strike it and where the temperature was below freezing part of the time. A third sample was kept in an unheated garage for 102.5 hours. After the period of desiccation, water was added to all samples. These were then left at room temperature for about two weeks. No hatching occurred, so they were exposed to freezing temperatures for 12 days and again permitted to come to room temperature. No hatching occurred in the first and second samples, but several eggs hatched in the third sample.

These experiments indicate that the eggs are capable of withstanding a limited amount of desiccation. This is probably an important factor in the survival of the species in the Oak Point habitat since the habitat is often exposed to drying conditions when seiches occur during periods of low water (Fig. 3). Since the eggs are intermixed with sand and debris which would protect them from the sun and wind, it would be possible for them to withstand relatively long periods of low water.

In order to check the resistance of the dormant eggs to low oxygen conditions, a large collection of eggs was taken from the natural habitat on November 30, 1949. This collection, containing the small particles of sand clinging to them, was placed in a four-ounce bottle which was filled with water, tightly sealed, and then placed into a beaker in a darkened corner of a sink where a continuous stream of very cold (1.5° to 4° C.) lake water was allowed to flow over it. Sixty-four days later, on February 1, 1950, the bottle was opened for the first time. Strong odors of a hydrogen sulfide or marsh gas nature were noted. The eggs and particles of sand had become very dark in color. It was hard to believe that anything could have survived in this unaerated water, but after the eggs had been washed and aerated, much of the dark color disappeared and the eggs appeared to be alive. The bottle was allowed to come from the near freezing temperature to room temperature and was connected to an aerating pump. A few days later hundreds of eggs hatched. Since the eggs were able to withstand these conditions, it appears that the oxygen consumption during dormancy is very low.

Number of Eggs Produced by Each Female

Joly (1876b:14) counted the eggs produced by *Ephoron virgo* (Oliver) of Europe and found that each ovary produced more than 400 eggs for a total of over 800 eggs per female.

Egg counts were made on 22 *Ephoron album* females collected at different dates between August 1 and September 13, 1949. Included in Table 1 are the results of these counts. The average number of eggs per individual

TABLE 1

NUMBER OF EGGS PRODUCED BY INDIVIDUAL *Ephoron album* FEMALES

Date of Collection	Number of Females	Number of Eggs Per Female	Ave. No. Eggs Per Female
Aug. 1, 1949	9	. .	1393
Aug. 10, 1949	2	1672	
		912	1292
Aug. 29, 1949	5	1020	
		949	
		838	
		778	
		670	851
Sept. 4, 1949	5	979	
		913	
	(2 females)	1652	891
Sept. 13, 1949	1	593	593

Average number of eggs per female for all collections—908.

based on the 22 females was 908. The largest number from a single specimen was 1672 while the smallest was only 593. It was expected that the individuals emerging late in the season would show a somewhat smaller number of eggs than those emerging early in the season. In general, the averages for the different collections do show a decrease in the number of eggs per female as the emergence season nears its end.

Distribution of Eggs in Water

The large swarms of mating *Ephoron album* adults and the accompanying deluge of females striking the water, ejecting their eggs, and dying, make it apparent that the number of eggs deposited during the entire emergence season must reach astronomical figures. Collections were made on seven evenings to determine the number of eggs deposited per given area. On none of these evenings was the emergence as great as it was at several other times. On August 8, 9, and 10, the emergence was extremely small. Table 2 gives the number of eggs collected in the battery jar each day and the calculated number per square meter of bottom. The largest number of eggs collected in one evening was 7,609, with a density of 442,235 per square meter.

This figure may be abnormally high due to a concentration of the swarm over the area of the collecting jar. Table 3 shows that on July 27 an average of 462 nymphs were found per square meter. If we assume that

TABLE 2

DISTBIRUTION OF *Ephoron album* EGGS IN WATER OFF OAK POINT

Date of Collection	Number of Eggs Collected	Number of Eggs/Square Meter
August 1, 1949	147	8544
August 3, 1949	303	17610
August 4, 1949	7609	442235
August 6, 1949	3908	229458
August 8, 1949	42	2441
Totals	12094	702903

before July 25, when the emergence season began, the population was twice this size and that 50%, or 462, were females, which deposit an average of 908 eggs, we arrive at an estimate of 419,496 per square meter of bottom produced by one population.

The Nymph

Joly (1876b:47) figured the egg and the young nymph of *Ephoron virgo* (Oliver). His drawing of the nymph, however, appears to be rather diagrammatic. Ide (1935a:118) made drawings of structures of the first and second instars of *Ephoron leukon* which appear to be almost identical to the corresponding structures of *Ephoron album* nymphs of the first and second instars.

TABLE 3

Number of *Ephoron album* Nymphs per Square Meter of Bottom at Oak Point

Date of Collection	No. of Samples Per Collection	Nymphs Per Square Meter	Daily Average
July 27, 1949	5	485	
July 27, 1949	5	439	462
Aug. 1, 1949	5	277	
Aug. 1, 1949	5	254	265.5
Aug. 10, 1949	10	127	
Aug. 10, 1949	10	219	173

First Instar

The nymphs were quite active from the moment of hatching. They were negatively phototactic and escaped the light by crawling under particles of sand and debris. Within a few minutes after hatching, they began to feed on the material (probably of bacterial and plankton nature) covering the small particles of sand and masses of eggs.

They had relatively long compodeiform bodies ranging in length from .732 mm. to .904 mm. and averaging .850 mm. exclusive of the caudal filaments. Their bodies were almost transparent, except for the yolk material extending along each side of the digestive tract. There were no gills at this stage (Fig. 15). Each of the three caudal filaments had four joints. The middle filament was the longest having an average length of .346 mm. while the lateral filaments were only .253 mm. long. The end of each filament had three hairs, the third joint had two to three hairs while the second joint had at least one hair. There was a pair of long, stiff hairs on each of the abdominal segments 8 and 9, while there may or may not have been a pair of short ones on segments 6, 7, and 10. On the foreleg there was one spur on the tarsus and one on the tibia. The head was about .106 mm. in width, and had a pair of poorly developed compound eyes, three ocelli, and a pair of antennae. Each antenna was composed of two basal joints and a three-jointed flagellum (Fig. 15). Measurements of segments 1 to 5, respectively, were as follows: .012 mm., .028 mm., .057 mm., .065 mm., and .085 mm. The total length of each antenna was .247 mm.

The length of time required to complete this stage probably varies with the conditions of temperature and food. In three instances, where accurate records were kept on laboratory specimens, it was found that five days were required for completing this stage. In the natural habitat, when conditions are favorable, probably less time is required.

Second Instar

The general form of the second instar nymph was much like that of the first instar; however, there were some noticeable changes. The length of body averaged about 1.091 mm. The most striking change in the second instar was the appearance of six pairs of short, lateral gill filaments on abdominal segments 2 to 7. These filaments had no trachea and were ap-

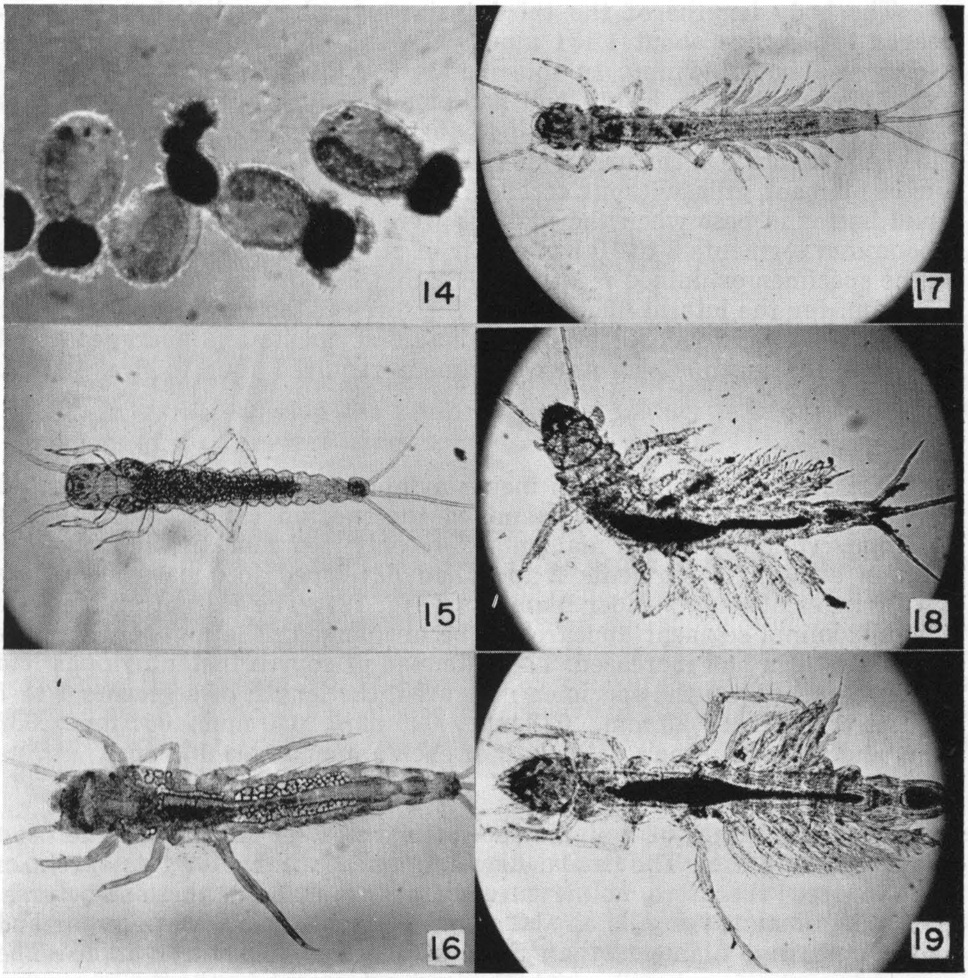

PLATE I—Photomicrographs showing some early stages in the development of *Ephoron album* (Say).

FIG. 14—Eggs showing the eyes of the well-developed embroys inside.
FIG. 15—A first instar nymph (ventral view).
FIG. 16—A second instar nymph (ventral view).
FIG. 17—A third instar nymph (dorsal view).
FIG. 18—A fourth instar nymph.
FIG. 19—A fifth instar nymph.

proximately the length of the abdominal segments to which they were attached (Fig. 16). A pair of stiff hairs were found on each of the abdominal segments 5 to 10. The foreleg had one spur on the tarsus and two on the tibia. The antennae had the same number of segments as those of the first instar nymphs, but there was an increase in size. In the case where measurements were made, the segments from 1 to 5 gave the following measurements respectively: .020 mm., .028 mm., .073 mm., .081 mm., .085 mm., and a total length of .287 mm. In the laboratory, this stage appeared to last from 4 to 6 days, depending on the conditions in the rearing bottle.

Third Instar

The body lengths of the third instar nymphs varied, but they appeared to average about 1.131 mm. while the head-width measurements averaged about .134 mm. In this instar, the gill filaments on segments 2 to 7 had doubled in length and had small protuberances about midway between the point of attachment and the tip (Fig. 17). In this stage the gills had trachea. On the first abdominal segment there was a pair of small single filament gills without trachea. These were difficult to locate, but could be found best when the nymphs were viewed from the dorsal side. Abdominal segments 3 to 10 had a pair of stiff hairs. The caudal filaments of the specimen examined measured .532 mm. for the median filament and .359 mm. for the lateral filament. On the foreleg, the tarsus had one spur and the tibia had four. Each antenna had 6 segments and averaged about .334 mm. in length. Laboratory specimens required four to five days to complete this stage.

Fourth Instar

The body length of fourth instar nymphs varied from 1.144 mm. to 1.463 mm. On the specimen examined the median caudal filament was .668 mm. while the lateral filaments were only .387 mm. In this stage the gills on abdominal segments 2 to 7 had developed into flattened plates with fringes of long, slender filaments (Fig. 18). The pair of gills on the first abdominal segment appeared to be unchanged. The number of spurs on the forelegs had increased. The antennae of fourth instar nymphs had seven segments. On the specimen measured, the length of segments 1 to 7 respectively were: .020 mm., .037 mm., .045 mm., .040 mm., .057 mm., .089 mm., and .089 mm. The total length of each antenna was .377 mm.

Fifth Instar

The body length of a single specimen was 1.565 mm. while the head width was .173 mm. The caudal filaments and antennae of this specimen were injured; therefore, no measurements were made of these structures. In the fifth instar, the gills on abdominal segments 2 to 7 were larger and had more fringe filaments than those of the fourth instar nymphs. The second branch of each gill which began development in the fourth instar had become partially fringed and was about half the length of the other filament (Fig. 19). The pair of gills on the first abdominal segment was still quite small. Long, parallel hairs, arranged in the form of an oval on the forelegs and side of the head, appeared for the first time in this instar. The mandibular tusks became prominent in the fifth instar. The tusks of the specimen studied extended .067 mm. beyond the rostrum. Each antennae of this fifth instar nymph was composed of 8 segments.

Sixth Instar

The body length of the single specimen studied was 1.512 mm. This was slightly less than that of the fifth instar nymphs described above. This apparent decrease in body length was probably due to individual variations which are quite noticeable from the time of hatching. There is also the possibility that sexual differentiation had begun at this stage. The head width was .186 mm., or slightly greater than that of the fifth instar nymph. The gill filaments on segments 2 to 7 showed an increase in area with the smaller branch of each between one-half and two-thirds the length of the other. The mandibular tusks of nymphs in this instar were about twice the length of those of the fifth instar nymphs. Each antenna consisted of 9 segments, although segments 3 and 4 were not distinctly separated. The total length of each antenna was .633 mm.

