

Life history, distribution and production of
Hexagenia limbata (Serville) and Ephemera simulans Walker
in Dauphin Lake, Manitoba

by

Brian A. Heise

A thesis
presented to the University of Manitoba
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ABSTRACT

The life history, distribution and production 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-central Manitoba. A system of wing pad developmental stages was used to assist in the separation of overlapping cohorts of H. limbata. During the two year study seven cohorts of this species were distinguished as evidence of three different life histories. The dominant life history followed by four of the seven cohorts was two years. A second life history was of two years (24 months) duration, nine months of which was spent as overwintering eggs, and fifteen months in the nymphal stage. Two cohorts had this length of life. The third life history, followed by only one cohort, was of 1.16-1.25 years (14-15 months) growth. The weighted average for all seven cohorts was 1.9 years (22.6 months). The degree-days above 10°C accumulated by each life history type was 1848, 2030 and 1806 respectively. Ephemera simulans had a two year life history in Dauphin Lake.

Hexagenia limbata was always found at stations having a silt-clay component. This included all offshore silty clay stations as well as those on a matrix of clay, silt, sand and gravel along the east and north shores.

Ephemera simulans was found on the gravelly matrix substrate only. Neither species was found on a substrate consisting entirely of sand.

The size-frequency estimates of production for H. limbata in 1982 and 1983 were $12.6 \pm 2.68 \text{ g/m}^2$ (wet weight) and $10.1 \pm 2.10 \text{ g/m}^2$ respectively. Instantaneous growth production estimates were 9.51 and 9.76 g/m^2 (1982) and 9.49 and 8.55 g/m^2 (1983) based on calculations using four versus seven cohorts respectively. P/\bar{B} ratios ranged from 1.68 to 2.38. Preservation in 10% formalin followed by 75% ethanol produced a production underestimate of 25% for H. limbata.

Production of E. simulans in 1983 was $9.02 \pm 3.10 \text{ g/m}^2$ (wet weight) and 9.90 g/m^2 using the size-frequency and instantaneous growth methods, respectively.

FOREWORD

This thesis has been written in the paper style format. Manuscript one, "Life history and distribution of Hexagenia limbata (Serville) and Ephemera simulans Walker (Ephemeroptera) in Dauphin Lake, Manitoba" will be submitted to the Canadian Journal of Zoology, and follows the format of that journal. The second manuscript, "Production of Hexagenia limbata (Serville) and Ephemera simulans Walker in Dauphin Lake, Manitoba, with a note on weight loss due to preservatives" will be submitted to the Canadian Journal of Fisheries and Aquatic Sciences, and follows the format of that journal.

INTRODUCTION

In 1981 the Department of Fisheries and Oceans Canada started a pilot walleye, Stizostedion vitreum vitreum (Mitchill), enhancement and rehabilitation project on Dauphin Lake, Manitoba. Techniques such as habitat rehabilitation, fishing regulation adjustments and hatchery and pond reared stock enhancement developed during the project could then be applied to other aquatic habitats in need of fisheries rehabilitation (J.F. Flannagan et al., Freshwater Institute, unpublished report). One aspect of this project was the identification and quantification of the benthic fauna of the lake.

The burrowing mayflies Hexagenia limbata (Serville) and Ephemera simulans Walker are dominant members of the macrobenthic community, are consumed by various species of fish, including walleye (Neave 1932; Hunt 1953; Britt 1962; Ryder and Kerr 1978), and due to their large size were potentially important fish food items in Dauphin Lake.

The first objective of this study was to investigate the life history and substrate preference of these mayfly species. The term "life history" is used throughout this study to mean the voltinism, duration of the nymphal stage, emergence phenologies, and other aspects of the cohorts of both species of mayfly (sensu Butler 1984).

This is not to be confused with the "life cycle" of these mayflies, which refers to the stages in the life of the organism, i.e. egg, nymph, subimago and imago. These terms are often used interchangeably, which can cause confusion (Butler 1984). The life history of these organisms is important to their potential as fish food, as semivoltine populations provide a supply of medium to large sized nymphs at all times of the year, whereas univoltine populations do not provide nymphs immediately following emergence (Neave 1932). Knowledge of the life history of a population is also an important factor to consider in the calculation of its production (Waters 1979).

Hexagenia limbata may require one year, two years, or a combination of 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 studies cohort analysis was complicated by the size overlap of cohorts, and by the presence of more than one species in the community. In this study these problems were overcome by monitoring developmental age in addition to growth using a system of wing pad developmental stages. 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 the studies of Britt (1962) and Speith (1936), reports on the life history of E. simulans have been restricted to accounts of emergence events. There is clearly a need for more information on the life history of this mayfly.

Production values reported for H. limbata cover a wide range, and may depend upon the life cycle and type of lake (Hudson and Swanson 1972; Horst and Marzolf 1975; Riklik and Momot 1982; Flannagan and Cobb 1984). There are no published production estimates for E. simulans. The second objective of this study was to calculate production and biomass estimates for these two species.

A third objective was to assess the influence of the interpretation of four versus seven cohorts present in the H. limbata population on the production estimates for this species.

The final objective was to determine the effect of length and weight changes caused by preserving fluids on the estimates of H. limbata production. Various degrees of weight loss caused by preservatives have been reported for other taxa (Howmiller 1972; Stanford 1973; Donald and Paterson 1977).

LITERATURE REVIEW

Life history of Hexagenia limbata

Hexagenia limbata is reported as having both a wide range of life cycles, and a high degree of flexibility within populations. The shortest recorded life cycles are 17 weeks in Utah canals (Edmunds et al. 1976), and 3 months for a mixture of H. limbata and H. bilineata (Say) in the Upper Mississippi River (Fremling 1967). All reports of a one year cycle for H. limbata have been in locations where it occurs with H. bilineata.

A Hexagenia population in an Oklahoma reservoir showed evidence of a one year cycle, with two emergence peaks (Craven and Brown 1969). The authors concluded that the peaks could have been the result of the two species having different emergence periods, or of a lengthening of the emergence period of one of the species due to a long growth period. These two species have a one year life cycle in pool 19 of the Mississippi River, with a possible two year cycle of abundance (Carlander et al. 1967).

The most commonly reported life cycle for H. limbata is a mixture of one and two years. Ninety-six percent of the Hexagenia limbata population in a Kansas reservoir completed their development in one year, and only 4% required two years (Horst and Marzolf 1975). In Lewis and Clark Lake, a large reservoir bordering South Dakota and

Nebraska, one and two year life cycles were present, and the proportion of each depended on the temperature, as expressed in degree-days above a 10°C threshold (Hudson and Swanson 1972). If eggs were oviposited in June or July, nymphs matured in 13-14 months, emerging the following August-September. Nymphs hatching from this oviposition period needed 22 months to develop, as they could not grow during their first fall. They then emerged the following June-July after two years. The two year cycle dominated because a short growing season lead to a two year cycle and because although a long growing season produced a one year cycle, their offspring initiated a two year cycle again (Hudson and Swanson 1972).

The most complex life history documented to date is that for H. limbata in Lake Winnipeg, Manitoba, where it occurs with H. rigida McDunnough (Flannagan 1979). In the colder north basin H. limbata has a two year life cycle, although some individuals may take longer, based on the evidence of large nymphs being present in early October (Flannagan 1979). In the south basin the population has an alternating 14/22 month cycle, and in the narrows, where the north and south water masses mix, there is a combination of all three developmental times.

In Brandenburg Pond, Ohio, most of the H. limbata population took two years to develop, but nymphs hatching from eggs oviposited in May, June or early July probably matured in only one year (Rutter and Wissing 1975).

Two year life cycles have been determined for H. limbata populations in a northern Ontario lake (Riklik and Momot 1982), the St. Marys River, Michigan (Schloesser and Hiltunen 1984), and Little Pine Creek, Indiana (McCafferty and Pereira 1984).

Hunt (1953) conducted the most detailed study of H. limbata populations, in three Michigan lakes. In the field he found that a one year cycle dominated, but that a small percentage of the population required an extra year of growth. In laboratory rearing experiments, nymphs completed development in only 5.5 months at elevated temperatures, while nymphs placed in colder water in transplantation experiments required two years to develop. The author concluded that temperature was the limiting factor, with nymphs showing negligible growth below 48°F (8.9°C - this number is widely misquoted in the literature as 10°C).

The most common method of quantifying the relationship between temperature and life cycle in Hexagenia populations is to calculate the number of degree-days above this 10°C growth threshold. The number of degree-days accumulated by the one and two year life cycle nymphs of Hudson and Swanson (1972) were 2370 and 2604 respectively (my calculations, based on the average monthly degree-days over an eight year period). McCafferty and Pereira (1984) calculated degree-days for H. limbata under four different thermal regimes in the

laboratory. The overall mean minimum degree-days accumulated at the two cooler regimes was 2588, but this is probably an underestimate, as the authors started with nymphs which were 8-10 mm long. Mayflies at the higher temperature regimes required more degree-days, possibly due to higher metabolic levels at these temperatures (McCafferty and Pereira 1984).

Temperature thresholds may also be important in determining the life cycle of Hexagenia. The minimum water temperature for emergence of H. limbata in the laboratory is reported to be 14.5°C (Fremling 1970, 1973b) and 12°C (McCafferty and Pereira 1984). Degree-day inputs appear to control development of H. bilineata up to a certain point (Wright et al. 1982), after which a threshold temperature must be reached before emergence takes place (L.L. Wright and J.S. Mattice, Env. Sci. Div., Oak Ridge Nat. Lab., pers. commun.).

There are many factors which make exact determinations of the length of Hexagenia life cycles difficult. Uncertainty as to the timing of recruitment can occur because of the protracted flight period of H. limbata caused by adverse weather conditions (Hunt 1953), and delayed egg hatching (Swanson 1967). Although the rate of embryonic development in Hexagenia is temperature dependent (Flattum 1963; Friesen et al. 1979; Hunt 1953; Wright et al. 1982), egg hatch may be protracted when egg masses are clumped together or buried in mud (Hunt 1951). In H.

bilineata egg masses, those eggs on the outside of the clumps hatch first because they are better oxygenated (Fremling 1967). Sexual dimorphism (Hunt 1953), and the presence of more than one species of Hexagenia at a study site, also complicate life history analysis of H. limbata.

A powerful technique for the elucidation of complex life cycles is to monitor developmental age independent of growth (Butler 1984; Clifford 1970). One method is the use of wing pad stages. This technique has only been used by McCafferty and Pereira (1984) for the analysis of a H. limbata population.

Life history of Ephemera simulans

E. simulans has a one year life cycle in western Lake Erie (Britt 1962). A one year life cycle was also reported for this species in an Indiana lake by Speith (1936). In the Speed River, Ontario, E. simulans has a two year life history, with the two generations overlapping in size in September (Coleman and Hynes 1970).

Substrate preference of Hexagenia limbata

The preferred substrate of H. limbata is one variously described as soft mud, silt, or marl-mud (Carlander et al. 1967; Craven and Brown 1969; Hunt 1953; Neave 1932; Swanson 1967; Walker and Burbanck 1973). This type of

substrate is apparently selected because H. limbata's large prothoracic legs can only be used in fine, adhesive sediments (Eriksen 1964; Lyman 1943). Although nymphs show a strong preference for this substrate type, they are also found, in smaller numbers, in other substrates. Hexagenia limbata is rare or absent in pure or shifting sand (Lyman 1956; Swanson 1967), and in substrates where sand constitutes greater than 30-55% of the sediment mixture (Hunt 1953; Walker and Burbanck 1973). Hexagenia limbata nymphs do not burrow into coarse substrates (Carlander et al. 1967; Eriksen 1968), but are found in mixed substrates of clay, sand and gravel (Neave 1932; Rutter and Wissing 1975).

Hexagenia distribution is also affected by low oxygen levels (Britt 1955a,b; Eriksen 1963,1964; Fremling 1967; Hunt 1953; Lyman 1943; Rutter and Wissing 1975; Swanson 1967) and strong winds during the flight period (Fremling 1970; Hunt 1953; Lyman 1944; Rutter and Wissing 1975).

Nymphs of H. limbata migrate to areas of lower density (Hudson and Swanson 1972; Swanson 1967), from areas of sand to silt (Hunt 1953), and to areas previously exposed due to drawdown (Walker and Burbanck 1973).

Substrate preference of Ephemera simulans

This species occurs in gravel, sand, sandy mud, marl, and combinations of all of these substrates (Britt 1962;

Eriksen 1968; Hunt 1953; Lyman 1956). Their usual absence from fine sediments is due to the respiratory inefficiency of their small gills at low oxygen levels (Eriksen 1968).

Secondary production methodologies

The measurement of secondary production is very important to the study of ecosystem dynamics, as production is a major pathway of energy flow. Production of benthic macroinvertebrates is of great importance to managers of fishery stocks (Waters 1977). Production is usually referred to as the rate of tissue elaboration, regardless of its fate (Clarke 1946; Ivlev 1945). The units are weight or energy per unit area per unit time. Biomass, or standing stock, is the amount present at a point in time, and has units of weight or energy per unit area.

One of the earliest production studies was that of Boysen-Jensen (1919), who examined the benthic macroinvertebrates of the Limfjord, Denmark. Since then many techniques have been developed, the majority of them since the early 1970's and the emphasis of the International Biological Program on production. While only the instantaneous growth and size-frequency methods of production calculation will be reviewed here, many other methods presently exist. Excellent reviews of these can be found

in Benke (1984), Downing and Rigler (1984), and Waters (1977).

The instantaneous growth rate method was developed independently by Ricker (1946) and Allen (1949). Production is calculated as the product of the instantaneous growth rate and mean biomass. i.e. $P = G \cdot \bar{B}$, where P = production in weight per unit area per unit time, for a given time interval, G = instantaneous growth rate during the time interval, and \bar{B} = mean biomass, in weight per unit area, for the time interval. G is calculated as the natural logarithm of the ratio of the mean weight at the end of the time period to the mean weight at the beginning of the time period. The mean biomass is calculated as the average of the total biomass at the beginning and end of the time interval. This method assumes that growth and mortality are exponential and constant, or vary similarly (Waters 1977). Identification of individual cohorts is necessary for use of this method.

