ASPECTS OF THE BIOLOGY OF *Pontoporeia hoyi* Smith IN LAKE WINNIPEG AND A COMPARISON OF *Hexagenia limbata* (Serville) AND *P. hoyi* PRODUCTION

by

JOHN F. FLANNAGAN

A Thesis
Submitted to
the Faculty of Graduate Studies
University of Manitoba

In Partial Fulfillment
of the Requirements for the Degree of
Master of Science

Department of Zoology

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ABSTRACT

During the open water season of 1969, three Birge-Ekman or Ponar grab samples were taken six times at up to fifty-five stations in Lake Winnipeg. Eighteen thousand one hundred and nine specimens of Pontoporeia hoyi Smith and one thousand and forty of Hexagenia limbata (Serville) were identified from these samples.

P. hoyi was collected in the greatest densities in the Narrows, was common in the North Basin and has almost disappeared from the South Basin. Multi-linear regression analyses of the density distribution of P. hoyi indicated significant negative correlations with depth, temperature and water transparency and a significant positive correlation with percent. sand on a whole lake basis. These four factors together explained 69.5% of the variation in the density data. A second analysis, including only data from the two basins, North and Narrows, where sustaining populations of P. hoyi were considered to exist, showed that a negative correlation with depth and a positive correlation with percent. sand could explain 55.3% of P.hoyi density variation in these two areas.

Unlike populations in other shallow, warm, unstratified water bodies, the Lake Winnipeg population had a 2+ yr life cycle. P. hoyi were found to grow only in fall, winter and spring in the North Basin and only in spring and fall in the Narrows. It is suggested that this cessation of growth in both basins in the summer, and in the Narrows in the winter, prevents this population from reaching maturity in one year. Regression analyses of 1+ yr and 2+ yr life cycle populations of Pontoporeia spp. from various localities in the Northern Hemisphere, indicated that a good correlation exists between their turnover ratio and the latitude of the water body where they were found.

Annual whole lake production, using the instantaneous growth method, was estimated at 67,015 tonnes of *P. hoyi* and 66,972 tonnes of *H. limbata*. These two species, which utilise similar food resources and which between them represent over 36%, by number, of the macrobenthos of the lake apparently coexist by dividing the resources of the lake temporally and physically: *P. hoyi* producing most of its biomass in the colder parts of the year in the North Basin and most of the Narrows; *H. limbata* growing only in summer and distributed throughout the South Basin, in the shallower parts of the Narrows, and in a very restricted area of the North Basin.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

INTRODUCTION

The bottom fauna of Lake Winnipeg has been investigated sporadically over the past 50 years. Bajkov (1930a, b) studied the organism/substrate relationships of the benthos of the Lake over the period 1927, '28 and '29 and showed that the dominant benthic animals on the "mud- bottom" areas of the Lake (≃ 85% of the Lake) were _Pontoporeia hoyi_ Smith and _Hexagenia limbata_ (Serville), accounting for 63% and 10% by numbers respectively, of the fauna. He specifically pointed out that animals were concentrated in some areas and reduced in number or absent in adjacent areas with apparently identical environmental conditions. Of particular interest to the present work was the frequent occurrence of _P. hoyi_ in the South Basin in 1927-29.

Neave (1932) studied tbe distribution and biology of the profundal mayflies (_Hexagenia limbata_ and _H. rigida_ McDunnough) of the Lake, and Flannagan (1979) showed that a significant decline in populations of _Hexagenia_ spp. in the South Basin, and a shift in the relative abundance of _H. limbata_ and _H. rigida_ in the whole Lake, occurred in the intervening period. In addition, Flannagan (1979) established that the _Hexagenia_ spp. had a two year life cycle in the North Basin, an alternating 22/14 month life cycle in the South Basin, and a mixture of these two life cycle types in the Narrows.

Similarly, Neave (1933) studied the distribution and biology of profundal Trichoptera in the Lake and Flannagan and Cobb (1981) showed that a third species, not found in Neave's samples, was apparently in the process of replacing the original two species.

In the period between the work of Neave (1932,'33,'34) and Bajkov (1930a, b) and the present survey, Manitoba government biologists studied the benthos of the Lake and noted changes in the fauna, especially in the South Basin (see Doan (1975) for listings of some of these unpublished reports). These changes indicated a general deterioration in the habitat of the South Basin, especially for the species considered by Bajkov (1930b) to be important as fish food items.

Though *P. hoyi* was considered to be of prime importance in the diet of the commercial fish of Lake Winnipeg (Bajkov 1930b), unlike the other important benthic species, no attempt has been made to study their life history, distribution or abundance in the Lake. This thesis will attempt to fill this gap by:

1. Investigating the life history, distribution and abundance of *P. hoyi* in the Lake and reviewing the published information on these subjects.

2. Will provide, and compare, production estimates for *P. hoyi* and *H. limbata*, the two most important benthic fish food sources in the Lake.

3. Will compare the production estimates obtained for *P. hoyi* with published production estimates for the genus.

Previous attempts to correlate distribution of *Pontoporeia* with environmental variables have not often been very successful (Marzolf 1963, Dermott 1978). The obvious concentration of animals along the north and east shores of the Lake (i.e. largely, but not entirely, the areas of Precambrian shield shoreline) suggested that a correlation with environmental parameters exists.

Thus the fourth objective of this thesis is to attempt to correlate the distribution of P. hoyi in the Lake with the environmental variables measured by other participants in the survey.

THE LAKE

Lake Winnipeg, maximum length 436 km, maximum breadth 111 km, area 23,750 km^2, is the 13th largest lake in the world and the 7th largest in North America (Hutchinson 1957). The Lake has a maximum depth of 36 m and mean depth of 12 m (Brunskill et al. 1980). The small mean depth combined with the large surface area allows almost continuous wind mixing of the water column and the surface sediments. This, together with the high sediment load from some of the rivers, results in high turbidity (Secchi disc: 0.5-3 m in the North Basin, 0.1-1.0 m in the South Basin), near saturated dissolved oxygen tensions at all depths, and little or no temperature or chemical stratification throughout the Lake (Brunskill et al. 1980). Local horizontal gradients of physical and/or chemical parameters may occur, however, as the result of lake morphometry and orientation of major rivers inflows (Brunskill et al. 1980).