Other Nymphal Stages

The nymphs were difficult to rear above the fourth instar; however, a few were kept in individual petri dishes with some sand and water until they had reached the fifth or sixth instar. If they were placed in bottles of water and sand, some lived and continued to grow for some time. However, it was difficult to recover the cast skins and thus keep a record of the stages through which the nymphs passed. On one occasion, a nymph was reared in this manner until it was about half the size of a mature nymph, but the number of stages it had passed through was unknown.

Since the life of the nymph is relatively short and the growth quite rapid, it is believed that the total number of instars is less than that of members of the genera *Ephemera* and *Hexagenia.*

Growth

Ephoron album nymphs were not successfully cultured beyond the sixth instar in the laboratory. Therefore, in order to study growth, it was necessary to make frequent collections of nymphs from their natural habitat. The nymphs were collected by the use of the shovel and sieve method described earlier in this paper. The specimens were brought into the laboratory, killed, preserved, and eventually measured. Three measurements were made of each: (1) total length exclusive of the long cerci and mandibular tusks, (2) width of the head just back of the antennae, and (3) diameter of the eye.

From these measurements and from some measurements taken on recently hatched nymphs in the laboratory, the range of total length was found to be from .732 mm. for a recently hatched nymph to 20.700 mm. for a female nymph just before emergence. The head widths varied from .106 mm. to 1.760 mm. The eye diameter was not determined on the very small individuals, but the maximum eye diameter for a male was 1.12 mm. while that of a female was only .93 mm.

Britt (1953b:802) has shown that head-width measurements are the least variable under the different states of preservation; therefore, this measurement was used in the plotting of the size-frequency distribution shown in Fig. 20.

Since it is known that the eggs of *Ephoron album* began to hatch about the first of May in 1949, there should have been a large population of small individuals in the May 26 collection. As only three specimens were

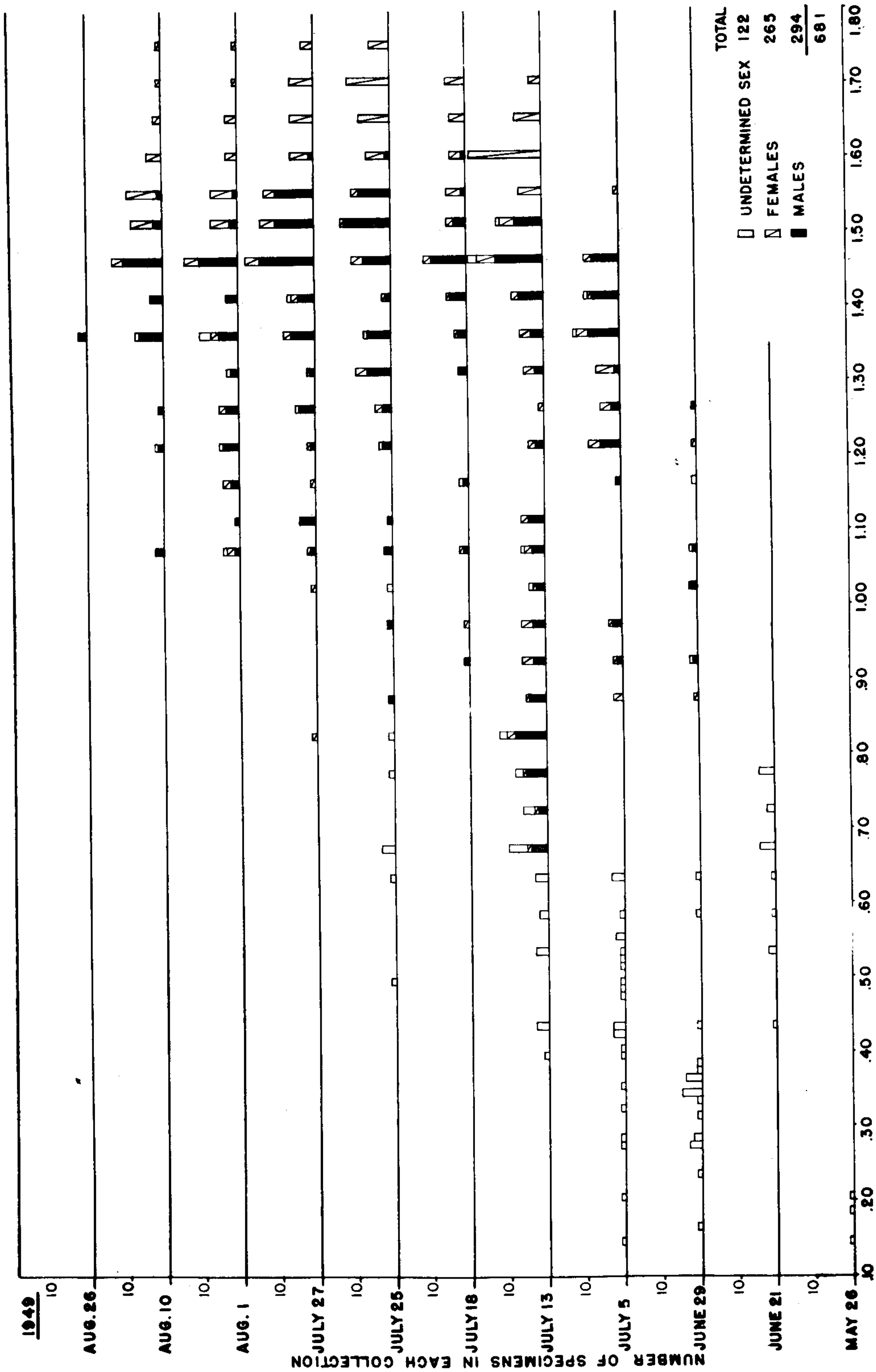

FIG. 20—Graph showing size-frequency distribution of *Ephoron album* nymphs at different dates.

found, it was assumed that the sieves used did not have small enough openings to retain them. The June 21 collection was a relatively large collection, but the vial containing it was accidently broken and all the smaller specimens lost. The July 18 collection also was not a representative sample since it was taken only to determine the size of the large individuals in order to see if they were ready to emerge. The small ones were not removed from the sieves.

In the graph (Fig. 20) it can be seen that there was a gradual increase in the maximum size of the individuals in each of the collections up to and including that of July 25. It can also be seen that from about the middle of July until August 10 increasingly greater numbers of individuals fall into the size groups between 1.20 mm. and 1.76 mm.

The size group containing the largest number of males was that of 1.47 mm. This seems to indicate the point at which the emergence of the males began. The corresponding point for the females was not quite as distinct, but seems to have been between 1.61 mm. and 1.71 mm., thus indicating that the emerging females were larger than the males.

In the graph (Fig. 21), the date and the average head width for each collection for the 1949 and 1950 seasons are given along with a graph of water temperature. The eggs of *Ephoron album* began to hatch on the last day of April, 1949. As the water became warmer, the nymphs grew at a very rapid rate, completing their growth before the end of July. The eggs which they deposited did not begin to hatch until May 9, 1950.

While making measurements of the nymphs, it was noted that if the specimen was well preserved there seemed to be a rather close correlation between the head width and the total body length. In an attempt to check this observation, specimens of each sex were grouped according to their head width. The average body length of each group was determined. This was then plotted on a graph opposite the head width (Fig. 22). A study of this graph indicates that in males body length is directly proportional to head width. There appears to be the same relationship in the females until they reach a head width size of 1.4 mm. and a total length of 13 to 14 mm. At this stage, the total length of the female increases more rapidly than the width of the head. This is about the stage when the eggs begin to develop.

While collecting well developed nymphs, it quickly became apparent that the males had much larger eyes than the females. This is not a characteristic peculiar to *Ephoron album* alone, but is shared with many other species of mayflies. In the small nymphs where sex determination was difficult, there seemed to be no noticeable difference in the size of the eyes.

A total of 285 males and 261 females were grouped according to head width. The average eye diameter for each group along with its head width was plotted on the graph (Fig. 23). On this graph, nymphs having head widths of .68 mm. and .73 mm., which is the smallest size that can be sexed accurately, show no divergence between the males and females. As the nymphs increase in size, the eyes of the males grow much faster than those of the females, thus giving two widely separated lines on the graph.

At the time of emergence, the eyes of the male nymphs vary from .95 mm. to 1.12 mm. in diameter while those of the females vary from .60 mm. to .93 mm.

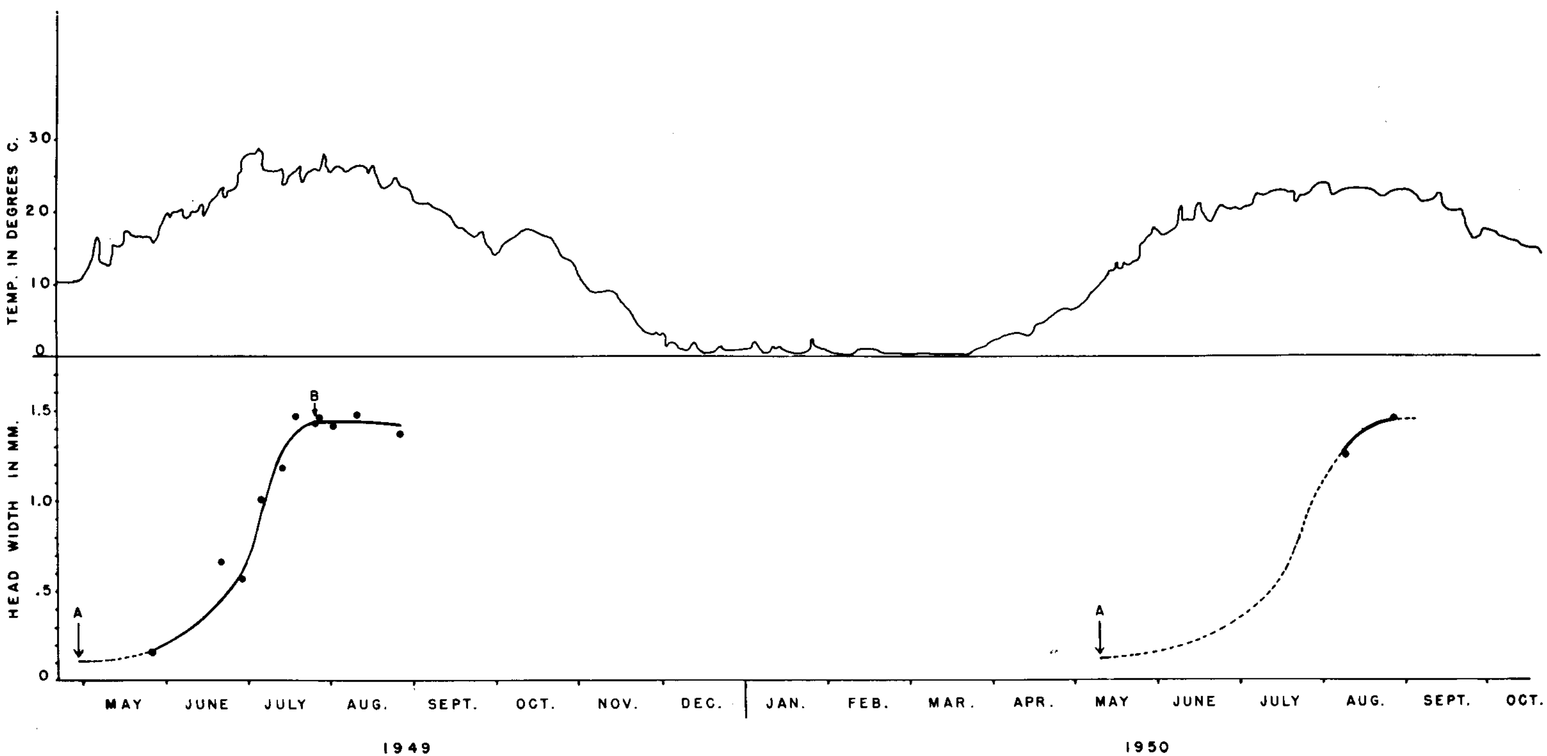

FIG. 21—Graph showing average growth of *Ephoron album* nymphs in 1949 and 1950 along with a graph of water temperatures for the same period,

Food

The contents of the digestive tracts of several *Ephoron album* nymphs were examined. Much of the material was indistinguishable, probably as the result of being ground by the well developed molar surfaces on the mandibles. There were fragments of filamentous algae, some plankton forms such as *Pediastrum, Navicula,* and *Fragilaria,* and one colonial protozoan.