The size-frequency method of production calculation was developed to permit production calculation for an entire community, without the necessity of cohort identification. Originally proposed by Hynes (1961), it was later modified by Hynes and Coleman (1968) and Hamilton (1969). The method is similar to the removal-summation method, except that the losses between size classes, and not time periods, are calculated. An average size-frequency distribution is calculated from samples

taken over a year, which will approximate the survivorship of an "average cohort" (Benke and Waide 1977; Hamilton 1969). To calculate production, 1. determine the mean standing stock in numbers for the entire sampling period for each size class, 2. calculate the loss in numbers between successive size groups and multiply by the mean weight to get loss in weight, 3. multiply by the number of size groups, 4. sum these products for total production.

The assumptions underlying the size-frequency method are that growth between size classes is linear, that all individuals are capable of growing to the same maximum size, and that the organisms are univoltine (Hamilton 1969). Violation of the assumption of linear growth probably does not produce large errors in production (Benke and Waide 1977; Hamilton 1969). However, if the organisms take more or less time than a year to complete growth serious errors will result. These can be overcome by multiplying the production estimate by $365/\text{CPI}$, where 365 is the number of days in a year, and the CPI is the Cohort Production Interval, or mean length of nymphal life, in days (Benke 1979). Confidence intervals for the production estimate, based mainly on sample variance, can be calculated using the method of Krueger and Martin (1980). Although originally developed to provide estimates within an order of magnitude, it appears that this method provides estimates similar to cohort based methods (Giberson and Galloway 1985; Riklik and Momot 1982; Waters

and Crawford 1973). Although generally accepted as a valid technique (Benke 1984), the size-frequency method has recently been criticized by Rigler and Downing (1984) for substituting assumptions about the age class development times for their actual measurement.

Production of Hexagenia limbata

Production estimates for H. limbata range from 3.09 g/m² (wet weight) for a population in Tuttle Creek Reservoir, Kansas (Horst and Marzolf 1975), to 11.5 g/m² in Lewis and Clark Lake, South Dakota/Nebraska (Hudson and Swanson 1972). The low values for Tuttle Creek Reservoir may be due to the short period of time that the reservoir population had been established prior to the study (Horst and Marzolf 1975). H. limbata production in Savanne Lake, Ontario was estimated at 4.78 to 5.59 g/m², depending on the method of calculation (Riklik and Momot 1982). In Lake Winnipeg, Manitoba, mayfly populations in the different basins of the Lake had very different production values (Flannagan and Cobb 1984). Estimates ranged from 1.0 g/m² in the north basin to 7.07 g/m² in the narrows.

In addition to geographic variation, annual fluctuations of 60% have been reported (Hudson and Swanson 1972).

P/ \bar{B} ratios reported for H. limbata have been lower (2.01-2.6) for semivoltine populations (Flannagan and Cobb

1984; Riklik and Momot 1982), and higher (3.48-5.38) for primarily univoltine populations (Horst and Marzolf 1975).

Preservative effects

Howmiller (1972) examined weight loss of tubificid oligochaets in 10% formalin, 70% ethanol with 5% glycerine, and 70% isopropanol with 5% glycerine. He found that weight loss varied from 10 to 38% after 24 hours and 24 to 74% after 44 days. Formalin consistently caused the least amount of loss. Stanford (1973) found that weight loss in 70% ethanol varied between 5 and 31% (after 35 days) for various taxa of aquatic insects. Donald and Paterson (1977) recommended the use of 10% formalin over 70% ethanol despite lower weight loss in ethanol. They found that the ethanol produced flaccid larvae and that weight changes in ethanol showed a more inconsistent pattern than those in formalin. The effects of first fixing specimens in formalin, and then preserving them in ethanol, have not been reported.

Production of Ephemera simulans

There are no published production estimates for E. simulans.

Life history and distribution of Hexagenia limbata
(Serville) and Ephemera simulans Walker
(Ephemeroptera) in Dauphin Lake, Manitoba

Abstract

The life history and substrate preference 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-central Manitoba. A system of wing pad developmental stages was used to assist in the separation of overlapping cohorts of H. limbata. During the two year study seven cohorts of this species were distinguished which indicated three different life histories. The dominant life history followed by four of the seven cohorts was two years. A second life history was of two years (24 months) duration, nine months of which was spent as overwintering eggs, and fifteen months in the nymphal stage. Two cohorts had this length of life. The third life history, present in only one cohort, was of 1.16-1.25 years (14-15 months) growth. The weighted average for all seven cohorts was 1.9 years (22.6 months). The degree-days above 10°C accumulated by each life history type was 1848, 2030 and 1806 respectively. Ephemera simulans had a two year life history in Dauphin Lake.

Hexagenia limbata was always found at stations having a silt-clay component. This included all offshore silty clay stations as well as those on a matrix of clay, silt,

sand and gravel along the east and north shores.

Ephemera simulans was found on the gravelly matrix substrate only. Neither species was found on a substrate consisting entirely of sand.

Introduction

In 1981 the Department of Fisheries and Oceans Canada started a pilot walleye, Stizostedion vitreum vitreum (Mitchill), enhancement and rehabilitation project on Dauphin Lake, Manitoba. Techniques such as habitat rehabilitation, fishing regulation adjustments and hatchery and pond reared stock enhancement developed during the project could then be applied to other aquatic habitats in need of fisheries rehabilitation (J.F. Flannagan et al., Freshwater Institute, unpublished report). One aspect of this project was the identification and quantification of the benthic fauna of the lake.

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 objectives of the current research were to investigate the life history and substrate preference of these species. The life history of these organisms is important to their potential as fish food. In semivoltine populations there is a supply of medium to large sized nymphs at all times of the year, whereas there are few or no nymphs present immediately following emergence in univoltine populations (Neave 1932). The life history of a population is also an important factor affecting the estimation of its production (Waters 1979), as it affects the

estimation of voltinism and growth rate. Biomass and production values for H. limbata and E. simulans will be reported in a separate paper (manuscript two).

Hexagenia limbata may require one year, two years, or a combination of 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 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 this study these problems were overcome by monitoring developmental age in addition to growth, using a system of wing pad developmental stages. 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 the studies of Britt (1962) and Speith (1936), reports on the life history of E. simulans have been restricted to accounts of emergence events. There is clearly a need for more information on the life history of this mayfly.

Methods and materials

Study area

Dauphin Lake is located in south-central Manitoba ($51^{\circ}15'23''\text{N}$; $99^{\circ}46'12''\text{W}$). It has a surface area of 519.3 km^2 (Anon. 1973) and mean and maximum depths of only 2.1 m and 3.5 m respectively (Fig. 1). There is a control structure on the outflow which restricts annual lake level fluctuations to 0.5 m. The Lake forms part of the Nelson River drainage basin which empties into Hudson Bay. The surface deposits of the surrounding area are lacustrine clay and silt plus glacial drift, which is primarily limestone (Weir 1960).

The ranges of selected physical and chemical parameters in the Lake, measured in May through October of 1982 and May through September of 1983, are listed in Table 1 (from J. Babaluk and M. Friesen, Freshwater Institute, Winnipeg, pers. commun.). Water samples taken during the period of ice cover in 1982 and 1983 contained dissolved O_2 levels of 77.8 to 162.6% saturation.

The Lake bottom was divided into three zones based on the sediment particle size. Description of sediments follows the sand-silt-clay ratio nomenclature of Shepard (1954). All of 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

Figure 1. Depth contours (m) and location of sampling stations on Dauphin Lake, Manitoba.

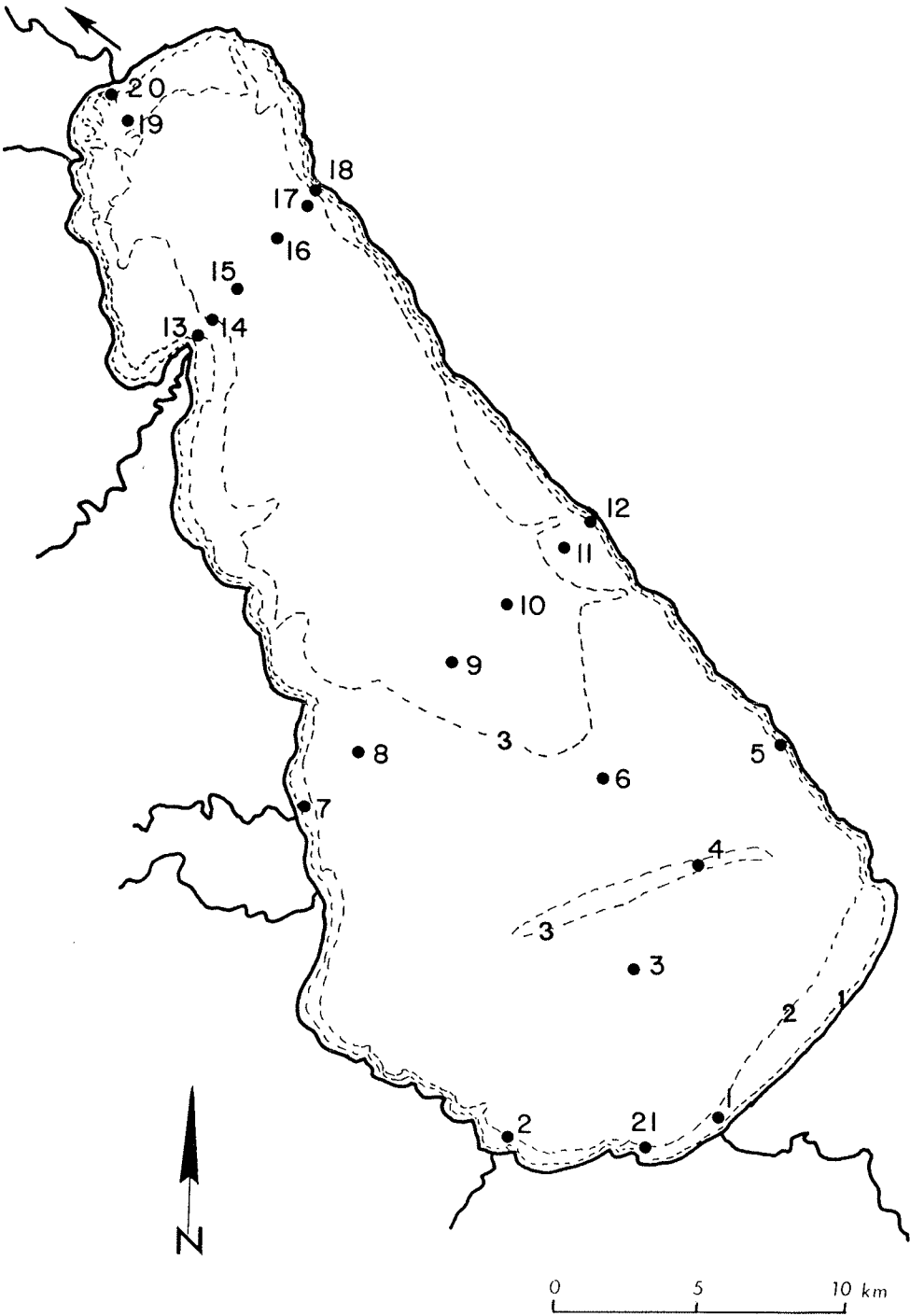


TABLE 1. Range of selected physical and chemical parameters in Dauphin Lake measured in May-October 1982 and May-September 1983. (from J. Babaluk and M. Friesen, pers. commun.).

Bottom temperature	2.4 - 24.8 ^o C
Dissolved oxygen	73.6 - 140.0 % saturation
pH	7.89 - 8.91
TSS	2 - 363 mg/l
Secchi disk	0.1 - 1.2 m

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 stony matrix type.

Emergent aquatic vegetation is sparse and found only along the shoreline. It includes reed-grass (Phragmites), bullrushes (Scirpus), sedges (Carex), and pondweed (Potamogeton). The filamentous algae Cladophora is also present (Stewart-Hay 1951).

Sampling

Twenty-one sample stations were arranged along transects originating at the mouths of inflow rivers (Fig. 1), in order to compliment benthic faunal studies of these rivers. Offshore stations were located by compass triangulation using onshore landmarks. In 1982 marker buoys with flags were used to mark stations, but buoys were destroyed by wave action and discontinued in 1983.

Triplicate grab samples were taken randomly at all stations monthly from May to October in 1982 and from May to September in 1983 (Appendix 1). Not all stations were sampled in late fall and winter due to inclement weather and ice conditions. 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 stony matrix substrate a pneumatic grab sampler (Burton et al. 1985), was used. Submerged funnel emergence traps modified from Hamilton (1965) were used in 1982 in an attempt to quantify adult emergence.

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 a high organic matter content were hand-picked under low power of a dissecting microscope. Samples with a low organic content and large particle size were floated in a sucrose solution (S.G.= 1.20 to 1.25), and sorted using a magnifying lens.

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 as the width across the eyes. All measurements were made using an ocular micrometer.

Hexagenia limbata nymphs were sexed using both the interior angle of the eyes (Neave 1932) and the presence or absence of male genitalia. Ephemera simulans nymphs were sexed using the latter method only.

Life history and substrate preference

Length frequency and head width frequency histograms

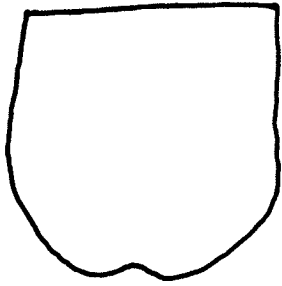
were constructed for both species. A linear regression of \ln length vs \ln head diameter was calculated for H. limbata (\ln length = $1.08 \ln$ head diameter + 2.01, $n=1052$, $R^2=0.98$, $P=0.0001$) and E. simulans (\ln length = $1.17 \ln$ head diameter + 2.07, $n=295$, $R^2=0.98$, $P=0.0001$). These equations were then used to predict total body length measurements for those nymphs having a damaged body, but an intact head.

