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PRODUCTION OF HEXAGENIA LIMBATA (SERVILLE) AND H. RIGIDA (MCDUNNOUGH) IN LAKE WINNIPEG, MANITOBA

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Abstract. Production of *Hexagenia* spp. in Lake Winnipeg in 1969 was estimated to be =87, 000 tonnes, about half of which was produced in the Narrows area of the Lake, which represents only 20% of the Lake area. Production estimates, assuming no change in turnover ratio, for the period 1927-30 were calculated from previously published summer standing crops of *Hexagenia* spp. Comparison of the production estimates for these two periods suggests that *Hexagenia* production in the whole lake has declined by 28%. The reduction in production was greatest in the more southerly 2/3rd of the Lake, ie. the area of the Lake closest to the main urban and agricultural centres. An apparent increase in *Hexagenia* production, over the same period, has occurred in the North Basin, suggesting a progressive south to north decline in the habitat of the Lake.

Production changes, turnover ratio

The fauna of Lake Winnipeg, the thirteenth largest (in area) lake in the world (Table 1) has been sporadically investigated over the past 50 years. Bajkov (1930) studied the organism/substrate relationships of the benthos of the Lake and recorded *Hexagenia limbata* as accounting for 10% of the fauna in the "mud-bottom" areas. Neave (1932, 1933, 1934) carried out extensive studies of the caddisflies and mayflies over the period 1927 - 1932. Manitoba provincial government biologists have been studying the fauna of the Lake since then, and noted a decline in the density of the benthos in the sixties (J.A. Crowe, personal communication). Flannagan (1979) showed a significant decline in the density of Hexagenia in the South Basin of the Lake and a shift in the relative abundance of H. limbata and H. rigida since Neave's (1932) study. He also established that there were two generation types in the Lake for Hexagenia spp. - a 2 year life cycle in the North Basin and a 14 month alternating with a 22 month life cycle in the South Basin. Flannagan and Cobb (1981) showed that of three species of profundal Trichoptera in the Lake in 1969, only two were present in Neave's (1933) time: Oecetis inconspicua (McLachlan) had replaced Molanna flavicornis Banks and Phryganea cinerea Walker in the South Basin and was apparently in the process of replacing them in the Narrows and North Basin of the Lake.

These various changes and reductions in the fauna of the Lake have not been definitely associated with any single cause. The lake has undergone considerable change in the past thirty years including, increased turbidity in the South Basin, decreased turbidity in the North Basin, raised lake water level, mercury pollution, increased input of pesticides, nutrients etc. (Brunskill 1973, Brunskill et al. 1979a, b; Flannagan 1979; Flannagan and Cobb 1981). Any one or all of these changes could well be involved in the faunal disturbances.

Although, as mentioned above, extensive studies of the distribution and abundance of the Lake benthos have been carried out, no attempt has been made to estimate the production of any of the benthic species. The Freshwater Institute survey of the Lake (Brunskill et al. 1979a, b; Flannagan 1979; Flannagan and Cobb 1981) and the definition of the life cycle of the two Hexagenia spp. (Flannagan 1979) allows production estimates of the profundal mayflies to be made. Comparisons of present day (1969) production with the estimated production from Neave (1932) were carried out to estimate the change in production over that period.

In 1969, Hexagenia species accounted for between <1% (North Basin) and 6% (South Basin), mean 3%, by number, of the benthos of Lake Winnipeg. However, because of their large size, compared to other benthic macroinvertebrates, they are, with the possible exception of Pontoporeia hoyi Smith, the most important single benthic food item in the diet of the lake fishes (Neave 1932, 1933, 1934; Bajkov 1930).

METHODS

During the open water season of 1969 three Birge-Ekman grab samples were taken approximately monthly at up to sixty sampling stations. In areas where the substrate was too hard a Ponar grab was used.

