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SEASONAL DISTRIBUTION AND LIFE CYCLES OF EPHEMEROPTERA¹

F. EARLE LYMAN, Department of Zoology, Southern Illinois University

The seasonal distribution and life cycles are recorded for relatively few species of mayflies occurring in lakes. Such knowledge is limited primarily to species of the genera *Hexagenia* and *Ephemera* (Neave 1932; Spieth 1936; Berner, 1950). The present paper presents data on seasonal distribution and life cycles of 22 species obtained during a four-season ecological study of mayflies of Douglas Lake, Cheboygan County, Michigan.

METHODS

The main portion of the field work covered a period of four consecutive summers. To supplement the summer material, collections were made in the spring at two-week intervals following the disappearance of the ice cover and also during the fall. A total of 240 collections, including approximately 25,000 specimens, were taken. Both nymphs and adults were preserved in 80 percent ethyl or isopropyl alcohol; however, representative adults were preserved dry on pins or in papers.

Collecting equipment consisted of circular pan screens (20 and 30 mesh) for sifting bottom materials and washings from stones. In deeper water a long-handled, aquatic dip-net, a triangular-mouth tow dredge, or an Ekman dredge was used to bring up aquatic plants and bottom materials which were then screened. To obtain nymphs less than 3 mm. in length, unsifted bottom materials were brought to the laboratory and examined under magnification.

In making collections from any one habitat, population samples were taken either along a line transect from the shore line into the deeper water or by random selection at various depths. Because of the scarcity of nymphs of certain

species, and because of the reduction in numbers of a better represented species toward the end of an emergence period, a thorough search was made in selected favorable habitats to determine the presence or absence of nymphs. Observations on swarming of adults were made whenever possible. Vegetation along the shore was examined for adults whenever collections of nymphs were made.

The terms *abundant*, *common*, *scarce*, and *rare* as used in this paper designate relative numbers of individuals and refer to one species as compared with all others in Douglas Lake but not as compared to those of other lakes. Since general descriptions of Douglas Lake are already available elsewhere (Scott 1921; Welch 1928; Eggleton 1931; Moffett 1943), it seems unnecessary to review this subject again; however, a map of Douglas Lake (FIG. 1) is included to show the specific locations referred to in this paper.

DISCUSSION

A graphic summary of the emergence periods of Douglas Lake mayflies is presented in Table I and in the following section the life cycle and seasonal distribution is discussed for each species using the order of taxonomic sequence given by Needham, Traver, Hsu (1935).

Ephemera simulans Walker

The imagoes of *Ephemera simulans* are fairly common around the shore of Douglas Lake during two months of the year. The emergence period extends from about June 10 to August 1, the maximum number of adults appearing in early to middle July.

Interesting comparisons may be made on the relative length of the emergence period of this species in various localities. Eaton (1883) and

¹Accepted for publication February 9, 1954.

Burks (1953) have reported the enormous swarms which appear yearly from Lake Michigan at Chicago, Illinois, about the third week in July. Clemens (1915) has given June 5 to July 27 as collection dates for *E. simulans* in the Georgian Bay region. For Lake Nipissing, Ontario, Ide (1930) has stated the emergence dates June 30 to July 24. The writer has observed numerous imagoes in the vicinity of the Straits of Mackinac during June and July while in Lake Erie at Put-in-Bay, Ohio, adults were

E. simulans. In southern Michigan the writer has collected *E. simulans* as early as May 17 although the principal emergence usually occurs at the end of May and is of short duration. For example, during the last of May and first part of June, prodigious numbers of imagoes emerge from the Huron River near Ann Arbor, from Bass Lake in Livingston County, and from other lakes in southern Michigan.

Thus, it is observed that real differences occur in the over-all length of the emergence period of