The Lake, which is a relict of a glacial Lake Agassiz, is situated between latitudes 50° 24' N and 53° 22' N on the boundary of the igneous rock, and generally acid soils, of the Precambrian Shield and the sedimentary rock and overlying glacial Lake Agassiz sediments of the Manitoba Prairie. Thus rivers entering the Lake from the east tend to have low concentrations of inorganic salts, though they may be relatively high in dissolved and suspended humic materials, while rivers entering from the south, west and north are high in both suspended and dissolved solids (Brunskill, Schindler et al. 1979). Brunskill et al. (1980) estimated that 9,030 tonnes of phosphorus and 100,540 tonnes of nitrogen were added to the Lake in 1969 from all sources, and that by the year 2,000 A.D.

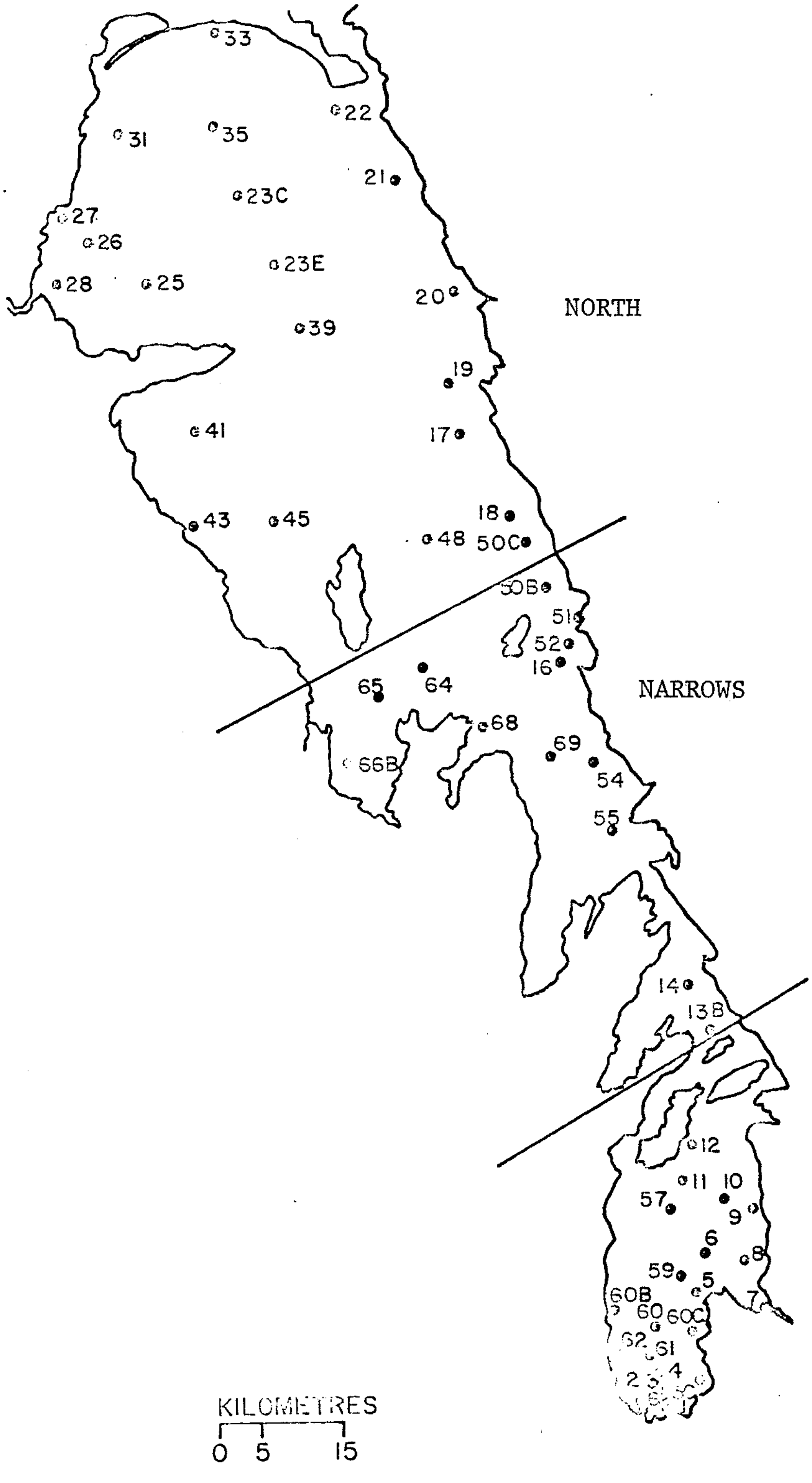

Figure 1. Lake Winnipeg showing the three basins and the benthos sampling stations.

the input of phosphorus and nitrogen would increase 628% and 317%, respectively. Primary production, at least in the South Basin, appears to be limited by turbidity rather than nutrients (Brunskill 1973, Brunskill, Schindler *et al*. 1979). Exceptions may occur in the inlets and bays off the mouths of the soft water streams and, on calm days extensive blooms of *Aphanizomenon flos-aquae* Raffs and *Anabaena* spp. have been recorded in the upper 0.5-1.0 m of the open water column (Bajkov 1934; Brunskill, Schindler *et al*. 1979).

The Lake, though apparently always turbid, has been changed considerably since the drainage basin was first farmed by the "Selkirk settlers" in 1820. The several hydro-electric dams on the Saskatchewan River, both in Saskatchewan and Manitoba, have drastically reduced the load of silt and nutrients carried by this, the largest inflow to the North Basin, resulting in an apparent increase in transparency in the North Basin from Bajkov's (1930a) time. In contrast, the South Basin appears to have suffered an increase in turbidity over the same period (Brunskill *et al*. 1980, Flannagan and Cobb in press).

Similarly, mercury, pesticides and industrial and domestic sewage effluents have all likely increased significantly since the last major survey of the Lake (Brunskill *et al*. 1980).

The above changes in Lake Winnipeg, the long interval since the Neave (1932, 1933, 1934) and Bajkov (1930a) survey of the Lake and the importance of the commercial fish catch from the Lake (over 10% of the total commercial freshwater fish in Canada ≃ 5,000 tonnes/yr (D.M. Cauvin, personal communication)) prompted a limnological survey by staff of the Freshwater Institute.

Detailed physical and chemical results of this survey are presented in Brunskill (1972), Brunskill _et_ _al_. (1979), Brunskill and Graham (1979), Brunskill, Schindler _et_ _al_. (1979) and Brunskill _et_ _al_. (1980).

