

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

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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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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 (\approx 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 the 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 km², 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.

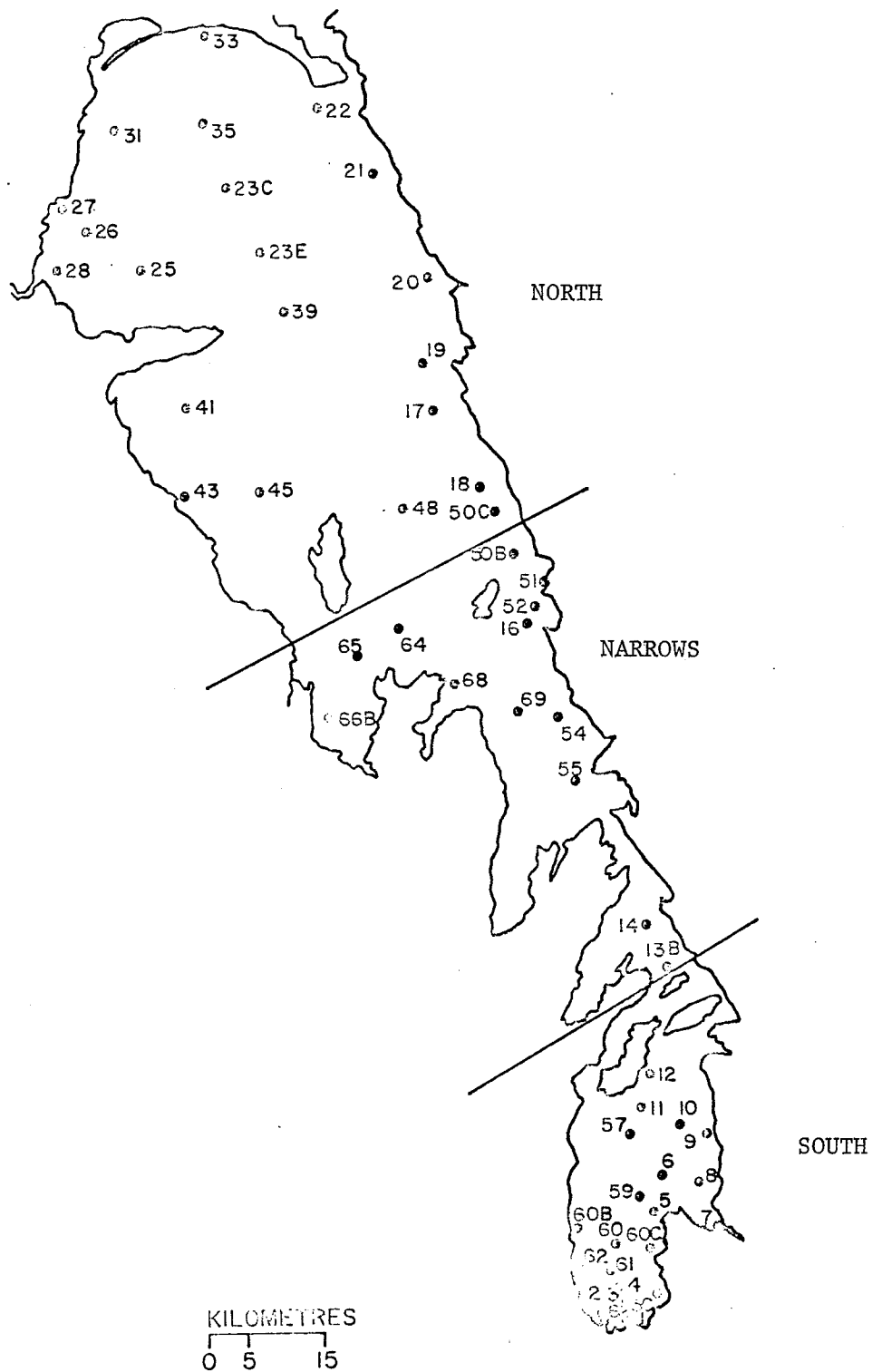


Figure 1. Lake Winnipeg showing the three basins and the benthos sampling stations.

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 Ruffs 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 \approx 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 cm², 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.

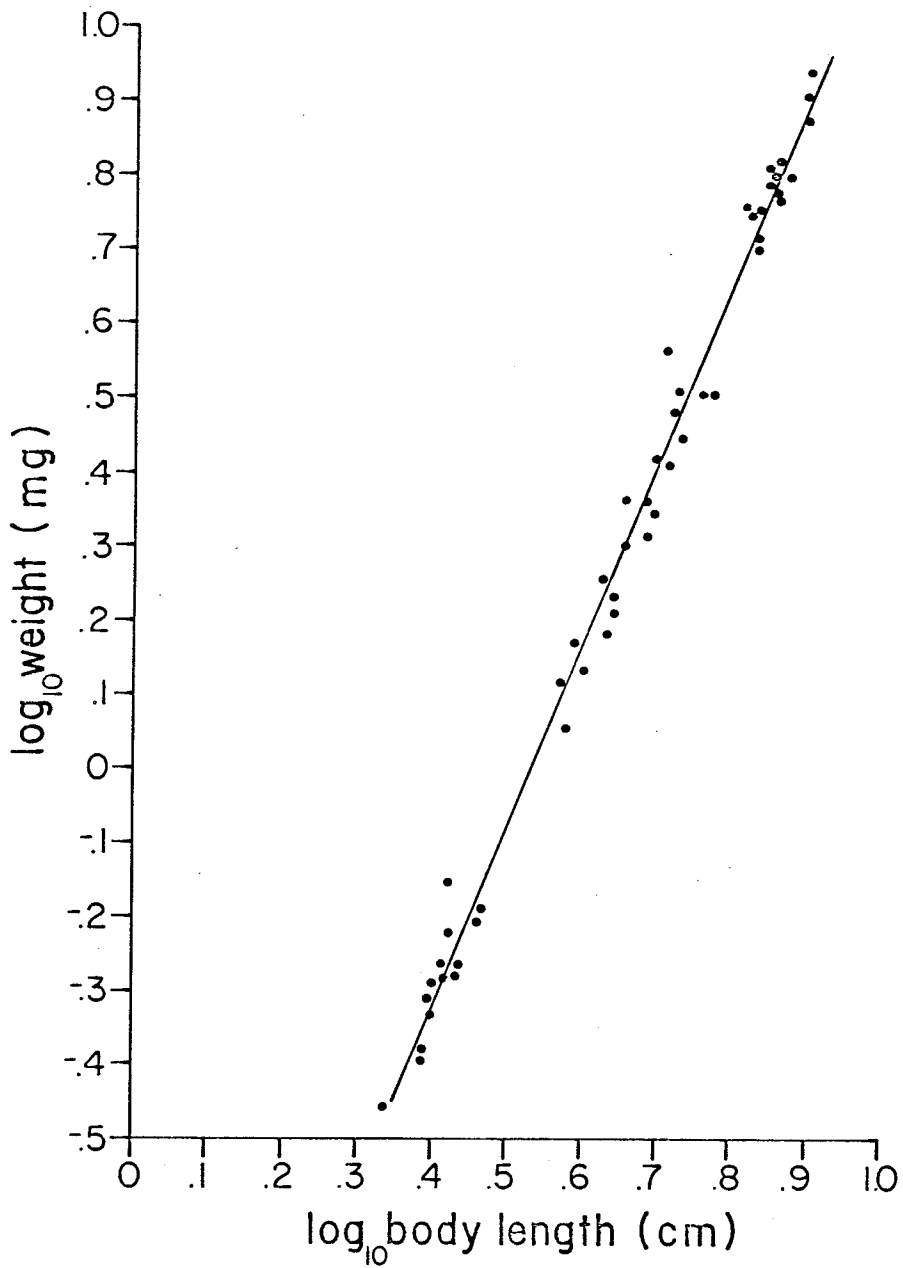


Figure 2. Relationship between length and weight (wet) of *P. hoyi* in Lake Winnipeg (N = 50).

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

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

(r=0.996)

b) H. limbata

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

(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: -

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

Where P = production, G = instantaneous growth rate
and \bar{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 (\bar{w}_t) minus the natural log of the mean weight at the start of the period (\bar{w}_0) divided by the number of days in the period (Δ_t) i.e.