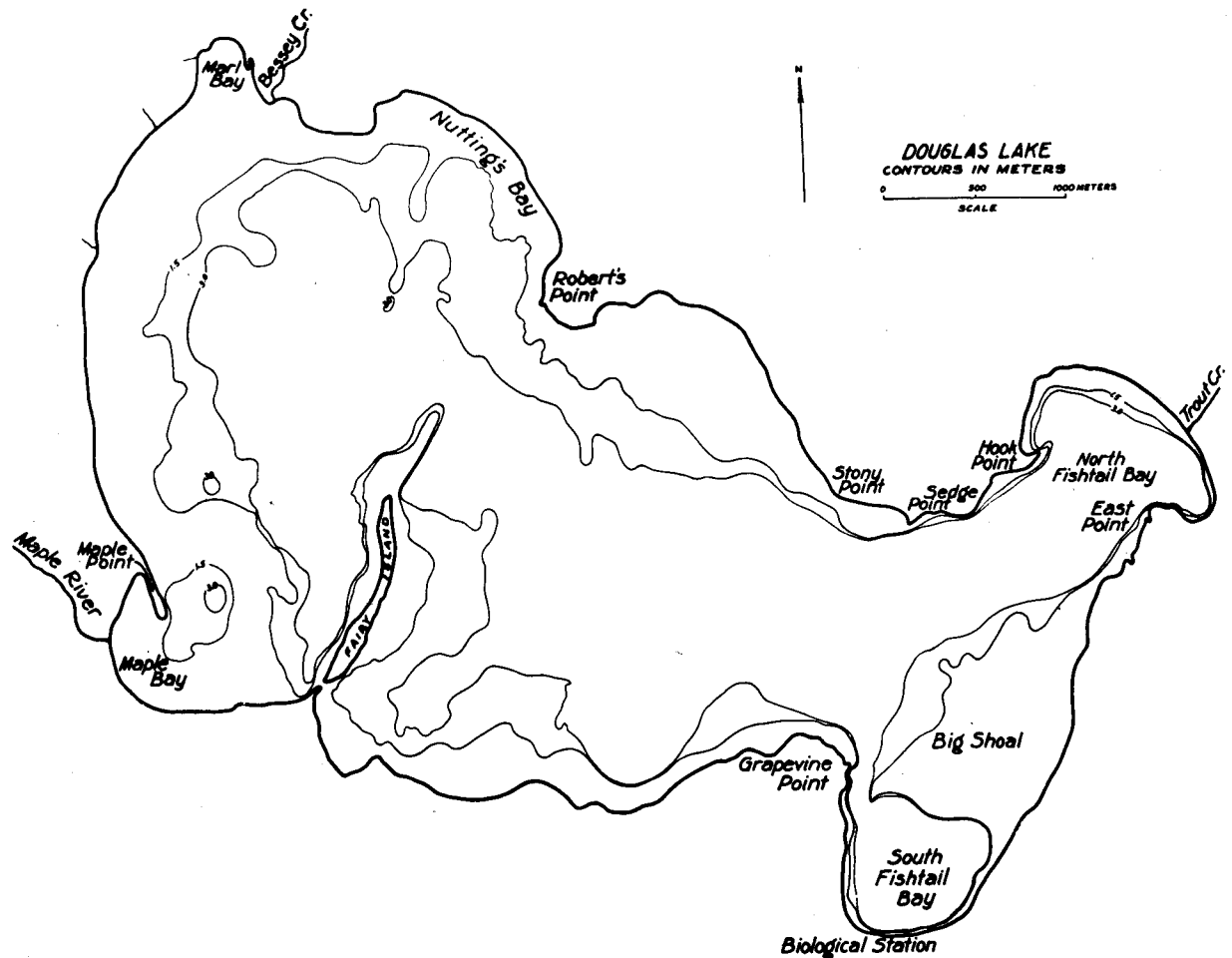


FIG. 1. Map of Douglas Lake, Michigan.

collected between June 11 and July 23 with the peak of emergence occurring about July 1. In contrast with the foregoing, Spieth (1936) has shown that in northern Indiana lakes and at Spencer, Indiana (White River), the main emergence of huge numbers of individuals of *E. simulans* is relatively short and occurs during the last of May and the first few days in June, although stragglers precede and follow this period by several days. For Illinois, Burks (1953) gives the earliest collection date of May 16 for

E. simulans over its wide geographical range. Ide (1935) has indicated already that the form of *E. simulans* inhabiting streams will eventually prove to be specifically different from the form inhabiting lakes. Although, on preliminary evidence, temperature appears to be an important factor correlated with the abundance of adults and the seasonal emergence pattern of *E. simulans*, further studies should be made to discover the reason for this phenomenon. A short emergence period in this species seems to be correlated

with a more southerly distribution and, consequently, a higher average water temperature over a longer seasonal period. For example, *E. simulans* emerges over a long period from the Great Lakes and from other lakes of more northerly latitudes where water temperatures are relatively colder during a shorter season of the year. On the other hand in the small, warmer bodies of water with higher average summer temperatures over a longer season, such as occurs in the lakes and streams of more southerly latitudes, *E. simulans* emerges over a relatively short period. As a result of this short emergence period, greater numbers and concentrations of adults are observed at the time of the annual seasonal emergence.

The burrowing nymphs of *E. simulans* are difficult to find and seemingly occur in com-

and summer until around August 1 at which time very young nymphs, a few millimeters in length, are found. Spieth (1936) also concluded that the life cycle was completed in one year in Indiana. In Bass Lake the writer found that *E. simulans* nymphs reach nearly their full growth by November. Growth essentially ceases until the following spring when final maturity of these nymphs occurs rapidly just prior to emergence.

Hexagenia limbata (Serville)

Hexagenia limbata is abundant at Douglas Lake. During the emergence period dense drifts and windrows of the bodies of imagoes and nymphal exuviae may be found floating in the water and piled along the shore. It was noted that these drifts and windrows consisted almost

TABLE I
EMERGENCE PERIODS OF DOUGLAS LAKE MAYFLIES

| SPECIES | MAY | JUNE | JULY | AUGUST | SEPTEMBER | OCTOBER |
|---------------------------------------|-----|-------|----------|--------|-----------|---------|
| <i>Ephemera simulans</i> | | | —XXXX*— | | | |
| <i>Hexagenia limbata</i> | | | —X XXX— | | | |
| <i>Hexagenia affiliata</i> | | | —X— | | | |
| <i>Stenonema femoratum</i> | | —XXX— | —XX— | —X— | | |
| <i>Stenonema interpunctatum</i> | | | —XXX— | —XX— | X— | |
| <i>Heptagenia lucidipennis</i> | | | —X— | | | |
| <i>Siphloplecton basale</i> | —X— | | | | | |
| <i>Siphonurus rapidus</i> | —X— | | | | | |
| <i>Leptophlebia nebulosa</i> | X— | | | | | |
| <i>Choroterpes basalis</i> | | | | —XXX— | | |
| <i>Baetisca obesa</i> | | ?-X-? | | | | |
| <i>Ephemerella bicolor</i> | | —XX— | | | | |
| <i>Ephemerella lutulenta</i> | —X— | | | | | |
| <i>Ephemerella temporalis</i> | | —XX— | | | | |
| <i>Tricorythodes allectus</i> | | | ?-X-? | | | |
| <i>Brachycercus lacustris</i> | | | | —X— | | |
| <i>Caenis simulans</i> | | —XXXX | X— | | | |
| <i>Callibaetis ferrugineus</i> | | | | | | |
| <i>Baetis phoebus</i> | | | —XXX— | | | |
| <i>Centroptilum fragile</i> | | | —XX— | | | |
| <i>Pseudocloeon dubium</i> | | | —XX— | | | |
| <i>Cloeon rubropictum</i> | | —XX— | XXXXXXXX | XX— | | |

*X indicates time of greatest abundance.

paratively small numbers in Douglas Lake. Clemens (1915) found this to be the case at Go-Home-Bay, Ontario, where, although adults were numerous, he was unable to find nymphs. Nymphs are found in Douglas Lake only as widely scattered individuals in loose, fine sand of that part of the littoral region included within the 1 and 3 meter contours. It might be emphasized that in situations where nymphs are seemingly scarce or rare, yet adults are common, these nymphs are widely distributed over a large area of the littoral zone while the emerging adults are always concentrated in a relatively narrow strip along the shore.