MATERIALS AND METHODS

During the open water season of 1969, three tall Birge-Ekman grab samples were taken, approximately monthly, at up to 55 stations (Fig. 1, see Brunskill et al. 1979 for exact locations of stations). In addition, benthic samples were taken at various stations from under the ice during the winter of 1969/70. Since none of these grabs contained specimens of P. hoyi they are not further mentioned here. In areas where the substrate was too hard, a Ponar grab (Powers and Robertson 1967) was used. Flannagan (1970) showed that the tall Birge-Ekman grab was the most efficient grab, in soft mud, of twelve samplers tested, and that the Ponar grab was the best multipurpose grab. The Birge-Ekman and Ponar grabs sampled 225 and 528 cm^2, respectively, of the substrate. All summer samples were taken from the Canadian government ship 'Bradbury'. Since the Bradbury draws 1.8m, shallow areas of the Lake could not be sampled. In addition, the other duties of the crew of the ship, such as laying and retrieval of navigation aids, limited the amount of time available for benthic and other sampling, especially during the first and last cruises.

Samples were sieved, immediately, through a 0.2 mm nylon mesh screen, labelled, preserved in 10% formalin, and later all of the macrobenthos was sorted and counted using the low power of a dissecting microscope.

Eighteen thousand one hundred and nine P. hoyi and one thousand and forty H. limbata were identified from these samples. Their total body length was measured as the distance from the front of the head to the base of the telson, in the case of P. hoyi, and between the front of the frontal process and the base of the cerci of the H. limbata.

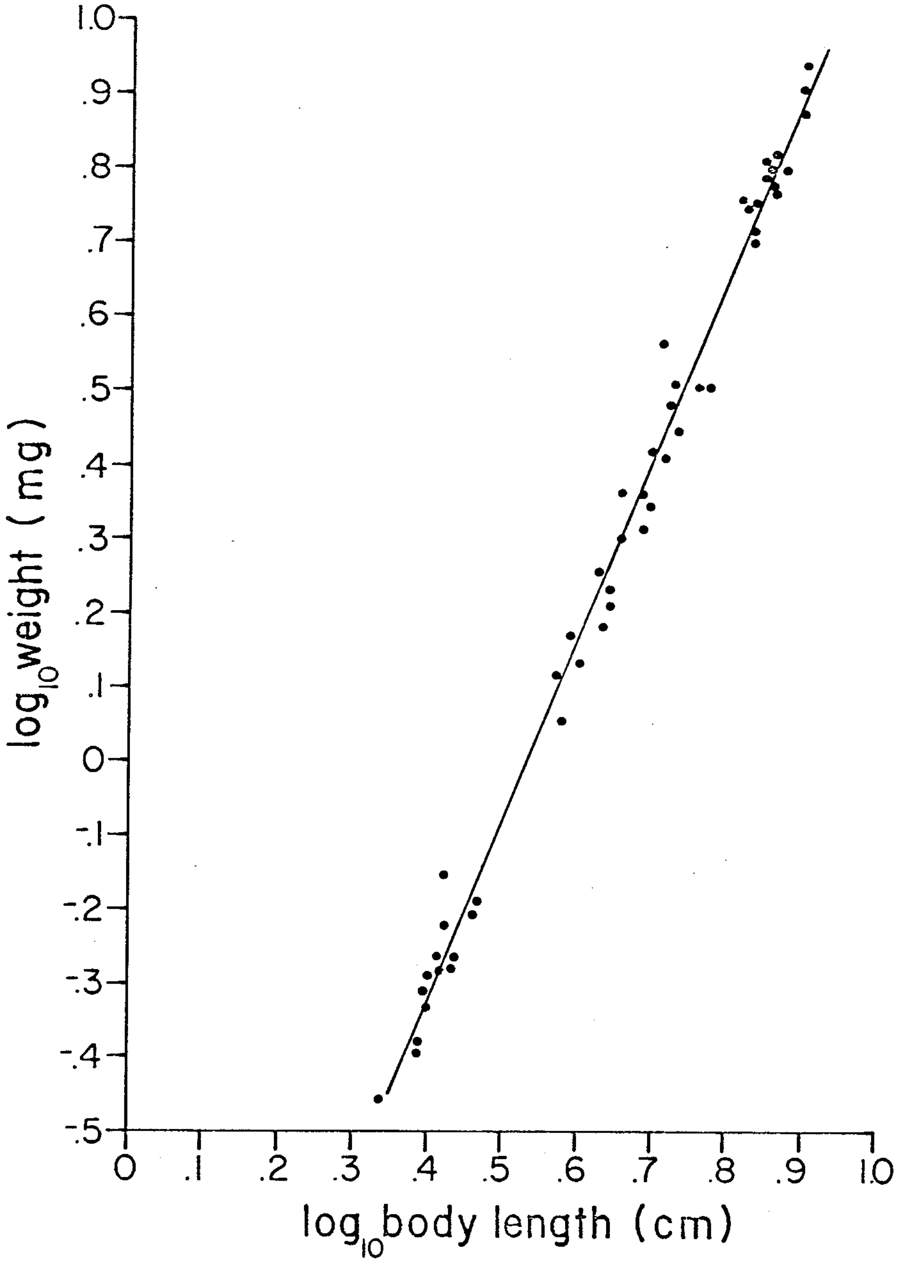

Figure 2. Relationship between length and weight (wet) of P. hoyi in Lake Winnipeg (N = 50).

Fifty well preserved specimens of each species, including representatives from all three basins, from both sexes, and from different times during the summer, were surface dried with filter paper and weighed to the nearest 0.01 mg. Ulomskii (1951) showed that length/weight relationships derived using this method were valid. The length/weight relationships were (Figs. 2, 3): -

a) P. hoyi

$$\log_{10} \text{wet weight (mg)} = 2.3560 \log_{10} \text{length} - 1.2360 \quad (r=0.996)$$

b) H. limbata

$$\log_{10} \text{wet weight (mg)} = 2.815 \log_{10} \text{length} - 1.8335 \quad (r-0.994)$$

Biomass, production estimates and turnover ratios were then calculated using weights derived from these regressions in the instantaneous growth method outlined by Chapman (1968). This method uses the formula: -

$$P = G \overline{B}$$

Where P = production, G = instantaneous growth rate and $\overline{B}$ = mean biomass in mg/m^2.