$$G_w = \frac{\ln \bar{w}_t - \ln \bar{w}_0}{\Delta_t}$$

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

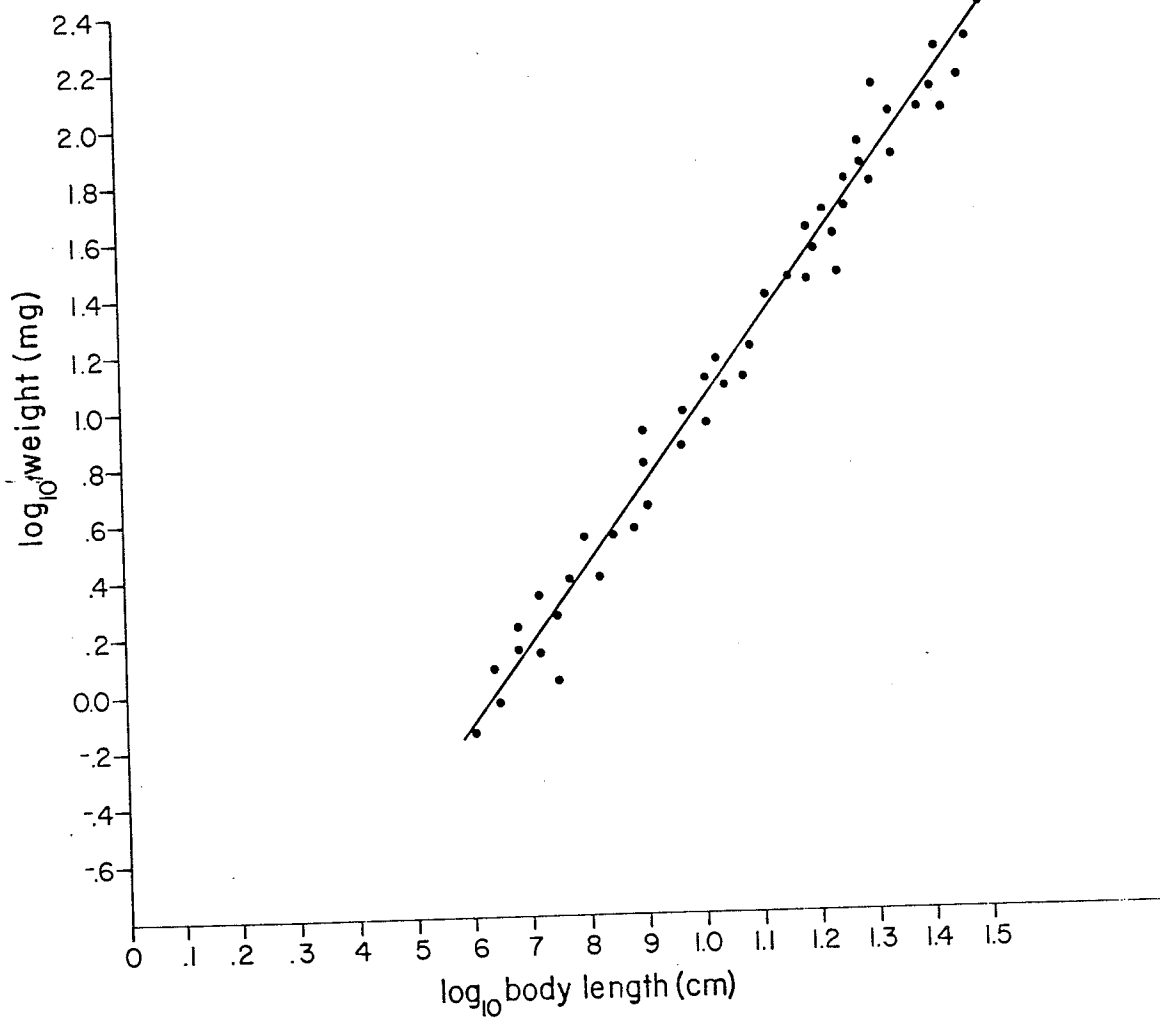


Figure 3. Relationship between length and weight (wet) of *H. limbata* in Lake Winnipeg (N = 50).

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

$(\log_n \text{ number}/m^2+1)$ 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

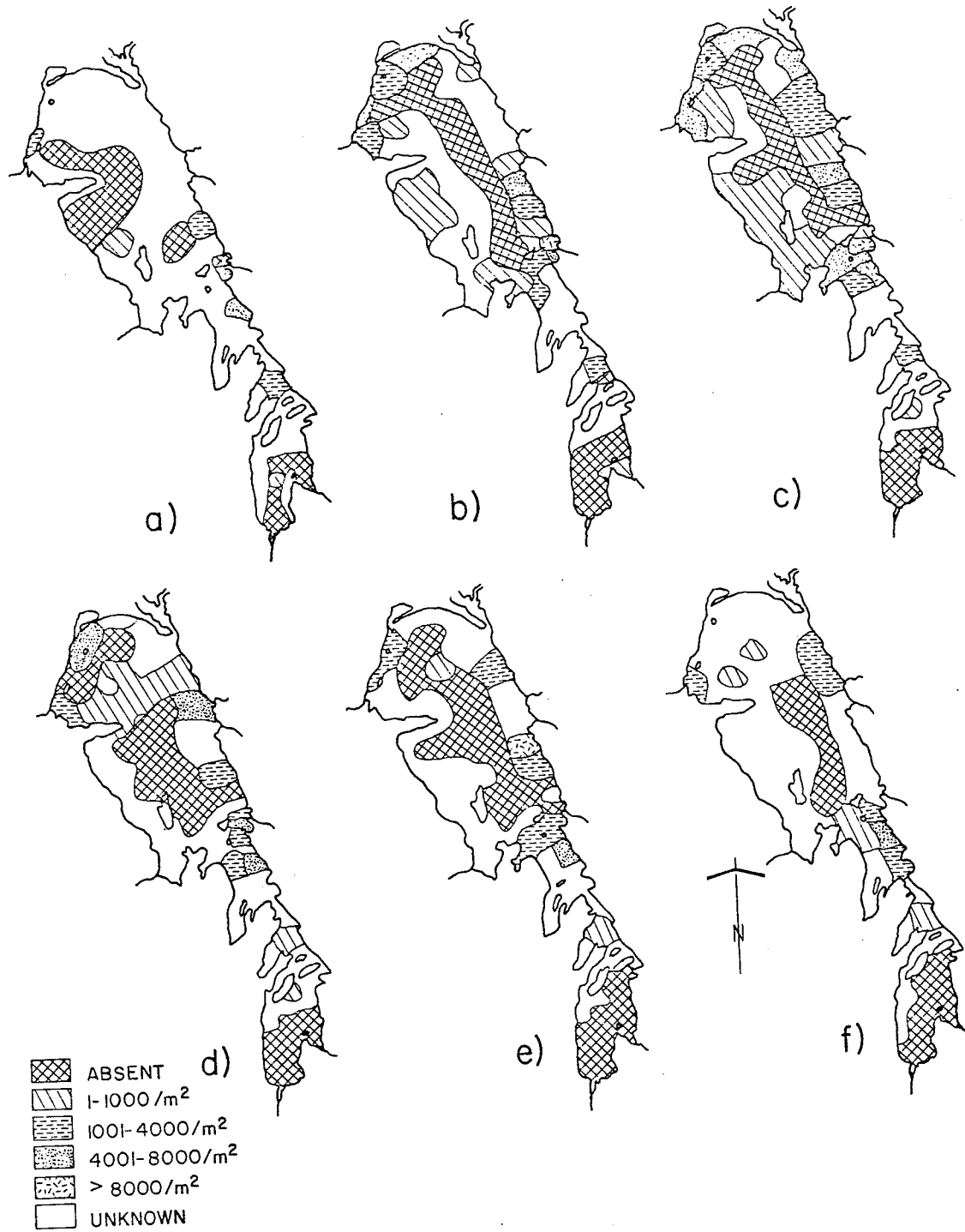


Figure 4. Density distribution of *P. hoyi* in Lake Winnipeg in a) June; b) early July; c) late July/August; d) September; e) early October; f) late October.

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.

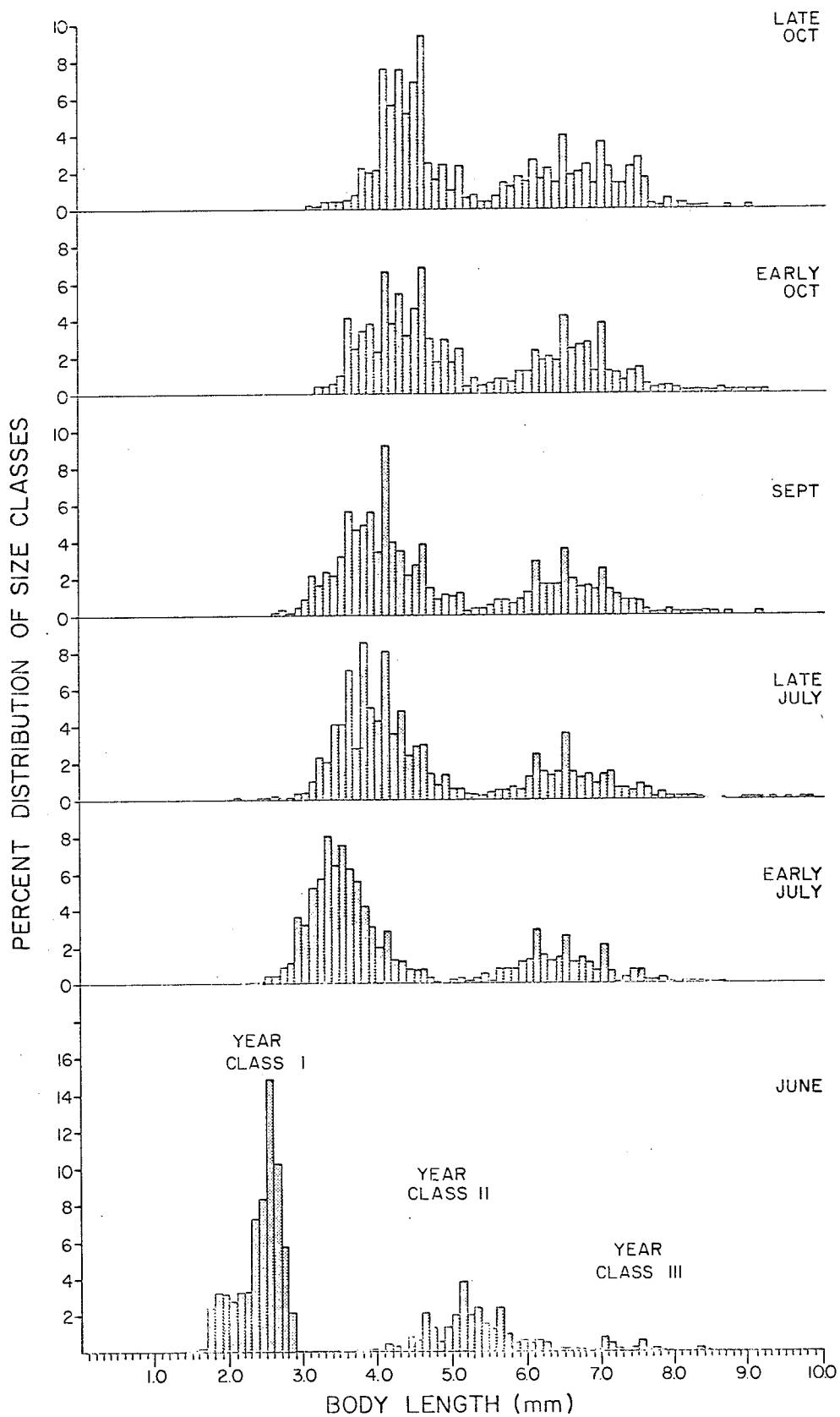


Figure 5. Percent distribution of size classes (1 mm intervals) of *P. hoyi* in the whole lake at each of the six sampling times.

