Production of *Hexagenia limbata* (Serville) and *Ephemera simulans* Walker (Ephemeroptera) in Dauphin Lake, Manitoba, with a Note on Weight Loss due to Preservatives

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Heise, B. A., J. F. Flannagan, and T. D. Galloway. 1988. Production of *Hexagenia limbata* (Serville) and *Ephemera simulans* Walker (Ephemeroptera) in Dauphin Lake, Manitoba, with a note on weight loss due to preservatives. Can. J. Fish. Aquat. Sci. 45: 774–781.

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 (±2 SE) of production for *H. limbata* were 12.6 ± 2.68 g/m² (wet weight) in 1982 and 10.1 ± 2.10 g/m² in 1983. Instantaneous growth production estimates were 9.51 and 9.76 g/m² (1982) and 9.49 and 8.55 g/m² (1983) based on life history interpretations of four versus seven cohorts, respectively. Elucidation of complex life histories involving overlapping cohorts may not be necessary in order to make accurate production estimates for similar semivoltine populations. Annual $P/\bar{B}$ ratios for *H. limbata* ranged from 1.68 to 2.38. Production estimates for *E. simulans* in 1983 were 9.02 ± 3.10 and 9.90 g/m², using the size–frequency and instantaneous growth methods, respectively. *Hexagenia limbata* weight loss due to preservation in 10% formalin followed by 75% ethanol resulted in a production underestimate of 25%. Length changes of *H. limbata* in the same preservatives were not significant ($p > 0.05$). *Hexagenia limbata* was found at all stations having a silt/clay component. *Ephemera simulans* was found only on a matrix substrate of clay, silt, sand, and gravel.

On a déterminé la production annuelle et la biomasse de *Hexagenia limbata* (Serville) et de *Ephemera simulans* Walker à partir d'échantillons recueillis de mai à septembre 1982 et 1983 dans le lac Dauphin (Manitoba). Les estimations de la production selon la fréquence de tailles (±2 ET) chez *H. limbata* se situaient à 12,6 ± 2,68 g/m² (poids humide) et 10,1 ± 2,10 g/m² en 1982 et 1983 respectivement. D'après une interprétation du cycle vital de 4 et 7 cohortes, la production en terme du taux de croissance instantanée a été fixée à 9,51 et 9,76 g/m² (1982) et 9,49 et 8,55 g/m² (1983) respectivement. L'explication de cycles vitaux complexes comprenant des cohortes chevauchantes peut ne pas être nécessaire afin d'effectuer des estimations précises de la production dans le cas de populations semivoltines semblables. Les rapports annuels $P/\bar{B}$ chez *H. limbata* ont varié de 1,68 à 2,38. En 1983, les estimations de la production chez *E. simulans* s'élevaient à 9,02 ± 3,10 g/m² et 9,90 g/m², basées respectivement sur les fréquences de tailles et le taux de croissance instantanée. La perte de poids chez *H. limbata*, entraînée par la conservation dans le formol à 10 % puis dans l'éthanol à 75 %, a mené à une sous-estimation de la production de 25 %. Les variations de la longueur chez *H. limbata* dans les mêmes agents de conservation n'étaient pas significatives ($p > 0,05$). *Hexagenia limbata* était présente à toutes les stations d'échantillonnage où le substrat était composé d'argile et de limon. Par contre, *E. simulans* n'était présente que sur des substrats consolidés d'argile, de limon, de sable et de gravier.