The instantaneous growth rate, G_W(=G), was calculated between sampling intervals, as the natural log of the mean weight at the end of the period ($\overline{w}_t$) minus the natural log of the mean weight at the start of the period ($\overline{w}_o$) divided by the number of days in the period (Δ_t) i.e.

$$G_W = \frac{\ln \overline{w}_t - \ln \overline{w}_o}{\Delta_t}$$

The production/day for each period was then calculated and summed over

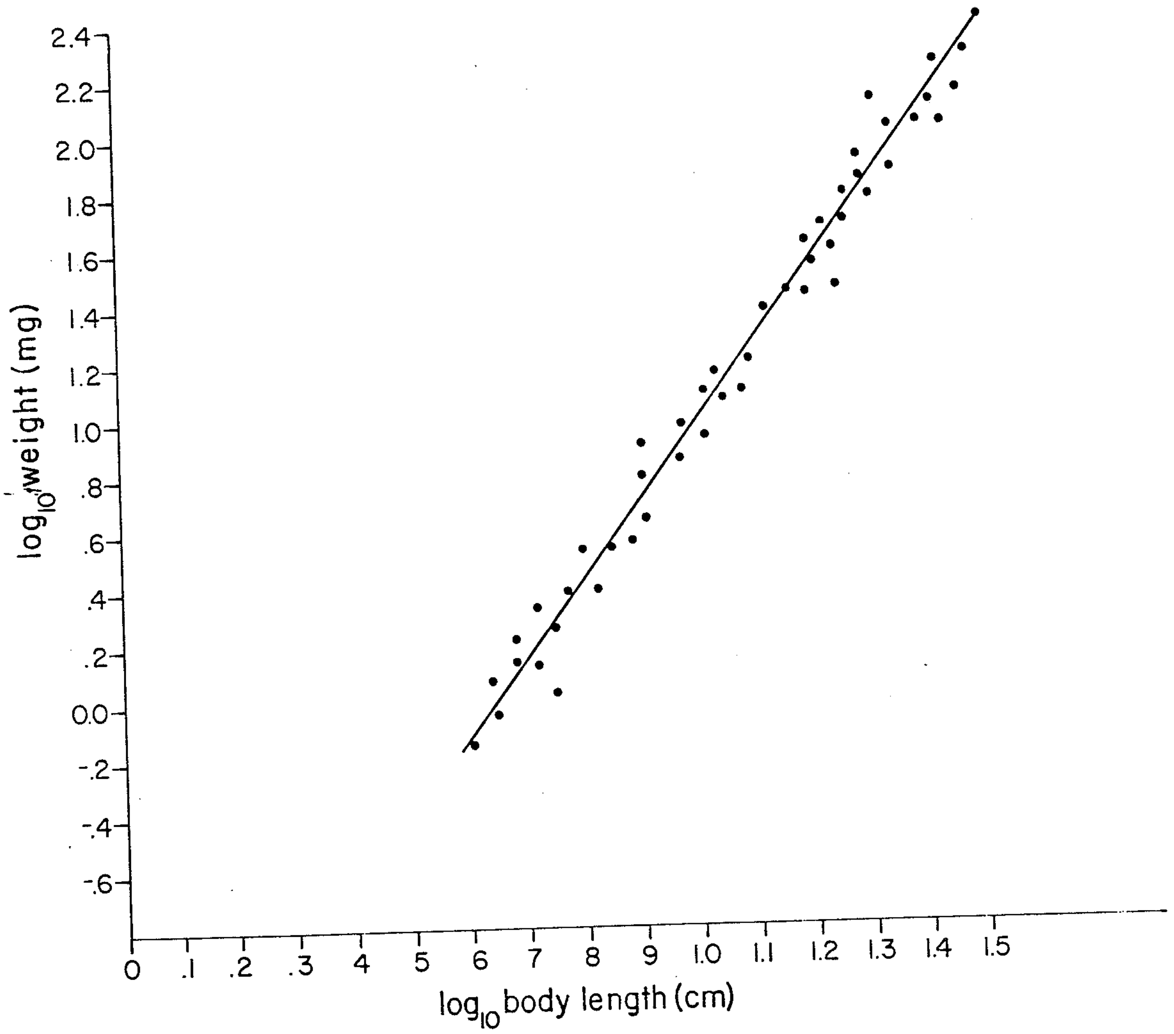

Figure 3. Relationship between length and weight (wet) of *H. limbata* in Lake Winnipeg (N = 50).

the duration of the animals' life cycles to give an estimate of total life cycle production.

Both of these animals have life cycles extending over more than one year and since the size classes were distinct, it was possible to follow them through the whole life cycle although only one season's samples were available. This assumes that the year classes found during this survey are representative of the growth of any one generation in the lake. In addition, G_w for P. hoyi was plotted over its life-cycle in each basin as a comparison of relative rates of growth throughout the year, and between basins. Turnover ratios were calculated for each basin to provide a basis for comparing the productivity of P. hoyi both within the basins of the Lake and with estimates from elsewhere.

In all of the production estimates in both species, mean numbers were calculated on a whole basin basis by using results from all samples whether or not they contained the animals under study. This allowed direct conversion to basin production.

Since the horizontal distribution of P. hoyi in the Lake appeared to be related to environmental factor(s), and with their published background of temperature and depth sensitivity, attempts were made, using a Hewlett-Packard multi-linear regression pack #9830, to relate the density distribution of P. hoyi to the temperature, depth, conductivity, transparency and substrate data collected during this survey by Brunskill and Graham (1979), Brunskill et al. (1979) and Brunskill, Schindler et al. (1979). Preliminary analyses of the P. hoyi samples indicated that variances were often larger than means, suggesting a clumped distribution (Elliott 1973). The raw data were therefore transformed to mean

($\log_n$ number/m^2+1) which according to Elliott (1973) makes the variances homogeneous and thus gives 'truer' values of statistical significance. Similarly an arcsin transformation was used on the substrate data to minimise the intercorrelations due to proportions (Snedecor and Cochran 1967). The data used in these analyses are listed in Appendix III. Substrate data were available from only 32 stations, thus the analyses were limited to these stations. On the first analyses, i.e. the whole Lake analyses, maximum water temperature was found to be the most important single factor influencing the density of P. hoyi. Since it was felt that this was largely due to the lack of P. hoyi in the large, turbid, shallow, warm South Basin, the analysis was rerun with the South Basin data excluded. Unfortunately, environmental data were not available for enough stations for individual analyses of the population of each basin