Sampling, sorting and handling methods for Hexagenia limbata and H. rigida were as described previously (Flannagan 1979). A total of 1,043 H. limbata and 240 H. rigida nymphs were measured. A total of 20 nymphs of various sizes of each species were, in addition, weighed after being surface dried

Table 1. Selected physical and chemical characteristics of Lake Winnipeg.*

Maximum Length	436 km
Maximum Breadth	111 km
Surface Area	23.750 km^2
Mean Depth	12.0 m
Maximum Depth	36 m
World Ranking	13th largest
Water Renewal Time	3.1 yrs
Secchi Disc	
North Basin	0.5-2.6 m
South Basin	0.1-1.0 m
Dissolved Oxygen	Near saturation throughout the year at all depths.
Nutrient Loading	
P	5.000 tonnes/yr
N	62.000 tonnes/yr

* From Brunskill /1973/; Brunskill, Schindler, Elliot and Campbell /1979/; Brunskill et al. /1979, 1980/.

with filter paper and the length/weight relationship calculated (Ulomskii (1951) showed that this method yielded adequate results). No significant difference was found between the two species. The length/weight relationship from (Fig. 1):

$$\log^{10} \text{wet weight (mg)} = 2.815 \log^{10} \text{length (mm)} - 1.8335 \quad (r=0.9941)$$

was used to convert the lengths of the remaining mayfly nymphs to wet weight. These weights, in conjunction with the life history data from Flannagan (1979) were then used to calculate production of each species, in each basin, and in the whole lake using the method of Winberg et al. (1971):

$$P = \frac{N_t + N_o}{2} \quad (W_t - W_o)$$

In this method the mean density between sampling times ($N_t + N_o$) is multiplied by the difference in mean biomass over the same period ($W_t - W_o$). Annual production is the sum of the production so calculated over the year/

Is should be noted that since only a single summer's data was available, it has been assumed that the two or three cohorts present during that summer were representative of any two

