

Life histories of *Hexagenia limbata* and *Ephemera simulans* (Ephemeroptera) in Dauphin Lake, Manitoba

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Abstract. The life histories of *Hexagenia limbata* (Serville) and *Ephemera simulans* Walker were investigated in Dauphin Lake, a large (surface area of 519.3 km²) but shallow (mean depth of 2.1 m) prairie lake in south-western Manitoba. Wing pad developmental stages helped to separate overlapping cohorts of *H. limbata*. During the 2-yr study, seven cohorts of this species were distinguished, indicative of three different life history patterns. Four of the seven cohorts had a 2-yr life history in which the eggs hatched soon after oviposition. Another type of 2-yr pattern was evident in two cohorts which spent nine months as overwintering eggs, and fifteen months in the nymphal stage. One cohort required 1.16 to 1.25 years (14 to 15 months) growth. The weighted average for all seven cohorts was 1.9 years (22.6 mo). The degree-days above 10°C accumulated by each life history type were 1848, 2030 and 1806, respectively. Three or four cohorts were present at all times of the year in the population, which provides a large range of nymphal sizes and emergence times for feeding fish. In contrast, *Ephemera simulans* had a simple 2-yr life history in Dauphin Lake.

Key words: life history, *Hexagenia limbata*, *Ephemera simulans*, cohorts, wing pads, Ephemeroptera, Ephemeridae.

Investigations into the benthic fauna of Dauphin Lake were begun in 1981 as part of a rehabilitation project for walleye, *Stizostedion vitreum vitreum* (Mitchill), carried out by the Department of Fisheries and Oceans Canada. One aspect of this project was the identification and quantification of the benthic fauna.

The burrowing mayflies *Hexagenia limbata* (Serville) and *Ephemera simulans* Walker are common in the lake and are consumed by various species of fish, including walleye (Britt 1962, Hunt 1953, Neave 1932, Ryder and Kerr 1978). The life history of these organisms is important to their potential as fish food. In semivoltine populations a supply of medium- to large-sized nymphs is available at all times of the year, whereas in univoltine populations there are few or no nymphs present immediately after emer-

gence (Neave 1932). Both voltinism and growth rate affect production estimates (Waters 1979). Biomass and production values for *H. limbata* and *E. simulans* are reported in Heise et al. (1988).

Populations of *Hexagenia limbata* may require one year, two years, or both to complete development (Carlander et al. 1967, Flannagan 1979, Horst and Marzolf 1975, Hudson and Swanson 1972, Hunt 1953, Riklik and Momot 1982, Rutter and Wissing 1975). In many of these studies cohort analysis was complicated by the size overlap of cohorts, and by the presence of more than one *Hexagenia* species in the community. In our study these problems were overcome because only *Hexagenia limbata* occurred in Dauphin Lake and developmental age was determined in addition to growth, using stages of wing pad development. McCafferty and Pereira (1984) used wing pad stages in a study of *H. limbata*, but were not able to determine the exact length of life for each cohort.

With the exception of reports by Britt (1962)

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and Speith (1936), life history accounts of *E. simulans* are restricted to emergence. Clearly more information is needed on the life history of this mayfly, especially for more northern populations.

The objective of our research was to investigate the life histories of these species. These data are valuable in assessing the temporal availability of the burrowing mayfly food supply for fish in Dauphin Lake.

Study Area

Dauphin Lake is located in south-western Manitoba (51°15'23"N; 99°46'12"W). It has a surface area of 519.3 km² (Anon. 1973) and mean and maximum depths of 2.1 m and 3.5 m, respectively (Fig. 1). A control structure on the outflow restricts annual lake level fluctuations to 0.5 m. The lake forms part of the Nelson River drainage basin which empties into Hudson Bay. Surface deposits of the surrounding area are lacustrine clay and silt plus glacial drift, which is primarily limestone (Weir 1960).

The lake is turbid; the range of total suspended solids was 2–363 mg/L in 1982 (May through October) and 1983 (May through September) (J. Babaluk and M. K. Friesen, Freshwater Institute, Winnipeg, personal communication). Dissolved oxygen levels in bottom water samples exceeded 77% saturation throughout 1982 and 1983.