In Douglas Lake the life cycle of *E. simulans* is completed in one year. Mature and almost mature nymphs are present during the spring

entirely of bodies of female imagoes with only an occasional male being found. This result arises from the fact that, following copulation, the female flies out over the water to oviposit, does not usually return to land but dies on the water. The mating flight, however, occurs over land and after copulation, the male generally alights on nearby vegetation or rejoins the swarm for further matings, ultimately dying on land rather than on water. Bodies of males are found rather commonly scattered among vegetation along the shore, whereas, in that situation, the body of a female lacking egg packets is exceedingly rare. Moreover, a living female imago without egg packets was rarely seen resting on vegetation. When specimens are collected from vegetation during the day, there

is a conspicuous preponderance of males over females. Yet, at the height of the emergence period the windrows of a morning, following a large swarming of an evening before, will consist primarily of prodigious numbers of females. This apparent difference in number may be due either to more secretive habits of females during the day or to longer life of the male. The latter alternative would result in an accumulation of males present.

During the four seasons it was observed that the largest emergence occurred in the summer of 1938 while the emergences of 1936, 1937, and 1939 were much smaller but more or less equal in relative numbers of individuals. Also, this large emergence was correlated with Ekman dredge samples taken during the summer of 1937 which contained more nymphs per dredge than did similar samples during either of the subsequent years. A cyclical trend in population numbers was also observed for *Hexagenia* in Lake Erie (Lyman 1944a).

The emergence of *H. limbata* occurs from about June 15 to July 20 with a maximum between June 20 and July 5. At the beginning of the emergence period the surface-water temperature ranges between 18° and 20° C. and by July 1 the temperature varies around 21°–22° C. The subimago usually emerges from the nymph during the early morning and after a quiet night, the lake surface will be found speckled with cast skins of nymphs floating on the calm water. The subimago period covers 36–48 hours depending to a large degree upon the air temperature and weather conditions (Lyman 1944). If the weather is warm and fair, the period is shortened, whereas it is lengthened by cold and rainy conditions.

The swarming or mating flight of *H. limbata* takes place over land in the evening. The nature of the swarm depends upon wind and other weather conditions. During cloudy, windy, or rainy weather, swarming is more or less sporadic and confined to small groups in well-protected situations. The most favorable time appears to be during calm, fair, and warm weather or when only a slight breeze is blowing.

Large swarms were observed mainly during the last of June over Grapevine Point. During the sunny hours of the day most of the imagoes rest quietly on the underside of leaves; those on the upper surface are in densely shaded areas. As the sun approaches the horizon they begin to move more and more to the upper-side of the leaves. Early on a calm evening the foliage is literally covered by thousands of imagoes. As the light fades a restless stirring develops and here and there an individual leaves its resting place for another, usually a little higher. If a breeze begins to move the leaves, a few males take wing and soon a large number of them are flying low over small open

areas of low vegetation. Should this breeze cease, they gradually settle again on the vegetation and remain there until the main swarming begins at about 9:00 p.m. (E.S.T.). If the breeze persists, the swarming continues although females do not approach the swarm until much later. On a completely calm evening, swarming does not take place earlier than 9:00 p.m. At 8:55 p.m. a few males begin to swarm over the low trees and shrubs. Within two minutes hundreds are in the air and by 9:00 p.m. thousands of males are swarming. Thus, the number of individuals taking part in a swarm increases rapidly in a remarkably short length of time. At first the swarm flies just above the lowest small trees and shrubs in the more or less open areas in the surrounding woods and numerous specimens come within easy reach of the insect net. As the light fades, the swarm rises gradually higher and higher. By 9:20 p.m. all members of the swarm are well out of reach of a net and concentrated slightly above the tops of the highest trees fringing the lake shore. Females enter the swarm from time to time from the surrounding vegetation. They do not fly up and float down as do the males but fly in a more or less zigzag oblique course upward through the swarm until grasped by a male. The swarming continues until well after 9:30 p.m. when darkness makes impossible further observations. Only females in flight and in oviposition were observed over the deeper waters between 9:30 and 10:00 p.m. but no males were seen at this time flying over the lake. The main swarming of males takes place along the shore of the lake over the tops of the trees, not over the open areas along the shore or out over the lake. At Put-in-Bay, Ohio, in Lake Erie swarming activities of *Hexagenia* begin about one hour earlier than at Douglas Lake (Lyman 1944a) which seems to indicate that there may be a correlation between the initiation of the mating flight and light intensity. The factors involved in initiating the mating flight of mayflies need more investigation.

The burrowing nymphs of *H. limbata* may be found in Douglas Lake at water depths of 1–15 meters. Those specimens taken in shallower depths (1–6 meters) were usually very young, recently hatched nymphs or those of comparatively small size (up to 10 mm.). Nymphs of larger size were very rarely encountered on sandy bottoms in shallow water. The greatest number of large specimens (20–25 mm.) were taken in soft mud at water depths of 11–13 meters on the west side of South Fishtail Bay and opposite Grapevine Point proper. They occur at 8–10 meters in North Fishtail Bay near Hook Point. In this area the transition from sandy to muddy bottom begins at a shallower depth than in South Fishtail Bay. The reasons for the restriction of *Hexagenia* nymphs to muddy

bottoms and to water depths not greater than 15 meters were given in a previous paper (Lyman 1943). The largest number of nymphs collected in a single haul with a 15 x 15 cm. Ekman dredge in Douglas Lake was 6 and often many samples taken at a given depth contained no nymphs. In comparison, Neave (1932) recorded taking 401 nymphs of *Hexagenia* in 10 hauls of a 23 x 23 cm. Ekman dredge from Lake Winnipeg.