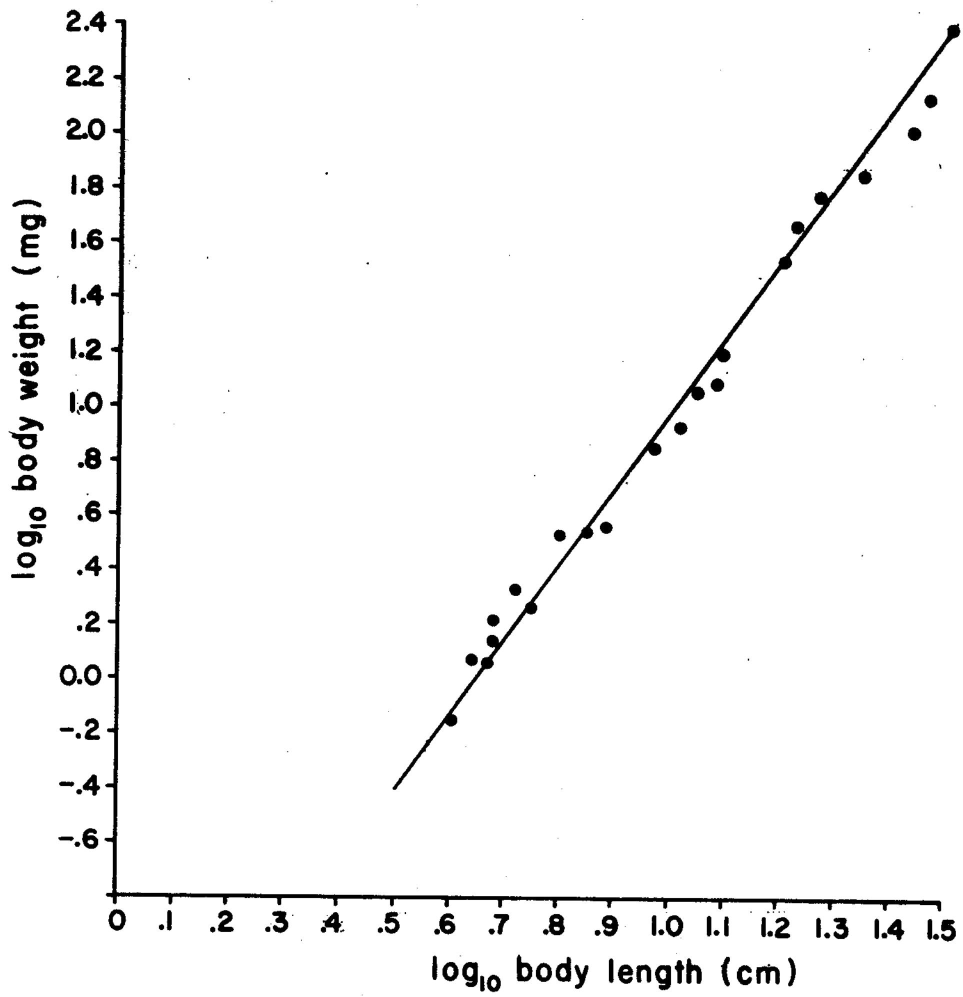

Fig. 1: Relationship between length and weight of Lake Winnipeg <u>Hexagenia</u> spp.

years growin in the Lake.

In addition to calculating the production for each species, each basin and the whole lake, turnover ratios (P/B) were calculated for <u>Hexagenia</u> spp.

Neave (1932) published mean densities for each species of <u>Hexagenia</u> and for each basin of the lake for the months of June and July. Using the difference between his mean densities and ours for the same months we calculated a production estimate for <u>Hexagenia</u> spp. for 1927 - 1930 for comparative purposes.

Since this estimate depends largely on there not being a significant change in turnover ratio between his sampling years and ours (production = turnover ratio x mean biomass) a regression analysis between latitude of occurrence of <u>Hexagenia</u> spp. and turnover ratio was carried out. The resultant regression line (Fig. 2, turnover ratio = 11.14 - 0.164 latitude) suggested that there was a significant relationship between