Received December 19, 1986
Accepted January 7, 1988
(J9054)

Reçu le 19 décembre 1986
Accepté le 7 janvier 1988

In 1981 the Department of Fisheries and Oceans (Canada) started a walleye (*Stizostedion vitreum vitreum*) 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 pilot project could then be applied to other aquatic habitats (J. F. Flannagan, J. A. Mathias, and W. G. Franzin, Freshwater Institute, Winnipeg, Man., unpubl. rep.). The Dauphin Lake fishery is important both commercially and for sport. However, over the past 50 yr the fishery has changed from one of walleye and lake whitefish (*Coregonus clupeaformis* to primarily northern pike (*Esox lucius*) and white sucker (*Catostomus commersoni*). The walleye catch has declined from 202 169 kg, with a landed value of $68 288 in 1947–48 (Malaher 1948), to 10 200 kg worth $15 100 in 1982–83

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(V. Grande, L. Inkster, and D. Topolniski, Freshwater Institute, Winnipeg, Man., unpubl. data). One aspect of the rehabilitation 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 known to be consumed by various species of fish including walleye (Neave 1932; Hunt 1953; Britt 1962; Ryder and Kerr 1978), and, because of their large size, are potentially important fish food items in Dauphin Lake. Published estimates of *H. limbata* production range from 3.09 to 11.5 g/m^2 (wet weight) and may depend on the animals' 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 estimate production and biomass for these two species.

Hexagenia limbata has a complicated life cycle of multiple overlapping cohorts in Dauphin Lake (Heise et al. 1987). A second objective of this study was to assess the influence of a simple (four cohorts present over 2 yr) versus a complex (seven cohorts present) interpretation of the life history of *H. limbata* on the calculation of the production estimates for this species.

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 in invertebrates (Howmiller 1972; Stanford 1973; Donald and Paterson 1977; Giberson and Galloway 1985), but the effects have not been examined for *H. limbata*.

Study Area

Dauphin Lake is a relatively large (519.3 km^2) prairie lake located in southwestern 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 shallow depth (maximum 3.5 m, mean 2.1 m). There is a control structure on the outflow which restricts annual lake level fluctuations to 0.5 m. From May to October 1982 and from May to September 1983, bottom temperature varied from 2.4 to 24.8°C, dissolved oxygen from 73.6 to 140.0% saturation, pH from 7.89 to 8.91, and total suspended solids from 2 to 363 mg/L (J. Babaluk and M. Friesen, Freshwater Institute, Winnipeg, Man., pers. comm.). Water samples taken under the ice in 1982 and 1983 contained dissolved oxygen levels of 77.8–162.6% saturation.

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 except one of the offshore stations 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. The sediments at the exceptional offshore station were either a clay/silt mixture or of the heterogeneous matrix type.

Materials and Methods

Preservative Effects

Fifty-five *H. limbata* nymphs collected on 23–25 June 1982 were held individually in vials containing dechlorinated water for 4–7 d to allow evacuation of the gut. Fresh blotted wet weight was measured to the nearest 0.1 mg on a Mettler AE 160 balance. Total body length was measured to the nearest 0.25 mm using an ocular micrometer. Nymphs were placed into 10% formalin for 1 yr then reweighed and remeasured, and placed into 75% ethanol for 12 d and once again weighed and measured.

TABLE 1. Mean percent wet weight loss (±95% CL) of *Hexagenia limbata* nymphs, by sex, after preservation in 10% formalin and 10% formalin followed by 75% ethanol.

	Formalin	Formalin followed by ethanol
All sexes combined	5.5 ± 2.9	24.9 ± 2.4
Females	4.0 ± 4.5	23.6 ± 3.8
Males	7.6 ± 4.2	26.2 ± 3.4
Immatures[a]	1.9 ± 17.6	24.0 ± 13.2

[a]Too young to sex.

Sampling

Twenty-one sample stations were arranged along transects originating at the mouths of major inflowing rivers, in order 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 each station monthly from May to October in 1982 and from May to September in 1983. A tall modified Ekman grab (Burton and Flannagan 1973) with a semiautomatic release mechanism (Burton 1974) was used on clayey silt and sand substrates. On the matrix substrate a pneumatic grab sampler (Burton et al. 1985) was used during all but the first 2 mo.

Samples were sieved in the field through 200-μm-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 – 1.25) and sorted using a magnifying lens. The amount of time nymphs spent in each preservative varied from approximately 4 to 11 mo in formalin and 1 to 4 wk in ethanol.