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.

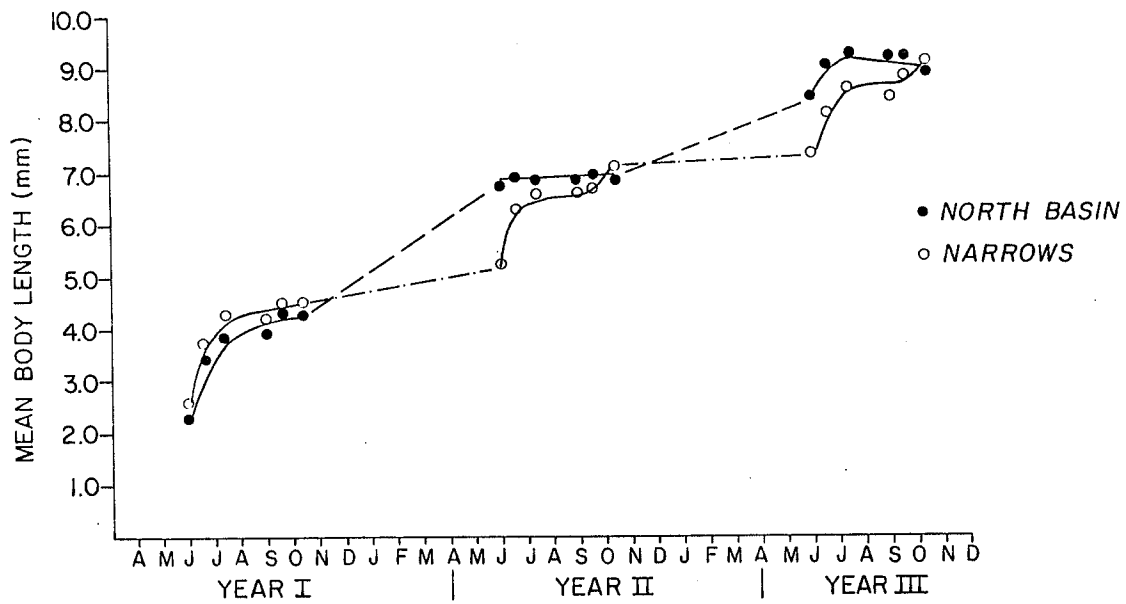


Figure 6. Mean body length of *P. hoyi* throughout its life cycle in the North and Narrows Basins of Lake Winnipeg.

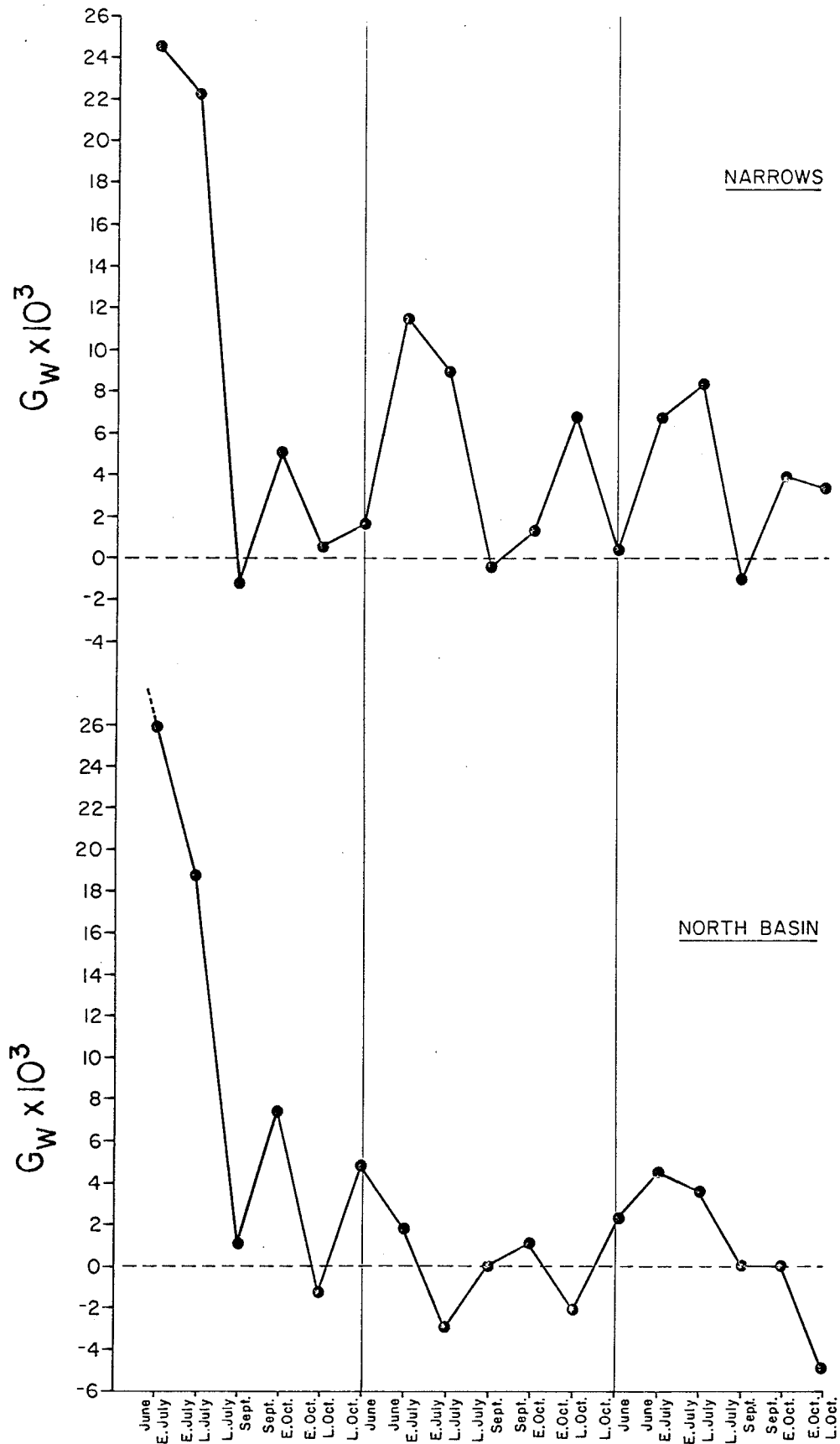


Figure 7. Instantaneous growth (G_W from Tables 3 and 4) throughout the life cycle of *P. hoyi* in the Narrows and North Basins of Lake Winnipeg.

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 ($7.37 \text{ g/m}^2/\text{yr}$, Table 2) was found to be much more productive than the North Basin ($2.34 \text{ g/m}^2/\text{yr}$, 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 ($\text{g/m}^2/\text{yr}$)	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, $P = GB$ (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	-	523.57 ^{a)}
June	1914.33	.547					
Early July	1885.85	1.32	36	0.0245	1768.23	43.32	1559.58
Late July	1988.68	1.80	14	0.0222	3034.48	67.37	943.12
September	1921.67	1.71	41	-0.0013	3432.84	-4.46	-182.97
Early October	886.97	2.01	32	0.0051	2534.43	12.93	413.62
Late October	1236.17	2.03	21	0.00047	2146.12	1.009	21.18
June	1206.04	2.40	222	0.0016	3004.34	4.807	<u>1067.14</u>
<u>Year Class II</u>							
Early July	1000.34	4.39	36	0.0115	3945.38	45.37	1633.39
Late July	1014.22	4.97	14	0.0089	4716.08	41.97	587.62
September	848.09	4.92	41	-0.00025	4606.64	-1.152	-47.22
Early October	774.96	5.11	32	0.0012	4066.32	4.880	156.15
Late October	522.29	5.90	21	0.0068	3520.78	23.94	502.77
June	27.30	6.36	222	0.00034	1627.57	0.553	<u>122.85</u>
							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
<u>Year Class III</u>							
Early July	28.14	8.09	36	0.0067	200.64	1.34	48.39
Late July	6.74	9.09	14	0.0083	144.46	1.20	16.79
September	5.55	8.67	41	-0.0011	54.69	-0.060	-2.47
Early October	2.64	9.83	32	0.0039	37.04	0.144	4.622
Late October	2.12	10.56	21	0.0034	24.17	0.082	1.726
							<u>69.058</u>