In Douglas Lake the length of the life cycle of *H. limbata* is two years (FIG. 2). This substantiates the same conclusion reached by Neave (1932) for this species in Lake Winnipeg. It

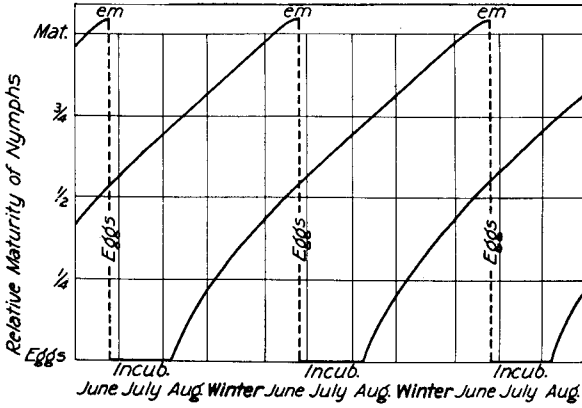


FIG. 2. Diagrammatic representation of seasonal life cycle of *Hexagenia limbata* in Douglas Lake. Mat.—mature nymphs; em—emergence; incub.—incubation period of eggs.

should be stressed, however, that not all species of the genus *Hexagenia* have a life cycle of two years (Lyman 1943a). Eggs are deposited in Douglas Lake during late June and early July and very young nymphs which hatch from these eggs are found during early August. Thus, the approximate length of the incubation period under natural conditions agrees well with Hunt (1951) who found that *H. limbata* eggs hatched in 20–26 days under laboratory conditions at a temperature range of 62°–73° F. At the beginning of the following summer these nymphs have become half grown, and by late August they are almost fully grown and emerge the next summer. The basis for this conclusion is that following the emergence of early summer, numerous nymphs, about three-fourths grown, but no fully mature nymphs, may be found during July and August (FIG. 2), while in August, the very small recently hatched nymphs are found. Thus, two distinct age groups are present at this time of year and continue until the following summer when emergence of the older one occurs.

Hexagenia affiliata McDunnough

The earliest date of collection of *Hexagenia*

affiliata was July 10, the latest July 31. This species is rare, since the total number of specimens collected was 25. All adults were taken in the vicinity of South Fishtail Bay resting on vegetation and none were taken from swarms. No nymphs known to be of this species were found.

Stenonema femoratum (Say)

Stenonema femoratum is one of the most abundant species around Douglas Lake throughout most of the summer. Imagoes are particularly numerous from about June 5 to July 15 although specimens may be found from the last of May to the end of August. During the day they usually rest on vegetation close to the water's edge. Swarming of males and mating take place between 7:30 and 9:00 p.m. along the shore of the lake over both land and water. No swarms were observed during the day. Swarming in this species stops at approximately the same time that the swarming of *Stenonema interpunctatum* begins. From reared specimens the length of the subimago period was determined as approximately 24 hours but this period is lengthened by a spell of cool weather (Lyman 1944).

The life cycle of *S. femoratum* in Douglas Lake is completed in one year. The long emergence period is best represented by a trimodal seasonal curve the peaks of which represent three periods of relative abundance of the adults as shown in FIGURE 3. The nymphs are present in large numbers at all seasons of the year in the shallow

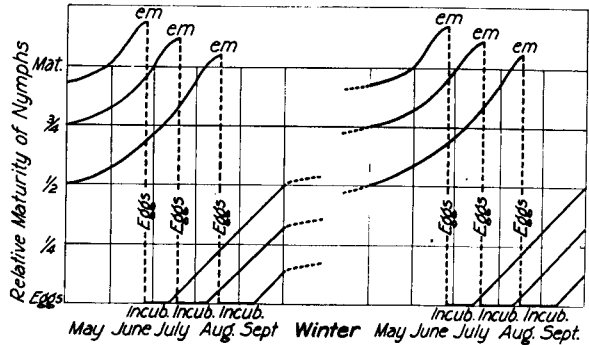


FIG. 3. Diagrammatic representation of the seasonal life cycle of *Stenonema femoratum*. Height of curve above maturity line indicates relative size of the emergence. Mat.—mature nymphs; em—emergence; incub.—incubation period of eggs.

littoral region wherever rocks or other similar objects are present. Collections of nymphs in May consist mainly of mature or almost mature specimens; however, many smaller nymphs are also present and the entire size range of all collected was from about one-half grown to fully mature. The degree of maturity was determined from the length and development of

the wing pads, since nymphs ready to emerge have large, much darkened wing pads, while in earlier instars, they are smaller and light colored. In May there appear to be three distinct age and size groups, all of which have come from eggs deposited at different times during the previous summer. Of these three groups of nymphs, the first emerges during June and early July, is the largest in number and size of individuals, and produces the largest emergence of the summer. The second group which emerges during July is the next in size and in number of individuals, while the third group which comes in August is the smallest in number and size of individuals. These facts are supported by collections taken throughout the summer. Such collections show two distinct groups of nymphs maturing, one in mid-July and the other in mid-August. No mature nymphs, or adults, were ever taken after late August. The three groups are also correlated with swarming activity of adults and the relative abundance of individuals found at different times during the summer. Although from collections of imagoes alone, the conclusion might be reached that there is only a single, long, unimodal emergence period rather than three more or less distinct ones, each relatively smaller than the previous one. Also, collections taken in September and October show three distinct size groups coming from eggs deposited by each of the three groups present in the spring and which matured separately at three different times during the summer. According to Needham, Traver, Hsu (1935) the incubation period of the eggs of *S. tripunctatum* (= *S. femoratum*) is 11-23 days under laboratory conditions, which time coincides with field observations at Douglas Lake. Eggs laid in June hatch during July, since collections taken in mid-July consist of numerous newly hatched, three-fourths mature, and fully mature nymphs. Collections made in mid-August consist of numerous recently hatched, one-fourth mature, and a few mature nymphs.

***Stenonema interpunctatum* (Say)**

Stenonema interpunctatum is common to abundant during most of the summer. Imagoes were collected either on vegetation or in swarm from about June 15 to September 15. The maximum of abundance is reached about July 15. A smaller emergence occurs during early August and a still smaller one consisting of comparatively few individuals takes place in late August and early September. Adults of *S. interpunctatum* seem to be more numerous on vegetation farther back from the shore line while *S. femoratum* is usually found on vegetation near the shore line.

Swarming of males in this species occurs at dusk in the evening over a comparatively short period of time. In July, swarming of the males does not begin until almost 9:00 p.m. and lasts

until dark (9:30 p.m.). Females were seen to enter the swarm about 9:15 p.m. but not before. This species seems to swarm with more regularity each evening from day to day, whereas, *S. femoratum* swarms one evening and then may not be seen again for several days. Both *S. interpunctatum* and *S. femoratum* have the same general type of swarming flight, which consists of hovering in one place for a time then darting elsewhere. Neither of these two species flies up and glides down in the type of flight characteristic of *Ephemera* and *Hexagenia*. *S. femoratum* appears to have a slower flight than *S. interpunctatum* and was often seen swarming over land close to the shore line while *S. interpunctatum* was always observed over water near the shore line but not over land.