Nymphs were brought into the laboratory and kept in glass containers partially filled with sand and water. Usually, within a few minutes after release in the water, the nymphs had buried themselves in the sand. When

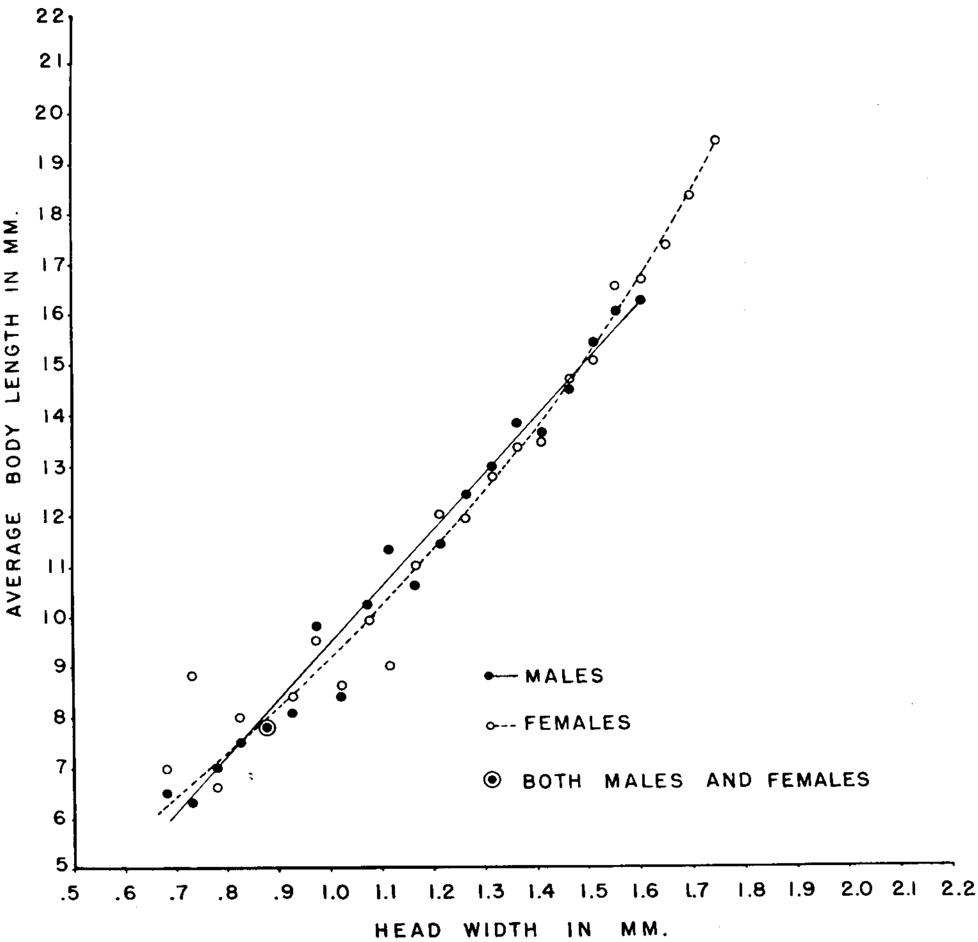

FIG. 22—Graph showing the relationship between head width and average body length of male and female *Ephoron album* nymphs.

the burrow was in contact with the glass, the activity of the nymph could be observed. Its behavior appeared to be about the same as that of other burrowing forms of mayflies. It kept its gills in motion most of the time, thus creating a very noticeable current in the burrow. Small particles suspended in the water were quickly drawn into the burrow where they were caught in the brushes on the forelegs and head of the nymphs. The nymphs were observed to bring the forelegs together beneath the mouth occasionally, and from the movements of the mandibles it was evident that something was being eaten. By suddenly flashing on a light at night, the nymphs often were observed to be either partially or completely out of their burrows. Individuals were observed to extend the head and thorax out of the burrow and with the forelegs rake up a quantity of the slime and debris covering the sand and draw it into their burrows where they proceeded to eat some and sweep the remainder out of the burrows by creating a current with their gills.

From these and other observations, it was concluded that in nature the nymphs probably utilize the bacteria, algae, plant debris, and plankton organisms that are found on or near the bottom. In the laboratory

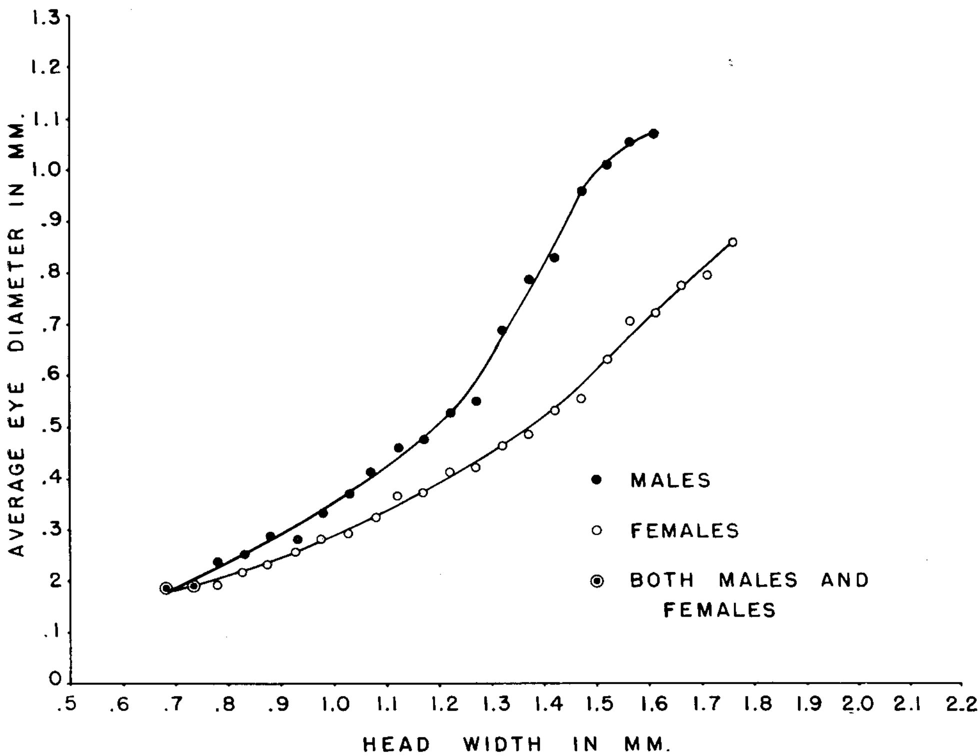

FIG. 23—Graph showing the relationship between head width and average eye diameter of male and female *Ephoron album* nymphs.

some nymphs were fed on yeast, but these died after a few days of feeding. It was not determined whether death was caused by the consumption of the yeast or by the fouling of the water resulting from the decomposition of the excess yeast.

The food and feeding habits of nymphs of mayflies have been subjects of interest and speculation for many years. As far back as 1737, Swammerdam (Needham, Traver, and Hsu, 1935:6) found that the food of the nymphs of *Ephoron virgo* (Oliver) consisted largely of clay and bottom mud. Joly (1876b:47) in discussing the food of this same species, stated that he believed they got their nourishment not from the mud, but from the animal and plant debris mixed with the mud. He considered the mud to be only incidental, being swept into the digestive tract along with the organic matter. In 1926 Wissmeyer reviewed previous literature on the feeding habits of mayfly nymphs and added the results of his own experiments on this subject. He concluded that in nature mayfly nymphs depend largely on plant food, while there are a few species that are definitely carnivorous. Morgan (1913:386) found that diatoms were the principal food of *Hexagenia* and *Blasturus*.

In his description of *Ephoron album* nymphs, Argo (1927:321–322) mentioned the elaborate strainers of parallel bristles of the forelegs and mouth parts. He assumed that these were used as sieves for getting the available food from the ooze and silt of the bottom. These assumptions appear to be substantiated by the result of laboratory observations and by the study of the stomach contents of nymphs taken from Lake Erie.

Maturation

In Lake Erie the nymphs of *Ephoron album* completed their growth and emerged within approximately three months after hatching from eggs. As the nymphs neared the stage where emergence was imminent the wing pads became dark along the borders. These dark areas were actually the developing veins of the front edge of the wing which showed through the transparent sacs that enclosed them. In the last nymphal instar the wings grew more rapidly than the enclosing envelope. This caused the wing to be crowded and resulted in the folding of the wing. This crowding causes the dark lines inside the wing pads of some specimens to show up as convolutions (Fig. 5B).

Since the adult life of *Ephoron album* is so brief, one is led to wonder if maturation of the egg and sperm may not take place before the emergence of the subimago. Examination of the reproductive organs of the male nymphs revealed very active sperm. The maturity of the eggs could not be readily ascertained; therefore, two experiments were made to check for hatching. In one, eggs from a nymph were mixed with sperm from an adult, using only a drop or two of Hobson's Ringer Solution. In the other, eggs from a nymph were mixed with sperm from a nymph in the same manner as above. Each of these groups of eggs were then transferred to small bottles of lake water and given the treatment described earlier for hatching eggs. Many eggs hatched in each bottle, thus indicating that the eggs are mature before the nymphs leave the water.

Another observation resulting indirectly from the above experiments is interesting when the short lives of the adults are considered. In one case spermatozoa were found to still be active in an adult that had been dead for 16 hours. This represents many times the adult life span of an individual of this species.

THE WINGED STAGES

Emergence

In Lake Erie the first emergence of *Ephoron album* adults of the year was recorded on July 25, 1949. From this date until September 20, at least a few adults could be found; however, the number at this later date was very small. Quantitative collections of nymphs were made on July

27, August 1, and August 10, 1949. The results are shown in Table 3. From these results it can be seen that the population decreases rather rapidly during the first two weeks of the season. This decrease is assumed to be due to the emergence of the maturing nymphs.

Many observations were made on their daily emergence and flight during the long emergence season of about sixty days. Notes on the air temperature, water temperature, light, sky conditions, and times of maximum emergence have been included in Table 4. From this it can be seen that the longest period of time from the first emergence in an evening until

TABLE 4

TENT TRAP COLLECTION DATA

Date	Water Temp. C.	Light*	First Adult Observed E.S.T. P.M.	Last Living Adult Observed E.S.T. P.M.	Tent Trap Results		
					Time P.M.	Number Caught	Total
July 27, 1949	26.5	..	8:10	9:15	8:40	12	
					8:55	4	
					9:10	0	16
July 28, 1949	27.0	..	8:08	9:15	8:30	24	
					8:45	23	
					9:00	10	
					9:15	5	62
July 29, 1949	27.0	..	8:00	9:25	8:15	2	
					8:30	47	
					8:45	38	
					9:00	4	
					9:15	0	91
July 30, 1949	24.0	..	7:46	9:10	8:00	0	
					8:15	4	
					8:30	17	
					9:00**		21
July 31, 1949	26.0	3.2	8:04	8:57	8:15	0	
					8:30	0	
					8:45	0	
					8:55	1	1
August 1, 1949	25.5	6.5	7:59	9:20	No emerging individuals caught		
August 2, 1949	25.5	.2	8:08	9:05	8:15	0	
					8:30	1	
					8:45	0	
					9:00	0	1
August 3, 1949	26.8	3.2	8:01	9:12	8:15	0	
					8:30	0	
					8:45	3 F***	
					9:00	0	
					9:15	0	3
August 4, 1949	26.5	3.2	7:59	9:23	8:15	2 M	
					8:30	3 M, 3 F	
					8:45	5 F	
					9:00	0	
					9:15	0	13
August 5, 1949	26.5	1.6	7:44	9:25	8:15	2 M	
					8:30	11 M, 14 F,	
					:	12 U	
					8:45	1 M, 3 F	
					9:00	1 M	
					9:15	0	44
August 6, 1949	26.5	6.5	7:48	..	No observations made on traps		

* Light readings based on Weston Master Photoelectric Meter pointed toward sky.
** Strong winds and wave action made collecting impossible.
*** Some collections were checked for sex. M = males, F = females, and U = undertermined sex.

all adults were dead was on August 5, when the period extended from 7:44 p.m. until 9:25 p.m., i.e., a period of one hour and forty-one minutes. This represents the time during which live adults were seen, but it is believed that the emergence period is much shorter. The records of the tent trap collections that same evening confirm this belief (Table 4). According to these records only one specimen was collected at 9:00 p.m., and none was collected after that time. On the evening of July 29 there was a very large emergence. From 8:00 to 8:15 p.m. only two specimens were trapped and only four were trapped between 8:45 and 9:00 p.m. During the thirty minutes between these two periods 85 specimens were trapped. From this and other observations it was concluded that the emergence period usually lasted considerably less than an hour, and that it usually occurred between 8:15 and 9:00 p.m., E.S.T. This was several minutes after sunset when there was still just enough light for one to be able to recognize the white mayflies.

The manner in which a mayfly nymph suddenly changes into a subimago and takes to the air has long been a subject of interest. Many records of observations on the different species show that in some species the usual manner of making this change is for the nymph to crawl up above the surface of the water on a stone or other object, there shed the nymphal skin, and then fly to some object on shore. In some species the nymphal skins are shed either at the bottom or in the water between the bottom and the surface. There are others that rise to the surface as nymphs, shed their skin, and then take flight in a matter of seconds. *Ephoron album* appears to be in this latter group. The transformation and flight are so rapid that there seems to be hardly a pause at the surface. The subimagos appear to fly directly out of the water. In order to check this, attempts were made to catch the nymphs in nets on the way to the surface. Several nymphs were caught in this manner, but when lifted to the surface they molted almost instantaneously and the subimagos flew away. The transformation took place so quickly that before one could seize the nymph with his hands, it had transformed and the subimago was on its way.