A system of mesothoracic wing pad developmental stages was used to help elucidate the life history of H. limbata, which had overlapping cohorts (Fig. 2).

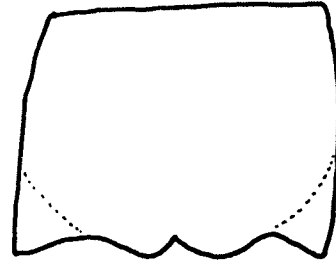
The number of nymphs of each species in each substrate type was compared for each month using the Kruskal-Wallis test (Conover 1971) to determine substrate preference. Comparison of densities in two habitats at a time was performed using the Mann-Whitney U-test (Elliott 1977).

Figure 2. Wing pad developmental stages for Hexagenia limbata, defined as follows: 1. pads absent 2. pad tips do not extend beyond mesonotum 3. pad tips exceed mesonotum, but angle between pads greater than 0° 4. pads parallel 5. pads elongate; tips point towards each other or meet 6. pads dark due to wing vein pigmentation.

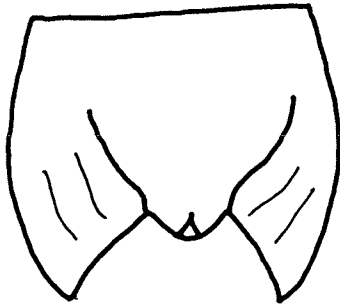
1



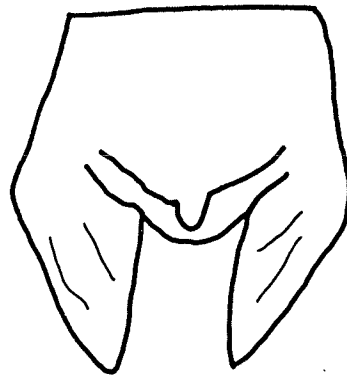
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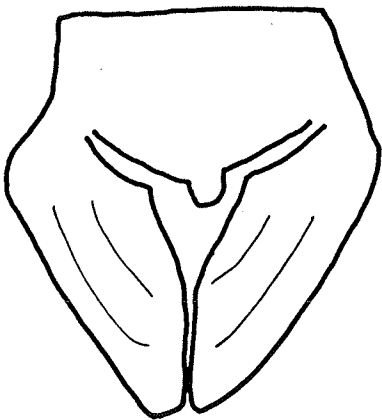
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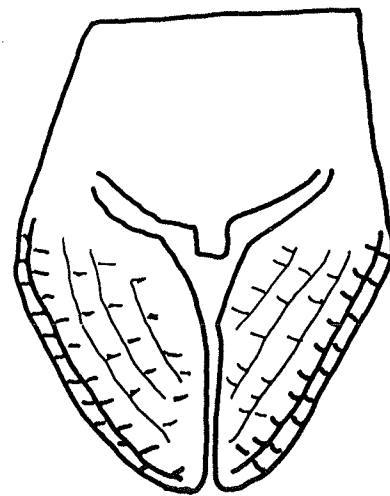
4



5



6



RESULTS

Life history

Hexagenia limbata

The total number of nymphs collected from May through September of 1982 and 1983 were 108, 94, 66, 138, 100, 116, 155, 60, 97, and 92 respectively. The length-frequency distribution of nymphs was bimodal on seven dates (Fig. 3), as evidence of at least two cohorts in the population. By superimposing the wing pad stage (WPS) of each individual on the size-frequency histograms of each sex plotted separately, (Appendix 2), a total of seven cohorts were discernible over the two year study period. The proportion of the population in each WPS is illustrated in Fig. 4, and the growth of each cohort, as indicated by change in mean length, is shown in Fig. 5.

Cohort 1 is represented by the large individuals in May and June of 1982, which emerged in early July and August of that year. Cohorts 2 and 3 appeared together as one large grouping in Fig. 3 but cohort 2 had more advanced WPS's (Fig. 4). Cohort 2 emerged in August and September, although in smaller numbers than the July emergence. Cohort 3 grew to wing pad stages 4 and 5 by September and did not emerge until July and August of 1983. Cohorts 4 and 5 were oviposited approximately one

Figure 3. Length frequency distribution of Hexagenia
limbata nymphs in Dauphin Lake from May to September
1982 and 1983.

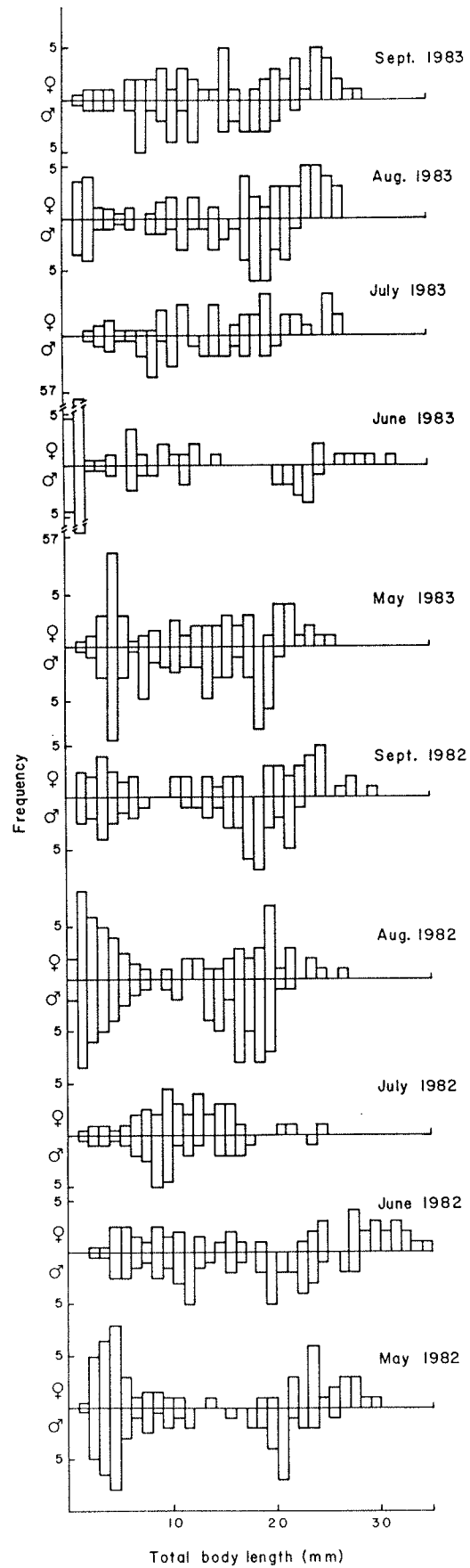


Figure 4. Percentage of Hexagenia limbata nymphs in each wing pad developmental stage in samples from May to September in 1982 and 1983 in Dauphin Lake. Numbers above lines denote cohorts.

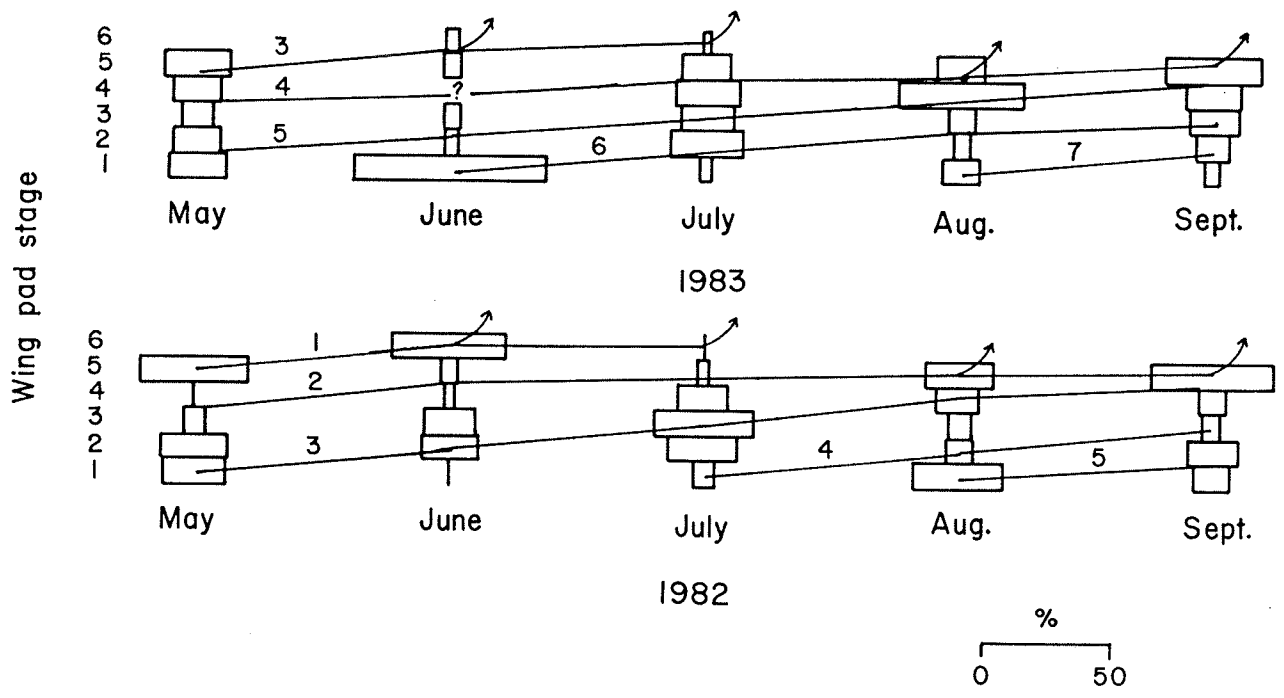
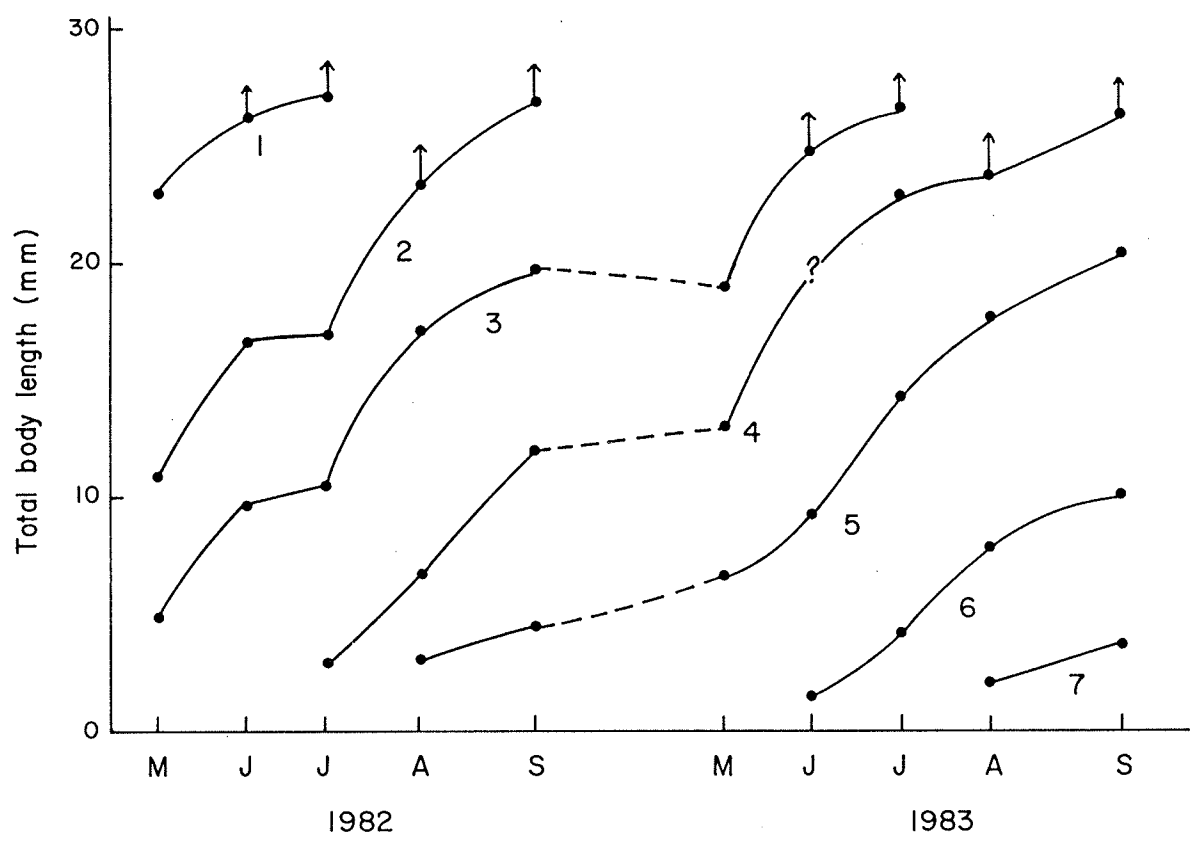