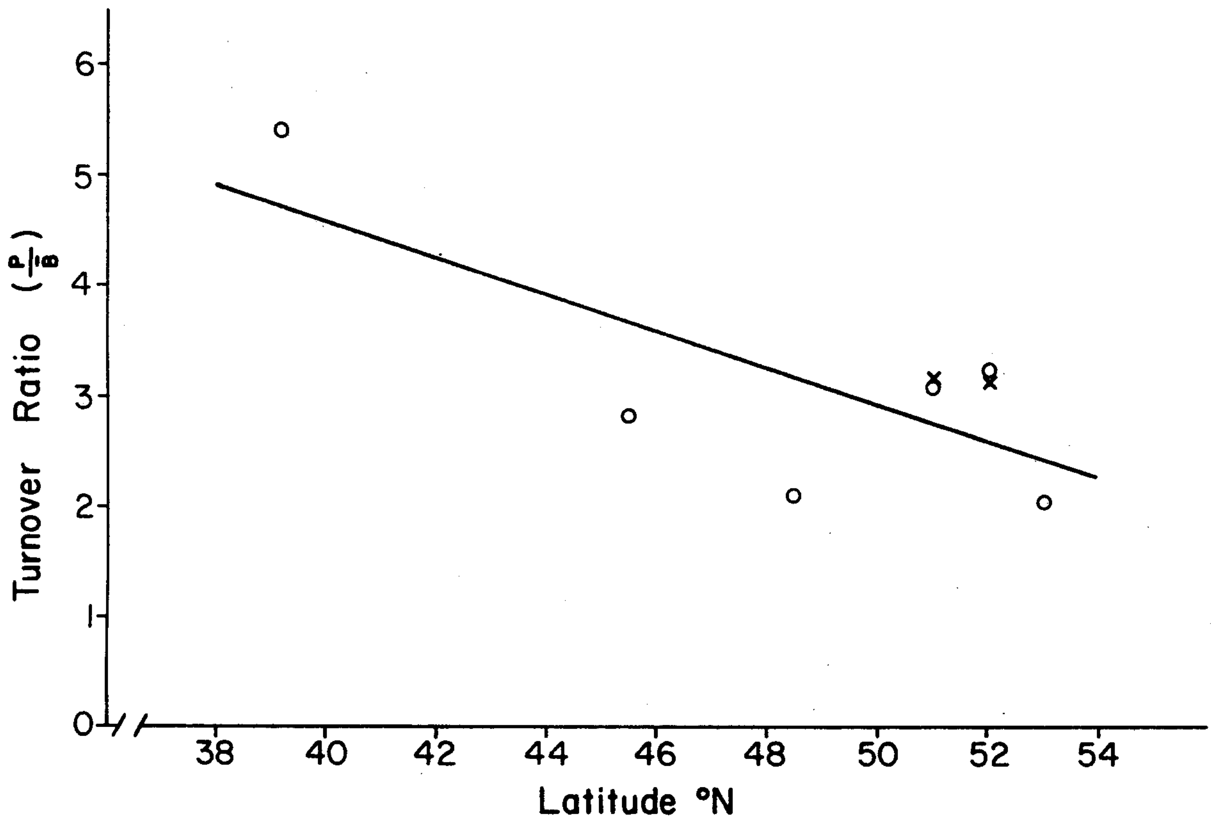

Fig. 2: Relationship between latitude of occurrence and turnover ratio in *Hexagenia* spp.

latitude and turnover ratio ($r = -.735$, $P < 0.05$). In addition, all of the Lake Winnipeg results for the South Basin and Narrows lie above the regression line perhaps suggesting that Lake Winnipeg *Hexagenia* turnover ratios have not changed.

RESULTS

Annual production for *Hexagenia* spp. varied from 6331 to 27,326 tonnes per year depending on the species and lake basin (Table 2). *H. limbata* contributed more than 2/3 of the mayfly production of the Lake and was the major contributor in each Basin. The Narrows, which comprises <20% of the total lake area contributed almost exactly 50% of the *Hexagenia* production, while the eutrophic South Basin produced little more than the much larger, deeper and more oligotrophic North Basin.

The ratio of annual production to mean biomass or Turnover Ratio (P/B, Table 2) indicates, as might be expected in a two year life cycle population (Hudson and Swanson 1972), the lowest turnover ratio occurred in the North Basin. Higher turnover ratios were found for the 14/22 month populations in the Narrows and South Basin.

Flannagan (1979) showed that considerable reductions in

Table 2. Production of Hexagenia species in the three basins of Lake Winnipeg in 1969.

	H. limbata tonnes/yr	H. limbata gm/m^2	H. rigida tonnes/yr	H. rigida gm/m^2	Total Hexagenia spp. tonnes/yr	Total Hexagenia spp. gm/m^2	Turnover Ratio
South Basin	21,991.08	6.738	6,331.66	1.940	28,32.74	8.678	3.10
Narrows	27,326.21	7.072	14,215.66	3.679	41,541.87	10.751	2.97
North Basin	17,045.21	1.035			17,045.21	1.035	2.03
Totals	66,326.50	14.845	20,547.32	5.619	86,909.82	20.464	

Table 3. Changes in the production /P/ of Hexagenia spp. in Lake Winnipeg 1932 vs. 1969.

	$\#/m^2$ /June and Early July only/	Differs by X	Mean Annual Standing Crop gm/m^2	P $gm/m^2/yr$	P for Basin tonnes/yr
South Basin					
H. limbata					
1932	62.00	1.50	3.273	10.110	32,996.41
1969	40.45		2.182	6.738	21,991.08
H. rigida					
1932	4.50	.95	.583	1.843	6,015.07
1969	4.76		.615	1.941	6,334.92
Narrows					
H. limbata					
1932	93.70	1.12	2.800	7.918	30,595.15
1969	83.60		2.500	7.070	27,318.48
H. rigida					
1932	44.00	3.30	3.858	12.140	46,908.96
1969	13.28		1.169	3.679	14,215.66
North Basin					
H. limbata					
1932	10.10	.28	.143	.290	4,775.95
1969	36.37		.509	1.035	17,045.21

Total P. Hexagenia spp.