$$\bar{B} = 2188.21$$

$$\Sigma P = 7369.86$$

$$\text{Mean Biomass} = 2.19 \text{ g/m}^2$$

$$\text{Production} = 7.37 \text{ g/m}^2/\text{yr}$$

$$P/\bar{B} = 3.37$$

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, $P = G\bar{B}$ (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	-	-	-	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	<u>474.38</u>
June	98.2	5.22					1950.32
<u>Year Class II</u>							
Early July	297.7	5.57	36	0.0018	1077.04	1.94	69.79
Late July	612.6	5.33	14	-0.0031	2453.32	-7.61	-106.47
September	376.62	5.35	41	0.00009	2640.04	0.238	9.74
Early October	374.8	5.54	32	0.0011	2045.66	2.25	72.01
			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
<u>Year Class II (continued)</u>							
Late October	306.51	5.30					
June 5.9	5.9	8.74	222	0.0023	838.03	1.927	<u>427.80</u> 391.27
<u>Year Class III</u>							
Early July	.8	10.28	36	0.0045	29.80	0.135	4.84
Late July	3.9	10.83	14	0.0037	25.23	0.093	1.307
September	.9	10.83	41	0	25.99	0	0
Early October	4.6	10.83	32	0	29.78	0	0
Late October	1.9	9.75	21	-0.005	34.17	-0.17	<u>-3.57</u> 2.577

Mean Biomass = .987 g/m²
 Production = 2.34 g/m²/yr

P/ \bar{B} = 2.37

a) see Table 1

\bar{B} = 986.5

ΣP = 2344.17

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,

Table 4. Annual production (P) (wet weight) of *Hexagenia limbata* in North Basin of Lake Winnipeg using the instantaneous growth method $P + \overline{GB}$ (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
-	0	-	-	-	15.23	-	15.23 ^{a)}
June	25.18	1.21	36	0.0218	38.97	0.8495	30.58
Early July	17.91	2.65	14	0.0757	58.39	4.42	61.88
Late July	9.06	7.65	41	0.0112	62.72	0.7025	28.80
September	4.63	12.12	32	0.0141	89.59	1.2632	40.42
Early October	6.48	18.99	21	0.0171	108.21	1.8504	38.86
Late October	3.43	27.22	222	-0.0013	183.25	-0.2382	-52.88
June	13.33	20.49	36	0.0236	430.57	10.16	365.81
Early July	12.24	48.04	14	0.0255	522.04	13.31	186.37
Late July	6.64	68.58	41	0.0036	338.62	1.219	49.98
September	2.78	79.56	32	0.0090	550.21	4.95	158.46
Early October	8.33	105.55	21	0.0090	609.28	5.48	115.15
Late October	2.64	128.53					
				\overline{B}	<u>501.18</u>		<u>1038.66</u>
Mean Biomass =	.501 g/m ²						
Production =	1.039 g/m ²						
P/ \overline{B} =	<u>2.07</u>						

a) see Table 1

Table 5. Annual production (P) (wet weight) of *Hexagenia limbata* in the Narrows of Lake Winnipeg using the instantaneous growth method $P = GB$ (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>24 Month life cycle</u>							
-	0	-	-	-	18.69	-	18.69 ^{a)}
Late October	27.48	1.36	-	-	22.68	- .06	-12.59
June	10.26	.78	222	-0.0025	14.82	0.04	15.90
Early July	9.52	2.28	36	0.0295	24.60	1.93	27.00
Late July	4.04	6.82	14	0.0784	158.46	4.07	166.97
September	14.81	19.54	41	0.0257	342.78	3.36	107.50
Early October	14.81	26.75	32	0.0098	488.17	0.24	5.13
Late October	21.44	27.06	21	0.0005	674.08	0.12	26.94
June	27.35	28.08	222	0.00018	723.30	8.68	312.47
Early July	15.64	43.39	36	0.0120	815.87	17.87	250.15
Late July	16.16	58.98	14	0.0219	1047.12	6.8	279.06
September	14.81	77.05	41	0.0065	1563.23	16.10	515.24
Early October	18.52	107.20	32	0.0103			
					\bar{B} 982.3		$\Sigma P = 1712.46$
Mean Biomass =	.983 g/m ²						
Production =	1.712 g/m ² /yr						
P/B =	1.74						

...continued

Table 5. (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
<u>22 Month Life Cycle</u>							
-	0	-	-	-	151.50	-	151.50 ^{a)}
Late October	75.56	4.09	-	-	190.45	0.114	25.36
June	17.09	4.56	222	0.0006	54.76	0.986	35.48
Early July	3.59	8.80	36	0.0180	32.65	0.849	11.88
Late July	2.69	12.53	14	0.0260	297.16	7.13	292.41
September	16.67	33.63	41	0.0240	695.55	8.35	267.09
Early October	16.67	49.82	32	0.0120	810.56	12.16	255.33
Late October	11.48	68.87	21	0.0150	494.73	-0.346	-76.81
June	3.40	58.37	222	-0.0007	540.90	16.23	584.18
Early July	5.08	173.89	36	0.0300			
					$\bar{B} = 544.71$		$\Sigma P = 1546.42$

Mean Biomass = .545 g/m²
 Production = 1.546 g/m²/yr
 P/ \bar{B} = 2.84

...continued

Table 5. (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
<u>14 Month life cycle</u>							
-	0	-	-	-	95.28	-	95.28 ^{a)}
September	114.80	1.66	-	-	292.36	7.25	231.90
Early October	107.40	3.67	32	0.0250	330.63	15.34	322.09
Late October	27.48	9.72	21	0.0464	1090.55	7.71	1712.16
June	41.02	46.66	222	0.0070	1702.31	29.79	1072.45
Early July	17.12	87.07	36	0.0175	1116.48	18.84	263.72
Late July	6.73	110.30	14	0.0169	928.79	10.54	432.24
September	6.35	175.63	41	0.0114			
					$\bar{B} = 926.07$		$\Sigma P = 4129.84$

Mean Biomass = .926 g/m²
 Production = 4.130 g/m²/yr
 P/B = 4.46

Total production for Narrows *H. limbata* = 7.388 g/m²/yr
 Mean Biomass = 2.453 g/m²
 P/B = 3.01

a) see Table 1

Table 6. Annual production (P) (wet weight) of *Hexagenia limbata* in South Basin of Lake Winnipeg using the instantaneous growth method $P = GB$ (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>14 Month life cycle</u>							
-	0	-	-	-	35.73	-	35.73 ^{a)}
September	23.98	2.98	-	-	81.09	1.16	37.11
Early October	19.26	4.71	32	0.0143	350.42	15.31	321.58
Late October	51.53	11.84	21	0.0437	478.31	2.97	658.34
June	7.41	46.76	222	0.0062	434.48	1.82	65.69
Early July	9.59	54.48	36	0.0042	517.63	-0.83	-11.59
Late July	9.63	53.25	14	-0.0016	619.97	7.25	297.40
September	8.46	85.95	41	0.0117			
					$\bar{B} = 419.61$		$\Sigma P = 1404.26$

Mean Biomass = .420 g/m²

Production = 1.404 g/m²/yr

$P/\bar{B} = \underline{3.34}$

Table 6. (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
<u>22 Month Life Cycle</u>							
-	0		-	-	7.01	-	7.01 ^{a)}
Late October	16.16	.87	-	-	11.33	0.03	5.53
June	6.17	1.40	222	0.0022	71.81	1.43	51.44
Early July	47.05	2.87	36	0.0199	227.43	18.47	258.64
Late July	35.76	8.95	14	0.0812	811.87	24.44	1002.05
September	42.32	30.81	41	0.0301	2127.35	48.93	1565.73
Early October	45.92	64.26	32	0.0230	3950.48	62.81	1319.06
Late October	55.21	89.66	21	0.0159	2711.52	4.338	963.12
June	3.70	127.81	222	0.0016	652.07	-1.304	-46.95
Early July	6.97	119.21	36	-0.0020			
					\bar{B} 1761.81		$\Sigma P = 5125.63$

Mean Biomass = 1.762 g/m²
 Production = 5.126 g/m²/yr
 P/B = 2.91

Total Production H. limbata South Basin = 6.53 g/m²/yr
 Mean Biomass = 2.136 g/m²
 P/B = 3.06

a) see Table 1

H. limbata production (unlike that of P. hoyi) was almost as high in the South Basin. The production of H. limbata in the large North Basin was less than half that of P. hoyi, resulting in an almost identical total production for the two species on a whole lake basis: -

	Production (g/m ² /yr)	Area (Km ²)	Production (tonnes/yr, wet weight)
North Basin	1.039	16,468	17,111
Narrows	7.388	3,864	28,547
South Basin	6.530	3,265	21,313

Total production H. limbata = 66,972

Total production P. hoyi = 67,015

A more detailed examination of the production estimates shows that, contrary to what might be expected in a species in which life cycle length tends to vary directly with latitude/temperature (Flannagan 1979), the 22 month life cycle type was most productive in the South Basin, and the 14 month life cycle type was most productive in the Narrows. These two groups together produced 9.2 gm/m²/yr out of a total production for these two Basins of 13.9 gm/m²/yr.

In contrast to the above, the basin turnover ratios, 3.06 in the South (Table 6), 3.01 in the Narrows (Table 5), and 2.07 in the North Basin (Table 4), follow the expected indirect relationship with latitude/temperature.