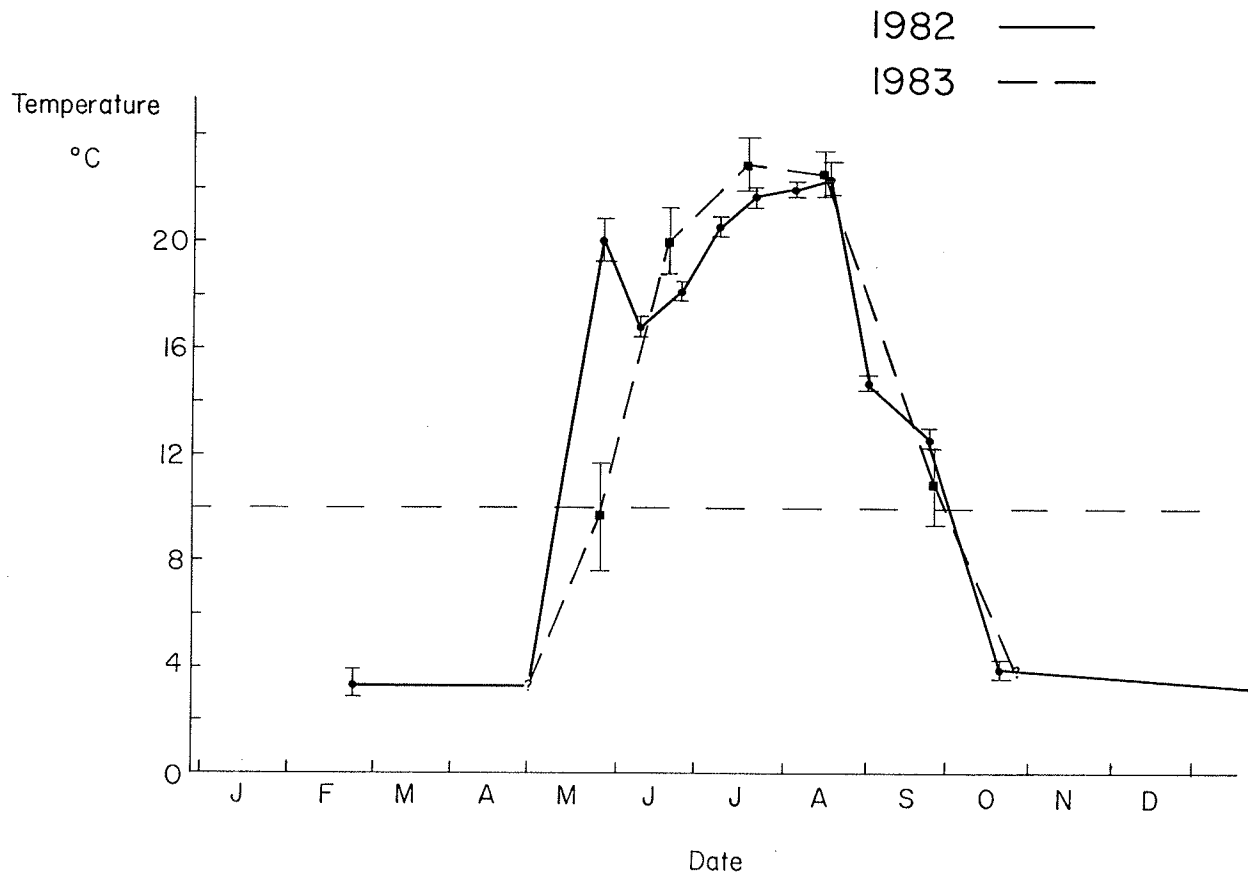
Figure 5. Growth of Hexagenia limbata nymphs, as indicated by change in mean length, for each cohort in Dauphin Lake from May to September 1982 and 1983. Numbers below lines denote cohorts. Curved arrows indicate emergence events following each sample date.



month apart, but cohort 4 was able to emerge in late August/September 1983, after only 14-15 months of development, whereas cohort 5 did not emerge by that date and presumably emerged in 1984. Cohort 6 first appeared in late June 1983. The main emergence in 1983 was again in the first few weeks of July, with smaller numbers emerging into early August. Hexagenia limbata eggs take 10-21 days to hatch at 25°C (Swanson 1967), 18-22 days at 19-27°C, and 20-26 days at 17-23°C (Hunt 1953). Dauphin Lake water temperatures in early July were approximately 21.5°C (Fig. 6), and so egg hatching probably took between 20 and 25 days. Therefore small nymphs resulting from the July oviposition could not show up until the end of July - early August. Cohort 6 nymphs first appeared in June, 4-5 weeks earlier than this and therefore most likely resulted from overwintering eggs oviposited the previous September by cohort 2 adults. 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 (Fig. 4).

The seven cohorts followed three distinct life histories. The predominant life history, which resulted in the major July emergence, was that of approximately two years of nymphal growth, from July-August of one year to July-August of the third year. Cohorts 1,3,5 and 7 were classified in this life history by growth curve and wing pad data. A second group was that oviposited in September

Figure 6. Bottom water temperatures \pm 95% C.I. 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.



which overwintered as eggs, and appeared as small nymphs in June. Cohort 6 was of this type. Its nymphs were in WPS's 2-late 3 by September 1983, and so did not likely emerge until late August or September 1984. They took 2 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 was that of an average 1.16-1.25 years (14-15 months) of growth shown by cohort 4. Nymphs first appeared in July 1982 and were probably oviposited in late June or early July, immediately preceding the July peak. They emerged in late August and September 1983. The average life history of the seven cohorts was 22.6 months, or 1.9 years.

Dauphin Lake warmed up in the spring and cooled off in the fall very rapidly (Fig. 6), which resulted in 99.9% of the degree-days above a 10°C threshold being accumulated between May and September (Table 2). The distribution of degree-days was different in the two years, as 1982 had a warm spring and 1983 had a warm fall. The early start of cohort 4 coincided with the warmer spring of 1982. 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 the 1.21 year life history (cohort 4). It accumulated 1728 degree-days. The degree-days based on the two year means

TABLE 2. Cumulative degree-days above a 10^oC threshold for Dauphin Lake, Manitoba, from May to September 1982 and 1983. All calculations were based on bottom water temperatures.

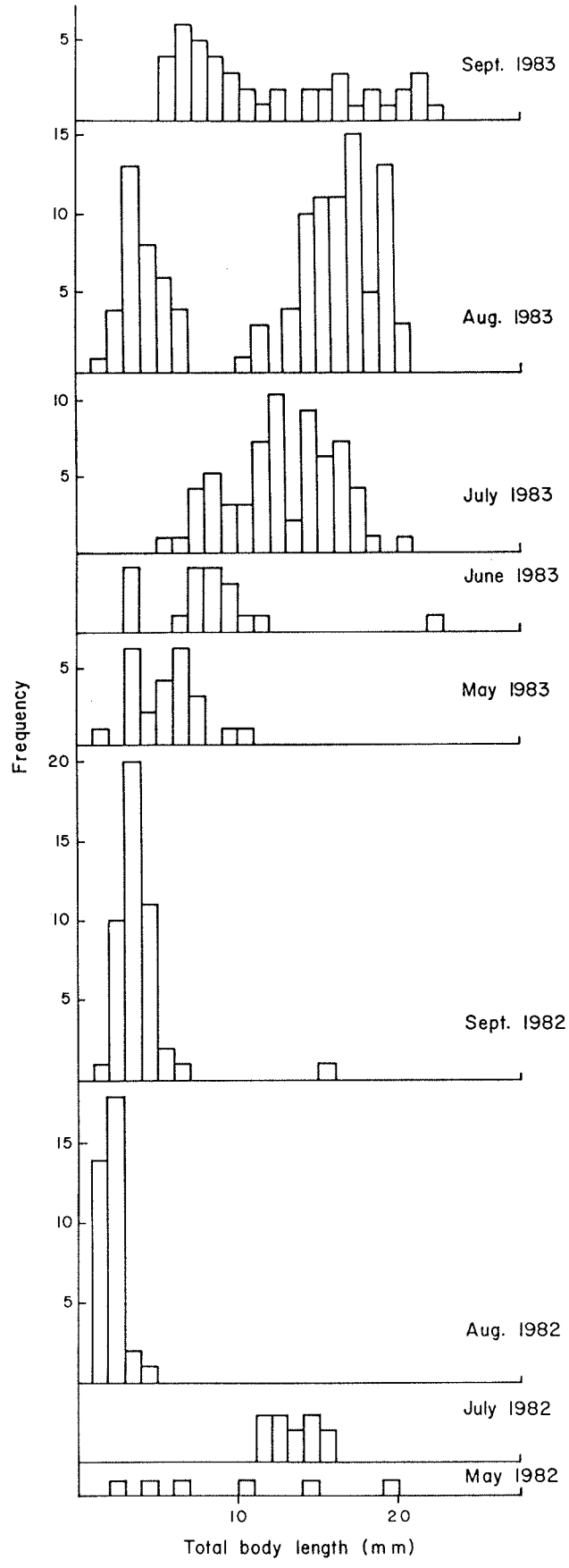
	1982	1983	mean
May	118.7	5.4	62.05
June	232.1	216.1	224.1
July	335.3	380.9	358.1
August	328.7	361.7	345.2
September	99.0	125.7	112.35
October	0.6	1.9	1.25
Total	1114.4	1091.7	1103.05
2-yr total		2206.1	

(Table 2) was 1806. The two year life history that grew from August to July used an estimated accumulation of 1848 degree-days, and the two year life history with overwintering eggs used 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 2).

Ephemera simulans

From the bimodal distribution of E. simulans nymphs in August and September 1983 (Fig. 7) it was concluded that two cohorts were present in the population. The smaller group of nymphs, which first appeared in August, resulted from a late July - early August oviposition. The larger group was traced back to its first appearance in August 1982. This group had not emerged by late September, and so emerged in 1984 after two years of growth. The cohort that first appeared in August 1983 was oviposited by a cohort represented by a single large individual in June 1983 and September 1982, all the nymphs present in July 1982, and by a few nymphs present in May 1982. This cohort was not collected during three months of this study, which led to the quite different appearance of the histograms for 1982 and 1983.

Figure 7. Length frequency distribution of Ephemera
simulans nymphs in Dauphin Lake, Manitoba, from May,
June, August and September 1982 and May to September
1983.



Substrate preference

Hexagenia limbata

With only one exception H. limbata nymphs were found in substrates having a clay-silt fraction. This included all offshore stations and the matrix east shore. On twelve occasions nymphs were found at west shore stations, but in eleven of these cases the substrate in the samples had some clay or silt component. In all other cases nymphs were not found in sandy substrates.

There was a significant difference (α varied from 0.05 to 0.001 depending on the month) between the number of H. limbata nymphs in the three substrate types in the lake (when the abnormal occurrences of nymphs at sandy stations, present on only three sample months, were excluded). Numbers of nymphs at the sandy stations were always significantly different ($\alpha=0.05$) from those at offshore stations, whereas there was no significant difference between the numbers at offshore vs rocky matrix stations ($\alpha=0.05$) in eight of ten months. The two months showing a difference were the first two months of the study, during which the pneumatic grab was not used on the rocky substrate.

The presence of very small (body length <3mm) nymphs was considered an estimator of oviposition localities. In 1982 very small nymphs were found in all three substrate

zones. In 1983 all nymphs present during the sudden appearance of large numbers in June and August were removed from stations along the rocky east shore.

Ephemera simulans

Nymphs of E. simulans were found only at stations 5, 12, 18 and 20 along the rocky matrix east and north shores.

Discussion

Life history

Hexagenia limbata

In the Hexagenia literature there is both a wide range of life histories reported, 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). In laboratory and transplantation studies nymphs from a single egg mass can

take from 5.5 months to two years to complete development, depending on temperature (Hunt 1953).

The use of a system of wing pad developmental stages in this study greatly aided the interpretation of the life history of H. limbata in Dauphin Lake. While WPS 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 due to the presence of multiple cohorts in the population, 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). In this study it was found that groupings (cohorts) were best followed by the use of total body length and WPS together. In this manner it was possible to monitor developmental age independent of growth (Butler 1984; McCafferty and Pereira 1984; Clifford 1970). While in other studies H. limbata cohorts split and completed their life history in one and two years, this study is unusual in that individuals in each cohort, or split cohort, were followed separately through time. Another important factor in determination of life histories is the

ability to accurately detect early instar nymphs. In this study this problem was overcome by the use of a small (200 μm) mesh size. Previous studies of H. limbata life histories have used mesh sizes as large as 800 μm (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).

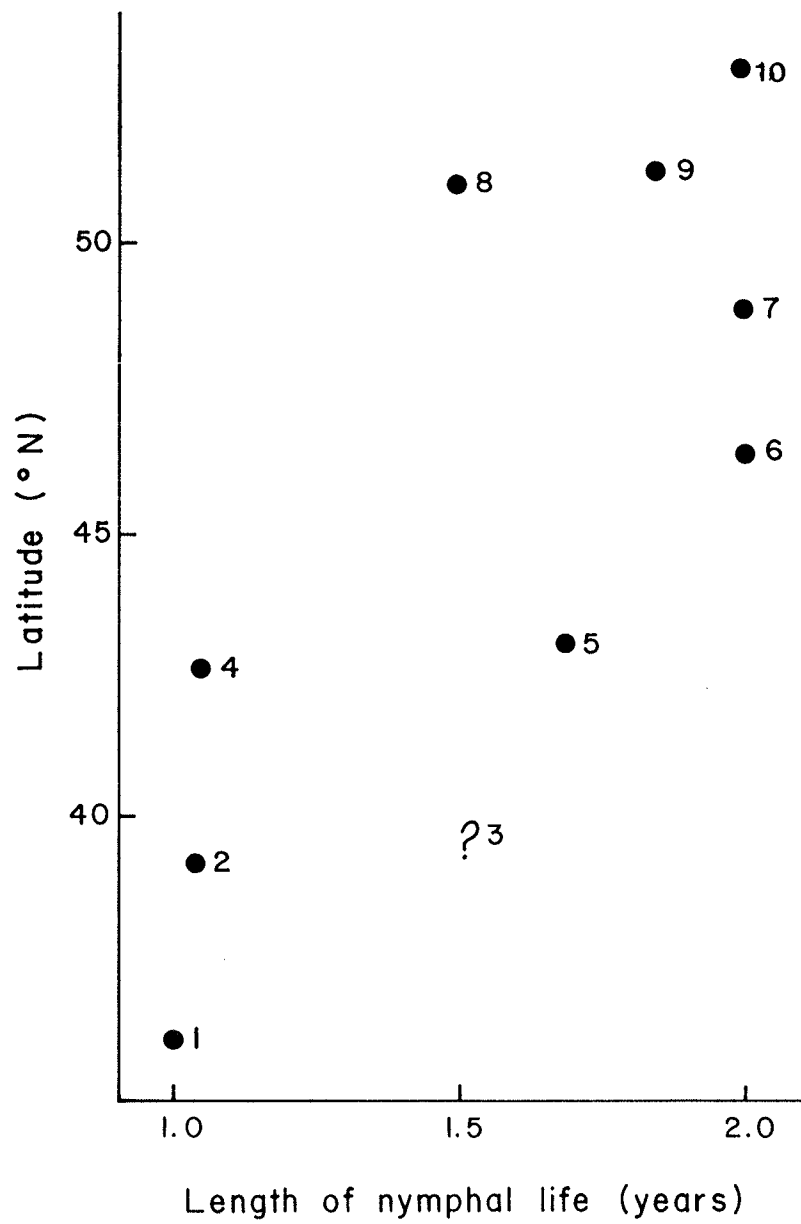
In this study the lack of good emergence data and the time interval between samples made exact separation of cohorts at the beginning and end of the nymphal stage difficult. Delayed egg hatching (Swanson 1967), which is affected by temperature and oxygen (Flattum 1963; Fremling 1967; Friesen et al. 1979;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

The "cohorts" identified in this study were defined as groups of nymphs which were of approximately the same length and wing pad stage, and which first appeared and emerged at approximately the same time. However, it is possible that groupings identified here as cohorts were actually oviposited at the same time, but developed at different rates to split apart later. Differential growth rates and number of instars are known to split cohorts in other mayflies species (Clifford 1970; Clifford et al. 1979; Fremling 1973a; Svensson 1977).