The nymphs of *S. interpunctatum* are present in relatively large numbers at all seasons of the year in the littoral region in such situations as Grapevine Point and Fairy Island where rocks are numerous. They are most abundant in deeper water (1-2 meters) and are much less numerous close to the shore line. They are less widely distributed than *S. femoratum* and are very rare at Hook Point, Marl Bay, and Stony Point where the latter species is common. These nymphs do not occur under isolated stones, old boards, or logs unless these objects are close to a rocky situation.

The life cycle is undoubtedly completed in one year in Douglas Lake and the pattern follows closely that of *S. femoratum*. Wodsedalek (1912) inferred that the life cycle required two years, a supposition which appears now to be incorrect. Collections of numerous individuals in late May show three age groups of nymphs which may be arbitrarily classified as approximately three-fourths, one-half, and one-fourth mature. Likewise, October collections contain three age groups but the largest nymphs are not more than about one-half mature and the smallest nymphs are those which recently hatched from eggs laid in late summer. There appears to be very little growth of nymphs during the winter months for nymphs collected early in May are only slightly larger than those collected in October. It thus seems that there is a marked increase in growth rate in the late spring, for the largest nymphs taken in early May are a little more than half grown yet they emerge during the last half of June and early July. Eggs of these individuals begin to hatch late in July and the nymphs become about one-half grown before winter when growth all but stops.

***Heptagenia lucidipennis* (Clemens)**

Representatives of *Heptagenia lucidipennis* are relatively uncommon and imagoes were collected from vegetation along shore in only two localities, Fairy Island and Stony Point. No

specimens were seen or taken in swarm. The emergence period is comparatively short and distinct and occurs from about June 25 to July 20 with a maximum of abundance around July 10.

The nymphs were found in numbers only on the northwest shore of Fairy Island, on Stony Point, and on Robert's Point where the rocks, lying close together, form an almost solid pavement over the bottom. A few specimens were collected at Grapevine Point and two at Hook Point.

The life cycle is completed in one year with a unimodal emergence period. On May 29 a series of nymphs was collected under stones from Fairy Island and Stony Point which averaged 1.0–1.5 mm. in length, the largest specimen being 2.5 mm. long and the smallest 1.0 mm. Twelve days later, on June 10, another series of nymphs collected from these localities averaged 5–6 mm. in length. The average size of mature nymphs is 7–8 mm. The surface-water temperature on May 29 was about 15.5° C. while on June 10 it was 20° C. Also, during this twelve-day period there was a marked increase in the growth of filamentous algae on the stones. This may be correlated with the rapid growth rate of the nymphs during this short period. An examination of the digestive tract of the nymphs collected on June 10 disclosed fragments of these filamentous algae. Although practically all nymphs collected on June 10 were of large size (5–6 mm.), a few small nymphs (2–3 mm.) were also taken. The first mature nymphs were collected about June 25 when the first imagoes were captured. The maximum abundance of both mature nymphs and adults occurs early in July. After July 20 no nymphs or imagoes were found. No nymphs of *H. lucidipennis* could be located during late summer or early fall. It thus appears that the incubation period in this species is a long one. Probably the eggs either hatch in the very late fall and the nymphs overwinter with little or no growth, or the eggs overwinter and hatch in the early spring just after the disappearance of the ice cover. Indications seem to favor the latter premise since this would account for the appearance of the scattered very small nymphs which occurred along with the large nymphs on June 10.

Siphloplecton basale (Walker)

The adults of *Siphloplecton basale* are rather common in May. This species is the first to emerge from Douglas Lake in the spring and the emergence period extends over about three weeks. Subimagoes were taken on May 12 as they emerged from the nymphal skins during the late morning while the water temperature was 15° C. and the ice cover had been off the lake for only two weeks. A male subimago taken on May 13 at 11:00 a.m. as it left the nymphal

skin, emerged as an imago on May 15 at 3:00 p.m. Males were observed swarming during a cloudy afternoon when the air temperature was 14° C. There was very little wind and most of the specimens flew at a height of 4–5 meters. They have a hovering and darting type of flight with a comparatively slow wing-beat. While hovering, the body is held with the anterior portion uppermost at an angle of about 45° with the horizontal. The tails and forelegs are spread apart during hovering and are brought together as the mayfly darts from one position to another. While hovering, it may move slowly up, down, or sideways without darting. Swarms were seen only over the water just beyond the shore line in the vicinity of Grapevine Point, North Fishtail Bay, and South Fishtail Bay. Swarming was also seen in the evening about 8:00 p.m.

Nymphs were collected only during May. They were common almost everywhere around the shore of the lake: in more protected coves, along open sandy beaches, in beach pools resulting from high water. Specimens were most abundant in stands of *Scirpus americanus* which appeared to afford them with temporary shelter during the shoreward migration. Individuals were often seen, usually near the water surface, swimming shoreward through the open water. During windy periods they were more or less carried along by the waves. Thus, in one way or the other the nymphs reached the shore and either clambered out of the water or were washed-up onto the sand where they emerged. From all indications this procedure seemed to be a normal one before emergence took place since no specimens were observed emerging from the open-water surface of the lake. During late morning, subimagoes were seen in North Fishtail Bay and other parts of the lake flying up from the sandy inner beaches where they had emerged from the nymphal skins. Nymphs and cast exuviae were common on the sands of the inner beach. No nymphal skins were found floating on the water surface out in the lake. Immature nymphs of *S. basale* were not collected from the shallow littoral zone or in the emergent plant beds. It is therefore concluded that they inhabited the submerged plant beds of the deeper water. However, efforts made to collect them in such places were unsuccessful. Since these nymphs are very strong, agile swimmers, they might easily have evaded the methods used for collecting them. It appears that the nymphs, when ready to emerge, leave the submerged plant zone, and either swim to the shore or allow themselves to be washed there by the waves.