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

Hexagenia limbata nymphs longer than approximately 9 mm were sexed using the interior angle of the eyes (Neave 1932) and the presence or absence of male genitalia. *Ephemera simulans* nymphs longer than approximately 8 mm were sexed using the latter method only.

Production Calculations

Blotted wet weight of preserved nymphs was measured to the nearest 0.1 mg on a Mettler AE 160 balance. Total length versus preserved wet weight linear regressions were calculated for *H. limbata* (ln wet weight = 2.99 ln length − 11.5, n = 80, R^2 = 0.99) and for *E. simulans* (ln wet weight = 3.13 ln length − 12.0, n = 33, R^2 = 0.99). These equations were then used to predict the weight of unweighed nymphs, based on their total body length. Mean weights used in production calculations were increased by a factor of 1.2488 (see Results section below) to correct for weight loss due to preservatives.

TABLE 2. Monthly mean density (no./m²) of *Hexagenia limbata* nymphs in each substrate zone in Dauphin Lake, Manitoba.

Date	Sandy	Offshore clay/silt	Heterogeneous matrix
May 1982	0	152.8	0
June 1982	2.8	98.6	5.2
July 1982	8.3	74.5	12.5
Aug. 1982	25.0	106.5	128.5
Sept. 1982	11.1	94.9	59.0
May 1983	0	123.8	24.3
June 1983	0	46.7	23.5
July 1983	0	70.7	10.6
Aug. 1983	0	63.8	109.0

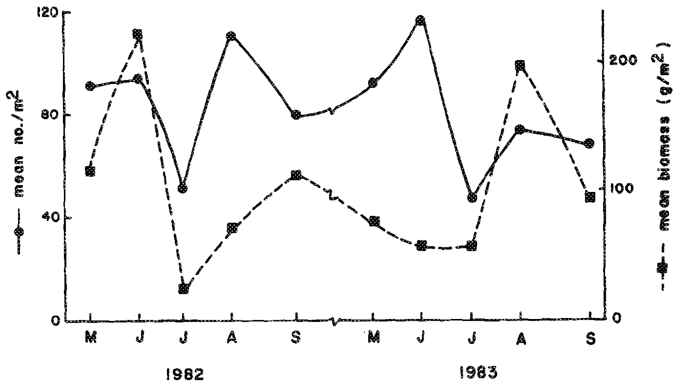

FIG. 1. Seasonal fluctuation in mean density and wet weight biomass of *Hexagenia limbata* in Dauphin Lake, Manitoba, in 1982 and 1983.

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. *Ephemera simulans* production was calculated 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 due to the small number of nymphs collected for the older cohort.

The sand, clay/silt, and heterogeneous matrix substrates made up approximately 2.7, 95.1, and 2.2%, respectively, of the whole lake area. Biomass and production estimates of *H. limbata* were made for the silt/clay and matrix substrates only. *Ephemera simulans* estimates were made for the matrix substrate only. Whole-lake production estimates were made using the area of the entire lake.

Hexagenia limbata in Dauphin Lake has a complex life history of seven overlapping cohorts present during a 2-yr period (Heise et al. 1987). The population at first appeared to have a simple 2-yr life cycle with only four cohorts present, but by examining wing pad developmental stages in addition to length frequency and emergence data, seven cohorts were detected. Many studies of *H. limbata* populations with overlapping cohorts have found simpler life histories with fewer cohorts (Rutter and Wissing 1975; Riklik and Momot 1982; Schloesser and Hiltunen 1984). Instantaneous growth production of *H. limbata* was calculated using both a complex (seven cohorts present) and a simple (four cohorts present) division of cohorts in order to assess the impact of these two different life history interpretations on the production estimate.