The lake bottom was divided into three zones based on sediment particle size. Description of sediments follows the sand-silt-clay ratio nomenclature of Shepard (1954). All the offshore stations except 17 (Fig. 1) were clayey silt or silty clay. Stations at river mouths along the west shore were sandy silt or silty sand, and stations along the rocky east and north shorelines were heterogeneous, with sediments ranging from silt, sand, and gravel to rocks approximately 0.5 m in diameter. Station 17 sediments were either a clay/silt mixture or of the heterogeneous matrix type.

Emergent aquatic vegetation was sparse and found only along the shoreline.

Methods

Sampling

Twenty-one sample stations were arranged along transects originating at the mouths of ma-

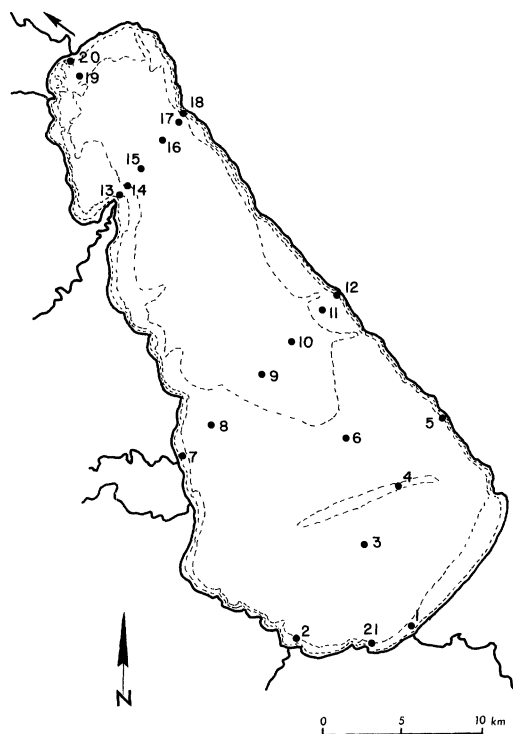


FIG. 1. Location of sampling stations on Dauphin Lake, Manitoba. Dotted lines indicate the 1-, 2- and 3-m depth contours.

ior inflowing rivers (Fig. 1) to complement benthic faunal studies of these rivers (Cobb and Flannagan 1987). Offshore stations were located by compass triangulation using onshore landmarks.

Triplicate grab samples were taken randomly at all stations monthly from May to October 1982 and from May to September 1983. Exact sample dates are listed in Heise (1985). Additional samples were taken in June 1982 and through the ice in April 1983. A tall modified Ekman grab (Burton and Flannagan 1973) with a semi-automatic release mechanism (Burton 1974) was used on clayey silt and sand substrates, while on the matrix substrate a pneumatic grab sampler (Burton et al. 1985) was used during all but the first two months.

Submerged funnel emergence traps modified from Hamilton (1965) were used in 1982 in an attempt to quantify adult emergence. Qualitative observations of emergence events were made by ourselves or Fisheries and Oceans field crews throughout the open water season in 1982

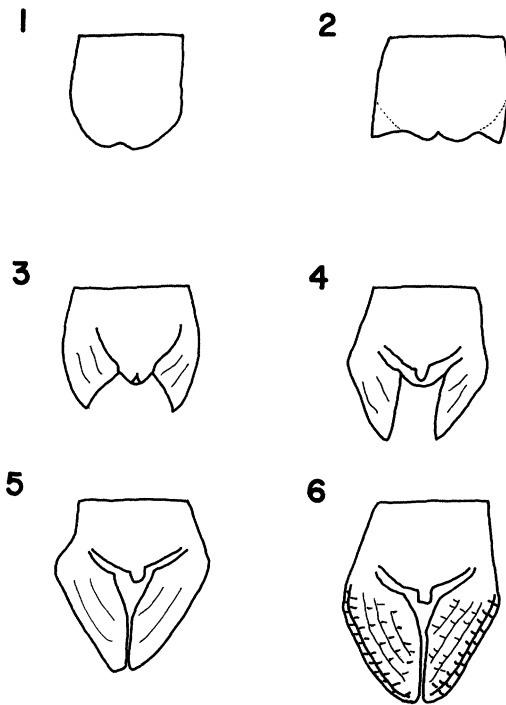


FIG. 2. Mesothoracic wing pad developmental stages for *Hexagenia limbata*: 1. wing pads absent; 2. wing pad tips not extending beyond mesonotum; 3. wing pad tips exceed mesonotum, but pads diverging; 4. wing pads parallel; 5. wing pads elongate, tips converging or touching; 6. wing pads with dark wing vein pigmentation.

and 1983. Adults were collected from vegetation and beneath lights on the shore of the lake.