Siphonurus rapidus McDunnough

Only the nymphs of *Siphonurus rapidus* were collected in Douglas Lake. During the last of

May in 1938, they were found in almost every pool located close to the lake shore but were rarely taken in the lake itself. At the time collections were made most of these pools were not directly connected with the lake but were usually separated from it by a narrow, relatively low strip of land. From all indications these pools had been connected with the lake earlier in the spring when the water level was higher and the nymphs had migrated into the pools during this period of higher water and were stranded there as the water level receded. They did not occur in those pools which had had no direct connection with the lake and which had been formed only by water seepage. In May of 1939 very few specimens were found in those pools in which they had been numerous the year before and many of the pools contained none at all. The spring of 1939 was much drier than the same period of 1938.

S. rapidus nymphs occur in abundance in most of the small streams of the countryside surrounding the lake. Emergence occurs at the end of May and early June. During a period of high water when the streams become swollen and overflow their banks, the nymphs migrate from the main channel of the stream into adjacent overflow areas. Here they remain to complete their nymphal development and usually emerge successfully even though the water level of the stream may drop rapidly and leave them stranded in shallow pools or ditches. During the high-water spring of 1938 many of the nymphs were probably swept downstream into the lake and as a result were found in the pools around the lake. Presumably this did not happen in the drier spring of 1939 and therefore very few nymphs were found around the lake. Yet, they were just as abundant as previously in the various streams. All the nymphs of *S. rapidus* collected were mature or almost mature a fact which leads to the conclusion that the more immature stages are probably confined to the streams and do not occur in Douglas Lake proper.

Leptophlebia nebulosa (Walker)

The imagoes of *Leptophlebia nebulosa* are common although the period of emergence is relatively short and occurs during the last of May and the first of June. The length of the subimago period is about 24 hours.

Swarming of the males was observed in both morning and afternoon but not in the evening. It consisted of flying up and floating down more or less over one spot and usually over the shrubs or low trees fringing the shore. Several females were seen ovipositing between 9:00 and 11:00 a.m. in the vicinity of Hook Point. They flew back and forth along the shore about 3 meters above the water. From time to time an individual of the group swooped down, alighted for an instant

on the water surface with wings held vertically and body resting on the water, deposited a group of eggs, and then resumed flight. This performance was repeated several times within a few minutes by the same individual until all the eggs were deposited. In some cases the abdomen was merely dipped in the water as the female skimmed along over it without alighting.

The nymphs are most common in the shallow littoral regions of the more quiet portions of the lake such as Hook Point, Marl Bay, and Maple Bay, although they do occur in typical rocky habitats in smaller numbers. The nymphs seem to be negatively phototactic as they are usually found under old wood, stones, or debris along the shore. In the spring the nymphs migrate shoreward and are usually found at the very water's edge. They do not normally occur along the open sandy shores where wave action is strong and where there is small chance for accumulation of debris. They are often found in small, shallow pools close to the shore line which are formed by high water but later become isolated from the lake proper by the drop in water level. These nymphs do not emerge from the open-water surface but clamber onto the shore and emerge 1-2 cm. above the water line. In captivity they readily eat all sorts of organic debris such as collects along shore or in the bottom of pools and they often consume the dead bodies of other nymphs or their exuviae.

Eggs laid in spring, hatch during the last of July and forepart of August. Numerous very small nymphs (1 mm.) were collected during this part of the summer. By the middle of October the nymphs attain a length of 3-4 mm. and by the following May are about 10 mm. long and ready to emerge. It appears that practically all the growth occurs during the winter. The life cycle is completed in one year.

Choroterpes basalis (Banks)

Choroterpes basalis imagoes were collected only in the vicinity of Hook Point. In this one place they are abundant, but considering the lake as a whole, representatives of this species may be cited as relatively scarce. The period of emergence occurs from the end of July to early September. Under aquarium conditions subimagoes almost invariably emerge in the early evening and imagoes on the following early morning, thus, the length of the subimago period is approximately 12 hours. Small groups of males were observed swarming only in mid-afternoon 3-5 meters above the water. Their flight was of the hovering and darting type.

During the course of four summers' collecting only two nymphs were taken outside the Hook Point situation. The nymphs are, however, abundant at Hook Point. Even here they are restricted to a relatively small area where they

occur under old logs and wood fragments which rest on the marl-covered bottom. The distribution of the nymphs ends abruptly along the line where the marl stops and the almost pure sand bottom begins. On one side of this artificial line nymphs are common while on the other side not a specimen can be found. The nymphs react negatively to light and remain under wood during the day coming out on top only at night. They feed on marl and the encrusting organisms found on the wood. When fed similar materials scraped off rocks from Grapevine Point they also ate it just as readily, although they do not occur in that type of habitat. *C. basalis* nymphs were found in other lakes near Douglas Lake but always in the same type of habitat characterized by collections of woody debris.

The life cycle of this species is completed in one year. Collections of nymphs seem to indicate that the eggs overwinter and hatch in late spring or early summer. No very small nymphs of this species were collected although nymphs about one-fourth to one-half grown were taken during July and early August. However, *C. basalis* nymphs were absent from all collections made in October and also from those made in May and June.

Baetisca obesa (Say)

During the four seasons over which collections were made only two male imagoes and two very immature nymphs of *Baetisca obesa* were taken. The adults were collected in flight on the evening of June 18 and the nymphs in mid-September.

Ephemerella bicolor Clemens

Ephemerella bicolor is a very common species emerging in early summer between June 5 and July 10 with a maximum abundance during the latter part of June. Swarming of males takes place along the edge of the lake in the evening about 8:00-8:30 p.m. The length of the sub-imago period is normally about 24 hours.

The nymphs of *E. bicolor* are numerous in the spring along the open shores on rocks, old wood, and stems of last year's growth of *Scirpus americanus*. No specimens were collected in quiet water situations such as prevail at Hook Point, Marl Bay, Maple Bay, or Sedge Point pools. When ready to emerge, the nymphs migrate shoreward, climb out of the water, and molt just above the water line of an exposed rock at the shore line. They do not seem to be able to emerge from the open-water surface. When mature nymphs were placed in water without a stone or other object on which they could climb out of the water to emerge, they soon died without emerging. However, if a stone, placed in the dish, projected slightly from the water, the nymphs emerged successfully.