3. Multi-linear regression analyses

The density distribution of P. hoyi in the Lake as a whole was inversely related to maximum temperature, depth and Secchi disc reading, and positively related to % sand (Table 7a). These four factors

Table 7. Results of stepwise multi-linear regression analyses between mean(\ln number/ m^2+1) of P. hoyi and possible environmental variables.

a) Whole Lake (N = 32)

Factor	Multiple correlation coefficient (R^2)	F (d.f.)	P
Max. Temperature	0.365	17.21 (1,30)	.001
Max. Temperature and Depth	0.586	20.48 (2,29)	.001
Max. Temperature; Depth and Secchi	0.649	17.28 (3,28)	.001
Max. Temperature; Depth; Secchi and % Sand	0.695	15.36 (4,27)	.001

Equation

$$\text{mean}(\log_n \text{ number}/m^2+1) \text{ P. hoyi} = 58.95 - 2.635 \text{ depth} - 0.470 \text{ max temperature} + 0.05 \text{ arcsin \% sand} - 2.22 \text{ Secchi}$$

b) North Basin and Narrows (N = 16)

Factor	Multiple correlation coefficient (R^2)	F (d.f.)	P
Depth	0.452	11.54 (1,14)	.001
Depth and Sand	0.553	8.04 (2,13)	.001

Equation

$$\text{mean}(\log_n \text{ number}/m^2 + 1) \text{ P. hoyi} = 12.39 - 0.628 \text{ depth} + 0.064 \text{ arcsin \% sand}$$

together accounted for 69.5% of the variation in the data ($R^2=0.695$). Maximum temperature alone explained 36.5% of the variance, and was therefore, as might be expected in a cold stenothermic species, the most reliable single predictor of P. hoyi density. In the equation predicting the densities of P. hoyi the coefficient associated with the slope for maximum temperature (0.470) is small, compared with those for depth and secchi. Thus, though the response in density changes to differences in maximum temperature is most predictable, the response to changes in depth and water transparency is of much greater magnitude. In addition, the possible range of depth is much larger than the range of either transparency or maximum temperature in the Lake. Thus depth is likely to be the largest single environmental factor, of those tested, affecting the density distribution of P. hoyi in the whole Lake.

As mentioned previously, it was felt that the possibly anthropogenic lack of P. hoyi in the shallow, turbid, warm South Basin unduly biased the analyses. Excluding the South Basin results from the analysis (Table 7b), excluded both maximum temperature and water transparency as significant variables. Depth, now with a much tighter fit, explained 45% ($R^2=0.452$) of the variation and % sand another 10%. Further, in the equation predicting densities of P. hoyi in the North Basin plus the Narrows (Table 7b) the coefficient associated with % sand, 0.064, is small and since the range of % sand is small compared to the range of depth, and made even smaller by the arcsin transformation, the contribution of % sand in predicting density of P. hoyi will be small.

Thus both on a whole lake basis or just on the basis of the Narrows and North Basin, P. hoyi appears to prefer shallower water, bearing in mind the 3-4 m depth limitation of the sampling, and coarser substrates.

DISCUSSION

1. Biology of P. hoyi

Although P. hoyi was collected only in samples taken during the open water season, (Fig. 5) three distinct year classes were identified. Year Class III, was composed of senescent females which gradually died out over the summer. Recruitment to year class I occurred only in spring. The life cycle length of the population is therefore 2+ yrs. and reproduction occurs annually. All other North American populations of P. hoyi which live in 'warm' water have a one year life cycle, two or more year life cycles being found only in deep, cold water (Alley 1968, Green 1971, Dadswell 1971, Lubner 1979, Moore 1979). Growth of P. hoyi in the Narrows (Fig. 6) was largely restricted to the spring and fall, with essentially no growth in summer or winter. In the North Basin, on the other hand, there was significant growth in winter, presumably because of the higher winter bottom temperatures in this Basin, but there was still no growth in summer. Each year class had, by fall, achieved about the same mean size. Brunskill et al. (1979) showed that in the South Basin and Narrows surface and bottom water temperatures were similar throughout the year. In winter, in the North Basin, bottom temperatures were about 2 C higher than surface temperatures (and 2 C higher than Narrows bottom temperature) with the reverse being true during spring and early summer.

Growth in most populations of Pontoporeia spp. is more or less continuous (Appendix 1; Green 1965; Kuz'menko 1969; Johnson and Brinkhurst 1971; Cederwall 1977) though in most two year life cycle populations maximum growth is recorded in spring (Johnson and Brinkhurst 1971,

Cederwall 1977).

The Lake Winnipeg populations of Pontoporeia were apparently exposed to a sufficiently high number of day-degrees to complete their life cycle in one year (2190-2445 degree-days, compared with 1060-2774 degree-days for 1 yr life cycle (Green 1965, Kuz'menko 1969, Greze 1951), and 511-1560 for 2 yr life cycle (Alimov et al. 1972, Greze 1951, Cederwall 1977). Since food supply is not likely to be limiting in Lake Winnipeg, it appears that the summer cessation of growth is the reason for the unexpectedly long life cycle length in the Lake Winnipeg population. This summer cessation of growth apparently prevents the animal from growing a sufficient amount to reach maturity in their first year. Since this species can reproduce only in cold water (Larkin 1948), they must then wait until the fall of their second year to achieve sexual maturity. Investigations of the life cycle and growth patterns of other warm water populations of P. hoyi e.g. Barton and Hynes' (1976) populations in the shallow water of the Great Lakes; Duffy and Liston's (1979) reservoir population would, if a similar 2 yr life cycle and summer "diapause" were found, confirm this hypothesis.

2. Distribution of P. hoyi

P. hoyi has been regarded as a cold stenothermic species (Dadswell 1971) and studies of its temperature tolerance (Smith 1972) confirm this. However, its collection in shallow waters of the Laurentian Great Lakes (Henson 1970, Barton and Hynes 1976), and the recent report of it colonizing a warm water reservoir (Duffy and Liston 1979) suggest that either more than one species is involved or that the species is more tolerance of high temperatures than was previously accepted. Its

distribution in Lake Winnipeg, and perhaps even its presence in a lake in which the continuous mixing of the summer warm surface waters raises bottom water temperatures to near those at the surface (Brunskill et al. 1980), suggest that the population in the Lake is not a cold stenothermic one.

Within the Lake, P. hoyi was present for at least part of the year in all three basins. The South Basin population was small (maximum density $489/m^2$) and had apparently disappeared by the last two sampling dates (Appendix II, Fig. 4e, f). The low population densities of P. hoyi and its elimination in late summer, may be due to high water temperatures (Table 4). However, Bajkov (1930a) in Ekman grab samples from the South Basin in the summers of 1928 and 1929, collected more than three times the maximum density recorded during the present survey and also collected the animal over all areas of the South Basin which he sampled, in spite of summer water temperatures of almost $30^{\circ}C$ in 1928 (Bajkov 1930b). Similarly, the water temperature results from the present survey (maximum water temperature at stations where P. hoyi was collected: - South Basin $20.2^{\circ}C$, Narrows $20.8^{\circ}C$ (Brunskill et al. 1980)), together with the collection of large numbers of P. hoyi from the Narrows, suggests that high water temperatures are not responsible for the low densities and/or elimination of P. hoyi in the South Basin.

Populations of P. hoyi are available, in the Winnipeg river system and other river systems (unpublished data) which enter the South Basin from the east. In addition Kenney (1979) showed that after strong south winds and during north winds large volumes of Narrows and North Basin waters enter the north part of the South Basin. Thus, the sporadic occurrence of P. hoyi may not represent a permanent population, but one

which is washed in under favourable conditions and which may not be able to sustain itself. Results from studies of the other benthic invertebrates (e.g. Flannagan 1979, Flannagan and Cobb 1981; Flannagan and Cobb, in press) suggest that anthropogenic changes in the South Basin may have, or may be, rendering it unsuitable for habitation by the more sensitive benthic aquatic invertebrates.

3. Production estimates of P. hoyi and H. limbata

a) General

The data available from this survey do not allow exact dates for release of young P. hoyi or H. limbata to be set. This knowledge is required to calculate exactly the initial production for the period from hatching to their first appearance in the samples, when the instantaneous growth method (Chapman 1968) is used. By assuming a biomass and density of zero at the start of the period before the first sampling date, an estimate of production (= 1/2 standing crop on the date of first appearance in the samples) was included in the production estimate. In addition to the above, sources of error in the production calculation arise from the lack of mature males and large gravid P. hoyi females in the growth/weight conversion curve (Fig. 2) and in the relatively small numbers of stations sampled in the June 4-12th cruise (Appendix II). The former has led to underestimation of the total P. hoyi production, while the latter may have contributed to an underestimation of the numbers of individuals at this time, resulting in an underestimate of total production. Additional errors inherent in calculation of production are discussed, among others, by Waters (1966), Hamilton (1969), Kajak and Hillbricht-Ilkowska (1972).