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. 8), 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. For H. limbata 10°C is usually used (Hudson and Swanson 1972; Hunt 1953; McCafferty and Pereira 1984). The value originally determined by Hunt (1953) was actually 48°F (8.9°C), but 10°C was used in the current study to allow comparison with other field studies (McCafferty and Pereira 1984). 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 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.

Figure 8. Relationship between the length of the life history 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).



Degree days regulate development of the closely related species H. bilineata (Say) up to a certain point (Wright et al. 1982), after which a threshold temperature must be reached before emergence takes place (L.L. Wright and J.S. Mattice, Env. Sci. Div., Oak Ridge Nat. Lab., pers. commun.). 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. 6).

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. More research is needed that covers a wider geographic range and reports degree-days and accurate emergence patterns. Water temperatures should be taken near the substrate, and not at the surface, in order to represent the conditions under which the nymphs grow. As well, some method of assessing development, such as wing pad stages, should be monitored in addition to growth characters such as length. Laboratory studies designed to compliment field studies would help

elucidate the factors critical to the length of the life history at any given locality.

Ephemera simulans

The length-frequency histograms of E. simulans in 1982 alone (Fig. 7) 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 that cohort oviposited in 1981. They grew to the 11-16 mm size by July 1982. These individuals 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 could not have emerged that year. This cohort was represented by the single 16 mm male nymph in September 1982, and by a 22.7 mm female in June 1983. In July they oviposited the 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 oviposited the eggs that resulted in the August 1982 cohort.

Despite its widespread distribution in Canada and the United States (Edmunds et al. 1976), little research has been done on the life history of this species 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 for this species 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. 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 when only the 1982 results of this study were considered.

Substrate preference

Hexagenia limbata

The preferred substrate of H. limbata is one variously described as soft mud, silt, or marl-mud (Carlander et al. 1967; Craven and Brown 1969; Hunt 1953; Neave 1932; Swanson 1967). This type of substrate is apparently selected because H. limbata's large prothoracic legs can

only be used in fine adhesive sediments (Eriksen 1964; Lyman 1943). Although nymphs show a strong preference for this substrate type, they are also found, in smaller numbers, in other substrates. Hexagenia limbata is rare or absent in pure or shifting sand (Lyman 1956; Swanson 1967), and in substrates where sand constitutes greater than 30-55% of the sediment mixture (Hunt 1953; Walker and Burbanck 1973). The nymphal distributions in silty clay and sandy substrates in Dauphin Lake agree with these studies.

Hexagenia limbata nymphs do not burrow into coarse substrates (Carlander et al. 1967; Eriksen 1968), but are found in mixed substrates of clay, sand and gravel (Neave 1932; Rutter and Wissing 1975). The approximately equal numbers of nymphs in the offshore and matrix east shore zones of Dauphin Lake indicate that both substrates were suitable for H. limbata in the lake. Nymphs were probably burrowing into the silty clay fraction of the gravelly matrix, but determination of the exact position of the nymphal burrows in the matrix was precluded by our sampling method.

Hexagenia distribution is also affected by low oxygen levels (Britt 1955a,b; Eriksen 1963,1964; Fremling 1967; Hunt 1953; Lyman 1943; Rutter and Wissing 1975; Swanson 1967) and strong winds during the flight period (Fremling 1970; Hunt 1953; Lyman 1944; Rutter and Wissing 1975). Oxygen levels were high in Dauphin Lake throughout the

year and so were never limiting. Wind did not appear to have a great effect as very small nymphs were distributed throughout the lake in 1982 despite strong NE winds during the peak July emergence period.

Nymphs migrate to areas of lower density (Hudson and Swanson 1972; Swanson 1967), from areas of sand to silt (Hunt 1953), and to areas previously exposed due to drawdown (Walker and Burbank 1973). While there was no direct evidence of nymphal dispersal in Dauphin Lake, the presence of early instar nymphs at only east shore stations following peak oviposition in 1983 indicated that movement of nymphs to populate the deeper offshore areas may have occurred during subsequent months.

Ephemera simulans

The occurrence of E. simulans nymphs in the heterogeneous matrix substrate along the east and north shorelines of Dauphin Lake is consistent with accounts of their occurrence in gravel, sand, sandy mud, marl, and combinations of all of these substrates (Britt 1962; Eriksen 1968; Hunt 1953; Lyman 1956). Their usual absence from fine sediments such as occurred at offshore stations in Dauphin Lake has been attributed to the respiratory inefficiency of their small gills at low oxygen levels (Eriksen 1968). This was probably not the case in Dauphin Lake, as O₂ levels were always well above the 1.20 ppm

minimum requirement of E. simulans (Eriksen 1964). It is more likely that the narrow tibiae and tarsi of this species, which allows it to easily penetrate most coarse substrates (Eriksen 1968), are inefficient in the clayey silt substrates of the Lake.

Production of Hexagenia limbata (Serville) and Ephemera simulans Walker in Dauphin Lake, Manitoba, with a note on weight loss due to preservatives

Abstract

Annual production and biomass of Hexagenia limbata (Serville) and Ephemera simulans Walker were estimated from samples taken from May through September of 1982 and 1983 in Dauphin Lake, Manitoba. The size-frequency estimates of production for H. limbata in 1982 and 1983 were $12.6 \pm 2.68 \text{ g/m}^2$ (wet weight) and $10.1 \pm 2.10 \text{ g/m}^2$ respectively. Instantaneous growth production estimates were 9.51 and 9.76 g/m^2 (1982) and 9.49 and 8.55 g/m^2 (1983) based on calculations using four versus seven cohorts respectively. P/\bar{B} ratios ranged from 1.68 to 2.38.

Production of E. simulans in 1983 was $9.02 \pm 3.10 \text{ g/m}^2$ (wet weight) and 9.90 g/m^2 using the size-frequency and instantaneous growth methods, respectively.

H. limbata weight loss due to preservation in 10% formalin followed by 75% ethanol produced a production underestimate of 25%.

Introduction

Investigations into the benthic fauna of Dauphin Lake were initiated in 1981 as part of a Department of Fisheries and Oceans Canada rehabilitation project for walleye, Stizostedion vitreum vitreum (Mitchill), in the Lake. The burrowing mayflies Hexagenia limbata (Serville) and Ephemera simulans Walker are dominant members of the macrobenthic community, are consumed by various species of fish, including walleye (Neave 1932; Hunt 1953; Britt 1962; Ryder and Kerr 1978), and, due to their large size, were potentially important fish food items in Dauphin Lake. Estimates of H. limbata production range from 3.09 to 11.5 g/m² (wet weight), and may depend upon the life history and type of lake (Hudson and Swanson 1972; Horst and Marzolf 1975; Riklik and Momot 1982; Flannagan and Cobb 1984). There are no published production estimates for E. simulans. The primary objective of the current research was to calculate production and biomass estimates for these two species.

Hexagenia limbata has a complicated life cycle of multiple overlapping cohorts in Dauphin Lake (manuscript one). A second objective of this study was to assess the influence of the use of four versus seven cohorts in the calculation of the production estimates for H. limbata.

A third objective was to determine the effect of length and weight changes caused by preserving fluids on H. limbata production. Preservatives result in various degrees of weight loss (Howmiller 1972; Stanford 1973; Donald and Paterson 1977), but the effects have not been examined for H. limbata.

Methods

Study area

Dauphin Lake is a relatively large (519.3 km²) prairie lake located in south central Manitoba (51°15' 23"N; 99°46'12"W). The Lake is thoroughly mixed at all times during the ice-free period due to wind action and the Lake's mean depth of only 2.1 m. Selected physical and chemical features of the Lake can be found in manuscript one.

Preservative effects

Fifty-five H. limbata nymphs collected on 23-25 June 1982 were kept alive individually in vials containing de-chlorinated water for 4-7 days to allow evacuation of the gut. Fresh blotted wet weight was measured to the nearest 0.1 mg on a Mettler AE 160 balance and total body length to the nearest 0.25 mm. Nymphs were then placed into 10% formalin for one year, then re-weighed and

re-measured, and placed into 75% ethanol for 12 days, and once again weighted and measured.

Production calculation

Nymphs were sampled monthly from May through September in 1982 and 1983. The sampling, sorting and length measurement methods are described in manuscript one. Blotted wet weight of nymphs was measured to the nearest 0.1 mg on an Mettler AE 160 balance. Total length vs wet weight linear regressions were calculated for H. limbata (\ln wet weight = $2.99 \ln$ length - 11.5, $n=80$, $R^2=0.99$, $P=0.0001$) and for E. simulans (\ln wet weight = $3.13 \ln$ length - 12.0, $n=33$, $R^2=0.99$, $P=0.0001$). These equations were then used to predict the weight of unweighed nymphs, based on their total body length.

The instantaneous growth (Waters 1977) and size-frequency (Hynes and Coleman 1968; Hamilton 1969) methods of production calculation were used. For the size-frequency method the cohort production interval (CPI) correction of Benke (1979) was used, and confidence intervals calculated using the method of Krueger and Martin (1980). Production estimates were calculated for H. limbata for 1982 and 1983, and for E. simulans for 1983 only, due to the small number of nymphs of this species collected in 1982. The instantaneous growth estimate for E. simulans was based on one cohort only.

In Dauphin Lake H. limbata was always found at stations having a silt-clay component, and E. simulans was restricted to the clay-gravel-sand east and north shores (manuscript one). For this reason stations 1,2,7,13 and 21 were excluded from analysis of H. limbata biomass and production, and only stations 5,12,18 and 20 were used in calculations of E. simulans production.

Instantaneous growth production of H. limbata was calculated using both a complex (7 cohorts present) and a simple (4 cohorts present) division of cohorts in order to assess the impact of these two different life cycle determinations on production. Cohorts in the complex situation were separated based on wing pad developmental stage, size-frequency distribution of nymphs, and emergence observations (manuscript one). Separation of cohorts in the simple scenario was performed using the latter two methods only.

Results

Preservative effects

Length changes of H. limbata in formalin and formalin followed by ethanol, calculated as a percentage of fresh length, were not significant ($\alpha=0.05$) regardless of sex (Fig. 1). Weight losses in formalin, calculated as a percentage of fresh weight, were significant for males and

all sexes combined, averaging 5.5% for all sexes combined (Fig. 2). Weight loss in formalin followed by ethanol, calculated as a percentage of fresh weight, was much greater for males, females and all sexes combined, averaging 24.9% overall (Fig. 2). No clear relationship between percent weight loss in formalin followed by ethanol and fresh total length of nymphs was evident (Fig. 3). The larger percent weight loss values and degree of scatter for larger individuals may be an artifact of the smaller number of small nymphs studied.

Biomass and production

Hexagenia limbata

The seasonal pattern of H. limbata densities was similar in 1982 and 1983 (Fig. 4). Densities decreased between June and July concurrent with the major summer emergence, and increased between July and August as the newly hatched nymphs appeared in the population. Numbers declined again in the fall as a second, smaller emergence took place. The minimum and maximum densities recorded at a single station were $0/m^2$ and $2331/m^2$ respectively.

The mean biomass curves for the two years were very different (Fig. 4), with the maximum values occurring in June in 1982 and August in 1983. In June 1982 the larger cohort was still present in the lake, whereas most of the corresponding cohort had emerged by the June sampling date

Figure 1. Length change of Hexagenia limbata nymphs, by sex, after preservation in 10% formalin (—●—) and 10% formalin followed by 75% ethanol (—■—), calculated as a percentage of fresh length.