Benthic samples were sieved in the field through 200- μ m mesh Nitex[®] screens, fixed and preserved in 10% formalin, and transferred to 75% ethanol in the laboratory. Samples with high organic matter content were hand-picked at 6 \times magnification using a dissecting microscope. Samples with low organic content and large particle size were floated in a sucrose solution (S.G. = 1.20–1.25), and sorted at 2 \times magnification.

Total body length of nymphs was measured from the tip of the frontal projection to the base of the caudal filaments. Head width was measured across the eyes. All measurements were made using an ocular micrometer.

Hexagenia limbata nymphs longer than approximately 9 mm were sexed using both the

interior angle of the eye (Neave 1932) and the presence or absence of male genitalia. *Ephemera simulans* nymphs longer than approximately 8 mm were sexed using the genitalic method only. For both species the sex ratio of smaller nymphs was presumed to be equal.

Life history

Length frequency and head width frequency histograms were constructed for both species. A linear regression of \ln length vs. \ln head diameter was calculated for *H. limbata* (equation 1) and *E. simulans* (equation 2).

$$\ln \text{ length} = 1.08 \ln \text{ head diameter} + 2.01, \\ n = 1052, r^2 = 0.98 \quad (1)$$

$$\ln \text{ length} = 1.17 \ln \text{ head diameter} + 2.07, \\ n = 295, r^2 = 0.98 \quad (2)$$

These equations were then used to predict total body length measurements for those nymphs having a damaged body, but an intact head.

The developmental stage of mesothoracic wing pads was used to help elucidate the life history of *H. limbata*. Wing pad stages are shown in Figure 2.

Results

Hexagenia limbata

Three or four cohorts were present in the population at all times of the year. By superimposing the wing pad stage (WPS) of each individual on the size-frequency histograms of each sex plotted separately, seven cohorts were discernible over the two-year study period (Fig. 3). The "cohorts" identified in this study were defined as groups of nymphs that were of approximately the same length and wing pad stage, and which first appeared and later emerged at approximately the same time. The growth (change in mean body length) of each cohort is shown by the diagonal lines in Figure 3. All emergence observations are qualitative as there was a 95% failure rate of the emergence traps, mainly owing to their destruction by wave action.

Cohort 1 is represented by the large individuals in May and June of 1982, which emerged in late June and July of that year. In 1982 the main emergence took place on 3–7 July. Swarms

of adults were a few hundred metres long, and spent females were found in piles (1 m high) at the base of lights. Cohorts 2 and 3 appeared together as one large group of smaller (<17 mm) individuals in May and June of 1982 but cohort 2 had more advanced WPSs (Fig. 3). Cohort 2 emerged in late August and September (Fig. 3), although in smaller numbers than the July emergence. Individual adults appeared sporadically as late as 20 October. Cohort 3 grew to WPSs 4 and 5 by September 1982 and did not emerge until June, July and August of 1983. The peak emergence date for this cohort in 1983 was 7–8 July, with smaller numbers emerging into early August. Cohorts 4 and 5 began approximately one month apart, but cohort 4 was able to emerge in late August/September 1983, after only 14 to 15 months of development (Fig. 3), whereas cohort 5 presumably emerged in 1984. Cohort 6 first appeared in late June 1983. *Hexagenia limbata* eggs take 10 to 21 days to hatch at 25°C (Swanson 1967), 18 to 22 days at 19–27°C, and 20 to 26 days at 17–23°C (Hunt 1953). Dauphin Lake water temperatures in early July 1983 were approximately 21.5°C (Fig. 4), and so egg hatching probably took at least 20 to 25 days. Therefore small nymphs resulting from the July 1983 oviposition could not be expected to appear until the end of July to early August. Cohort 6 nymphs first appeared in June, 4 to 5 weeks earlier than this and therefore most likely resulted from overwintering eggs oviposited the previous September (1982) by cohort 2 adults. Cohort 7 nymphs first appeared in August 1983, having been oviposited by cohort 3 adults in June and July. Cohort 6 nymphs had two months more summer growth than cohort 7 nymphs, and by September were accordingly larger and at a more advanced WPS than cohort 7 nymphs.