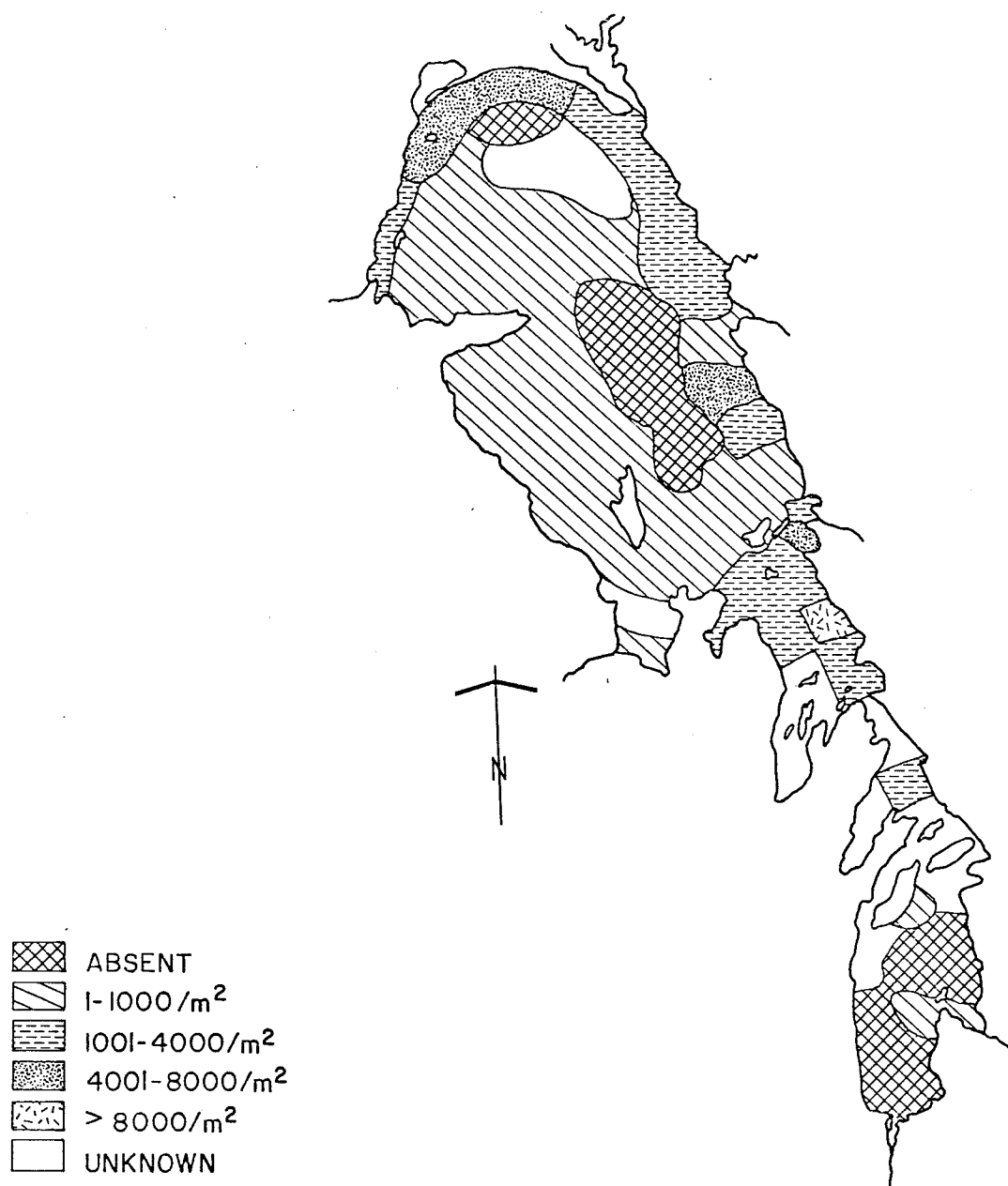


Figure 8. Mean density of *P. hoyi* in Lake Winnipeg, all samples combined.

b) P. hoyi and H. limbata

The total production of these two important fish food species is almost identical. In both species production rate is highest in the Narrows, both producing in an area of less than 4,000 Km² (\approx 16.4% total Lake area), about 42% of their total production. The remainder of the P. hoyi production occurs in the North Basin of the Lake. H. limbata in contrast, produces 32% in the South Basin and only 25% of its total in the North Basin.

Although the South Basin appears to have changed considerably due to the activities of man, Flannagan and Cobb (1981) have shown a 27% decrease in Hexagenia production over the last fifty years, it appears from Bajkov (1930a) that it never had a population of P. hoyi comparable with those of the other two basins. P. hoyi although generally exhibiting maximum densities at the junction of the profundal and sublittoral, is a species distributed into the deepest parts of lakes (Dadswell 1971). Although the Lake Winnipeg distribution was not typical, this animal appeared to be able to inhabit deeper water than the essentially littoral and/or sublittoral H. limbata (Flannagan 1979). The shallow South Basin has no true profundal area, thus H. limbata could colonize most of it. In the North Basin, H. limbata was restricted to the shore areas, while P. hoyi showed a more extensive distribution. Similarly, in the Narrows, which contains a long narrow deep area bounded by shallow areas, H. limbata dominated at the shallower stations, was generally not present at the deeper ones (Flannagan 1979) and P. hoyi was present at all but the shallowest stations (Fig. 8).

H. limbata is a southern species, able to develop significantly only at temperature $\geq 10^{\circ}\text{C}$ and not limited by maximum Lake Winnipeg water

temperature (Friesen et al. 1979) while P. hoyi is a northern species, able, in Lake Winnipeg to grow at temperatures of 2°C but limited by high summer temperatures. In addition, Hexagenia spp. are tunnelers requiring a more adhesive substrate than the sand preferred by P. hoyi.

Thus these animals, both of which are relatively indiscriminate detritus feeders (Pennak 1953), though having a similar total production, have divided the available resources of the Lake spacially, both in terms of depth and substrate, and temporally.

4. Lake Winnipeg P. hoyi and Pontoporeia spp. production

Estimates of production of Pontoporeia spp. in the literature are variable, ranging from a high of 19.39 g/m²/yr in the Baltic Sea (Cederwall 1977) to a low of 0.439 g in Lake Krivoe (Alimov et al. 1972). Cederwall's (1977) results are based on only one station, in a part of the Baltic Sea where Pontoporeia is abundant, and thus are not comparable with those of Lake Winnipeg, and most of the others, where production is estimated over whole lakes or large areas of lakes. Kuz'menko (1969) reported 3.46 and 2.81 g/m²/yr production of P. affinis in mesotrophic Lake Krasnoe. This is intermediate between the 7.37 g (Table 2) estimated for the Narrows and the 2.34 g (Table 3) for the North Basin of Lake Winnipeg. Green (1971) estimated 1.81 g for P. hoyi in the more oligotrophic Lake Cayuga which is lower than those for either basin of Lake Winnipeg. If production of Pontoporeia can be used as a measure of trophic in lakes, the North Basin of Lake Winnipeg could be classified as being mildly oligotrophic, while the Narrows would be mesotrophic to eutrophic. Using the chironomid species as indicators of trophic level would also result in similar classifications for these two basins (Saether 1975).

Table 8. Comparison of published and calculated turnover ratios for Pontoporeia spp.

Author	Water Body	Species	Mean bottom water T ^o	Calculated TR (TR = $\frac{T^2}{10}$)	TR of author
-	L. Winnipeg (North Basin)	<u>P. hoyi</u>	6.0	3.6	2.37
-	L. Winnipeg (South Basin)	<u>P. hoyi</u>	6.7	4.49	3.37
Green (1971)	Cayuga L.	<u>P. hoyi</u>	3.9	1.5	4.2
Bekman (1959)	L. Baikal	<u>P. affinis</u>	3.2 - 3.7	1.03 - 1.37	3.0
Cederwall (1977)	Baltic Sea	<u>P. affinis</u>	4.3	1.85	1.9
Kuz'menko (1969)	Krasnoe L.	<u>P. affinis</u>	7.5 - 7.7	5.6 - 5.9	3.8 - 4.4
Alimov et al.(1972)	L. Krivoe	<u>P. affinis</u>	4.0	1.6	1.0
Greze (1951)	Yenisei R.	<u>P. affinis</u>	2.9	0.84	3.44

Turnover ratio, the rate at which biomass is renewed, is perhaps a better measure of the productivity of water bodies. Johnson and Brinkhurst (1971) found that turnover ratio ($TR = \frac{\text{production}}{\text{mean biomass}}$) of benthic invertebrates was correlated with mean annual bottom temperature (T) in Lake Ontario in the following fashion:

$$TR = \frac{T^2}{10}$$

As far as I am aware this has not been tested with populations other than those they worked on and certainly not on any other Pontoporeia populations.

The mean annual temperatures of the North Basin and Narrows were estimated to be 6.0 and 6.75 respectively from the data in Brunskill et al. (1979) and assuming that winter bottom temperatures were similar in the South Basin and Narrows - not an unreasonable assumption, since under the ice the flow in the lake is from south to north.

The predicted TR for the North Basin using the Johnson and Brinkhurst (1971) formula would be 3.6 and that for the Narrows 4.49, while the TR derived from the production calculation were 2.41 and 3.33 respectively. This suggests that either the TR prediction formula is not accurate, or the results from Lake Winnipeg are out by a factor of around 30%. Comparison of predicted TR values with those derived from production estimates by other authors (Table 8) indicates that, at least for Pontoporeia spp., there is little or no correlation between mean temperature and turnover rates.