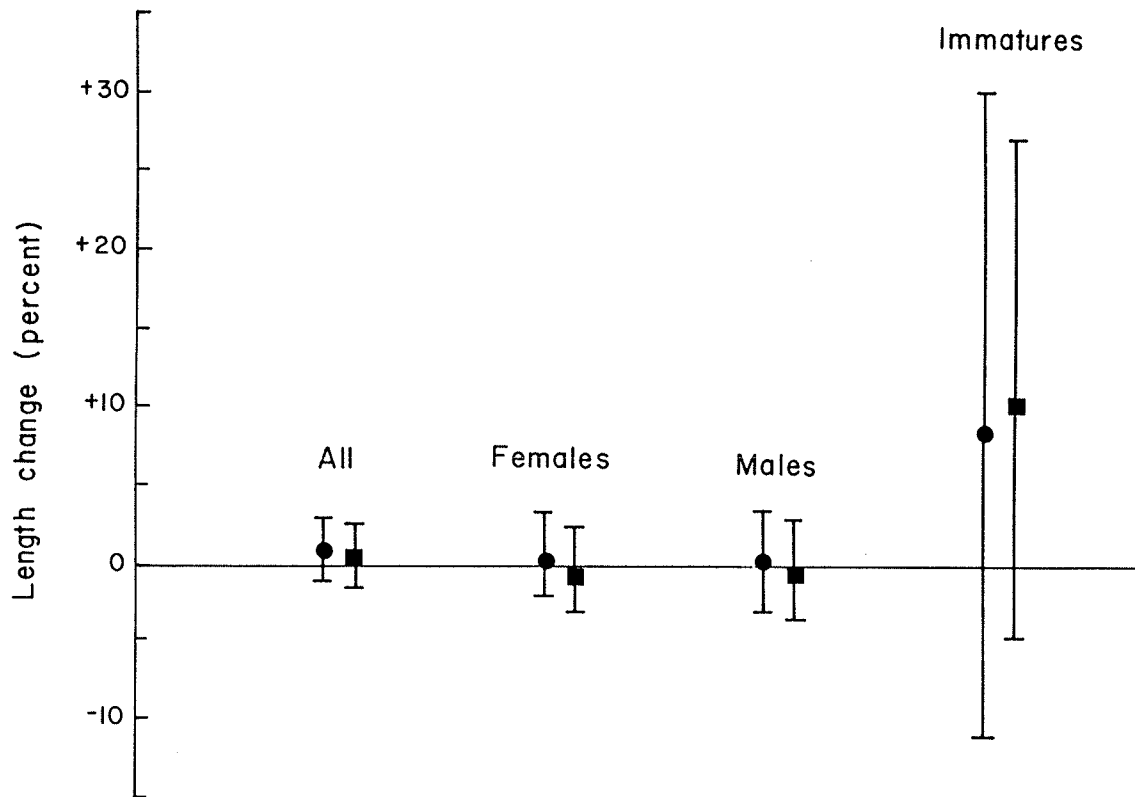


Figure 2. Wet weight change of Hexagenia limbata nymphs,
by sex, after preservation in 10% formalin (—●—)
and 10% formalin followed by 75% ethanol (—■—),
calculated as a percentage of fresh weight.

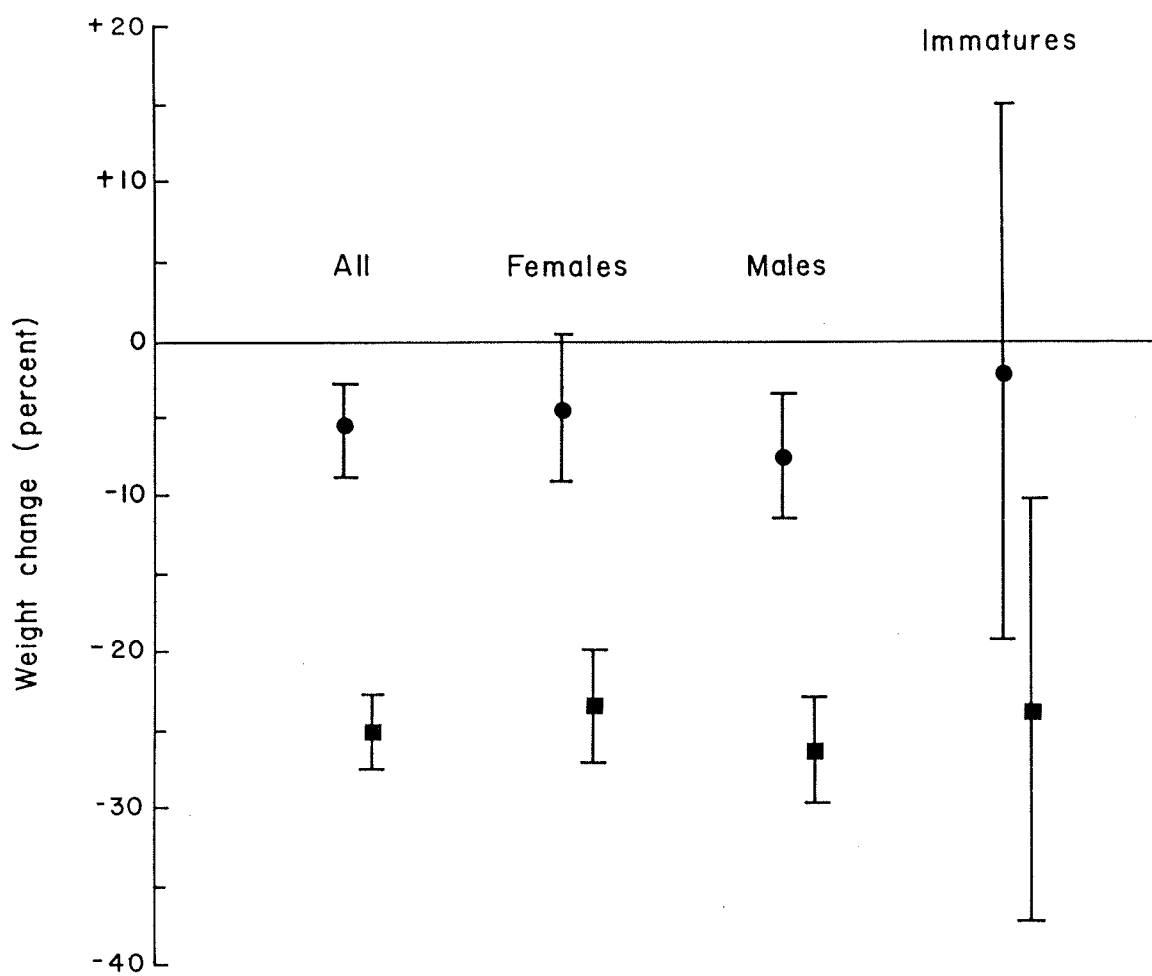
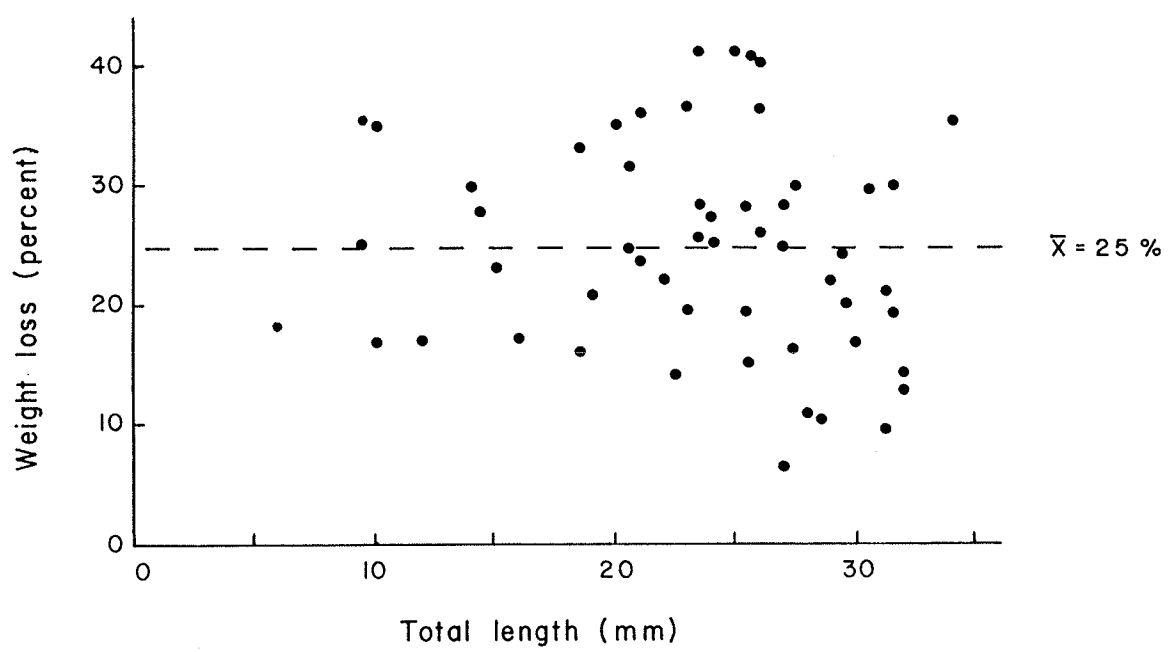


Figure 3. Weight loss of Hexagenia limbata nymphs, by fresh total body length, after preservation in 10% formalin followed by 75% ethanol, calculated as a percentage of fresh weight.



in 1983 (Appendix 2).

The annual production of H. limbata as calculated using the simple and complex instantaneous growth methods were very similar. For 1982 the complex estimate of 9.76 g/m² (Table 3) was slightly higher than the simple estimate of 9.51 g/m² (Table 1), and in 1983 the simple estimate of 9.49 (Table 2) exceeded the complex estimate of 8.55 (Table 4).

The size-frequency method, which does not require the identification of cohorts, produced estimates of 12.6 ± 2.68 g/m² for 1982 (Table 5) and 10.1 ± 2.10 g/m² for 1983 (Table 6). Both of these estimates are higher than the corresponding instantaneous growth estimates for each year.

Calculation of production using the size-frequency method with separate sexes, using a "times loss factor" (Hamilton 1969) of six for males and seven for females, resulted in estimates of 11.0 g/m² for 1982 and 8.34 g/m² for 1983. Both of these estimates are lower than the corresponding size-frequency estimate using the sexes combined.

The mean production estimates from all four methods for 1982 and 1983 were 10.72 and 9.12 g/m² respectively. These estimates adjusted to 10.43 and 8.87 g/m² for 1982 and 1983 respectively when the sandy shoreline habitat was included in the calculation of area. Hexagenia limbata production over the entire lake was 5416 tonnes in 1982, and 4606 tonnes in 1983.

Figure 4. Seasonal fluctuation in mean density and biomass of Hexagenia limbata in Dauphin Lake, Manitoba, in 1982 and 1983.

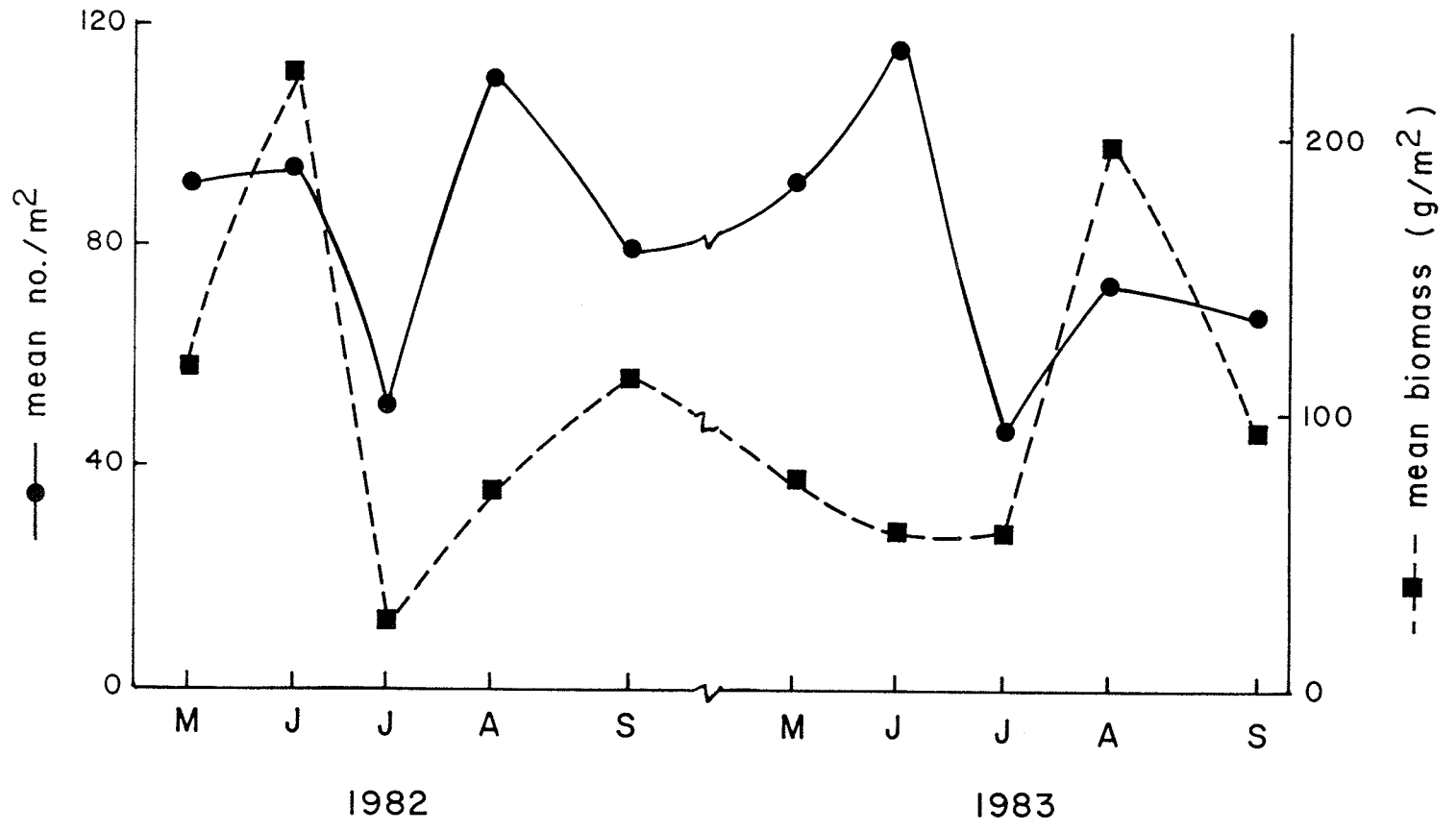


TABLE 1. Annual production of *Hexagenia limbata* in Dauphin Lake for 1982 using the instantaneous growth method and assuming a simple cohort structure.