The seven cohorts followed three distinct life history patterns. The predominant life history, which resulted in the major July emergences of 1982 and 1983, was that of approximately two years of nymphal growth, from July to August of one year to July–August of the third year. Cohorts 1, 3, 5 and 7 were classified in this life history pattern by growth curve and wing pad data. A second group was oviposited in September, overwintered as eggs, and appeared as small nymphs in June. Cohort 6 was of this type. Its nymphs were in WPSs 2 or late 3 by September

TABLE 1. Cumulative degree-days above a 10°C threshold for Dauphin Lake, Manitoba, from May to September 1982 and 1983. All calculations were based on bottom water temperatures.

	1982	1983	Mean
May	118.7	5.4	62.1
June	232.1	216.1	224.1
July	335.3	380.9	358.1
August	328.7	361.7	345.2
September	99.0	125.7	112.4
October	0.6	1.9	1.3
Total	1114.4	1091.7	1103.1
2-yr total		2206.1	

1983, and so did not likely emerge until late August or September 1984; they took two years (24 months) to develop, 15 months of which was in the nymphal stage. Cohort 2 was most likely of this type also.

The third life history pattern was shown by cohort 4 which appeared to average 1.16 to 1.25 years (14 to 15 months) of growth. Nymphs first appeared in July 1982 and were probably oviposited in late June or early July, immediately preceding the July peak emergence. They emerged in late August and September 1983. The average generation time of the seven cohorts was 22.6 months, or 1.9 years.

The threshold temperature chosen for degree-day calculations was 10°C because of its use in other studies (Hudson and Swanson 1972, McCafferty and Pereira 1984). Nearly all (99.9%) of the degree-day accumulation above the 10°C threshold was accumulated between May and September (Table 1) because Dauphin Lake temperatures rose and fell rapidly in the spring and fall respectively (Fig. 4). The distribution of degree-days was different in the two years, as 1982 had a warm spring and 1983 had a warm fall. The yearly totals of degree-days differed by only 2% despite the differences in their distribution.

An accurate estimate of accumulated degree-days for the entire life of a cohort was possible only for cohort 4, which accumulated 1728 degree-days in 1.16 to 1.25 years. The degree-days based on the two-year means (Table 1) was 1806. Cohorts 1, 3, 5 and 7 grew from July/August to July/August (two years) and accumulated an estimated 1848 degree-days. Cohort 6, which

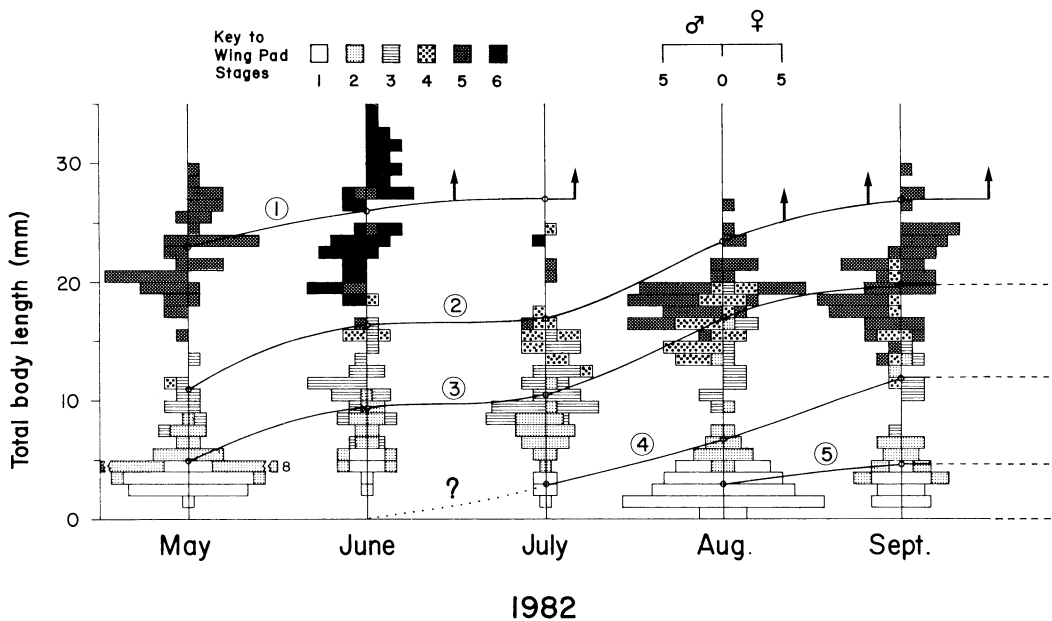


FIG. 3. Length-frequency distribution of *Hexagenia limbata* nymphs from Dauphin Lake showing the wing pad developmental stage of each nymph sampled in 1982 and 1983. Circled numbers and solid diagonal lines indicate growth of cohorts. Arrows show emergence observations. Dotted line with a ? indicates a possible alternative interpretation of the starting date of cohort 4.

had a two-year life history with overwintering eggs, accumulated 2030 degree-days (not counting the months of egg overwintering). These estimates for the two-year life histories are based on the monthly means (Table 1).