To study the manner of emergence in detail, a tall glass hatchery jar containing some sand was filled with water, and last-instar nymphs were placed into this jar. A wire ring with cheesecloth over it was then pushed down a few inches below the surface of the water thus blocking any nymphs on the way to the surface. On August 11, 1949, a nymph was observed to rise in the water until it was against the cheesecloth net. It seemed to be unable to stay down, apparently being buoyed up by some form of gas. This nymph was quickly removed from the water and thrust into a bottle of Bouin's Fixative for future study. Some other nymphs, on rising, found a hole in the net and reached the surface where transformation took place within a few seconds.

Table 4 appears to show evidence that changes in the temperature of the water affect the emergence of subimagos. When the water temperature was 27° C. on July 27 to 29, there were very large emergences. When the water temperature dropped to 24° C. on July 30, there was also a drop in the number of emerging mayflies, but an even greater drop was noted the next day even though the water temperature had come back up to 26° C. After the water temperature had been around 26.5° C. for a few days the number of mayflies emerging gradually increased.

Although this appears to indicate that a change of a few degrees in temperature may have a decided effect on the emergence, there were other factors associated with the drop in temperature that may have been equally important. Strong northeast winds caused strong wave actions at the area where the observations were being made. Strong wave action in shallow water causes turbulence along the bottom, and probably influences the amount of light reaching the bottom. It is possible that these disturbances may have been at least partially responsible for the decrease in emergence on July 30.

A rough attempt was made to correlate the time of emergence each evening and the light intensity as measured by a Weston Master Photoelectric Exposure Meter pointed toward the lightest part of the sky. Emergence began each evening when the light intensity was between 1.6 and 6.5 foot candles (Table 4). On August 5, while the light intensity was still at 25 foot candles, one individual was observed, but the main emergence began after the light intensity dropped below 3.2 foot candles. By measuring the light reaching the bottom, probably more accurate results could have been obtained as this would have automatically compensated for such factors as turbidity of the water, angle of lighting, cloudy sky, and any others that might influence the amount of light reaching the habitat of the nymphs.

During the period of large emergences no attempt was made to determine the relative number of each sex caught in the tent trap. However, at a later date it was considered desirable to know whether the females emerged at the same time as the males or after the flights of males were already under way each day.

On August 4 and 5, 1949, random net samples were taken from the mating swarm at fifteen to twenty minute intervals. The number of males and females collected in each sample was recorded. Table 5 shows that in the early part of the emergence the females constituted from about thirty per cent to more than fifty per cent of the mating swarm while later in the evening only males were to be found. It appears that the females emerge at the same time as the males, but having a shorter adult life, they die within a few minutes thereby leaving a relatively greater number of males in the swarm.

Molting of Subimagos

When *Ephoron album* females emerge from the water, they fly directly into the mating swarm where they mate, drop to the water, expel their eggs, and die. Unlike most mayflies, the females of this species do not undergo transformation from subimago to imago. However, the males transform within a few minutes after emergence. Since adult males of this genus were often seen flying with the subimaginal pellicle still attached, it was believed by some of the early workers that the process of exuviation, or transformation, took place while the insect was in flight. Riley (1881:395) studied this problem and concluded that exuviation commenced while the insect was on the surface of the water. More recently, Burks (1953:33) stated that in *Ephoron leukon* molting takes place in the air, during flight. It is difficult to understand how the first stages of the molting process can be accomplished while the insect is in flight.

The present study on *Ephoron album* showed that when the male subimagos emerge they fly either to some object on shore or settle on the surface of the water, depending on the condition of the water. On calm days almost all the subimagos molt on the surface of the water. When there is a wind and the water is choppy they fly to shore. Since the legs of the subimagos, especially the middle and hind ones, are very weak, the subimagos usually settle on a relatively flat or horizontal object, where they immediately begin to shed the subimaginal skin. As soon as the wings are free, the adult usually flies away with the subimaginal pellicle still hanging to the cerci to be lost somewhere over the water while he is engaged in the mating flight (Fig. 24).

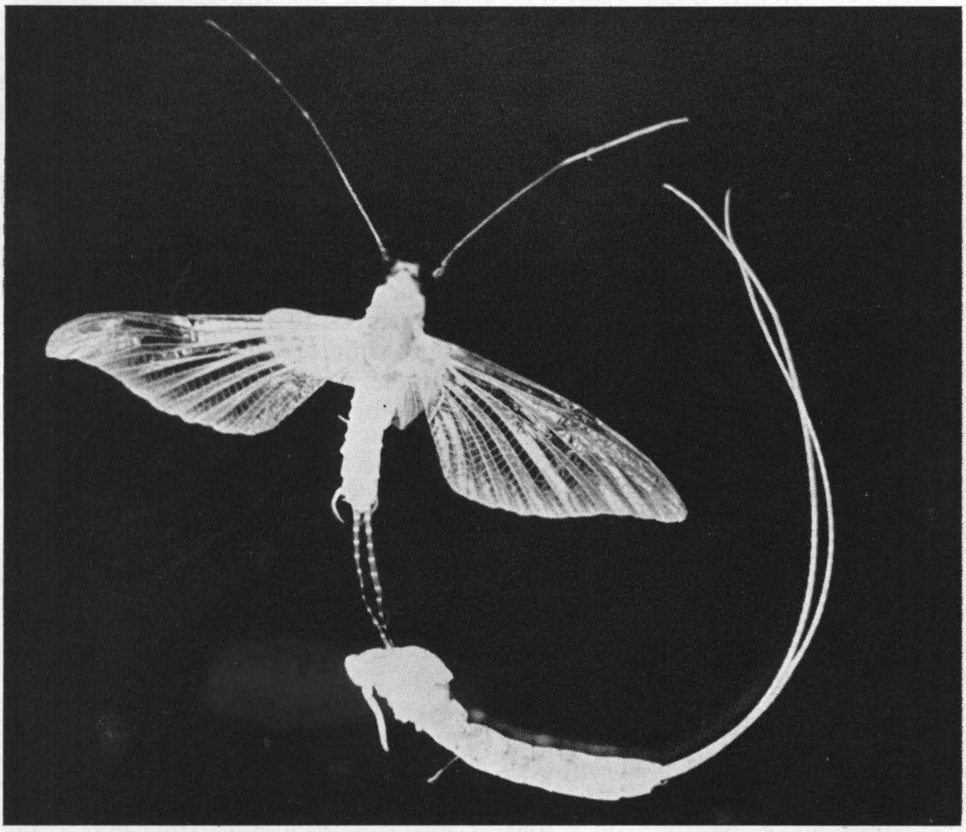

FIG. 24—Male *Ephoron album* just after molting and with the subimaginal pellicle still hanging to caudal filaments.

The amount of time required for *Ephoron album* subimagos to molt was checked on 19 individuals. The 14 individuals observed on July 30 required an average of seventy-five seconds to complete the change while the 5 individuals observed on July 31, at one degree lower temperature, required on the average only 60 seconds. One individual observed on July 26, required only thirty-four seconds to complete the transformation. The number of observations was not sufficient to warrent conclusions about the effects of temperature and humidity on molting. Lyman (1944:113-

115) conducted some experiments on *Stenonema femoratum* and concluded that temperature was a major factor controlling the length of the subimaginal stage while humidity played a minor role.

These observations appear to verify Ide's belief (Ide, 1935a:114) that the subimago stage of Nearctic species of *Ephoron* lasts only a few minutes as in the case with the European species of this genus. *Ephoron album* subimagos observed by Edmunds, Nielsen, and Larsen (1956:145) required from 55 to 80 seconds to molt.

Sex Ratio

Joly (1876b:12) observed a numerical preponderance of females over males in *Ephoron virgo* (Oliver). This is just the opposite of what one would be led to believe concerning *Ephoron album* if only the results of Table 5 were studied. This table shows a definite preponderance of males. This is probably due to the longer life of the male. Those that emerge early may still by flying thirty minutes later, thus new emergences continue to increase the number of males in the swarm until the peak of the emergence is over. The females emerge and fly directly into the swarm, mate, deposit their eggs, and die in probably less than fifteen minutes. Probably as many females as males emerged, but in a random net collection only those females that had just emerged were taken, the ones that had emerged earlier having already died. The few observations made on the sexes of the subimagos caught in the tent traps appeared to indicate that the percentages of males and females were approximately equal. Nymph collections (Fig. 20) also indicate that the numbers of males and females are about equal. Thus the sex ratio appears to be approximately one to one.

TABLE 5

NUMBER OF MALES AND FEMALES COLLECTED IN RANDOM NET COLLECTIONS AT DIFFERENT PERIODS OF TIME ON AUGUST 4 AND 5, 1949

Date	Time P.M., E.S.T.	Number of Males	Number of Females
August 4, 1949	8:10	21	7
	8:35	37	25
	8:50	79	0
	9:05	31	0
August 5, 1949	8:05	18	11
	8:20	49	5
	8:55	100	6
	8:50	69	0
	9:05	67	0

The Mating Flight

On emerging from the water, *Ephoron album* males flew a short distance and again settled on the water or on some object on shore, where they immediately cast off their subimaginal skins. The adults now being lighter in weight were better suited for flight. They usually skimmed along about a foot above the surface of the water and seldom rose more than four or five feet. The flight did not have the up and down movement so characteristic of the *Ephemera* and *Hexagenia* mating flights. Each evening the swarms appeared to form at the same spots along the shore near the nymphal habitat. The male imagos would fly back and forth near this spot. Emerging females joined the males in the flight until they had mated, then they immediately dropped out of the swarm, settled on the water, expelled their eggs, and died.

In the semi-darkness at which the mating flights took place it was rather difficult to observe the details of the mating process. By using flashlights, it was sometimes possible to observe a pair in the process of copulating. Copulation appeared to last only a few seconds. The position of the pair was the same as that which has been observed in *Hexagenia, Ephemera, Stenonema,* and others and was briefly described by Needham, Traver, and Hsu (1935:104). In this description it is stated that probably the necessary position could only be assumed while in flight. However, a few instances of copulation occurring on a substratum have been reported. Reaumur (1742:501) observed that males, probably *Ephoron virgo* (Oliver), settled on females which were resting on a napkin on his knee, but he was not sure that effective copulation occurred. Eaton (1883-1888:10) reported that *Plethogenesia papuana* (Eaton) copulated on the surface of the water. Spieth (1940b:384) observed a pair of *Ephemera guttulata* copulating on the underside of a leaf.

In the present study no actual copulation was observed to take place on a substratum. Occasionally in early evening males were seen hovering over or even alighting momentarily on a female resting on the water. If the female remained on the water, the male flew back into the mating swarm.

In their normal position for copulating while in flight, the male attaches himself below the female. Obviously this position would be difficult for the male to assume when the female was already on the water surface. Copulating pairs often fell on the water before they were able to separate. The individuals of each pair usually separated as quickly as their awkward position permitted, but to a casual observer it might appear that copulation occurred regularly on the surface of the water.

It has already been stated that as soon as copulation was completed the females deposited their eggs and died, while the males went back to the mating swarm and continued to fly. After about thirty to forty-five minutes from the beginning of emergence, only males were left in the swarm. Late in the evening when most of the females were spent, the males frequently appeared to attempt to mate with each other. The reason for this behavior is not known, but it is possible that the dim light at the time prevented recognition of the sex of the individuals until they were very close together.

Usually all members of the swarm were dead and floating on the water surface within one and a half hours from the time emergence began.

Some phases of the emergence and mating flight of the American species of this genus have been observed by previous workers. The first record of such observations was that of Williamson (1802), mentioned earlier in this paper. In the narrative of Long's second expedition, Keating (1824:365) gave the following account of observations on the emergence of *Ephoron album* (Say):

"They became so abundant on Rainy River toward sunset, that they presented the appearance of a snow storm. They continued for some time, until they were driven by the wind into a small tributary valley where they formed white clouds beautifully relieved against the dark green of the forest, deepened in its shade by the approach of night. The ensuing morning their dead bodies were seen floating on the stream, and drifted by the wind into small coves near the shore. From their great abundance, Mr. Say was led to believe that this short-lived insect never witnesses a rising sun, but that after each performance, in a short time, all the duties assigned to it in its perfect state, it deposits its eggs and expires in the night, a few hours after it has been evolved from the chrysalis. The next evening the ephemera were again seen very abundantly, but it was evident that this was a new swarm, and not a part of that previously observed."

Since these early observations, there have doubtless been many others but few of these have been recorded. Thew (1958:9) does give an interesting account of his observations on the mating flight of *Ephoron album* at Rock Island, Illinois. In general his observations agree with those made by the author at Lake Erie.

Parthenogenesis

Viviparity and parthenogenesis are known to occur in various groups of mayflies, but there seems to be no record of either having been observed in any American members of the genus *Ephoron.*

On August 5, 1949, a female *Ephoron album* emerged from an aquarium in the laboratory. There was no known way that the eggs could have been fertilized. They were submerged in a bottle of water and kept aerated for several months. On January 31, 1950, they were examined and found to contain embryos. The eggs were then divided and placed into three bottles which were subjected to temperature treatments similar to those explained earlier in the section on the hatching of eggs. After a period of time, there was an average of about 8 to 10 per cent hatch in each of the bottles.