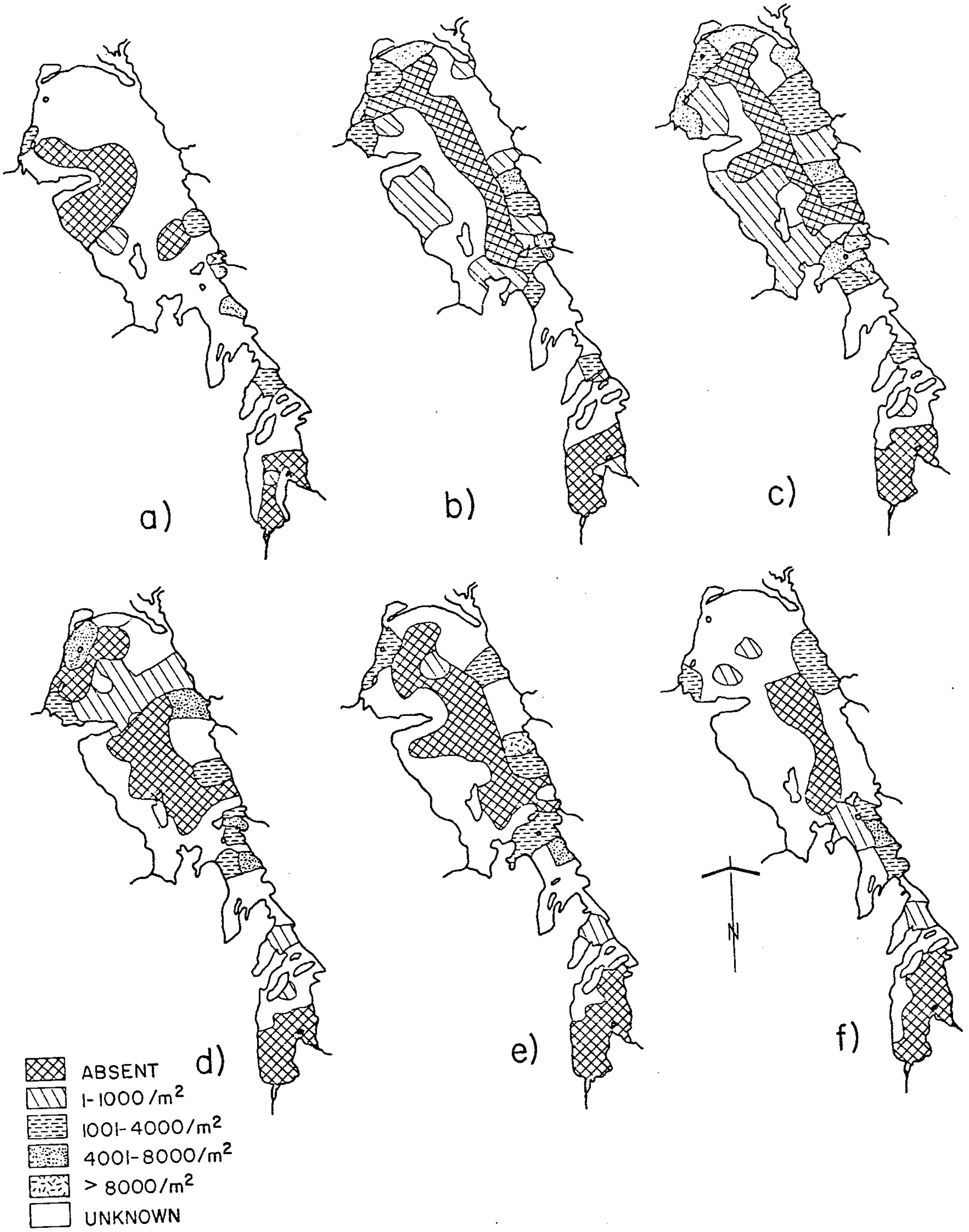

Figure 4. Density distribution of *P. hoyi* in Lake Winnipeg in a) June; b) early July; c) late July/August; d) September; e) early October; f) late October.

RESULTS

1. Biology of *P. hoyi*

Considerable variation in *P. hoyi* densities, both between stations and between times at any given station, was evident (Fig. 4, see also Appendix II). Maximum densities of *P. hoyi* recorded during the present survey were: The North Basin 8,547/m^2, The Narrows 11,243/m^2 and The South Basin 489/m^2. On average, they represented 36% by number of the macrobenthic fauna of the whole Lake, 39% in the North Basin, 70% in the Narrows and 1% in the South Basin. They are, at least in numbers, the dominant benthic macroinvertebrate species in the Lake. In the Narrows and North Basins the *P. hoyi* depth distribution patterns were slightly different from each other. In the Narrows Basin they were collected in depths ranging from 3-14 metres while in the North Basin they ranged over slightly deeper water, 6-17 metres. In both of these Basins, their maximum densities occurred at 12 metres (Appendix II).

Body length measurements (Fig. 5) show three fairly distinct year classes: Year Class I, consisting of juveniles and as might be expected, the year class with the highest numerical abundance; Year Class II consisting of immature males and females, the females showing small brood plate buds in September and October, i.e. in the antepenultimate stage (Bousfield, personal communication). No mature males or females were found in this year class; Year Class III, consisting exclusively of large, spent, senescent females, and though not always distinct in Fig. 5, were easily separable in the samples because of their translucent appearance and lack of oil globules.