Ephemera simulans

The *E. simulans* population was smaller than *H. limbata*; only 366 nymphs were collected during the study. From the bimodal distribution of *E. simulans* nymphs in August and September 1983 (Fig. 5) we concluded that two cohorts were present in the population. The most readily identifiable cohort was the one which first appeared in August 1982. This cohort had not emerged by late September 1983, and presumably emerged in 1984 after two years of growth. The cohort represented by the larger nymphs present in May 1982 presumably emerged in midsummer and oviposited the cohort that first appeared in August 1982. The smaller nymphs present in May 1982 were part of a cohort represented in our samples by all the nymphs present in July 1982, by a single large male in September 1982, and by a single large female in June 1983. This cohort presumably emerged in

late July or early August, ovipositing the cohort that first appeared in August 1983.

Discussion

Hexagenia limbata

Using wing pad developmental stages to classify nymphs collected from Dauphin Lake greatly aided the interpretation of *H. limbata* life history. Although WPSs have been defined for various mayfly species (e.g., Cianciara 1979, Clifford et al. 1979, Humpesch 1979, McCafferty and Huff 1978, Svensson 1977), only McCafferty and Pereira (1984) have used WPS in analysis of *Hexagenia* life histories. In that study the population consisted of at least two cohorts, but the exact length of life was not determined. The interpretation of *Hexagenia* life histories is often difficult owing to the presence of multiple cohorts in the population, inadequate sample sizes, differential growth of the sexes, delayed hatching of the eggs, and the wide variability in the growth rate of individuals from the same egg mass (Hunt 1953). By using total body length and WPS together we were able to monitor developmental age independent of growth, and

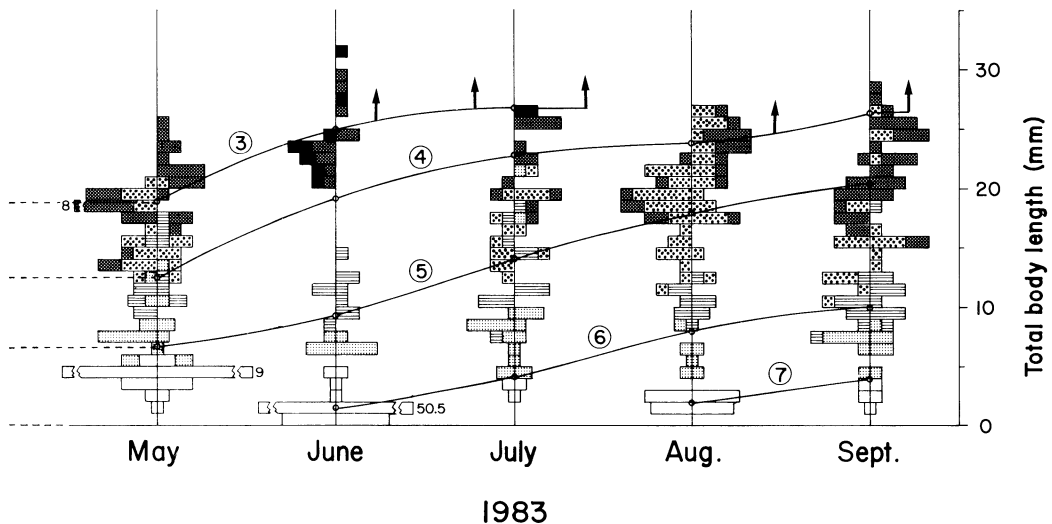


FIG. 3. Continued.

follow individual cohorts, or split cohorts, separately through time. The cohort structure reported here for *H. limbata* is more complex than most reported in the literature, and may be due, in part, to the increased resolution of cohorts made possible by the use of wing pad stages. Consideration of the nymphal frequency distribution without developmental age could have led us to conclude incorrectly that this species had a simple two-year life history with only four cohorts present during the study.