Sample date	No./m ²	Mean wet weight (mg)	Biomass (mg/m ²)	Mean biomass (mg)	Inst. growth rate (G)	Production (mg wet weight/m ²)
			Cohort 1			
May	38.15	146.2	5579			
June	48.73	214.4	10449	8014	0.383	3067
July	0.816	240.9 ^b	196.7	5323	0.116 ^a	619.0
Aug.	0			98.32	0.421 ^c	41.44
			Cohort 2			
May	53.76	3.477	186.9			
June	45.68	15.07	688.3	437.6	1.466	641.7
July	46.53	22.70	1056	872.3	0.410	357.6
Aug.	65.04	68.51	4456	2756	1.105	3044
Sept.	57.90	96.31	5576	5016	0.341	1709
			Cohort 3			
July	4.082	0.319	1.301			
Aug.	45.96	0.625	28.74	15.02	0.674	10.12
Sept.	22.33	1.393	31.10	29.92	0.801	23.96
Total (cohorts 1-3)=						9514

^a calculated using males only

^b extrapolated from G for June to July and June mean weights

^c based on assumed growth to maximum observed weight

TABLE 2. Annual production of Hexagenia limbata in Dauphin Lake for 1983 using the instantaneous growth method and assuming a simple cohort structure.

Sample date	No./m ²	Mean wet weight (mg)	Biomass (mg/m ²)	Mean biomass (mg)	Inst. growth rate (G)	Production (mg wet weight/m ²)
Cohort 2						
May	54.85	67.62	3709	3195	0.996	3181
June	14.65	183.0	2681	1517	0.226	342.3
July	1.542	229.3	353.6	176.8	0.126 ^a	22.30
Aug.	0					
Cohort 3						
May	37.10	2.510	93.12	128.4	1.393	178.8
June	16.19	10.10	163.6	1306	1.725	2252
July	43.18	56.69	2448	4142	0.525	2175
Aug.	60.91	95.83	5837	5099	0.176	900.0
Sept.	38.15	114.3	4361			
Cohort 4						
June	87.13	0.040	3.524	2.278	2.400	5.466
July	2.313	0.446	1.031	6.100	0.485	2.961
Aug.	15.42	0.724	11.17	161.5	2.667	430.8
Sept.	29.92	10.43	311.9			
Total (cohorts 2-4)=						9490

^a based on assumed growth to maximum observed weight

TABLE 3. Annual production of Hexagenia limbata in Dauphin Lake for 1982 using the instantaneous growth method and assuming a complex cohort structure.

Sample date	No./m ²	Mean wet weight (mg)	Biomass (mg/m ²)	Mean biomass (mg)	Inst. growth rate (G)	Production (mg wet weight/m ²)
Cohort 1						
May	38.15	146.2	5579	7984	0.398	3178
June	47.71	217.7	10388	5292	0.092 ^a	488.8
July	0.816	238.8 ^b	194.9	97.47	0.430 ^c	41.92
Aug	0					
Cohort 2						
May	7.804	15.70	122.5	202.8	1.268	257.1
June	5.076	55.76	283.1	409.5	.0680	27.87
July	8.980	59.69	536.0	671.5	0.955	641.2
Aug.	5.203	155.1	807.0	889.1	0.415	368.7
Sept.	4.135	234.8	971.1			
Cohort 3						
May	45.96	1.402	64.43	265.0	2.077	550.2
June	41.62	11.18	465.5	492.9	0.214	105.6
July	37.55	13.85	520.3	1630	1.494	2437
Aug.	44.39	61.74	2741	3606	0.412	1485
Sept.	47.97	93.21	4471			
Cohort 4						
July	4.082	0.319	1.301	9.325	2.477	23.10
Aug.	4.569	3.797	17.35	78.14	1.710	133.6
Sept.	6.617	21.00	138.9			
Cohort 5						
Aug.	30.68	0.335	10.28	18.12	1.281	23.22
Sept.	21.50	1.207	25.95			
Total (cohorts 1-5)=						9761

^a calculated using males only

^b extrapolated from G for June to July and June mean weights

^c based on assumed growth to maximum observed weight

TABLE 4. Annual production of *Hexagenia limbata* in Dauphin Lake for 1983 using the instantaneous growth method and assuming a complex cohort structure.

Sample date	No./m ²	Mean wet weight (mg)	Biomass (mg/m ²)	Mean biomass (mg)	Inst. growth rate (G)	Production (mg wet weight/m ²)
Cohort 3						
May	40.33	82.47	3326	3003	0.797	2394
June	14.65	183.0	2681	1517	0.226	342.3
July	1.542	229.3	353.6	176.8	0.204 ^a	36.10
Aug.	0					
Cohort 4						
May	12.10	27.14	328.4	625.4	1.158	724.1
June ^b	10.68	86.40	922.4	1135	0.522	592.8
July	9.252	145.7	1348	2361	0.107	251.8
Aug.	20.82	162.0	3374	2100	0.3105	652.0
Cohort 5						
May	39.52	3.728	147.3	155.5	0.951	148.0
June	16.96	9.653	163.7	629.8	1.303	820.7
July	30.84	35.53	1096	1762	0.634	1118
Aug.	36.24	67.00	2428	2981	0.427	1274
Sept.	34.41	102.7	3534			
Cohort 6						
June	86.35	0.039	3.390	4.285	3.196	13.70
July	5.397	0.960	5.179	25.24	1.812	45.73
Aug.	7.710	5.875	45.30	177.0	0.755	133.7
Sept.	24.68	12.51	308.7			
Cohort 7						
Aug.	11.56	0.120	1.389	2.318	1.641	3.805
Sept.	5.236	0.620	3.247			

Total (cohorts 3-7) = 8550

^a based on assumed growth to maximum observed weight

^b all data for cohort 4 in June are interpolations from May and July data

TABLE 5. Annual production of Hexagenia limbata in Dauphin Lake for 1982 using the size-frequency method.

Size group (mm)	No./m ²	Mean weight (mg)	Standing crop (mg/m ²)	No. lost /m ²	Geometric mean weight (mg) at loss	Biomass lost (mg/m ²)	7 production (g/m ²)
0- 5	20.80	0.544	11.31	6.587	1.764	11.62	0.081
5-10	14.21	5.723	81.34	0.371	11.92	4.419	0.031
10-15	13.84	24.84	343.8	-6.17	41.61	-256	-1.80
15-20	20.01	69.70	1395	7.708	97.80	753.8	5.277
20-25	12.30	137.2	1688	7.302	186.5	1362	9.531
25-30	5.003	253.4	1268	2.997	315.7	946.0	6.622
30-35	2.007	393.3	789.2	2.006	393.3	789.2	5.524

Total= 25.27

$$\text{Annual production} = 25.27 \times \frac{365^a}{730} = 12.63 \pm 2.68^b$$

^a this is the Cohort Production Interval (CPI) of Benke (1979)
^b confidence interval = ± 2 standard errors, calculated using the method of Krueger and Martin (1980)

TABLE 6. Annual production of Hexagenia limbata in Dauphin Lake for 1983 using the size-frequency method.

Size group (mm)	No./m ²	Mean weight (mg)	Standing crop (mg/m ²)	No. lost /m ²	Geometric mean weight (mg) at loss	Biomass lost (mg/m ²)	x 7 production (g/m ²)
0- 5	30.96	0.2639	8.170				
				22.28	1.272	28.34	0.1984
5-10	8.681	6.134	53.25				
				-2.053	12.23	-25.10	-0.176
10-15	10.73	24.37	261.6				
				-3.198	41.42	-132.5	-0.927
15-20	13.93	70.40	980.8				
				-0.141	98.22	-13.84	-0.097
20-25	14.07	137.0	1928				
				9.288	174.8	1624	11.37
25-30	4.785	223.0	1067				
				4.590	292.3	1342	9.391
30-35	0.196	383.1	74.91				
				0.196	383.1	74.91	0.524

Total= 20.28

$$\text{Annual production} = 20.28 \times \frac{365^a}{730} = 10.14 \pm 2.10^b$$

- ^a this is the Cohort Production Interval (CPI) of Benke (1979)
^b confidence interval = ± 2 standard errors, calculated using the method of Krueger and Martin (1980)

The annual P/\bar{B} ratios and their corresponding production estimates are listed in Table 7. The P/\bar{B} values ranged from 1.7 to 2.4.

Ephemera simulans

Annual production of the one cohort of Ephemera simulans in 1983, calculated using the instantaneous growth method, was 9.90 g/m^2 (Table 8). The size-frequency estimate for all cohorts present during 1983 was 9.02 ± 3.10 (Table 9). The mean of the two estimates was 9.46 g/m^2 , or 110 tonnes in 1983. Total burrowing mayfly production in the rocky matrix habitat was 18.33 g/m^2 .

The annual P/\bar{B} ratios for E. simulans, calculated using the instantaneous growth and size-frequency methods, were 2.94 and 2.15 respectively.

Discussion

Weight loss

The weight loss in preservative and subsequent underestimate in production of 25% for H. limbata is one of several large sources of potential error in the production estimate. This source of error is not addressed by the confidence limit calculations of Krueger and Martin (1980), which mainly concern sampling variance. Many

TABLE 7. Summary of production and P/\bar{B} ratio estimates for Hexagenia limbata in Dauphin Lake, for 1982 and 1983.

Calculation method	1982	1983
Instantaneous growth (simple)	Prod. = 9.51 P/ \bar{B} = 1.68	9.49 2.38
Instantaneous growth (complex)	Prod. = 9.76 P/ \bar{B} = 1.78	8.55 2.05
size-frequency (sexes together)	Prod. = 12.6 \pm 2.68 ^a P/ \bar{B} = 2.26	10.1 \pm 2.10 ^a 2.32
size-frequency (sexes separate)	Prod. = 11.0 P/ \bar{B} = 2.04	8.34 2.11

^a confidence interval = \pm 2 standard errors

TABLE 8. Annual production of Ephemera simulans in Dauphin Lake for 1983 using the instantaneous growth method. The calculation is based on one cohort only.

Sample date	No./m ²	Mean wet weight (mg)	Biomass (mg/m ²)	Mean biomass (mg)	Inst. growth rate (G)	Production (mg wet weight/m ²)
May	64.01	2.450	156.9	197.3	0.845	166.8
June	41.66	5.706	237.7	2136	1.563	3339
July	148.1	27.24	4035	6693	0.669	4475
Aug.	175.9	53.16	9351	6214	0.309	1922
Sept.	42.50	72.42	3078			
Total=						9903

TABLE 9. Annual production of Ephemera simulans in Dauphin Lake for 1983 using the size-frequency method.

Size group (mm)	No./m ²	Mean weight (mg)	Standing crop (mg/m ²)	No. lost /m ²	Geometric mean weight (mg) at loss	Biomass lost (mg/m ²)	x 7 production (g/m ²)
0- 3	4.098	0.142	0.581				
3- 6	27.08	0.848	22.96	-22.98	0.347	-7.971	-0.064
6- 9	24.30	4.232	102.8	2.782	1.894	5.269	0.042
9-12	17.19	12.74	219.0	7.106	7.342	52.17	0.417
12-15	19.57	28.04	548.9	-2.379	18.90	-44.96	-0.360
15-18	35.45	48.90	1734	-15.88	37.03	-588.0	-4.704
18-21	15.57	81.15	1263	19.89	63.00	1253	10.02
21-24	2.589	119.4	309.1	12.98	98.43	1277	10.22
				2.589	119.4	309.1	2.472

Total= 18.05

$$\text{Annual production} = 18.05 \times \frac{365^a}{730} = 9.02 \pm 3.10^b$$

$$P/\bar{B} = \frac{9.02}{4.20} = 2.15$$

^a this is the Cohort Production Interval (CPI) of Benke (1979)
^b confidence interval = ± 2 standard errors, calculated using the method of Krueger and Martin (1980)

researchers either do not comment on weight loss effects (e.g. Horst and Marzolf 1975; Flannagan and Cobb 1984), or consider the effects negligible after citing other studies performed using different organisms (e.g. Riklik and Momot 1982).

In other studies where preservative effects have been examined differences occurred due to taxa, preservative, and length of time in the preservative (Howmiller 1972; Stanford 1973; Donald and Paterson 1977). All production studies should consider weight loss by applying methods such as using fresh weights in biomass determinations, or applying a correction factor to the preserved weights, as was done in this study. Reducing such systematic errors will increase the comparability of production estimates.

Production

The slightly higher production estimates for H. limbata using the size-frequency method compared to the instantaneous growth method are consistent with the findings in other studies (Hudson and Swanson 1972; Waters and Crawford 1973; Cushman et al. 1978; Riklik and Momot 1982). However, all of the production estimates within each year were within the 95% confidence interval of the size-frequency estimate.

Differences between the production estimates for 1982 and 1983 were small, ranging from 0 to 32% depending on the method of calculation. Annual fluctuations in

production could result from changes in the growth rate of nymphs, caused by fluctuation in temperature and the food supply. One of the assumptions of the size-frequency method is that all individuals reach the same maximum size (Hamilton 1969), a condition which is not met in H. limbata due to sexual dimorphism. This is the most likely reason for the slightly lower estimate resulting from the calculation of sexes separately (Table 7).

The accurate determination of voltinism and length of the life cycle is essential to cohort based production methods (Waters 1979). The agreement between the simple and complex instantaneous growth production estimates was unexpected, as they involved differing number of cohorts and growth rates. It is probable that the small differences between cohorts in the H. limbata population in Dauphin Lake were not large enough to influence the production estimate. If this result applies to other H. limbata populations then elucidation of complex life histories involving overlapping cohorts may not be necessary in order to make accurate production estimates for this species.