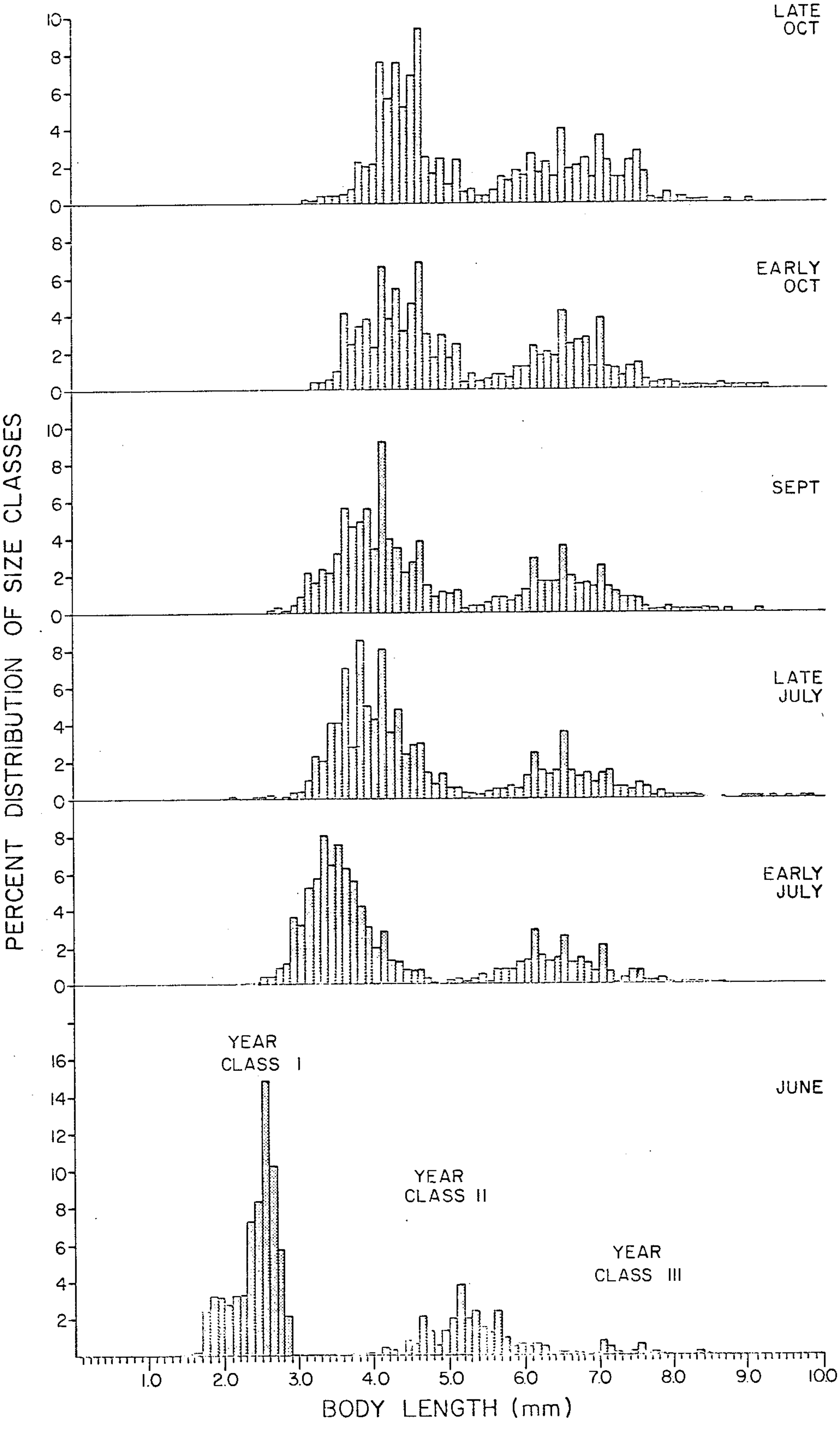

Figure 5. Percent distribution of size classes (1 mm intervals) of P. hoyi in the whole lake at each of the six sampling times.

Table 1. *t* values for differences between mean lengths of each year class of *P. hoyi* in the Narrows and North basin at each sampling time.

	YEAR CLASS I	II	III
June	13.78** (927)[1]	10.46** (417)	7.68** (10)
E. July	22.76** (2868)	19.71** (1129)	3.33** (18)
L. July	86.54** (4517)	8.73** (1224)	3.61** (12)
Sept.	12.27** (1936)	6.25** (881)	6.23* (2)
E. Oct.	6.0** (1460)	5.88** (910)	4.16** (5)
L. Oct.	5.90** (624)	5.92** (516)	-

[1] degrees of freedom

* difference significant at $P<0.05$

** at $P<0.01$

The relative frequencies of abundance of the three year classes in the North and Narrows basins as a mean of all samples together were: -

	Year Class I	Year Class II	Year Class III
North Basin	163	65	1
Narrows	99	49	1

From this table, on average, about 50% survival occurred into the second year and less than 1% survived into year Class III. Assuming, as before, that the year classes found were representative of any one generation, survival appears to be better in the warmer Narrows Basin since percentage survival is higher in year Class II and III.

Plots of the mean body size for each sampling time for each year class (Fig. 6) indicate slightly different growth patterns in each basin, though each year class achieved similar sizes by the end of "each" summer. The discrepancy growth apparently occurred as a result of the North Basin population achieving a large part of their growth during the winter (Fig. 7), while the Narrows population achieved all of its growth during spring and fall. Statistical analyses were not carried out on these curves because release of the young and the start and finish of each year class growth curve occurred under the ice in the period not sampled. Further, the various curves were different shapes which tended to produce a poor fit to any one model. However, *t*-tests for differences between means (Table 1) carried between each pair of points (one from North Basin, one from Narrows) in Figure 6 indicated that the differences in growth between the North Basin and Narrows populations were real. The *t* values are smaller in the late summer and fall pairs, suggesting that the size differences were decreasing.