Accurate detection of early instar nymphs is another important factor in determination of life histories. In our study this problem was overcome by the use of a small (200 μm) mesh size. In previous studies of *H. limbata*, mesh sizes as large as 800 μm were used (Riklik and Momot 1982). Large mesh sizes can lead to erroneous conclusions regarding life histories of aquatic insects (Mutch and Pritchard 1982, Suter and Bishop 1980, Zelt and Clifford 1972).

The lack of good emergence data and the time interval between samples made exact separation of cohorts at the beginning and end of the nymphal stage difficult. Delayed egg hatching (Swanson 1967), which is affected by temperature and oxygen (Flattum 1963, Fremling 1967, Friesen et al. 1979, Hunt 1953, Wright et al. 1982), and the protracted flight period of *Hexagenia* (Hunt 1953), also made exact length of

life determinations difficult. It is possible that groupings identified here as cohorts came from eggs oviposited at the same time, but developed at different rates to split apart later. Differential growth rates and variation in the number of instars are known to split cohorts in other mayfly species (Clifford 1970, Clifford et al. 1979, Fremling 1973a, Svensson 1977).

The cohort that was the most difficult to interpret was cohort 4, which took 14–15 months

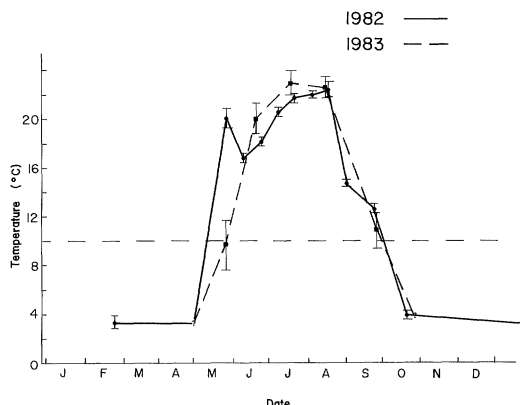


FIG. 4. Bottom water temperatures \pm 95% CI in Dauphin Lake, Manitoba, measured from February 1982 to October 1983. The horizontal dashed line represents a 10°C threshold temperature for growth of *Hexagenia limbata*.

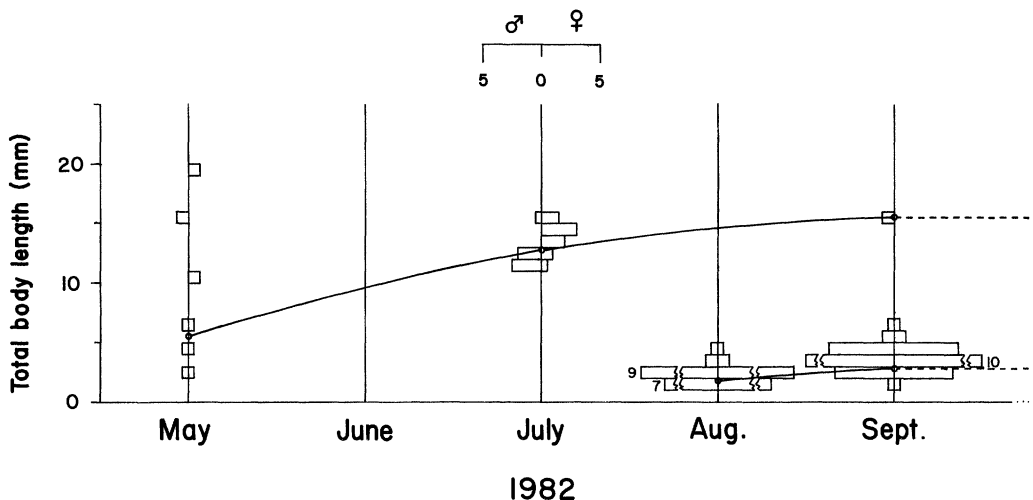


FIG. 5. Length-frequency distribution of *Ephemera simulans* nymphs in Dauphin Lake, Manitoba, from May, June, August and September 1982 and May to September 1983.

of growth. Our conclusions are based on our sampling data, but another interpretation is possible. This cohort may have been missed by our June sampling, as indicated by the dotted line for cohort 4 in Figure 3. This earlier start of the cohort would then correspond to the June start of cohort 6 in 1983. However, this would necessitate overwintering of eggs. May 1982 was very warm (Fig. 4), and so eggs should have hatched to produce abundant tiny nymphs in the June samples. Almost all of the tiny nymphs of cohort 6 collected in June 1983 were found in the rocky matrix substrate along the north and east shoreline of the lake. It is possible that nymphs of cohort 4 were in this habitat in June 1982, but it was not sampled effectively during the first two months of the study when the pneumatic grab was not used. This alternative interpretation of cohort 4 would mean that only two life history patterns appear in the population, but would not affect the total number of coexisting cohorts. Future studies should use laboratory rearing, in combination with field sampling, to help elucidate cohort structure.