Since mean temperature/turnover ratio relationships did not appear to provide a basis for comparison of Lake Winnipeg Pontoporeia productivity, and since there appeared to be a relationship between latitude, length

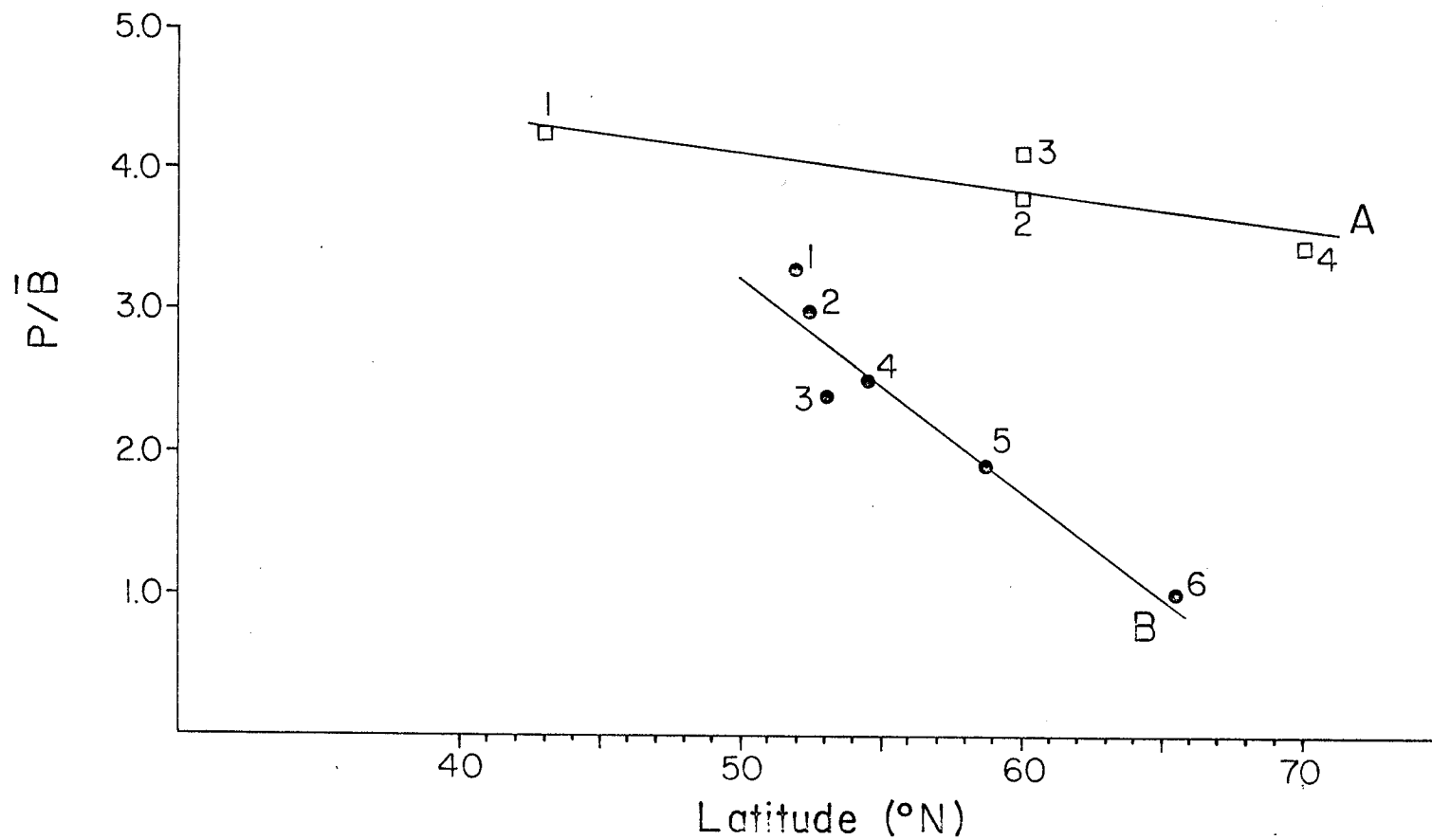


Figure 9. The relationship between life cycle length, latitude and turnover ratios of *Pontoporeia* spp. A. 1 yr life cycle; 1-Cayuga L; 2-L. Krasnoe; 4-Yenesei R. B. 2 yr life cycle: 1-Narrows L. Winnipeg; 2-L. Baikal; 3-North Basin, L. Winnipeg; 4-Angara R.; 5-Baltic Sea; 6-L. Krivoe.

of life cycle and TR, plots of the regression of the TR of one and two year life cycle Pontoporeia on latitude were drawn. These indicated (Fig. 9) that a good correlation, especially with the 2 yr cycle, existed. The formulae describing the relationships were:

$$\text{1 yr cycle TR} = 5.479 - 0.0272 \text{ latitude } (r = -0.869, P \leq .10)$$

$$\text{2 yr cycle TR} = 10.735 - 0.150 \text{ latitude } (r = -0.954, P < .001)$$

The Narrows TR (B1, Fig. 9) lies a little above the regression line and the North TR (B3, Fig. 9) lies a little below it suggesting that production of P. hoyi in the Narrows is a little above what might be expected, and in the North a little less, or that the production of P. hoyi in the two basins together is about what might be expected at these latitudes. As previously discussed, the TR in the Lake is among the highest, while the lake is near the lowest latitude for two year life cycles and perhaps only restriction of growth by the warm summer temperatures prevents these animals from completing their life cycle in one year.

5. Multi-linear analyses

Attempts to analyse the density distribution of P. hoyi in relation to the distribution of environmental variables in the Lake indicated (Table 7) a negative correlation with temperature, depth, Secchi disc reading and a positive correlation with sand. Eliminating the South Basin populations from the analyses removed temperature and Secchi disc as significant variables. This might be expected, if in fact the low densities of P. hoyi in the very turbid and warm South Basin, were due to anthropogenic changes, causing a spurious temperature and transparency correlation.

Although P. hoyi is generally considered to be a deep water

species (Dadswell 1971, Bousfield 1958) maximum abundance has been generally found in the 15-45 m depth range (e.g. Alley 1968, Henson 1970) except in lakes in the far North where maximum numbers occur in 0-5 m depth range (Rawson 1953). Thus the negative correlation with depth, in Lake Winnipeg, was expected. It should be noted that only depths of 3-4 m or greater were sampled, and if the shallower areas were included, the distribution of P. hoyi, because of the small mean depth of the Lake, might not show a depth correlation. However, Freitag et al. (1976) found a negative correlation between depth and P. hoyi density in Lake Superior, which has a high mean depth, suggesting that the Lake Winnipeg results are valid. The positive correlation with sand might also be expected, since analyses by some workers (Kraft 1979, Cook 1975, Nalepa and Thomas 1976) indicated a similar preference, though other workers (Marzolf 1965, Alley 1968, Dermott 1978, Freitag et al. 1976) were not able to show any, or only weak, correlation with substrate type.

Together depth and substrate type accounted for 55.3 percent of the variation in the distribution of P. hoyi ($R^2 = 0.553$). The remaining variation is unexplained. P. hoyi occurs, as previously noted, in the lakes and rivers which drain into Lake Winnipeg from the east. Redistribution from these lakes and from basin to basin by the water movements shown by Kenney (1979) and within basins by the internal wind-driven movements of water and sediment (Brunskill and Graham 1979) are all likely involved in the redistribution of animals within and into the Lake.

If, as suggested above, the inclusion of maximum water temperature and water transparency as significant variables contributing to the density distribution of P. hoyi (Table 7a) was spurious, only the equation for the Narrows plus North Basin need be discussed further. In this second equation (Table 7b), as previously mentioned, the slope associated with depth is steep while that of arcsin percent. sand is very shallow. Thus the density of P. hoyi could, without greatly affecting the accuracy, be predicted using only depth data.

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Appendix 1. Review of Pontoporeia hoyi

Taxonomy

Smith (1874) described Pontoporeia hoyi from specimens from the Laurentian Great Lakes, but it was regarded as, at most, a subspecies of P. affinis Lindström (Bousfield 1958) until Segerstråle (1977) in consultation with Dr. E.L. Bousfield, reinstated it as a valid species, distinct from the Eurasian P. affinis, and assigned all freshwater North American Pontoporeia to this species.

Today, two species of Pontoporeia, P. hoyi Smith and P. erythrophthalma Waldron, known only from L. Washington, are recognized from North America. However, the genus, including its marine representatives, is presently being revised by Dr. Bousfield, who suggested (personal communication) that several species may occur in North America.

The specimens from Lake Winnipeg were identified as P. hoyi by Dr. Bousfield, who mentioned the possibility, because of some small morphological differences between these and the eastern Canadian populations, that the Lake Winnipeg population may be a separate subspecies. My ecological data support this hypothesis.

Distribution

Until the taxonomy has been revised, it is not advisable to speculate on the distribution and origin of Pontoporeia spp.

P. hoyi species or species complex appears limited to those areas of North America covered by ice or directly connected to ice-covered areas, during, or immediately after, the Wisconsinan glaciation (Ricker 1959). Cook and Johnson (1974) suggested that P. hoyi is either a relict

species or a species which became dispersed through the glacial lake systems. Since Bousfield (personal communication) believes that P. hoyi existed as a species in freshwater long before the glacial periods, Cook and Johnson's (1974) latter statement is probably the more accurate one.

Abundance

P. hoyi has been recorded in densities up to 14,000/m² in the Great Lakes (Cook and Johnson 1974). Where they occur, they normally dominate the benthos in both numbers and biomass. Cook (1975) showed that P. hoyi contributed 34% by number and 51% by weight of the benthos of Lake Superior; Hamilton (1971, 1975) found it to numerically comprise 68.5% of profundal benthos of E.L.A. lakes and up to 93% of the benthos of the deeper parts of South Indian Lake; Loveridge and Cook (1976) found it to represent 48-51% by number and 69-70% of the biomass in Lake Huron; Larkin (1948) recorded it to be 58-84% by number and 49-85% by weight of the fauna of Great Slave Lake and 38-63% by number and 45-82% by weight of the fauna of Lake Athabasca. In Lake Winnipeg this species was found to comprise 63%, by number of the benthic fauna (Bajkov 1930a).