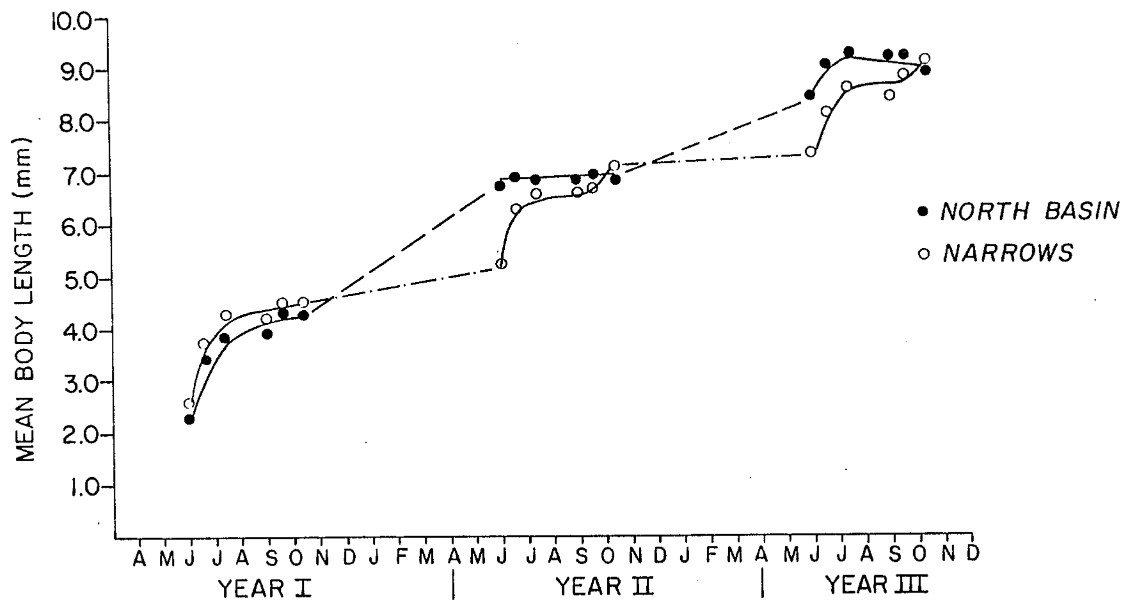

Figure 6. Mean body length of P. hoyi throughout its life cycle in the North and Narrows Basins of Lake Winnipeg.

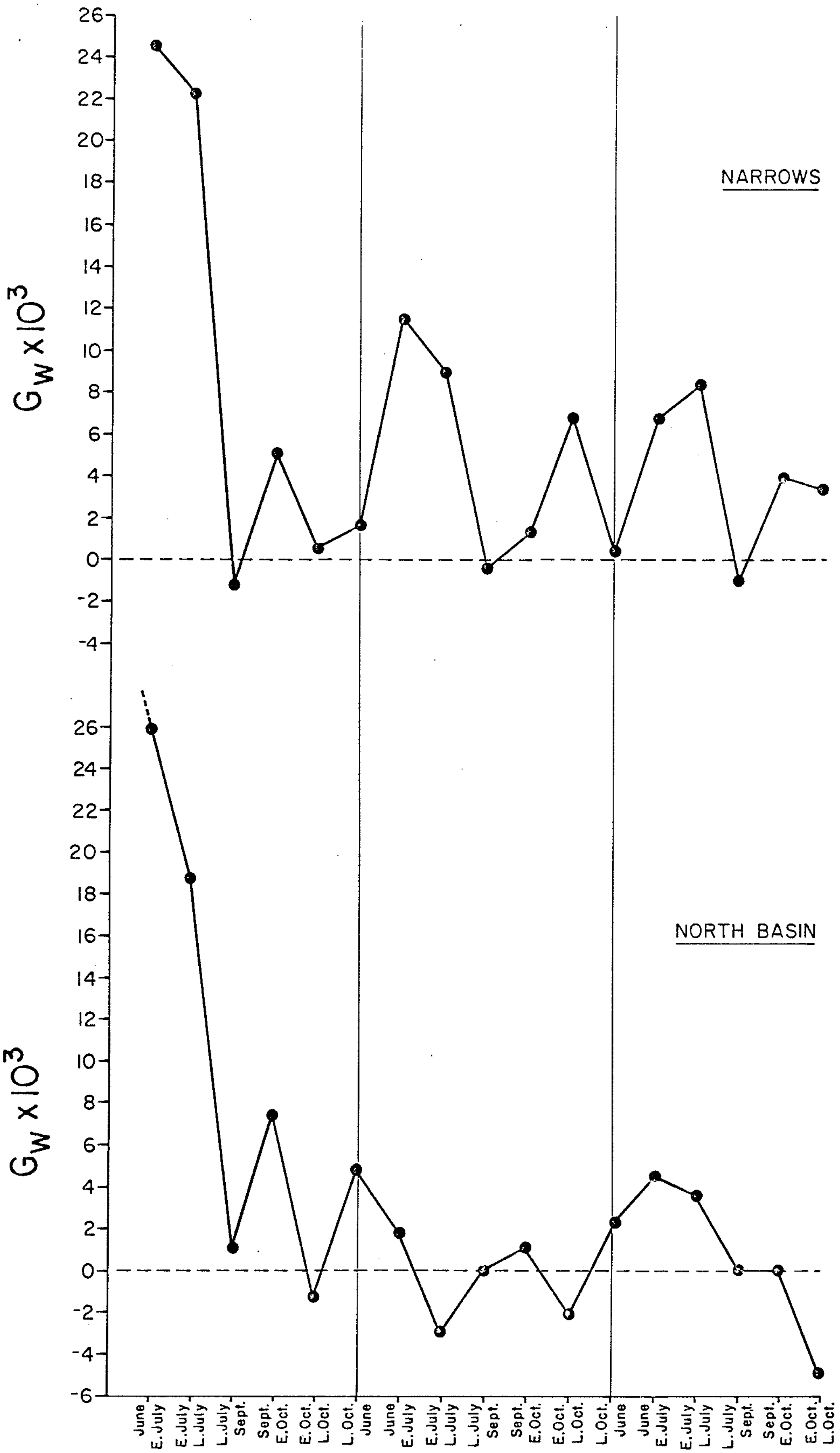

Figure 7. Instantaneous growth (G_W from Tables 3 and 4) throughout the life cycle of _P. hoyi_ in the Narrows and North Basins of Lake Winnipeg.

2. Production estimates

a) P. hoyi

Although three year classes, representing three different generations were present, the total annual production (assuming similar year class strength in each of the three years) is equal to the total life cycle production of any one generation.

Production calculations were not made for the South Basin of the Lake because it did not appear to have a permanent population (Fig. 4) The Narrows (7.37 $g/m^2/yr$, Table 2) was found to be much more productive than the North Basin (2.34 $g/m^2/yr$, Table 3).

Since all of the stations sampled, whether P. hoyi was present or not, were taken into account in the production calculations, it is possible to estimate the total production for each basin simply by multiplying the area of the basin by the production figures obtained: -

	Production ($g/m^2/yr$)	Area (Km^2)	Production (tonnes/yr, wet weight)
North Basin	2.34	16,468.8	38,537
Narrows	7.37	3,864	28,478
		Total	67,015

It is of interest to note that though the area of the North Basin is 4.3 x area of the Narrows, the North Basin total production is less than 1.4 times that of the Narrows.