Reported in the *Hexagenia* literature is both a wide range of life histories and a high degree of flexibility within populations. *Hexagenia limbata* life histories extend from one year (Carlander et al. 1967, Craven and Brown 1969, Fremling 1967), and two years (Flannagan 1979, Riklik and Momot 1982, Rutter and Wissing 1975, Schloesser and Hiltunen 1984), to mixtures of one and two years (Flannagan 1979,

Horst and Marzolf 1975, Hudson and Swanson 1972, Hunt 1953). The average generation time of 1.9 years for *H. limbata* in Dauphin Lake is consistent with the location of the lake in the northern third of the species' range. Although there is a general geographical trend of two-year life histories in the northern end of its range and one-year life histories in the south (Fig. 6), latitudinal differences alone do not adequately describe the variation in *H. limbata* life histories. Temperature is usually considered the most important parameter affecting length of life, but this relationship has been quantified in only a few studies. The most common method is to calculate the number of degree-days accumulated above a certain temperature threshold needed for growth. Degree-day accumulations calculated in the laboratory have proven accurate in predicting the onset of emergence of semivoltine mayflies in natural field conditions (Tokeshi 1985, Wright et al. 1982). The degree-days required for *H. limbata* in Dauphin Lake were fewer than those required for this species in South Dakota/Nebraska (2370 and 2604 for the one and two-year life histories, respectively, calculated by us using the average monthly degree-days reported by Hudson and Swanson (1972)). Dauphin Lake values were also lower than the 2588 minimum calculated by McCafferty and Pereira (1984) for laboratory-reared populations.

Temperature can also affect life histories in the form of minimum temperature thresholds

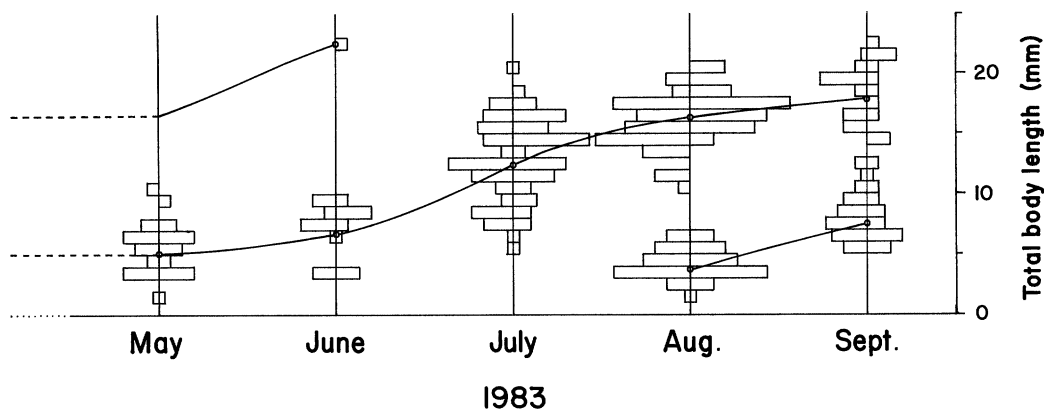


FIG. 5. Continued.

which must be reached before emergence can take place. The minimum water temperature for emergence of *H. limbata* in the laboratory is 12–14.5°C (Fremling 1970, 1973b, McCafferty and Pereira 1984). The former threshold was exceeded in Dauphin Lake from May through September (Fig. 4). Degree-days may regulate development of the closely related species *H. bilineata* (Say) up to a certain point, after which a threshold temperature must be reached before emergence takes place (Wright and Mattice 1985).

Given the high plasticity of response of *H. limbata* to varying thermal regimes it is possible that each population over this species' geographic range has a different thermal requirement. The length of life of each cohort may also vary temporally. The life histories calculated in this report for *H. limbata* in 1982 and 1983 are representative of these years only. Annual fluctuations in monthly temperatures could result in life histories of plus or minus one or two months.