In order to check the above results, nymphs were collected on August 26, 1950. The female nymphs were removed from the collection, placed into a separate pan of water, and covered with cheesecloth to prevent the escape of emerging females. The eggs were removed from two of the emerged unfertilized females and placed in bottles of water at room temperature. By October many of the eggs were well developed. By January, 1951, the eyes of the embroys were easily seen, and the eggs appeared to be ready to hatch. On February 26, the eggs were exposed to freezing temperatures. On March 10, they were brought back to room temperature, and on March 15, hatching began. Many of the eggs hatched, but the percentage of hatch appeared to be much lower than that of eggs from copulating females or eggs mixed with sperm in Ringer's solution.

There appears to be only two remote possibilities whereby fertilization could have occurred in the above case, i.e., the transfer of sperm to the incubating eggs by way of lake water, or by a mating of nymphs. In the laboratory, active sperm instantly became inactive and distorted when brought into contact with lake water; therefore, the possibility of fertilization in this manner is very low. Since the external reproductive organs of the males are not fully developed until they reach the adult stage, and the opening to the oviducts of the female nymphs appear to be closed by the cuticle, the possibility of the nymphs being able to effectively copulate appears to be rather remote. Therefore, it appears to be safe to conclude that this species is partially parthenogenetic. Since the life span of the adult is so short, this adaptation may be an important factor in the survival of the species.

EPHEMERA SIMULANS WALKER

LITERATURE REVIEW

Linnaeus (1746:226-227; 1758:546) described the genus *Ephemera* and used it to include all known mayflies. About one hundred years later, Francis Walker (1853:536) described the species, *Ephemera simulans*, from the St. Lawrence River. In a few instances since then this species has been reported under different names as follows:

Ephemera decora Walker (1853:537), Hagen (1861:38), Walsh (1863b:376), Hagen (Walsh, 1863a:177)

Palingenia natata Walker (1853:551)

Ephemera natata Hagen (1861:39), Hagen (Walsh, 1863a:177), Hagen (Eaton, 1873:393), Hagen (1874:580)

Ephemera guttulata Eaton (1871:69)

Since Eaton's monograph (1883-1888) this species has been known as *Ephemera simulans*.

Some phases in the life history of this species have been studied. The largest contributions to the knowledge of this species were those of Ide and Spieth. Ide (1935b) studied and figured the various instars in the development of *Ephemera simulans* nymphs. Spieth (1936) published a study on the life history of this species in Lake Wawasee, Indiana. The present paper attempts to supplement these studies. The data for this work have been collected concurrently with those used in the preceding study of *Ephoron album*. The stations where collections were made, and the materials and methods used were essentially the same as those reported in the above study of *Ephoron album*.

Ephemera simulans adults and nymphs can be identified from the descriptions and keys of Needham, Traver, and Hsu (1935:246-248, 252-253). Ide (1935a:444) described and figured some of the structures of the last instar nymphs.

GEOGRAPHICAL DISTRIBUTION

The genus *Ephemera* is Holarctic in distribution. In North America it includes six generally recognized species, of which *Ephemera simulans* was the second to be described. In 1853 Walker described it from the St. Lawrence River. Since that date this species has been reported from various localities from Maine to Alberta to Wyoming and Florida. Published records show that this species has been collected from the following localities, most of which are shown on the distribution map (Fig. 25):

Alberta, Maligne Lake (Needham, Traver, and Hsu, 1935:253), Pyramid Lake (Neave, 1929:187, 188); *Manitoba*, Lake Winnipeg (Neave, 1932:54; 1933:186, 193, 197; 1934: 160, 165); *Ontario*, Mad River (Ide, 1935c:13, 58), Lake Nipigon (Adamstone and Harkness, 1923:130-132), Nanticoke (Clemens and Bigelow, 1922:96-97), Lake Simcoe (Rawson, 1930:41), Georgian Bay (Clemens, 1913:332; 1915:116-117), Port Elgin, Long Lake, Moose Factory—Hudson Bay (Needham, Traver, and Hsu, 1935:253), Hudson Bay (Eaton, 1883-1888:69; Hagen, 1874:580-581-*E. Natata*=*E. simulans*); Quebec, St. Lawrence River (Walker, 1853:536; Hagen, 1861:38-39; 1874:580-581-*E. natata*=*E. simulans*), Ile Bizard (Needham, Traver, and Hsu, 1935:253); *Saskatchewan*, (Eaton, 1883-1888:69), Saskatchewan River (Hagen, 1874:580-581-*E. natata*=*E. simulans*).

Florida, Kingsley Lake (Berner, 1950:94); *Idaho*, Coolin (Needham, Traver, and Hsu, 1935:253); *Indiana*, Spencer, Lake Wawasee, Lake James, Winona Lake (Spieth, 1936:263); *Illinois*, Chicago (Needham, Traver, and Hsu, 1935:253; Eaton, 1883-1888:69; Hagen, 1874:580-581-*E. natata*=*E. simulans*; Daggy, unpublished thesis, 1941:63; Burks, 1953:

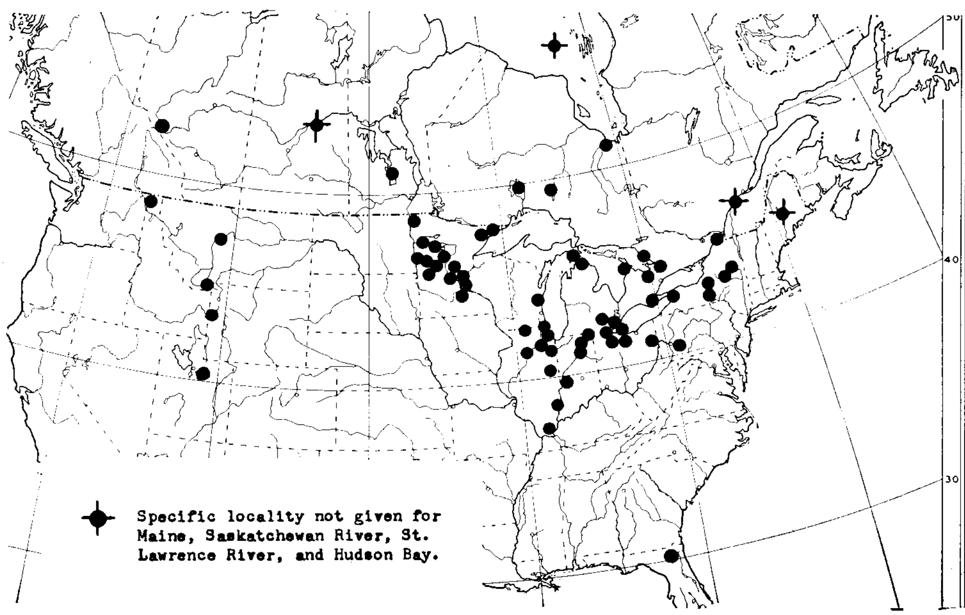

FIG. 25—Map showing reported geographical distribution of *Ephemera simulans* Walker. Based on Goode Base Map No. 102, Copyright 1937 by the University of Chicago. Used by permission of the University of Chicago Press.

36), (Desplains River (Walsh, 1863b:377=probably *E. simulans*), Cedar Lake, Eddyville, Evanston, Homer, Kankakee, Henry Muncie, Oakwood, South Beloit (Burks, 1953:36-37); *Maine*, (Hagen, 1874: 580-581-*E. natata*=*E. simulans*), West Beach (Eaton, 1883-1888:69); *Michigan*, Ann Arbor, Burt Lake, Walnut Lake (Needham, Traver, and Hsu, 1935:253; Lyman, unpublished thesis, 1940), Portage Lake (Needham, 1921:284), Straits of Mackinac, Douglas Lake (Lyman, unpublished thesis, 1940), Islands in Lake Erie near mouth of Detroit River (Eaton, 1883-1888:69); *Minnesota*, Muskoda (Needham, Traver, and Hsu, 1935:253), St. Paul, St. Cloud, Cass Lake (Needham, Traver, and Hsu, 1935:253; Daggy, unpublished thesis, 1941:62-63), Kawishiwi River, Hallock, Minneapolis, Green Lake in Chisago Co., Alexandria, Bemidji, Cass Co., Coon Creek in Anoka Co., Crookston, Cross Lake, Garrison at Mille Lacs Lake, Itasca

Park, Otter Trail Lake, Pope Co., Detroit Lakes, Credit River at Savage, Pine River, Kettle River at Rutledge, Brule Lake, Mississippi River at Fridley, Mink Lake in Cook Co. (Daggy, unpublished thesis, 1941:62-63); *Montana*, Great Falls, Yellow Bay, West Yellowstone (Needham, Traver, and Hsu, 1935:253); *New York*, Ithaca, Union Springs, Buffalo, North Fair Haven, Lake George, Sacandaga (Needham, Traver, and Hsu, 1935:253), Cayuga Lake (Needham, 1921:284), St. Martins Falls on Albany River (Eaton, 1883-1888:69; Hagen, 1874: 580-581-*E. natata*=*E. simulans*); *Ohio*, Millport (Needham, Traver, and Hsu, 1935:253), Island section of Lake Erie (Wright, Tiffany, and Tidd, 1955:258-*Ephemera* sp; Shelford and Boesel, 1942:184-*Ephemera* sp.), Sandusky, Toledo, Cedar Point, Gibraltar Island, South Bass Island, Middle Bass Island, North Bass Island (Jenkins, unpublished thesis, 1939:11), Put-in-Bay (Kennedy, 1925:395; 1926:61; Krecker, 1922:155); *Pennsylvania*, Westmoreland County (Needham, Traver, and Hsu, 1935:253); *Utah*, Uintah River at U. S. Hwy. 40 near Ft. Duchesne (Clyde Eriksen, Personal Communication); *Virginia*, Akhurst (Eaton, 1883-1888:69); *Wisconsin*, Lake Winnebago (Baker, 1924:122, 123, 128); *Wyoming*, Crayfish Creek in Yellowstone National Park near South entrance (Clyde Eriksen, Personal Communication), West Yellowstone (Needham, Traver, and Hsu, 1935:253. This appears to be an error since West Yellowstone is just inside the Montana line).

ECOLOGICAL DISTRIBUTION

The ecological distribution of the species, *Ephemera simulans*, has not been intensively studied. In a few instances the habitats of the nymphs have been reported. Clemens (1915:177) mentioned that the nymphs of this species were found at several places in Georgian Bay, Ontario, at a depth of two to nine feet, but the type of bottom was not discussed. Adamstone and Harkness (1923:131-132) showed that *Ephemera simulans* individuals were most abundant in Lake Nipigon at the depth of six to nine feet, but that they were also found less abundantly in water even thirty feet deep. More individuals were found in sandy bottom than in mud bottom. Baker (1924:122, 123, 128) reported *Ephemera* sp. from Lake Winnebago on sandy shores and on mud bottom in shallow water and in water 2.5 meters deep. The type of bottom in the deeper water was not given. Kennedy (1925:395) stated that the nymphs are negatively phototactic and burrow in the mud in the bottom of Lake Erie. Neave (1929:188) dredged nymphs of *Ephemera* sp. (probably *simulans*) from a depth of several meters in Pyramid Lake. In studies on Lake Winnipeg (Neave, 1932:54; 1934:165) stated that the nymphs lived in the bottom sand but not in water more than a few meters deep. In Lake Simcoe, Rawson (1930:41) found the nymphs in the littoral and sublittoral zones, usually less than nine meters in depth. They were usually associated with a bottom of marly clay and *Chara* or one of soft sand. Ide (1936b:437; 1935c:58) found the nymphs in large numbers in burrows in the gravel and marl bottom of the channel of the slow-flowing portions of the Mad River, Ontario. Spieth (1936:264) found the nymphs in the shallow littoral zone (0.5 to 1.25 meters in depth) of Lake Wawasee, Indiana. In this collection from deep water (3 meters or more in depth) he found only one specimen. The type of bottom was not stated. Lyman (unpublished thesis, 1940) found the nymphs in Douglas Lake only as scattered individuals in loose, fine sand at a depth of one to three meters. Eriksen (Personal Communication) found the nymphs in a mixture of pebbles, gravel, and sand with scattered fist-sized cobbles in the Uintah River. In Crayfish Creek they were in fine gravel and sand.

In the present study, nymphs were found in coarse gravel and sand overlying a clay substratum in water between one half meter and two meters in depth. During periods when the water level was low enough to permit direct observation, it was found that when large stones were moved, the burrows of nymphs could often be found in the gravel and sand beneath. No nymphs of this species were collected from the soft mud bottom inhabited by *Hexagenia*.

Since collecting the nymphs in deeper water is quite difficult, few reliable data are available on the distribution in the deeper water. K. G. Wood (personal communication) recently made a survey of the bottom fauna of western Lake Erie. He collected one nymph of this species from the gravel-sand bottom in water 27 feet deep and three miles west of Pelee Island, Ontario.

From the above records and from casual observation, it appears that the nymphs of this species may be found in water up to 30 feet in depth, provided suitable habitats are available and the area is not too far from shore. If better bottom samples could be obtained in the gravel, sand, and rubble bottom, perhaps the distribution of *Ephemera simulans* would be much greater than that indicated by present records.

THE EGG

The eggs of *Ephemera* were figured and described by Needham, Traver, and Hsu (1935:76, 86). They are ellipsoid, about .22 by .12 mm. No projections or filaments are present, but when they are deposited in water on a smooth surface such as a stone, an adhesive substance on the surface of the egg firmly attaches it to the stone.