A more detailed examination of the production of the three year classes (Tables 2, 3) show that in both basins Year class III contributed little, while year class I contributed considerably more than half the total production. Year class II, 17% of total in the North Basin, 40% in the Narrows, as was indicated earlier in the percent. survival

Table 2. Annual production (P) (wet weight) of *P. hoyi* in Narrows of Lake Winnipeg using the instantaneous growth method, P = G$\bar{B}$ (Chapman 1968).

Month	Mean Density (#/m^2)	Mean Individual Weight (mg)	Days in Period	Instantaneous growth rate (G_W)	Mean Biomass (mg/m^2)	Production for Day	Production for Period (mg/m^2)
<u>Year Class I</u>							
-	0						
			-	-	523.57	-	523.57a)
June	1914.33	.547					
			36	0.0245	1768.23	43.32	1559.58
Early July	1885.85	1.32					
			14	0.0222	3034.48	67.37	943.12
Late July	1988.68	1.80					
			41	-0.0013	3432.84	-4.46	-182.97
September	1921.67	1.71					
			32	0.0051	2534.43	12.93	413.62
Early October	886.97	2.01					
			21	0.00047	2146.12	1.009	21.18
Late October	1236.17	2.03					
			222	0.0016	3004.34	4.807	1067.14
June	1206.04	2.40					4345.24
<u>Year Class II</u>							
			36	0.0115	3945.38	45.37	1633.39
Early July	1000.34	4.39					
			14	0.0089	4716.08	41.97	587.62
Late July	1014.22	4.97					
			41	-0.00025	4606.64	-1.152	-47.22
September	848.09	4.92					
			32	0.0012	4066.32	4.880	156.15
Early October	774.96	5.11					
			21	0.0068	3520.78	23.94	502.77
Late October	522.29	5.90					
			222	0.00034	1627.57	0.553	122.85
June	27.30	6.36					2955.56

...continued

Table 2. (continued)

Month	Mean Density (#/m^2)	Mean Individual Weight (mg)	Days in Period	Instantaneous growth rate (G_W)	Mean Biomass (mg/m^2)	Production for Day	Production for Period mg/m^2
Year Class III							
			36	0.0067	200.64	1.34	48.39
Early July	28.14	8.09					
			14	0.0083	144.46	1.20	16.79
Late July	6.74	9.09					
			41	-0.0011	54.69	-0.060	-2.47
September	5.55	8.67					
			32	0.0039	37.04	0.144	4.622
Early October	2.64	9.83					
			21	0.0034	24.17	0.082	1.726
Late October	2.12	10.56					
							69.058
					$\overline{B}$ = 2188.21		ΣP = 7369.86

Mean Biomass = 2.19 g/m^2

Production = 7.37 g/m^2/yr

$P/\overline{B}$ = 3.37

a) estimate = 1/2 biomass on first appearance (see discussion)

Table 3. Annual production (P) (wet weight) of _P_. _hoyi_ in North basin of Lake Winnipeg using the instantaneous growth method, $P = G\overline{B}$ (Chapman 1968).

Month	Mean Density (#/m^2)	Mean Individual Weight (mg)	Days in Period	Instantaneous growth rate (G_W)	Mean Biomass (mg/m^2)	Production for Day	Production for Period mg/m^2 (mg/m^2)
Year Class I							
-	0	-					
			-	-	102.87	-	102.87$^{a)}$
June	487.53	.422					
			36	0.026	630.11	16.38	589.78
Early July	985.50	1.07					
			14	0.187	1498.65	28.02	392.35
Late July	1397.71	1.39					
			41	0.00120	1585.19	1.90	77.99
September	840.80	1.46					
			32	0.0074	1438.45	10.64	340.62
Early October	891.53	1.85					
			21	-0.0013	1013.54	-1.32	-27.67
Late October	209.86	1.80					
			222	0.0048	445.18	2.137	474.38
June	98.2	5.22					
							1950.32
Year Class II							
			36	0.0018	1077.04	1.94	69.79
Early July	297.7	5.57					
			14	-0.0031	2453.32	-7.61	-106.47
Late July	612.6	5.33					
			41	0.00009	2640.04	0.238	9.74
September	376.62	5.35					
			32	0.0011	2045.66	2.25	72.01
Early October	374.8	5.54					
			21	-0.0021	1850.45	-3.89	-81.60

...continued

Table 3. (continued)

Month	Mean Density (#/m^2)	Mean Individual Weight (mg)	Days in Period	Instantaneous growth rate (G_W)	Mean Biomass (mg/m^2)	Production for Day	Production for Period mg/m^2
Year Class II (continued)							
Late October	306.51	5.30					
			222	0.0023	838.03	1.927	427.80
June 5.9	5.9	8.74					
							391.27
Year Class III							
			36	0.0045	29.80	0.135	4.84
Early July	.8	10.28					
			14	0.0037	25.23	0.093	1.307
Late July	3.9	10.83					
			41	0	25.99	0	0
September	.9	10.83					
			32	0	29.78	0	0
Early October	4.6	10.83					
			21	-0.005	34.17	-0.17	-3.57
Late October	1.9	9.75					
							2.577
					$\overline{B}$ = 986.5		ΣP = 2344.17

Mean Biomass = .987 g/m^2
Production = 2.34 g/m^2/yr
$P/\overline{B}$ = 2.37

[a] see Table 1

calculation, was much weaker in the North Basin. Even if the production of year class II individuals in the North Basin was raised to the same proportion of the total as found in the Narrows, the North Basin would still be less than half as productive as the Narrows.

b) H. limbata

Flannagan (1979) described the distribution, growth and life history of the H. limbata collected during this survey. In the North Basin he found two cohorts, representing a 2 yr life cycle, with emergence occurring annually, in late summer, and eggs hatching the following spring. In the South Basin he found three cohorts in June, early July, September and late October and two cohorts in Late July and early October, indicating alternating 22/14 month life cycles with emergence in early and/or late summer, synchronous emergence of the two life cycles occurring every third year. Since H. limbata do not grow in winter at these latitudes, the offspring from the 14 month population, which had emerged in late summer, grew little in its first year and required all of the next summer plus part of a third summer (22 months) to complete their development. The offspring from this generation hatched in early summer and were able to complete their growth by late in their second summer (14 months). The population in the Narrows was comprised of all three life history types, emergence occurring more or less continuously throughout the summer.

The production estimates for the various life history types of H. limbata in the North, Narrows and South Basins of the Lake are given in Tables 4, 5 and 6, respectively. As was the case with P. hoyi, the Narrows was found to be the most productive area of the Lake, however,