The mean annual production estimates of 10.43 and 8.87 g/m² for 1982 and 1983 respectively are among the highest reported for this species. However, comparison of production estimates is difficult due to differences in methodology, such as the manner in which weights are measured. The whole lake production values of 5416 tonnes

(1982) and 4606 tonnes (1983) indicate that H. limbata provides a large potential food source for fish in the Lake. These high production values may be a result of elevated water temperatures and abundant algae in the Lake. The low P/\bar{B} ratios for H. limbata in Dauphin Lake are consistent with reports of values in the range of 2.0 to 2.6 for semivoltine populations (Riklik and Momot 1982; Flannagan and Cobb 1984). Higher P/\bar{B} ratios of 3.48 to 5.38 have been reported for populations that are at least partly univoltine (Horst and Marzolf 1975). These findings are in the range of 2 for semivoltine populations and 5 for univoltine populations predicted by Mann (1967) and Waters (1969).

The production estimates reported here are the first for E. simulans, despite the wide North American distribution of this species (Edmunds et al. 1976). The two methods of calculation produced similar results despite the inclusion of only one cohort in the instantaneous growth calculation.

The question of whether the cohort of large individuals present in very low numbers in the spring of 1983 was simply a poor year class, or represented an alternation of weak and strong year classes, is an important one. If the low numbers are "normal", then the calculated production estimates are representative of most years. If however, E. simulans frequently exhibits two equally strong cohorts, as suggested by the strongly bimodal distribution

of nymphs in August 1983 (manuscript one), then the production estimates calculated here should be doubled to represent the "normal" situation in Dauphin Lake. Either way, the combined production of E. simulans and H. limbata in the gravel matrix east shore is very high. The gravelly shore habitat in lakes may be analogous to the highly productive "snag" habitat of subtropical blackwater rivers (Benke et al. 1984). Difficulty in sampling this habitat type may be responsible for an underestimate of the productivity of rocky lake shorelines in the literature.

GENERAL DISCUSSION

The length of the life history of an organism is an important factor affecting its production (Waters 1979). As well, the life histories of H. limbata and E. simulans are important to their potential as fish food, as semivoltine populations provide a supply of medium to large sized nymphs at all times of the year, whereas univoltine populations do not provide nymphs immediately following emergence (Neave 1932). The distribution of both species in Dauphin Lake is of great importance in weighing the final production estimates to achieve a realistic whole lake production figure. For these reasons manuscripts one and two of this thesis are closely related.

Hexagenia limbata

The length of the life history of H. limbata is highly variable, ranging from one to two years, and more often a mixture of the two (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 this study the use of a system of wing pad stages permitted the monitoring of developmental age independent of growth (Butler 1984; Clifford 1970), and allowed individual cohorts to be followed through time.

Despite this advantage the estimated life histories in this study are only accurate to within one or two months due to species characteristics such as differential growth of the sexes, delayed egg hatching, the protracted flight period, and the wide variability in the growth rate of individuals from the same egg mass (Hunt 1953; Swanson 1967). The relatively small number of samples and the lack of more complete emergence data also reduced the precision for the life history determination.

The life history of H. limbata in Dauphin Lake was very complex, with a total of seven cohorts following three different life histories during the two year study (manuscript one). 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 (manuscript one; Fig. 8). Annual fluctuations in mean monthly temperatures could alter this figure from year to year.

The estimated degree-days above a 10°C threshold required for development of this species in Dauphin Lake were less than those reported for populations in South Dakota/Nebraska (Hudson and Swanson 1972), and for laboratory reared populations in Indiana (McCafferty and Pereira 1984). Degree-days control development of H. bilineata (Say) up to a certain point (Wright et al. 1982), after which a threshold temperature must be reached before

emergence takes place (L.L. Wright and J.S. Mattice, Env. Sci. Div., Oak Ridge Nat. Lab., pers. commun.).

Hexagenia limbata nymphs in Dauphin Lake were present in approximately equal numbers in the offshore soft sediment and the rocky matrix east shore (manuscript one). Nymphs were not present in sand-only substrates. These results are in agreement with published accounts of their distribution in other water bodies (Carlander et al. 1967; Craven and Brown 1969; Eriksen 1964, 1968; Hunt 1953; Lyman 1943; Neave 1932; Rutter and Wissing 1975; Swanson 1967; Walker and Burbank 1973). While there was no direct evidence of nymphal dispersal in Dauphin Lake, early instar nymphs were present only at east shore stations following peak oviposition in 1983. Nymphs may disperse to populate the deeper offshore areas during subsequent months.

The mean annual production estimates of 10.43 and 8.87 g/m² wet weight for 1982 and 1983 respectively (manuscript two), are among the highest reported for H. limbata (Flannagan and Cobb 1984; Horst and Marzolf 1975; Hudson and Swanson 1972; Riklik and Momot 1982). Comparison with production estimates in the literature is made difficult by differences in methodology, such as the manner in which weights were determined. In this study weight loss due to preservatives averaged 25%.

The similarity between the simple and complex instantaneous growth estimates was unexpected, and may have been

due to the small differences between the cohort regimes. If this result is representative of other H. limbata populations, errors in production estimates due to over-simplification of the life history may be minimal.

The P/\bar{B} ratios varied from 1.68 to 2.38, which is typical for a population which is mostly semivoltine (Flannagan and Cobb 1984; Mann 1967; Riklik and Momot 1982; Waters 1969).

Hexagenia limbata nymphs provide a large potential food resource for fish in Dauphin Lake, producing 5416 and 4606 tonnes (entire lake) for 1982 and 1983 respectively.

Ephemera simulans

The occurrence of E. simulans in the gravelly matrix substrate in Dauphin Lake is consistent with accounts of its occurrence in gravel, sand, sandy mud, marl and combinations of all of these (Britt 1962; Eriksen 1968; Hunt 1953; Lyman 1956).

Britt (1962), Coleman and Hynes (1970), and Speith (1936) reported that this species may take one or two years to complete development. Ephemera simulans was semivoltine in Dauphin Lake, with two cohorts present. The very low numbers of one cohort made interpretation of the life history difficult. The question of whether the cohort of large individuals present in very low numbers in the spring of 1983 was simply a poor year class, or

represented an alternation of weak and strong year classes, is an important one to the calculation of production. If the low numbers are "normal" then the calculated annual production estimates (mean = 9.46 g/m^2) are representative of most years. If however, the usual population structure of E. simulans is that of two equally strong cohorts, as suggested by the strongly bimodal distribution of nymphs in August 1983 (manuscript one), then the production estimates should be doubled to represent the "normal" situation in Dauphin Lake. Either way, the combined production of E. simulans and H. limbata in the gravelly matrix substrate (18.33 g/m^2 in 1983), is very high relative to the production in other substrate types of the Lake. Unfortunately this substrate type is also difficult to sample, which may have led to the paucity of data from similar substrates in other lakes.

Importance to the walleye fishery

Although the yellow walleye is a piscivore, it will feed on mayfly nymphs. Hexagenia comprised up to 40% of walleye food in five Saskatchewan lakes (Rawson 1960). The decline of the walleye stock in western Lake Erie is thought to be related to the decline in the Hexagenia population, although this has not been proven (Regier et al. 1969). Due to their burrowing nature the nymphs are usually not readily available to fish. However, nymphs of

H. limbata and E. simulans leave their burrows to disperse (Britt 1962; Hunt 1953; Swanson 1967), and so become available at this time. Hexagenia are most active from sunset to sunrise (Swanson 1967), which overlaps the preferred feeding period of the walleye (Ryder and Kerr 1978).

Mayflies are most readily available to fish predators at the time of emergence. The mature nymphs, at their maximum size, swim to the surface to transform to the subimago stage. Spent females on the lake surface following oviposition often accumulate in large numbers. Adult mayflies form a very important food source for adult walleye during the emergence season in boreal forest lakes (Ryder and Kerr 1978). The early instar nymphs of H. limbata do not burrow, but are epibenthic (Hunt 1953), where they are available for juvenile walleye. Under experimental conditions young juvenile walleye (>54 mm long) selected gammarids and mayfly nymphs over zooplankton (Mathias and Li 1982), and may do the same in Dauphin Lake. The multiple cohort population structure of H. limbata and E. simulans, coupled with the wide range of individual size within each cohort (manuscript one), provides a large range of prey sizes for the fish population in Dauphin Lake.

The burrowing mayflies of Dauphin Lake may also provide an indirect food source for walleye. Hexagenia limbata nymphs comprised 41% of the diet of yellow perch

in southern Michigan lakes (Hunt 1953). They foraged for the nymphs by standing on their head on the sediment, with their tails pointing towards the surface, and grubbing into the bottom. This behaviour is termed "tailing" (Hunt 1953). Suckers prey heavily on the nymphs of E. simulans (Hunt 1953). Potential fish prey species such as these could provide a pathway for energy transfer from mayflies to walleye.

The burrowing mayflies of Dauphin Lake provide a large (5416 and 4606 tonnes of H. limbata nymphs in 1982 and 1983 respectively; manuscript one), quantity of biomass to the lake ecosystem. Apart from providing food for fish, this biomass may be helpful to the lake system in providing nutrients for use by plankton and macrophytes.

From preliminary gut contents analysis of walleye from Dauphin Lake, burrowing mayflies do not comprise a major portion of the diet (J. Babaluk, Freshwater Institute, pers. commun.). However, gut analyses have not been performed on walleye sampled during the emergence period of the mayflies, when they are of much greater potential importance. Future research should attempt to quantify the importance of mayflies to the diet of walleye in the Lake, and the relationship between burrowing mayfly and walleye production.

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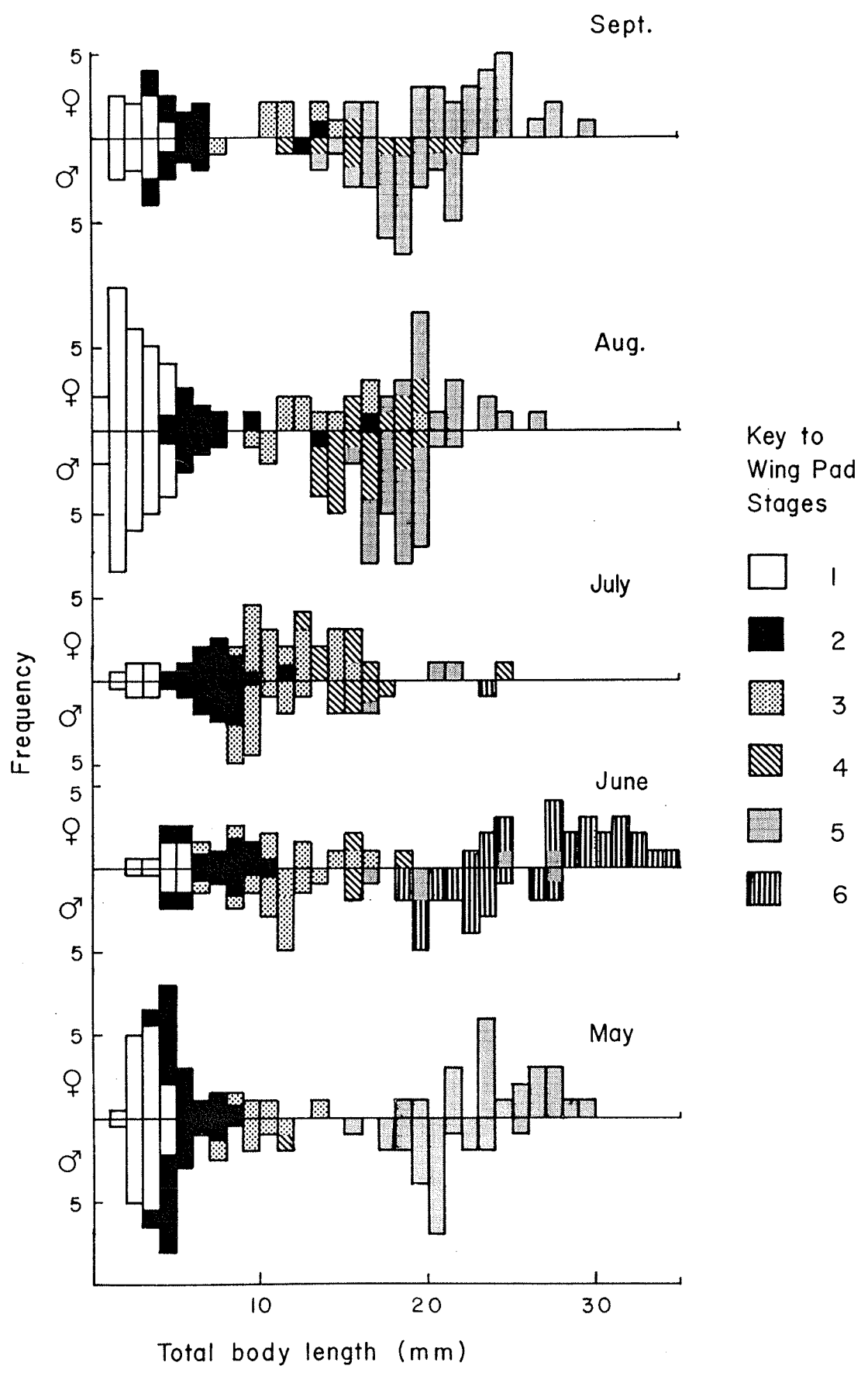
APPENDIX 1

List of the dates on which samples were taken in Dauphin Lake, Manitoba, in 1982 and 1983.

May 26,27	1982
June 10,11	1982
June 23-25	1982
July 19,20	1982
August 17-19	1982
September 24,25	1982
October 19,20	1982
April 1,2	1983
May 23-26	1983
June 20-23	1983
July 18-20	1983
August 15-18	1983
September 26-28	1983

APPENDIX 2

Appendix 2a. Length-frequency distribution of Hexagenia
limbata nymphs from Dauphin Lake showing the wing pad
developmental stage of each nymph sampled: 1982.



Appendix 2b. Length-frequency distribution of Hexagenia
limbata nymphs from Dauphin Lake showing the wing pad
developmental stage of each nymph sampled: 1983.