The life cycle of *E. bicolor* is completed in one year. Eggs deposited in early summer hatch in late summer or early fall. Recently hatched *Ephemerella* nymphs begin to make their appearance in the lake during the last half of August. At that time the writer found it impossible to specifically identify these very young nymphs since three closely allied species of *Ephemerella* belonging to the *bicolor* group occur in Douglas Lake and certain phases of the life and seasonal cycles of these three species run parallel to one another. However, by October characters appear in the developing nymphs by means of which *E. bicolor* can be separated from the other two species. Practically all of the growth of *E. bicolor* nymphs occurs in the spring after the ice cover disappears. In mid-October the nymphs average about 2 mm. in length and in early May are only around 3 mm. long. The average size of mature nymphs is 7 mm.

Ephemerella lutulenta Clemens

Ephemerella lutulenta imagoes are rather common during the last of May and early June. This species is not as abundant as the other two species of this genus in Douglas Lake. Emergence begins about May 15 and ends about June 10. Swarming activities were not observed.

The nymphs are found close to shore in almost all parts of the lake in the early spring but seem to prefer those areas in which debris collects; they are commonly found on the old stems of *Scirpus*. They do not occur on the open bottoms but under rocks, wood, or other objects to which they cling.

The life cycle is completed in one year. Eggs which are laid in late spring incubate through the summer and probably hatch in late summer or early fall. The small nymphs of *E. lutulenta* and *Ephemerella temporalis* found in the fall probably hatch from eggs at about the same time and although collections made in mid-October seem to contain both of these species, the writer does not feel sure of his ability to distinguish them. In fall collections taken at Hook Point where *E. bicolor* does not occur, there seem to be two sizes of nymphs present, the larger of which may be *E. lutulenta* and the other *E. temporalis*. However, the size groups are not distinct and graduate into each other so as to make impossible positive separation of the two species on this basis alone. Neither can they be separated on the basis of distribution since they occur together in the same situations. Nevertheless, by early May, *E. lutulenta* is readily separable from *E. temporalis* on the basis of size alone for at this time the nymphs of *E. lutulenta* are practically full grown and ready to emerge while those of *E. temporalis* are but little larger than they were in the autumn. Thus, *E. lutulenta* seems to continue its growth throughout

the winter and is the first of the three *Ephemerella* to emerge in the spring.

***Ephemerella temporalis* McDunnough**

Ephemerella temporalis is a very common species and compares equally with *E. bicolor* in relative abundance. The period of emergence is from about June 5 to July 15. It appears to last a few days longer than *E. bicolor* although this may be an apparent rather than an actual difference and may vary from year to year. No swarms of *E. temporalis* were observed although imagoes were readily collected resting on vegetation along the shore. The length of the subimago period is about 24 hours.

In the spring the nymphs of *E. temporalis* are found almost everywhere along the shore in shallow water where old wood, stones, debris, or old culms of *Scirpus* occur. They are more numerous in situations such as Hook Point or Sedge Point pools. In the latter situation, however, they occur only in that pool which is permanently connected with the lake and were not found in the second pool. On Grapevine Point or Fairy Island they are not as abundant as *E. bicolor*. In a quiet situation this species has been observed to emerge from the open-water surface.

As in the other two species of *Ephemerella* that occur in Douglas Lake, this species completes its life cycle in one year. However, there appears to be very little growth of the nymphs during the winter months since collections made in early May contain specimens only about one-half grown. Most of the growth takes place in the spring during the first month after the disappearance of the ice cover.

***Tricorythodes allectus* (Needham)**

Only imagoes of *Tricorythodes allectus* were collected at Douglas Lake. From a small group in swarm about 10:00 a.m. on July 26 at Hook Point three males and three females were taken. On July 29 between 9:00 and 10:00 a.m. a much larger number of specimens was observed swarming over the water along the shore of North Fishtail Bay in the area north of Hook Point and 19 males and 12 females were collected. No nymphal exuviae could be found either at the water's edge or out from the shore on the water surface. No nymphs were collected.

***Brachycercus lacustris* (Needham)**

Adults of *Brachycercus lacustris* were collected in late July. However, collections of nymphs indicate that the emergence period extends well into August and probably early September. No swarms were seen but specimens were reared from nymphs and some nymphal exuviae were

found floating on the water surface near the shore line in the early morning. This is a relatively rare species in Douglas Lake.

Nymphs were collected only at depths of 1-3 meters on marly sand bottoms during July and August from Grapevine Point, Hook Point, Big Shoal, Fairy Island, and Marl Bay. *B. lacustris* evidently has a one-year life cycle. It seems probable that the eggs laid in late summer overwinter and hatch in the late spring since only half-grown nymphs were collected in early July and none were found in the autumn or early spring. The emergence period is relatively long and occurs simultaneously with that of *Choroterpes basalis*.

***Caenis simulans* McDunnough**

Caenis simulans is abundant at Douglas Lake and imagoes were collected on various dates throughout most of the summer. The earliest date of adult collections was June 10 and the latest August 11, although a few mature nymphs were collected later which probably would have emerged during the last half of August. The peak of abundance is reached during the last half of June.

Emergence from the nymph, casting of subimago skin, swarming, and mating all occur in the same evening. Toward the end of June the subimago emerges about 7:00 p.m. from the surface of the water, where it leaves the nymphal skin, and alights on the nearest object it contacts, usually the vegetation fringing the lake shore. Molting occurs very shortly thereafter and the first small swarms of males are observed forming between 8:00 and 8:15 p.m. and by 8:30 p.m. dense groups are seen.

During swarming observations of *C. simulans* at Douglas Lake the writer noticed many specimens flying with exuviae fastened to the long tails or tip of the abdomen and trailing out behind as the insect flew. This led to the conclusion that the mayfly might be shedding its exoskeleton during flight. Close observations were made in an effort to see the early part of the process which would consist of molting the exuviae covering the head and thorax. If shedding of the exoskeleton during flight were possible, individuals should have been seen falling through the air during the process as flight would seem to be impossible during such a time. This falling of individuals was not observed. Later it was found that with subimagoes reared in captivity and those observed directly in the field resting on vegetation, exuviation took from forty-five to sixty seconds for completion. This time interval was observed repeatedly. The process was, however, sometimes incomplete to various degrees. Some exuviating specimens even began flight immediately following extrication of the head, thorax, legs, and only a portion

of the abdomen thus carrying the partially shed skin along with them, and giving the impression that molting might have occurred during flight. Burks (1953) states positively that he has observed *C. simulans* shedding the subimaginal skin during flight. On the other hand Berner (1950) observed that *Caenis diminuta* in Florida molted while at rest. Further studies might well be carried on to clarify this subject of exuviation in flight.