	1932	1969	% Δ
South	39,011.48	28,332.74	- 27 %
Narrows	77,504.11	41,534.14	- 46 %
North	4,775.95	17,045.21	+257 %
Total	121,291.54	86,902.09	- 28 %

Hexagenia spp. standing crop had occurred, especially in the South Basin, between the present survey and that of Neave (1932). To investigate how these changes in standing crop would be reflected in change of the production of mayflies in the Lake we assumed that the turnover ratio (P/B) had not changed from 1932 to 1969 and calculated production figures from Neave's (1932) standing crop data (note that Neave's figures were from June to July samples only, thus only our June and July standing crops were used). The results (Table 3) show an overall reduction of 28% in the production of profundal mayflies in the Lake (= 34,389 tonnes/yr). The only basin of the Lake to show an increase was the North Basin where conditions, at least in terms of water transparency and perhaps in chemical load, have improved since 1932. However, Neave (1932) did not sample the N.W. corner of the North Basin while the present study found quite large populations of mayflies there. Thus Neave's biomass figures for the North Basin may well have been underestimated. Similarly in the Narrows we sampled a large area, which was not sampled by Neave, and found few mayflies. Thus, in this case, Neave's standing crop figures may have been overestimated. There seems little doubt, however, that the reductions in production of *H. limbata*, in the South Basin, are real.

DISCUSSION

The mean annual production of *Hexagenia* spp. in Lake Winnipeg varied from 1.035 in the North Basin to 10.706 $g/m^2/yr$, in the Narrows. Hudson and Swanson (1972) recorded figures of 10.4 to 16.7 $g/m^2/yr$, in Lewis and Clarke reservoir, in several different years. Horst and Marzolf (1975) recorded mean annual production ranging from 2.75 to 6.49 $g/m^2/yr$, over several years, in a Kansas reservoir. Thus production was lower than what might be expected, in the North Basin, and near or above what might be expected, in the Narrows. (Note that, as a well established lake, Lake Winnipeg is likely to have a more consistent annual production, than reservoirs). The low production in the North Basin is undoubtedly related to its lower mean annual temperature (Flannagan 1979) and its subsequent effect on the rate of growth of *Hexagenia* spp.

Similarly the lower P/B ratio in the North Basin (2.03, Table 2) is related to the life cycle length (2yr). Mann (1967) suggested that animals with a two year life cycle should have a ratio of about 2, while those completing a life cycle in 1 yr should have a ratio of about 5. Hudson and Swanson (1972) calculated a turnover ratio of 2.7, and Horst and Marzolf (1975) calculated ratios of 3.48 - 5.38 both with populations of *Hexagenia* sp. with life cycles between 1 and 2 yrs, as in the Narrows and South Basin of Lake Winnipeg. Lake Winnipeg production and turnover rates are therefore in the expected range and the huge total production of mayflies is a direct result of the very large area and low mean depth of the Lake.

Using the results calculated from the 1969 survey and, as earlier mentioned, assuming that there was little or no change in turnover ratio from Neave's (1932) time to the present survey, a comparison of production figures for 1927 - 1930 and 1969 showed an overall reduction of 28%, or almost 35,000 tonnes, in the production of Hexagenia spp. in the Lake (Table 3) All of this reduction occurred in the South Basin and Narrows and is consistent with changes in the other fauna of the Lake (Flannagan 1979, Flannagan and Cobb 1981, Flannagan in press), suggesting a decline or at least a change, spreading from South Basin northward (ie. the direction of flow in the Lake), in the suitability of environmental conditions. In the period between Neaves (1932) sampling and ours there have been major changes in water level (Flannagan 1979), turbidity (Table 1), increased nutrient supply (Brunskill, 1973), metal and pesticide load (Flannagan and Cobb 1981). Since all of these stressors have occurred over the same time period, it is not possible to identity a single cause. Any one or any combination of these factors could well result in a decline of benthic animal populations.

CONCLUSIONS

Lake Winnipeg produced 187,000 tones of Hexagenia mayflies in 1969. Of this approximately half was produced in the Narrows which represents only 20% of the area of the Lake. Significant decline in mayfly production appears to have occurred in the last 40 years in the southern 2/3rds of the Lake, and a significant increase may have occurred in the North Basin. An overall decline of 28% in the production of Hexagenia mayflies was calculated for the whole lake. The change in mayfly production is consistent with other changes in the fauna of the Lake, but no single cause for these changes can be identified because a number of major physical and chemical changes have proceeded simultaneously.