Results

Preservative Effects

Length changes of *H. limbata* nymphs in formalin and formalin followed by ethanol, calculated as a percentage of fresh length, were not significant ($p > 0.05$) regardless of sex. Weight losses in nymphs held in formalin followed by ethanol, calculated as a percentage of fresh weight, were significant ($p < 0.05$) and much greater than weight losses in formalin only, averaging 24.9% overall (Table 1). There was no clear relationship between percent weight loss in formalin followed by ethanol and fresh total length of nymphs.

Substrate Preference

With the exception of one sample on one date, *H. limbata* nymphs were found in substrates having a clay/silt fraction. This included all offshore clay/silt stations and the matrix east shore. The density of nymphs in these two substrate types was usually similar (Table 2). On 12 occasions, nymphs were found at sandy west shore stations, but in 11 of these cases the substrate in the samples had some clay or silt component.

Nymphs of *E. simulans* were found only at stations along the heterogeneous matrix east and north shores. Mean densities per square metre were 63.4 (range = 0–121.5) in 1982 and 129.7 (range = 39.6–269.4) in 1983.

Biomass and Production

Hexagenia limbata

The seasonal pattern of *H. limbata* densities was similar in 1982 and 1983 (Fig. 1). 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. Densities at stations ranged from 0 to 2331/m² and standard deviations from 85 to 143% of the mean.

The mean biomass curves for the 2 yr were very different (Fig. 1), 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 in 1983.

The annual production estimates for *H. limbata* calculated using the instantaneous growth method with a simple, and a complex, interpretation of cohort structure were very similar. For 1982 the complex estimate was 9.76 g/m² (Table 3) and the simple estimate was 9.51 g/m² (Table 4). In 1983 the simple estimate was 9.49 g/m² and the complex estimate was 8.55 g/m².

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. Both of

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./m²	Mean wet weight (mg)	Biomass (mg/m²)	Mean biomass (mg)	Inst. growth rate (*G*)	Production (mg wet weight/m²)
			Cohort 1			
May	38.15	146.2	5 579			
				7984	0.398	3178
June	47.71	217.7	10 388			
				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	0.068	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	2 741			
				3606	0.412	1485
Sept.	47.97	93.21	4 471			
			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–July and June mean weights.
[c]Based on assumed growth to maximum observed weight.

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 6 for males and 7 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 became 10.43 and 8.87 g/m² for 1982 and 1983, respectively, when the sandy shoreline substrate, which was not inhabited by *H. limbata*, was included in the calculation of area. *Hexagenia limbata* production over the entire lake was 5416 metric tonnes (t) in 1982 and 4606 t in 1983.

TABLE 4. Annual production of *Hexagenia limbata* in Dauphin Lake for 1982 using the instantaneous growth method and assuming a simple cohort structure.

Sample date	No./m²	Mean wet weight (mg)	Biomass (mg/m²)	Mean biomass (mg)	Inst. growth rate (*G*)	Production (mg wet weight/m²)
			Cohort 1			
May	38.15	146.2	5 579			
				8014	0.383	3067
June	48.73	214.4	10 449			
				5323	0.116[a]	619.0
July	0.816	240.9[b]	196.7			
				98.32	0.421[c]	41.44
Aug.	0	—	—			
			Cohort 2			
May	53.76	3.477	186.9			
				437.6	1.466	641.7
June	45.68	15.07	688.3			
				872.3	0.410	357.6
July	46.53	22.70	1056			
				2756	1.105	3044
Aug.	65.04	68.51	4456			
				5016	0.341	1709
Sept.	57.90	96.31	5576			
			Cohort 3			
July	4.082	0.319	1.301			
				15.02	0.674	10.12
Aug.	45.96	0.625	28.74			
				29.92	0.801	23.96
Sept.	22.33	1.393	31.10			
					Total (cohorts 1–3) =	9514

[a]Calculated using males only.
[b]Extrapolated from *G* for June–July and June mean weights.
[c]Based on assumed growth to maximum observed weight.