Swarms of *C. simulans* males were particularly abundant just at dusk in the evening during late June. Swarming began with small numbers of individuals flying in little individual groups along the lake shore. Gradually as flying individuals became more numerous these smaller groups merged to form larger ones until finally only one or two large, compact swarms were seen in the immediate vicinity where before there had been a number of much smaller ones. Each group was composed of thousands of individuals and formed a dense flying mass 3-5 meters in diameter and 7-10 meters above the water surface. The wings of each individual beat continuously as it darted here and there between other members of the swarm. The members of the swarm faced into the wind and the entire group acting as a unit wove back and forth or up and down seemingly with the changing air currents. Swarming continued until dark after which time observations were impracticable. Both males and females of *C. simulans* were attracted in large numbers to strong lights at night during the height of an emergence period.

Nymphs were abundant at Sedge Point pools and Hook Point cove and common on the organic detritus bottoms of Marl Bay and Maple Bay coves. They were also common in the open lake at depths of 1-3 meters around the littoral zone of most of the lake wherever flocculent marl and organic detritus accumulate. Specimens were collected from the submerged plant zone where they occur both on the plants and the bottom. In the spring and autumn the nymphs are more widely distributed and some specimens were taken in less than 1 meter of water, usually under stones, in various parts of the lake subject to strong wave action such as Grapevine Point and Stony Point. But during the summer these nymphs were very rarely found in water less than 1 meter deep except in very protected situations. Indications are that the life cycle of *C. simulans* in Douglas Lake is completed in one year. Collections taken during May, June, and early July show a preponderance of mature nymphs in the lake. This is correlated with the principal emergence which occurs in June. During the last of July and early August many very young nymphs begin to appear in collections although mature nymphs are still present but in fewer numbers. In late August and early Sep-

tember only an occasional mature nymph was taken but young nymphs were very abundant.

Callibaetis ferrugineus (Walsh)

Callibaetis ferrugineus is a relatively rare species at Douglas Lake and but few specimens were collected during the four seasons. The only adult specimen taken was a female imago but a single male was reared. Nymphs were captured, usually only one or two to a collection, in such places as Sedge Point pools, Hook Point, Marl Bay, and Maple Bay on various dates throughout the summer. Nymphs were never taken along the wave-swept shores of the lake but only in extremely well-protected situations which approach ponded conditions.

Baetis phoebus McDunnough

Adults of *Baetis phoebus* are very common during the entire summer where they were collected resting in vegetation along rocky wave-swept shores. Swarming of this species was not observed. Subimagoes usually emerge during the afternoon by crawling just out of the water on a partially submerged stone at the shore line. The length of the subimago period is about 24 hours. There appears to be no definite period or periods of emergence except that of the whole summer since adults or mature nymphs were collected at all times between June 10 and October 20. However, mature nymphs and adults were most abundant during July.

The nymphs of *B. phoebus* were found generally distributed along the wave-washed shores of the lake wherever stones occurred at the shore line. They were very abundant on Grapevine Point and as many as 50-60 nymphs of all sizes were often found occupying an area of approximately 5 square cm. under a small stone. Depth distribution of these nymphs is very limited. Most of the specimens occurred on the sides or under partially exposed stones at the shore line and lakeward to a depth of about 15 cm. Very rarely were nymphs collected at depths of 15-30 cm.

Centroptilum fragile McDunnough

Centroptilum fragile was collected only as the adult. Approximately 80 specimens were taken in the course of four seasons, the majority of which were females. Specimens were captured either flying over the water near the shore about 6:00-7:00 p.m. or resting on vegetation. Several subimagoes were collected. The species was most abundant during mid-July; however, specimens were taken from the last of June to mid-August. Swarming seems to occur in late afternoon and early evening. About 7:30 p.m. on July 18, numerous females were seen flying

up from the vegetation along the shore of South Fishtail Bay and ovipositing in the water over a submerged plant zone. No individuals were seen depositing eggs close to the shore which is wave-swept and sandy but only over the deeper water 45-60 meters lakeward from the shore line. Nymphs of this species were not found. Since they occur nowhere else in the lake, it is concluded they are probably restricted to the submerged plant zone.

Pseudocloeon dubium (Walsh)

Only subimagos and imagoes of *Pseudocloeon dubium* were collected. A total of 16 specimens (10 males; 6 females) were taken on the following dates: July 1; August 8; August 18. On July 1, 10 males and 1 female were captured swarming at 7:30 p.m. along the shore of South Fishtail Bay. The nymphs may be inhabitants of the submerged plant zone since no specimens were found in any of the other habitats.

Cloeon rubropictum McDunnough

Adults of *Cloeon rubropictum* are rather common throughout the summer around Douglas Lake. Numerous imagoes were reared or collected from vegetation along the shore. Swarming usually occurred about 7:30 p.m. during mid-summer. The emergence period appears to be an extended one and lasts from about June 15 to October 15. Imagoes were most abundant between the last of June and the forepart of August.

Nymphs of *C. rubropictum* were found generally distributed around the entire littoral region of the lake at a depth of about 0.5-1.0 meter. They were most numerous on the top surface of marl encrusted rocks and rarely found on clean rocks of open bottom.

SUMMARY

Information obtained during a four-season investigation is presented on seasonal distribution and life cycles of 22 species of Ephemeroptera known to occur in Douglas Lake, Cheboygan County, Michigan. Data are given on the relative abundance of adults including total length of emergence period, time of maximum population density, and length of the subimago stage. Swarming activities of a number of species are discussed. A trimodal seasonal emergence of three separate broods, each with a cycle of one year, is postulated for *Stenonema femoratum* and *S. interpunctatum*. The relative length of the incubation period of the eggs of various species

based upon field observations under natural conditions is given. Also discussed are the seasonal differences in growth rate of nymphs. The littoral distribution and the type of habitat occupied by the different species of nymphs are reported. A life cycle of one year is typical for most species of mayflies in Douglas Lake; however, *Hexagenia limbata* requires two years to complete its development.

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