REFERENCES

Bajkov, A. 1930. Biological conditions in Manitoba Lakes. Contr. Can. Biol. Fish., 5: 383 - 422.

Brunskill, G.J. 1973. Rates of supply of nitrogen and phosphorus to Lake Winnipeg, Manitoba, Canada.

Brunskill, G.J., Campbell, P. and Elliot, S.E.M. 1979a. Temperature, oxygen conductance and dissolved major elements in Lake Winnipeg. Fish. Mar. Serv. Canada MS Rep., 1526: v + 127 p.

Brunskill, G.J., Elliot, S.E.M. and Campbell, P. 1980. Morphometry, hydrology and watershed data pertinent to the limnology of Lake Winnipeg. Fish. Aquat. Sci. Canada Ms. Rep., 1556: v + 32 p.

Brunskill, G.J., Schindler, D.W., Elliot, S.E.M. and Campbell, P. 1979. The attenuation of light in Lake Winnipeg waters. Fish. Mar. Serv. Canada MS Rep., 1522: v + 79 p.

Flannagan, J.F. 1979. The burrowing mayflies of Lake Winnipeg, Manitoba. p. 103 - 114. In: Proc. 2nd Int. Conf. on Ephemeroptera. Ed. K. Pasternak and R. Sowa. Krakow, Poland. 312 pp.

Flannagan, J.F. Growth in Pontoporeia sp. (Amphipoda) with emphasis on hot and cold effects. In: Crustacean Growth Vol. 2. Ed. A.H. Wenner. Balkema press, The Netherlands. In press.

Flannagan, J.F. and Cobb, D.G. 1981. Changes in the profundal Trichoptera of Lake Winnipeg 1928 - 1932 to 1969. p. 67 - 674. In: Proc. 3rd Int. Symp. on Trichoptera. Ed. G.P. Moretti Ser. Entomol. Vol. 20. Dr. W. Junk Publ., The Hague.

Horst, T.J. and Marzolf, G.R. 1975. Production ecology of burrowing mayflies in a Kansas reservoir. Verh. Interna. Verein. Limnol., 19: 3029 - 3038.

Hudson, P.L. and Swanson, G.A. 1972. Production and standing crop of Hexagenia (Ephemeroptera) in a large reservoir. Stud. Nat. Sci. (Portales N.M.) 1(4): 1 - 42.

Mann, K.H. 1967. The cropping of the food supply. p. 243 - 257. In: The biological basis of freshwater fish production. Ed. S.D. Gerking. Blackwell Sci. Pub., Oxford.

Neave, F. 1932. A study of the mayflies (Hexagenia) of Lake Winnipeg. Contrib. Can. Biol. and Fish., 7: 177 - 201.

Neave, F. 1933. Ecology of two species of Trichoptera in Lake Winnipeg. Int. Rev. ges. Hydrobiol. Hydrograph., 29: 17 - 28.

Neave, F. 1934. A contribution to the aquatic fauna of Lake Winnipeg. Int. Rev. ges. Hydrobiol. Hydrograph., 31: 157 - 170.

Riblik, L. and Momot, W.T. 1982. Production ecology of Hexagenia limbata in Savanne Lake, Ontario. Can. J. Zool., 60: 2317 - 2323.

Ulomskii, S.N. 1951. The role of crustaceans in the general biomass of lake plankton. Trans. Problematic Topical discuss. Zin., 1: 121 - 130.

Winberg, G.G., Patalas, K., Weight, J.C., Hilbricht-Ilkowska, A., Cooper, W.E. and Mann K.H. 1971. Methods for calculating Productivity. p. 296 - 354. In: Edmondson, W.T. and Winberg, G.G. eds. A manual on methods for the assessment of Secondary Productivity in Fresh Waters. IBP Handbook No. 17., Blackwell Sci. Publ., Oxford.