Number of Eggs Produced by Each Female

The eggs from 14 females were removed and counted. Table 6 shows the result of this count. On an average each female produced 4500 eggs.

TABLE 6

NUMBER OF EGGS PRODUCED BY INDIVIDUAL *Ephemera simulans* FEMALES

Total Length of Specimen in mm. (exclusive of appendages)	Number of Eggs Per Female
20.25	3979
20.79	5116
22.28	5441
21.60	5094
18.90	3375
19.58	4135
18.63	3443
21.33	4767
21.60	5879
20.52	4842
20.79	5266
17.96	3202
21.20	4534
18.50	3939

Average number of eggs per female—4500

The table also shows that the number of eggs produced was generally directly proportional to the body length of the female. It is known that in some species the number of eggs varies with the time of emergence. Those individuals emerging early in the season are often larger and thus produce more eggs than those emerging later in the season. Although no data were obtained on this, it is believed to be true of this species also.

Distribution of Eggs in Water

The mating flights of *Ephemera simulans* occurred over land. After mating, the females flew out over the water and deposited their eggs. The heavy females were rather poor fliers and usually settled on the water near the shore and deposited their eggs. It was not determined whether the eggs were all discharged at the same time or in several smaller groups, but the bodies of the females did not become badly ruptured and distorted when the eggs were extruded as did those of *Ephoron album* females.

Hatching of Eggs

Spieth (1936:264) found that 14 days were required for the hatching of *Ephemera simulans* eggs in an environment much warmer than the normal one, and he assumed that from 20 to 30 days would be required for hatching in the normal habitat. Clemens (1922:78) found that 15 days were required for the hatching of *Ephemera varia* eggs in the summer at Ithaca, New York, but he did not record the temperature.

On June 7, 1959, eggs were removed from copulating *Ephemera simulans* females. These were placed in bottles of lake water which were then placed on the bottom in the normal habitat of the species. The bottles were examined and the water was changed periodically. By June 27, several hundred of the several thousand eggs had hatched. Since several days had elapsed since the bottles were examined, the exact date when hatching began is unknown. On the basis of observations on other species, it is probable that hatching began one or two days earlier. The water temperature varied from 18° C. on June 7 to 20° C. on June 27. These results appear to support Spieth's assumption that 20 to 30 days are required for hatching in their natural habitat.

In 1950 the first *Ephemera simulans* adults were seen on June 6. In the above experiment the eggs were obtained just one day later. Thus it appears that the first nymphs of *Epherema simulans* should appear, in the natural habitat in Lake Erie, around the last part of July or the first part of August. It will be shown later that water temperature may cause a variation in the emergence date, which, in turn, may influence the date of hatching of the eggs.

The Nymph

Ide (1935a:436–446) gave detailed descriptions and figures of external characters of nymphs of instars 1 to 7, 9 to 11, 13, and the last eight or nine instars of this species. He was not able to determine the total number of instars, but he estimated that the nymphs passed through thirty or more such stages. No attempt was made to determine the number of instars in this study.

Growth

The average body length of the nymph at hatching was about .79 mm. At the time of emergence a few male nymphs reached a maximum length of 18-20 mm., exclusive of tusks and caudal filaments, and a head width of 1.6 mm. The females attained a maximum length of 23-24 mm. and a head width of 1.9 mm. The average size at emergence was less than this and probably varied with the season, those emerging earliest being slightly larger than those emerging at a later date. The eye diameter of mature male nymphs was noticeably greater than that of the females.

The graph (Fig. 26) shows the average growth of three populations (1949, 1950, 1951) of nymphs based on head-width measurements. Although a collection was made on June 21, 1949, no *Ephemera simulans* nymphs were recorded. On June 29, small nymphs were abundant. The largest specimens in the collection measured only 3 mm. in length and .29 mm. in head width. In the summer of 1949 the temperature of the water of the bay was unusually high. It was above 25°C. from June 28 to August 19 and reached a maximum of 29° C. on July 5. During this period the nymphs grew quite rapidly. As the water temperature dropped, growth rate of the nymphs dropped. By the middle of November, when the water temperature had dropped to around 5° to 7° C., the nymphs appeared to be ready to emerge. Several collections were made through the ice, but they revealed no increase in the average size of the nymphs.

The first emerging *Ephemera simulans* for the year were noticed on June 6, 1950. Since most of the nymphs were mature in the autumn, they did not have to complete growth in the spring; therefore, they were ready to emerge as soon as the water temperature became favorable. The emergence period was short, with very few stragglers left. The eggs deposited by this population began to hatch around June 26-27, 1950. No collections were made until August 8, after which date collections were made at more or less regular intervals. It can be seen from the graph that nymphs of the 1950 population remained smaller than those of the 1949 population and showed some increase in size throughout autumn, winter, and before emerging in the following spring of 1951. It can also be noted that the emergence period was longer than in the previous year. As the majority of the large individuals emerged, the smaller ones remaining outnumbered the large ones. This is shown in the drop in average size in June and early July. The long emergence period is further indicated in the July and possibly in the August collections. The remaining individuals of this population were collected along with the recently hatched nymphs of the 1951 population and is indicated by the large average size of specimens found in the July and August collections.

The 1951 population appeared to grow at approximately the same rate as the 1950 population. High water after January, 1952, prevented further collecting. Except for differences in water level and water temperature, the environmental conditions were essentially the same for the three years. It is not likely that the difference of two or three feet in water level would result in a significant difference in growth rate. In 1949 the water temperature was above 25° C. for 52 days with a peak of 29° C. In 1950 and 1951 the maximum water temperature was only 24° C. The unusually high water temperature was probably one cause for the rapid growth of the 1949 population. Another factor influencing the rapid growth is due indirectly to the high water temperature which caused the 1948 population to begin emerging on May 23, 1949. This was about 10 to 14 days earlier than was the case in 1950 and 1951. This gave the 1949

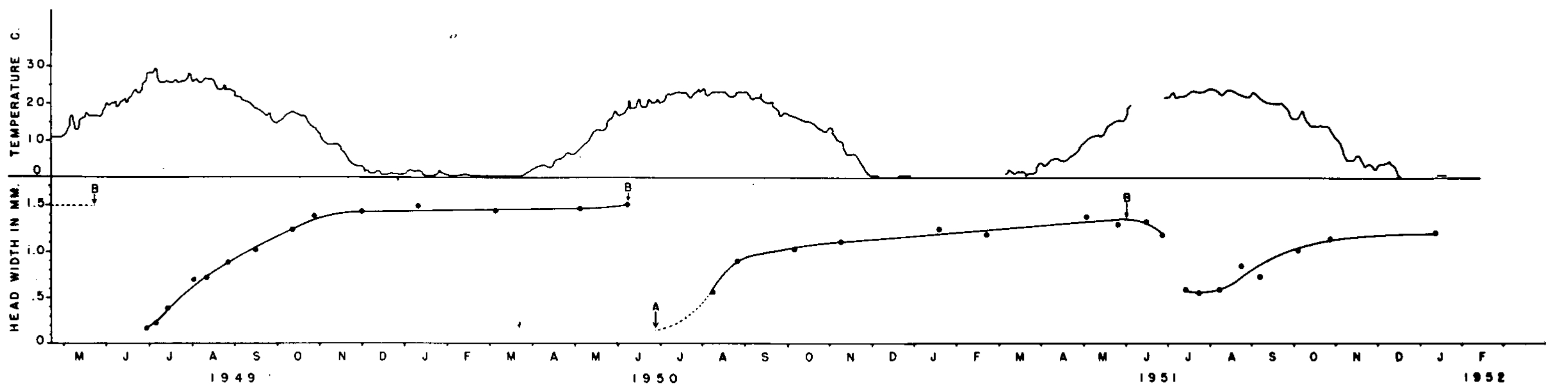

FIG. 26—Lower graph shows the average growth of three populations (1949, 1950, 1951) of *Ephemera simulans* nymphs based on head width. The minimum daily water temperatures for the corresponding periods are shown by the top graph.

population about 10 to 14 days extra growing time when the water temperature was most favorable for the hatching of eggs and for the growth of the nymphs.

Food

Wissmeyer (1926) made studies of the food consumed by several species of European mayflies including species of this genus. In the digestive tracts of *Ephemera* nymphs he found both plant and animal remains, but the proportion of plant material was much greater than that of the animal remains. However, the bulk of the material (50% to 86%) was unidentifiable and was classed as detritus.

It is generally assumed that the burrowing mayflies ingest the planktonic and littoral detritus which settles on the bottom of their habitat. Since the mandibles of the nymphs are well developed and rather efficient at grinding the food, only the forms with relatively strong walls or structures are likely to be recognizable in the contents of the digestive tract. The digestive tracts of some *Ephemera simulans* nymphs contained recognizable fragments of *Melosira, Diatoma, Fragilaria, Gomphonema, Pediastrum, Staurastrum, Navicula, Cymbella,* a protozoan, probably *Cothurnia,* some fragments of filamentous algae, sand, silt, and a mass of greenish debris which appeared to have no definite form. There appeared to be little selection on the part of the nymphs. The forms found in the digestive tracts appeared to vary with the seasonal abundance of the various species of plankton and algae in the surrounding area.

Maturation

It is evident from the graph (Fig. 26) that about one year is required for *Ephemera simulans* to complete a cycle in Lake Erie. It is also clearly shown that the population overwinters in the nymphal stage with many of the nymphs fully developed and ready to emerge as soon as the water temperature becomes favorable in the spring. Nymphs that are ready to emerge can be distinguished from others by their dark wing pads.

The Winged Stages

Emergence

When the nymphs of this species are ready to emerge, they swim or float to the surface and molt. The subimago then flies to the shore while the discarded nymphal skin floats on the water surface. Emergence in this species appears to occur principally at night, but unlike *Ephoron album,* it does not appear to be restricted to any particular hour or light intensity.

At Put-in-Bay, Ohio, *Ephemera simulans* subimagos began to emerge around the last part of May and early part of June with the greatest concentration around the middle of June. Imagos and subimagos of this species were first noticed on May 23, 1949; June 6, 1950; May 31, 1951; in the first week of June, 1952; and June 2, 1953.

In 1949, immense numbers emerged in a short period, leaving few stragglers. In 1950, although the emergence period began about fourteen days later, it was relatively short. The 1951 emergence began about seven days later than that of 1949. It was quite long, with stragglers continuing to emerge throughout most of the summer. The 1952 emergence was similar to that of 1951. The 1953 emergence period was relatively short.

Occasionally, when the water temperature remains high until late autumn, a few specimens may emerge before cold weather lowers the water temperature. In the evening of October 11, 1949, several subimagos of *Ephemera simulans* and *Hexagenia* sp. were collected around a lantern. None were collected in this manner in the autumn of the following years.

The time of emergence varies according to the geographical location. Clemens (1915:117) found *Ephemera simulans* imagos to be abundant around Georgian Bay, Ontario, from June 5 until July 27, 1912. Spieth (1936:263) states that in small lakes in Indiana, the main emergence of this species is relatively short and occurs in the last of May and first part of June with some individuals preceding and some following. Lyman (unpublished thesis, 1940) states that in Douglas Lake, Michigan, this species has a long emergence period that extends from about June 10 to August 1, with maximum numbers appearing in early to middle July. He further states that in southern Michigan the emergence periods are shorter and more concentrated, and that he has collected *Ephemera simulans* here as early as May 17. It is his belief that the length of the emergence period depends on the temperature of the water. Therefore, in northern lakes with low temperature, the emergence periods are long with no great concentration, while on the other hand in southern lakes with warm water the emergence period is short and concentrated.

Miller (1941:45–50) was able to predict the date of emergence of midges from different depths in Costello Lake by using the sum of the mean daily temperatures which he called day-degrees. Uvarov (1931) found the temperatures at which development begins to range from 0° C. to around 10° C. for most insects. The actual threshold of development for the mayflies is not known, but it probably varies with the species and habitat. In the growth curve for the 1950 population (Fig. 26) there appears to be some indication that growth occurred even under ice cover when the temperature at the bottom was near 0° C. That feeding and possible growth may continue at a reduced rate during the winter was also indicated by the contents of the digestive tracts of nymphs collected in winter. Many of these contained large amounts of planktonic forms which are predominant in winter.

Since a definite threshold of development is not known for this species, the date at which the last ice disappeared and the water temperature reached 1° C. was taken as the starting point for each year. The graph (Fig. 27) shows the day-degrees to which the mayflies in this study were exposed in the years 1949 to 1953. The points A to E represent the time of the beginning of emergence of the 1948 to 1952 populations, respectively. The year designations refer to the year of hatching of the eggs that produced the population.

As might be expected, there appears to be a correlation between the growth of the nymphs (Fig. 26) and the number of day-degrees (Fig. 27). The day-degree curve for 1949 has a consistently higher value than that for the other three years. On May 23, 1949, when the 1948 population began to emerge, it had been exposed to 606 day-degrees that spring. The eggs laid by this emerging population and the resulting nymphs were exposed to unusually favorable growing conditions which resulted in the unusually rapid growth as shown in the graph (Fig. 26). The total day-degree curves for the years 1950 to 1953 are similar but are lower than the one for 1949. The growth of the nymphs was slower also.