The annual $P/\bar{B}$ ratios and their corresponding production estimates are listed in Table 6. The $P/\bar{B}$ values ranged from 1.7 to 2.4. Cohort $P/\bar{B}$ ratios ranged from 0.832 to 3.58 (complex cohort structure) and from 0.832 to 2.65 (simple cohort structure) in 1982 and from 1.64 to 2.8 (complex) and from 2.06 to 7.75 (simple) in 1983. The lowest value was for a cohort in the few months prior to emergence, and the highest value was for a cohort newly hatched.

Ephemera simulans

Annual production of the one cohort of *E. simulans* in 1983, calculated using the instantaneous growth method, was 9.90 g/m². The size–frequency estimate for all cohorts present during 1983 was 9.02 ± 3.10 g/m². The mean of the two estimates was 9.46 g/m², or 110 t, in 1983.

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.

Production estimates for both species combined was possible for 1983 only. Total burrowing mayfly production in the rocky matrix habitat was 18.58 g/m². Whole-lake production was 9.08 g/m² (90.8 kg/ha), or 4716.7 t.

Discussion

Preservative Effects

The weight loss in preservative and subsequent underestimate in production of 25% for *H. limbata* is a large source of bias in the production estimate, one which is not addressed by the confidence limit calculations of Krueger and Martin (1980). Many researchers either do not comment on weight loss effects (e.g. Horst and Marzolf 1975; Flannagan and Cobb 1984), or they rely on shrinkage data for very dissimilar taxa (e.g. Riklik and Momot 1982).

In other studies, preservative effects were related to taxa, type of preservative, and length of time in the preservative (Howmiller 1972; Stanford 1973; Donald and Paterson 1977). All production studies should take this bias into account. The best way to do this is to use fresh weights. A second technique is the application of 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 with the instantaneous

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

Size group (mm)	No./m²	Mean weight (mg)	Standing crop (mg/m²)	No. lost/m²	Geometric mean weight (mg) at loss	Biomass lost (mg/m²)	×7 production (g/m²)
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	1362.0	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

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

[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. Summary of production (g/m²) and annual $P/\bar{B}$ ratio estimates for *Hexagenia limbata* in Dauphin Lake for 1982 and 1983.

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

[a]Confidence interval = ±2 standard errors.

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 6).

Accurate determination of voltinism and length of the life cycle is essential to cohort based production methods (Waters 1979), so the agreement between estimates based on simple and complex cohort structure was unexpected. The differences among cohorts in the *H. limbata* population in Dauphin Lake were probably not large enough to influence the production estimate. Elucidation of complex life histories involving overlapping cohorts may not be necessary for accurate production estimates in 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. Horst and Marzolf (1975) reported a value of 3.09 g/m² for a population in a Kansas reservoir, and Riklik and Momot (1982) estimated *H. limbata* production at 4.78–5.59 g/m² in Savanne Lake, Ontario. Production of *H. limbata* in Dauphin Lake is also higher than values of 1.0 and 7.07 g/m² in the north basin and narrows, respectively, of nearby Lake Winnipeg (Flannagan and Cobb 1984). 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 estimates of 5416 t (1982) and 4606 t (1983) indicate that *H. limbata* provides a large potential food source for fish in the Lake. The high Dauphin Lake values probably result from the high proportion (95.1%) of the total lake area which is suitable habitat for *H. limbata*. The shallow depth of the lake also provides adequate oxygen concentrations to all parts of the lake at all times of the year.

The calculation of burrowing mayfly production in each substrate zone of Dauphin Lake increased the precision of the estimates and facilitate comparisons of production estimates among locations. Production studies should be based on accurate estimates of organism densities in habitat types and of the proportions of the habitats within the study area.

The low annual $P/\bar{B}$ ratios for *H. limbata* in Dauphin Lake are consistent with reports of values in the range of 2.0–2.6 for semivoltine populations (Riklik and Momot 1982; Flannagan and Cobb 1984). Higher $P/\bar{B}$ ratios of 3.48–5.38 have been reported for populations that are at least partly univoltine (Horst

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