Ephemera simulans

The length-frequency histograms of *E. simulans* in 1982 alone (Fig. 5) could easily be misinterpreted as representing a single cohort, univoltine life history. This was not the case, based on the following evidence. The individuals less than 11 mm long in May 1982 represented a cohort oviposited in 1981. These nymphs grew to the 11–16-mm size by July 1982; but they

were still much smaller than the maximum size ranges of 18–20 mm (males) and 23–24 mm (females) reported by Britt (1962), and so probably did not emerge that year. Further growth of this cohort is suggested by the single 16-mm male nymph in September 1982, and by a 22.7-mm female in June 1983. In July the adults from this cohort oviposited eggs leading to another cohort that first appeared in August 1983. The cohort represented by the two nymphs larger than 14 mm in May 1982 emerged in July after two more months of growth and deposited the eggs that produced the cohort that first appeared in August 1982.

Despite its widespread distribution in Canada and the United States (Edmunds et al. 1976), little research has been done on the life history of *E. simulans* apart from emergence studies. The only detailed study to date is that of Britt (1962), in which *E. simulans* in western Lake Erie had a one-year life history. A one-year life history was also reported in an Indiana lake by Speith (1936). Coleman and Hynes (1970) reported a two-year life history for *E. simulans* in the Speed River, Ontario, with the two generations overlapping in size in September. This species does not appear to exhibit the wide range of life histories, including split and alternating cohorts, discovered for *E. danica* Mull. in Europe (Landa 1968, Macan 1970, Svensson 1977, Whelan 1980). Many more studies are needed, especially at higher latitudes, in order to determine the degree of flexibility in the life history of this widespread species of mayfly.

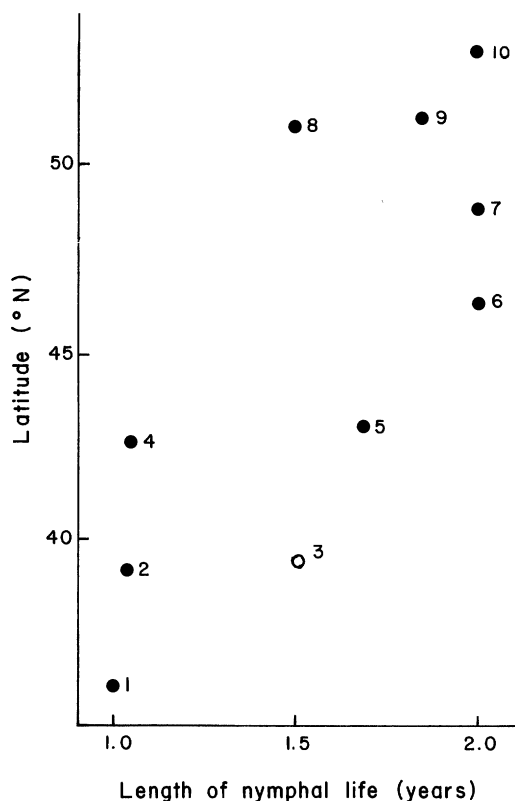


FIG. 6. Relationship between the length of the life cycle of *Hexagenia limbata* and latitude. Values were taken from the literature (●) or represent estimated means calculated from data provided in the original papers (○). Numbers denote source, as follows: 1. Craven and Brown (1969), 2. Horst and Marzolf (1975), 3. Rutter and Wissing (1975), 4. Hunt (1953), 5. Hudson and Swanson (1972), 6. Schloesser and Hiltunen (1984), 7. Riklik and Momot (1982), 8. Flannagan (1979; narrows), 9. this study, 10. Flannagan (1979; north basin).

General considerations

The complex population structure of *H. limbata* in Dauphin Lake provides an assortment of nymphal sizes at all times of the year, regardless of fluctuations in the timing of cohorts. The presence of more than one emergence time per year also increases the availability of mayfly biomass to fish populations, as the emergence period is one of greatly increased mayfly predation by fish (Britt 1962, Hunt 1953). Secondary production of *H. limbata* and *E. simulans* averaged over Dauphin Lake was 9.08 g/m² (90.8 kg/ha) in 1983 (Heise et al. 1988), and was 18.58

g/m² in the rocky matrix habitat. Future research will have to overcome the problem of sampling nymphs burrowing into the interstices of rocky substrates. Insufficient sampling can lead to incorrect assumptions about the life history, as was the case with *E. simulans* when only the 1982 results of this study were considered.

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