Since the 1949 population appeared to be ready to emerge in the fall, it was assumed that the emergence would occur early in the spring of 1950. However, the 1949 population emerged at a later date than any of the populations studied. Although there was as much as fourteen days difference in the emergence dates, the number of day-degrees required for emergence in the spring for the 1948 to 1951 populations was between

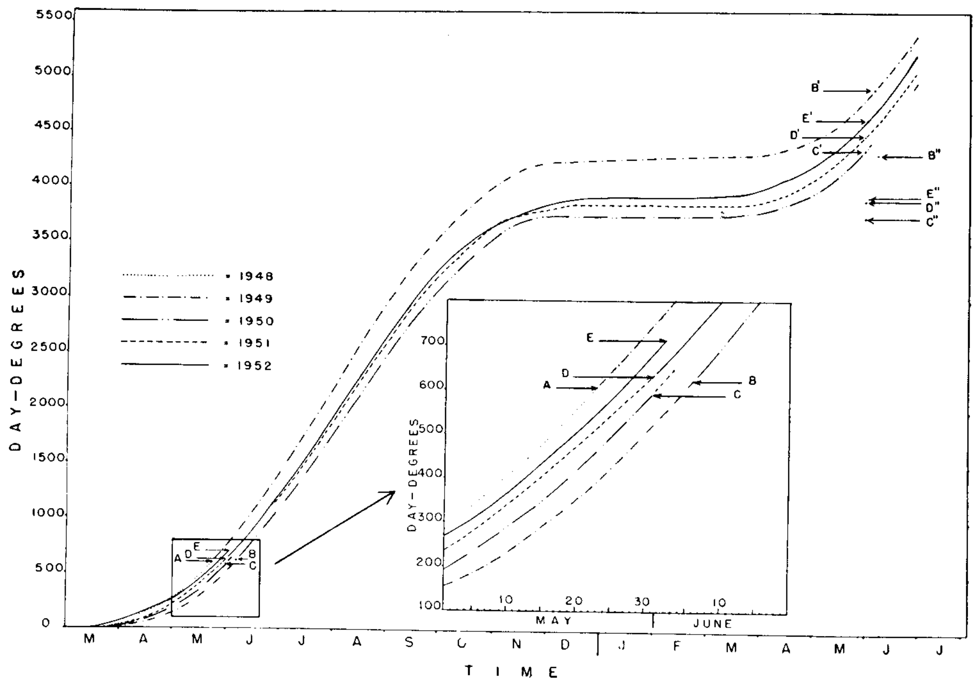

FIG. 27—Graph showing day-degrees to which the populations of *Ephemera simulans* nymphs were exposed during the years 1949 to 1953. Points A to E represent time of beginning of emergence of the 1948 to 1952 populations, respectively. Points B′ to E′ represent total day-degrees accumulated by the parent population in the spring before emergence plus the day-degrees to which their eggs and the resulting nymphs are exposed until emergence begins. EXAMPLE: B′ = 4904.5 day-degrees = 606 day-degrees accumulated by the 1948 population at point A plus 4298.5 day-degrees accumulated by the 1949 population from egg to emergence. Points B″ to E″ represent total day-degrees to which the 1949 to 1952 populations respectively were exposed from egg to emergence. These values are obtained by subtracting the day-degree values of A, B, C, and D from those of B′, C′, D′, and E′, respectively.

588 and 631, a range of only 43 day-degrees. The 1952 population apparently required 713 day-degrees. This larger value may have resulted from inaccurate emergence data. No observations had been made for several days prior to June 2 when a small number of adults was found; therefore, emergence may have started earlier than June 2. The points B′, C′, D′, and E′ also show emergence dates of the 1949 to 1952 populations, respectively. In this case, however, there was a range of over 550 day-degrees between the total day-degrees accumulated for each year. The number of day-degrees to which the eggs and nymphs of the 1949 to 1952

populations were exposed can be obtained by subtracting the day-degree value of A, B, C, and D from B′, C′, D′, and E′, respectively. These new values are shown on the graph as B″, C″, D″, and E″, respectively. Here again there is a difference in exposure of over 550 day-degrees between the 1949 (B″) and the 1950 (C″) populations. If the total day-degrees were the limiting factor in the emergence, the 1949 population should have emerged at an early date, but as stated above it emerged later than usual.

Although there was a difference of fourteen days in the dates of emergence of the 1948 and the 1949 populations, an examination of Fig. 27 A and B shows a difference of only 13.5 day-degrees between these populations at the time of emergence.

On the basis of this study the controlling factor in emergence appears not to be the total day-degrees to which the eggs and nymphs are exposed. Instead, it appears that about 600 to 700 day-degrees are required in the spring. In this study this requirement was reached when the water temperature was between 15° C. and 18° C.

Molting of Subimagos

The emerging subimagos of *Ephemera simulans* flew to some sheltering object on shore, usually shrubs or trees, and remained quiet for several hours. During this quiet period they moved only when disturbed. When strong sunlight struck them, they often crawled or flew to some shady spot. After a time, usually about 12 to 24 hours, the subimagos molted again. The pubescent skins of the subimagos were replaced by the glossy smooth skins of the imagos. Lyman (1944: 113-115) states that the temperature of the air is the major factor controlling the length of the subimaginal stage in many of the mayflies. During cold rainy weather the subimagos may require 72 hours or more before molting takes place.

Reproduction

Sex determinations were made on 1376 nymphs. Of these, 45.8% were males and 54.2% were females. It was easy to determine the sex in the larger specimens, but was quite difficult in the smaller ones. Generally those with a head width of .5 to .7 mm. or less were classed as sex unknown. The presence or absence of forceps was used to separate the males from the females. Where these structures were visible, the specimen was unquestionably a male, but since neither the females nor the small males possessed these structures, it is possible that some of the small ones were classified as females. When the possibilities of errors in sex determination are considered, it appears that this species has an approximate one to one sex ratio.

When adults were collected from a mating swarm, males predominated. This was due to the behavior of the two sexes. The males usually swarmed over shrubs or trees along the shore. The females entered the swarm only when ready to mate. They mated immediately and then left the swarm while the males usually joined the swarm again. Thus, at any specific time the number of females in the swarm was relatively small.

The males performed the characteristic dance of flying up a foot or more, then settling with wings, legs, and caudal and lateral filaments outstretched. This up and down motion was repeated time after time until a female entered the swarm. A male then rose from below the female and grasped her thorax above the wing bases with his long double-jointed front legs. By curling the tip of the abdomen up, he was able to grasp her abdomen with his forceps and to insert the double penis into the double genital openings of the female.

Copulation usually continued for less than a minute. The pair continued to fly, but since flight was impaired by the awkward position, it gradually lost altitude and sometimes even struck the substratum before separating. Usually the male released the female while several feet above the substratum. He usually returned to the swarm while the female flew out over the water and deposited her eggs. On one occasion a female was observed to enter a swarm three times. Each time a male attempted to copulate, but it is not known whether the attempts were successful or not. On the last attempt she continued flying out over the water while the male returned to the swarm.

Normally, mating occurs in mayflies only when they are in flight. No exceptions were observed in this study. Under some circumstances it may be possible that mating may occasionally take place on a firm substratum. Spieth 1940b: 384) observed a pair of *Ephemera guttulata* copulating on the lower side of a *Platanus occidentalis* leaf.

The mating flights of Ephemera simulans usually began about sunset, and the males were usually still flying when visibility was reduced to where they could not be seen. However, a short time after darkness set in there was no indication that the flight was continuing. The females died after depositing their eggs. Although the males returned to the swarm after mating, it is believed that most of them spent themselves before the evening flight was over.

Experiments similar to those used in the study of *Ephoron album* were used to check for parthenogenesis; however, there was no evidence of this form of reproduction in *Ephemera simulans.*

ECOLOGY

Physical Factors and Their Effect on the Population

The highest mortality rates of mayflies probably occur in the egg stage. In the case of *Ephoron album,* the egg stage is unusually long and extends over the winter months. Since the eggs of this species are usually deposited near the shore, they are subject to desiccation during low water periods and to the molar action of the sand and gravel in periods of stormy weather. The eggs, however, appear to have an unusually strong covering and, as shown elsewhere in this paper, are resistant to limited desiccation and to low oxygen conditions for long periods.

Probably one of the greatest limiting factors for this species is temperature. As shown earlier, low temperatures followed by temperatures above 10° C. are required for the hatching of the eggs. Along the southern boundary of its range where the winters are mild, there may not be sufficient cold weather to cause the eggs to hatch. On the other hand, eggs would not hatch in water where the maximum temperature remained below 10° C.

The eggs of *Ephemera simulans* have a short incubating period and do not have to withstand the rigorous conditions of winter. These eggs appear to have a rather thin covering and to secrete an adhesive substance which causes them to adhere to stones or other objects. This secretion also causes silt and debris to cling to them. This probably has some value as a protection against enemies. Since the eggs develop rapidly, the oxygen requirement must be relatively high. Therefore it is doubtful that they would be able to survive long in low oxygen conditions. However, it is not likely that oxygen is a limiting factor in their natural habitat on shallow gravel shoals of lakes and riffles of streams where wave action and currents keep the water in motion.

Nymphs may also suffer loss from molar action during storms, and from desiccation when water levels drop suddenly. If the water level drops gradually there is some evidence that the nymphs may migrate short distances, thereby keeping below the water surface. Another factor that may be effective in eliminating either of these species from some localities is the length of the growing season. This is especially true of *Ephoron album.* Unless the growing season is of sufficient length, the nymphs will not be able to complete their growth and distribute their eggs.

Unfavorable weather at the time of emergence is probably the most effective physical factor operating against the adults. Great losses of eggs can occur at this time if weather conditions prevent mating, or if strong winds sweep the mating swarm inland thus preventing the eggs from reaching the water.

Predation

Needham, Traver, and Hsu (1935: 213) state that small egg-eating enemies such as caddis worms, snails and other lesser invertebrates, doubtless destroy many of the eggs. The area where this study was made was inhabited by many forms such as caddis fly larvae, snails, other forms of mayflies, dragonfly and damsel fly nymphs, scuds, crayfish, small fishes, copepods, ostracods, water mites, and various worms. The extent of utilization of the eggs by these animals is unknown.

The nymphs of mayflies generally appear to be a choice item of food for almost all predaceous forms of aquatic life. The elusive habits of the nymphs of *Ephoron album* and to a lesser extent those of *Ephemera simulans* may help to reduce the mortality due to the predaceous fishes and other vertebrates. The predaceous invertebrates inhabiting the same area probably devour many of the nymphs, especially the very young ones. The periods of greatest danger for the nymphs appear to be that just after hatching and that just before emergence when the nymph leaves its hiding place to swim or float to the surface. In the study area, large schools of fishes were nearly always present during this latter period, and doubtless many of the nymphs fell prey to them before they reached the surface.

The adults of both species usually emerge at dusk or later. In the case of *Ephoron album* the mating flight takes place immediately. Thus the adults escape the predatory birds which would take a heavy toll if emergence and mating flight occurred during the day. In *Ephemera simulans* the subimagos require a period of several hours before molting takes place. Under favorable conditions the subimagos remain quiet usually on the underside of leaves until molting is complete, then on the following evening the adults go into the mating flight. This delay between emergence and mating flight exposes this species to predation by birds, insects, spiders, and other insectivorous animals. Birds, especially, take a heavy toll at this time.

Parasitism and Commensalism

It is known that mayflies are subject to many parasites, but these have been studied inadequately. In America the parasites of only a few species of mayflies have been studied.

A large number of nematodes appeared in the collections of *Ephoron album eggs*. Many of these eggs had been dissected from adult females and artificially fertilized by crushing the sex organs of a male in a depression slide with the eggs. Where these nematodes came from was not determined, but it is believed that they were dissected out of the bodies of the females along with the eggs.

The nymphs of both species were examined for external parasites. Out of a total of 586 *Ephoron album* nymphs examined, 577 (98.5%) were infested with a colonial ciliate of the genus *Carchesium*. Out of a total of 1126 *Ephemera simulans* nymphs examined, 1019 (90.5%) were infested with the same organism. The nymphs of *Ephemera simulans* were collected throughout the year while those of *Ephoron album* were collected only during the summer months. If this organism is more abundant during the summer, this may explain the differences in the percentages of infestation. This appeared to be a case of commensalism rather than parasitism since the protozoans obtained their food from the surrounding water independently of the nymphs. The nymphs, however, did provide them with a place for attachment, mobility, and a current of water which brought suspended particles within reach. Large nymphs infested with this protozoan showed no harmful effects of this relationship, but the effect on the very small nymphs is questionable. It appears that a large colony of protozoans attached to a small nymph might restrict the movements of the nymph thereby interfering with its movement into feeding and hiding places. This was found to be true, at least for specimens kept in the laboratory.

Competition

Some of the other species of animals living in the area studied are listed in the preceding section on predation. The nymphs of *Ephoron album* and *Ephemera simulans* had to compete with many of these species for food and space. Unfortunately, it is not possible at this time to estimate the degree of competition between these forms.

Since large populations of *Ephoron album* and *Ephemera simulans* nymphs live in the same habitat, strong competition might be expected between them. In order to better compare the growth rates of the two populations, the average growth rate curves for the 1949 and 1950 populations of *Ephoron album* (Fig. 21) have been superimposed upon those of the corresponding populations of *Ephemera simulans* (Fig. 26) resulting in the graph, Fig. 28.

Examination of this composite graph reveals a number of interesting points which were not so easily detected on the individual graphs: (1) The growth rate of *Ephoron album* is much more rapid than that of *Ephemera simulans*. The interval between the hatching of the eggs and the emergence of the adults in *Ephoron album* is only about twenty per cent of that required by *Ephemera simulans* in their natural habitat. (2) There is an alternation of populations, with *Ephoron album* overwintering as eggs, while *Ephemera simulans* overwinters as nymphs. (3) The overwintering eggs of *Ephoron album* hatch only a short time before the nymphs of *Ephemera simulans* emerge. The nymphs of *Ephemera simulans* are still relatively small when the *Ephoron album* nymphs emerge.

Both species belong to the same family (according to Needham, Traver, and Hsu, 1935), feed on the same type of food, and are prolific reproducers. Thus, if the eggs of both species hatched at the same time, it appears that competition between them would be very great. However, Fig. 28 indicates that the life cycles of the two species are sufficiently out of phase to reduce competition between them to a tolerable level.

Biotic Potential

Chapman (1931:182) defined biotic potential as "The inherent property of an organism to reproduce and to survive; i.e., to increase in numbers." Because of the limiting influences exerted by every environment, probably no species in nature ever attains complete fulfillment of its biotic potential.

Data obtained on the sex ratio, the average number of eggs per female (Table 1), and the number of eggs deposited per square meter for a few days during the emergence season (Table 2) indicate that *Ephoron album* has a relatively high biotic potential. There are many factors which prevent the fulfillment of its biotic potential; some of these have already been discussed in the preceding sections while there are probably other factors that are as yet unknown.

Table 3 shows the results of quantitative collections of nymphs made on July 27, August 1, and August 10, 1949. Emergence was first noticed

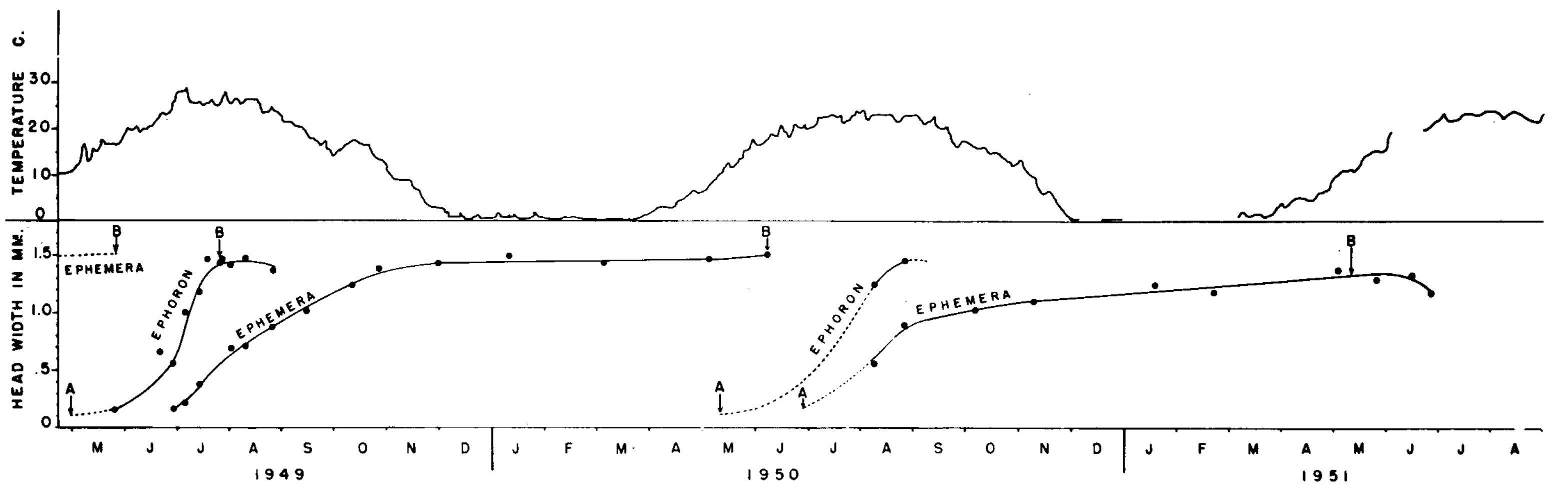

FIG. 28—Graph showing *Ephoron album* growth curves for 1949 and 1950 superimposed upon the corresponding growth curves of *Ephemera simulans*. A = date when eggs began to hatch. B = date of the beginning of emergence.

on July 25; therefore, the collection made on July 27 was probably somewhat smaller than it would have been two days earlier. If it is assumed that the average number of nymphs per square meter on July 25 was 924, or twice that of July 27, the number would still be rather small compared with the 442,235 eggs deposited per square meter of bottom during the one evening of August 4, 1949. It should be noted also that the number of nymphs represents the total production of this species for the year, yet the number of eggs produced in one evening was 478 times as great.

In the section dealing with the distribution of eggs in the water, the number of eggs possible per square meter based on the population of nymphs, the sex ratio, and the average number of eggs per female was shown to be 419,496 for the season. This represents a potential 454 times as great as the actual production. Thus it appears that only about 0.2 per cent of the potential population of *Ephoron album* survive.

No quantitative collections of nymphs or eggs were made in the case of *Ephemera simulans*, but in a population such as this where the sex ratio is about one to one, each female on the average needs to produce only two adult offspring in order to hold the population stable. During the five years in which *Ephemera simulans* populations were observed, there was no noticeable difference in their abundance. If we apply the above reasoning to this stable population, it then appears that each female produces on the average only two mature offspring. When this number is compared with the average number of eggs produced by each female (4,500), the potential productivity is found to be about 2,250 times as great as that actually attained. The survival rate for this species is only about 0.04 per cent. These figures indicate that the survival rate for *Ephoron album* is approximately five times as great as that of *Ephemera simulans*.

Economic Importance

The life-span of adult *Ephoron album* is so short that the individuals are unable to travel far from the place of emergence. They are likely to become a nuisance only in cases where lights are very close to the place of emergence, or when strong winds sweep the swarms inland. *Ephemera simulans*, having a longer adult life and being a stronger flyer, is more likely to travel inland to lights where many die, thus making streets and walks dangerously slippery. If the masses are not removed, unpleasant odors from the decomposition of the dead bodies may result.

The mayflies in general are recognized as an important food of aquatic and in some cases of terrestrial animals. There appears to be little literature dealing specifically with either of these species. Needham and Christenson (1927:16) listed *Ephoron album* with the economic aquatic insects of Utah. Clemens and Bigelow (1922:90) found that in June, 1919, the ciscoes *(Leucichthys prognathus)* of Lake Erie fed almost entirely on adult and subimago *Ephemera simulans*. Leonard (1947:688) studied the food of the rainbow trout (*Salmo gairdnerii irideus* Gibbons). He found that nymphs of *Hexagenia occulta* (Walker) were more abundant than *Ephemera simulans* in the stomachs of the fish that he examined. He concluded that, except for a brief period at emergence time, *Ephemera simulans* spends its nymphal life too deeply embedded in the substrate to be a reliable source of fish food.

Price recently studied the stomach contents of some Lake Erie fishes. In his report to the Natural Resources Institute of the Ohio State University, he showed that the mayflies are important in the diet of several species of fishes. Members of the genus *Hexagenia* were the most numerous of the mayflies found in the stomachs. Individuals of *Ephemera* were found infrequently, but no specimens of *Ephoron* were reported. The fishes used in Price's study were collected by trawl from the deep open water of the lake, often at long distances from the shoal habitats of *Ephemera* and *Ephoron;* therefore, it is not surprising that these mayflies were not found in significant numbers in the stomachs of these fishes.

In this study of *Ephoron album* and *Ephemera simulans* no fish stomachs were examined, but observations at the time of emergence and mating flight indicate that these species are important sources of food for fishes, birds, and some invertebrates, especially the spiders.

The best fly fishing that the writer has ever experienced on Lake Erie occurred during an emergence of *Ephoron album.* While using a small white fly, several species and in some instances several individuals of each species were caught. Rock bass (*Ambloplites r. rupestris*), white bass (*Roccus chrysops*), and smallmouth bass (*Micropterus d. dolomieu*) were caught most frequently; however, some yellow pikeperch (*Stizostedion v. vitreum*), sheepshead (*Aplodinotus grunniens*), and yellow perch (*Perca flavescens*) were caught. Sometimes the water appeared to contain schools of hundreds of small white bass. When the mating flight was over and the dead mayflies on the surface began to drift away, the schools of rising fish followed and continued to take them from the surface.

Since *Ephoron album* subimagos emerge only in the evening and have such a short adult life, they are not of much importance as food for birds. The subimagos and adults of *Ephemera simulans,* on the other hand, are important both as a food of fishes and as an item of food of many birds. As a food for birds, they are especially important since they emerge at a time when many of the birds are nesting.

The nymphs, due to the secretive habits of both species, are probably not an important item of fish food except at the time of emergence when they leave their hiding places and rise to the surface. However, they should be an important source of food for many of the invertebrates living in the habitat.

Of the larger groups of mayflies in Lake Erie, *Ephemera simulans* and some species of *Stenonema* are first to emerge, followed by the extremely abundant *Hexagenia.* Soon after the *Hexagenia emergence* season is over, *Ephoron album* begins to emerge. Thus it appears that both *Ephemera simulans* and *Ephoron album* may be quite important as a food supply during the periods when other forms are not available.

SUMMARY

1. A study of the biology of *Ephoron album* and *Ephemera simulans* in Lake Erie was made during the years 1948 to 1953.

2. *Ephoron album* is distributed across North America, but it is usually confined to a region between 40 degrees and 50 degrees north latitude. *Ephemera simulans* is distributed over a much wider area and in one case has been reported as far south as Florida.

3. Both species appear to be ecologically confined to riffles of relatively large streams or to gravel and sand shoals in lakes.

4. The eggs of *Ephoron album* are about .37 mm. by .21 mm. They have a hard outer shell and require eight to nine months for hatching in Lake Erie. The oxygen requirement appears to be very low during much of this time. *Ephemera simulans* eggs are about .22 mm. by .12 mm. They have an adhesive outer covering and will adhere to solid objects. Debris also becomes attached to the egg surface. Oxygen consumption of eggs is probably much greater per unit time than with *Ephoron album.*

4. A period of near freezing temperatures followed by a period with temperatures above 10° C. is necessary for the hatching of the eggs of *Ephoron album.* This is believed to be a factor limiting the geographical distribution of this species to a range between 40 and 50 degrees north latitude. Freezing temperatures are not necessary to cause the eggs of *Ephemera simulans* to hatch.

6. The average number of eggs produced by each *Ephoron album* female was 908. The average number by *Ephemera simulans* females was 4,500.

7. The number of eggs deposited on the bottom below a mating swarm of *Ephoron album* in one evening was as high as 442,235 per square meter.

8. In *Ephoron album* the first instar nymphs average .850 mm. in length, exclusive of caudal filaments. There are no gills in this stage. In the laboratory, nymphs remained in this stage for about five days. The second instar nymphs have six pairs of short gills on abdominal segments 2 to 7. In the third instar nymphs, the gills on abdominal segments 2 to 7 are about twice the length of those of the second instar. In this stage there is a pair of small gills on the first abdominal segment. In the fourth instar nymphs, the gills on abdominal segments 2 to 7 are flattened and have a fringe of small filaments along the edges. The mandibular tusks first become prominent in the fifth and sixth instars.

9. *Ephoron album* nymphs grow very rapidly. The eggs hatch about the first of May and the nymphs emerge as subimagos about the last part of July or first part of August. *Ephemera simulans* requires more time to go from egg to adult in Lake Erie. The eggs hatch in July, but the nymphs do not emerge until the following June.

10. In both species the eyes of the males develop much more rapidly and attain a larger size than those of the females.

11. The food of the nymphs of both species appears to be about the same. It consists chiefly of diatoms (both planktonic and sessile), other planktonic algae, filamentous algae, and plant detritus commonly found in the layer of ooze covering the gravel and sand particles on the bottom.

12. In *Ephoron album* emergence occurs at dusk. The males immediately settle on the water or on some object on shore, molt within about a minute, and join the mating flight. The females do not molt the second time, but fly directly into the swarm, mate, and expel their eggs, and die. In *Ephemera simulans* emergence usually occurs at night, but does not appear to be restricted to any particular time as is the case with *Ephoron album*. The subimagos of both sexes fly to some support on shore and remain quiet until they molt again, usually about 12 to 24 hours. The mating flights usually take place over vegetation. These occur at about sunset on the day the final ecdysis takes places.

13. *Ephoron album* was found to be partially parthenogenetic. Eggs removed from unmated females reared in captivity produced many nymphs.

14. A commensal relationship appeared to exist between a colonial protozoan and the nymphs of both species.

15. The life cycles of *Ephoron album* and *Ephemera simulans* appears to be sufficiently out of phase to reduce competition to a level that can be tolerated by both species.

16. From an estimate of the number of eggs and number of nymphs per square meter, it was estimated that an average of only about 0.20 per cent of the eggs of *Ephoron album* hatch and reach maturity. In *Ephemera simulans* only about 0.04 per cent reach maturity.

17. Both species are important sources of food for fishes for a short time during the emergence season. *Ephemera simulans* is a good source of food for nesting birds.

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