Life History

P. hoyi, in North America, exhibits a plastic life cycle length. Alley (1968) in Lake Michigan showed that at 10 m they had a 1 yr, at 20-35 m a 2 yr, and deeper than 35 m possibly a 3 yr life cycle length. Similarly, Cooper (1962) in Lake Huron collected two year classes (young of the year + parents) at 13 m and three year classes (young of the year + immatures + mature 2 yr olds) at 37 m. Green (1971) found a 1 yr life cycle in Cayuga L., N.Y. Kuz'menko (1969) working on the related

European species, P. affinis, showed that its 1, 2, or 3 year life cycle depended on the day-degrees to which the population was exposed.

Dadswell (1971) reviewed the available information on P. hoyi and suggested that the P. hoyi in Ontario lived in deep, cold lakes, matured in 16-18 months (2 yr life cycle) and reproduced only once in their life cycle. Copulation usually occurred in late fall or early winter, the eggs hatched about one month later, and the young were brooded for several more months and released between March and May (Moore 1979, Dadswell 1971, Marzolf 1963). After copulation the males died, and during incubation of the eggs the females degenerated and shortly after releasing their young generally died. At maturity the male apparently became free swimming and was adapted for this existence by developing very long antennae and setose uropods which were used for swimming. In addition, males stopped feeding and lived on stored oil globules (Dadswell 1971). Larkin (1948) suggested that the upper temperature limit for successful reproduction was 7 C. Baychorov and Semenchenko (1977) showed that a temperature of 2-3 C was necessary for successful reproduction and embryogenesis of the closely related Eurasian P. affinis.

Egg or brood size appears to be consistent throughout its range. Green (1965) recorded a brood size of 16-20 in P. hoyi from L. Cayuga (N.Y.) while Moore (1979) found a mean of 16.5 eggs in 6 mm long females and 22 eggs in 9 mm females P. hoyi in Great Slave Lake (N.W.T.). Both temperature and light are important in reproduction of Pontoporeia spp. Summer reproduction was recorded in P. hoyi living in deep water (reviewed by Segerstråle 1967, Green 1968). Segerstråle (1969) showed that constant light inhibited normal development of the gonads of P. affinis while constant dark allowed reproduction. He suggested that the lack of light at great depth in lakes allowed summer (or even continuous)

reproduction to occur in Pontoporeia species. Moore (1979) using a multivariate analysis technique, showed that reproduction of P. hoyi was influenced by light (35%) and temperature (24%).

Feeding

Marzolf (1963) suggested that P. hoyi fed indiscriminately, ingesting large quantities of bottom mud and digesting the associated bacteria. A similar feeding mode is suggested by Dadswell (1971). Moore (1976) in a more intensive study in Great Slave Lake, showed that P. hoyi gut contents contained significant amounts of algae, sandgrains and oligochaete remains. He further showed that they selected specific algae and that the sand grains in the guts were considerably smaller than the commonest particle sizes in the substrate, and that feeding did not occur during the winter (Oct. - Mar.). In contrast, Marzolf (1965) showed that algal material passed undigested through the gut. In another study, also in Great Slave Lake, Moore (1979), using a multivariate analysis showed that percent. feeding in this species depended on temperature (65.8%) + light (94.2%) - reproduction (97%). Thus feeding activity would be expected to be limited to the spring-summer-fall seasons of the year, being depressed during the winter by low light intensities, low water temperatures and reproduction.

Economic Importance

a) As Fish Food

P. hoyi is of prime importance in the diet on many species of fish. Larkin (1948) suggested that it was virtually the only food for deep-water fish. In Lake Michigan, Brandt (1980) studied the food of alewives (Alosa pseudoharengus (Wilson)) and showed that the adult fish

occurred in deeper and colder water than the juveniles and P. hoyi contributed a significant portion to their diet (up to 135 individuals/stomach). Griswold and Smith (1973), studying the food of the fishes of L. Superior, indicated that P. hoyi contributed 61-79% by volume of the diet of nine-spine stickleback (Pungitius pungitius (Linnaeus)), the main food item of Lake Superior lake trout. Rawson (1953) found that P. hoyi in Great Slave Lake contributed 45% of the diet of grayling (Thymallus arcticus (Pallas)), and a significant portion of the diet of lake trout (Salvelinus namaycush Walbaum) particularly juveniles. Dadswell (1971) suggested that P. hoyi contributed 50-80% of the diet of fish such as whitefish, young lake trout, burbot and deep water sculpins. In Lake Winnipeg P. hoyi was listed as the main food item in the diet of the whitefish of the lake (Bajkov 1930b). In addition P. hoyi also provides a food source for Mysis relicta (Lovén) (Parker 1980), a major food item of lake fish and ducks (Peterson and Ellarson 1978).

Where they occur, P. hoyi are extremely important, either directly or indirectly, in the diet of many fishes. They were also considered to be sufficiently important that both P. hoyi and M. relicta were introduced into Kootenay Lake, B.C. in an attempt to improve the growth of the fishes of the Lake. Sparrow et al. (1964) claimed a significant increase in growth of both rainbow trout and kokanee salmon 10 years after the introduction.

b) As an indicator species

P. hoyi because of its low position in the food web (Yaguchi et al. 1974), its apparent sensitivity to heavy metals (Gannon et al. 1979), organic pollution, temperature and various pesticides (Peterson and Ellarson 1978), has been extensively used as an indicator species, especially in the Laurentian Great Lakes.

Kidd (1970) investigated and evaluated P. hoyi from Lake Michigan as a potential monitor of radioactive fall-out. He showed that this species concentrated strontium, manganese and zinc isotopes X 260, 5840 and 3540 respectively. This work led to investigations such as those of Yaguchi et al. (1974) who showed that fish in a Lake Michigan detritus P. hoyi food chain, concentrated ^{239}Pu to a higher degree than zooplankton feeding fish because the plutonium sedimented to the lake sediments and the former food chain was shorter. Radionuclides concentration factors apparently decreased up the food chain. The concentration factors of ^{239}Pu in Lake Michigan algae was X 6100, in P. hoyi was X 1600 and in other animals was much lower (Marshall et al. 1974). Robbins et al. (1977) suggested that P. hoyi was responsible for mixing ^{210}Pb and ^{137}Cs into the top 3 cm of Lake Huron sediments, as a result of its burrowing activity.

Gannon et al. (1979) attributed the disappearance of P. hoyi from Glen Lake (Michigan) to either copper poisoning from treatments for swimmer's itch or pesticide run off from nearby orchards. Kraft (1979) found a negative correlation between density of P. hoyi in Lake Superior and copper concentrations in the sediment. Peterson and Ellarson (1978) showed that both Lake Michigan whitefish and old squaws (Clangula hyemalis (Linnaeus)) concentrated P.C.B.'s and D.D.E. x 4-21 from their main food source - P. hoyi. In addition, Nalepa and Thomas (1976) and Hiltunen (1969) used the absence of P. hoyi in parts of Lake Ontario as an indicator of deteriorating environmental conditions.

In laboratory cultures, P. hoyi preferred silty substrates, still water and low temperatures (Smith 1972). He established its 96 hr mean tolerance limit (TL_m) at 10.8 C and 30 day TL_m at 10.4 C. Gannon

and Beeton (1971) used P. hoyi in sediment selection tests to assay the effects of dredging sediments on freshwater benthos.

c) As an intermediate host for fish parasites

P. hoyi is the intermediate host for a number of acanthocephalan, cestode and nematode fish parasites. Brownell (1970) found that P. hoyi was an important intermediate host for Echinorynchus salmonis (Müller) (Acanthocephala) which can be transmitted to lake trout when they feed on P. hoyi. Amin (1978) found immature E. salmonis, Acanthocephalis parksidei Amin (acanthocephelans) and Cyathocephalus truncatus (Pallus) (cestode) in Lake Michigan P. hoyi. Of interest is his collection of C. truncatus only in P. hoyi from stomachs of slimy sculpins and not in P. hoyi from bottom samples. He postulated that the bright orange colour of P. hoyi infected by C. truncatus encouraged selective predation by the fish host.

Other records of P. hoyi as the intermediate host of fish cestode and acanthocephalan parasites include: C. truncatus, (Wardle 1932; Larkin 1948; De Guisti and Budd 1959), E. salmonis, (Green 1965; Van Cleave 1920; DeGuisti and Budd 1959).

Smith and Lankester (1979) confirmed experimentally that the swim bladder nematode, Cystidicola farionis Fischer, a parasite of salmonid fishes, developed to the infective stage in P. hoyi.

P. hoyi is therefore of considerable economic importance to man both as an indicator of environmental conditions and as the main food source for many commercially and recreationally important fish species. As an intermediate host to several debilitating fish parasites it also has considerable economic impact, especially in fish stocking and restocking

programmes where disease-free stocks might well be introduced into infected lakes or infected stocks introduced into disease free lakes.

Ecological Parameters

a) Temperature

P. hoyi (mostly as P. affinis until 1977) has been considered a cold stenothermic deep water, glacial relict species. Laboratory studies (Ricker 1959, Smith 1972) and field observations (e.g. Larkin 1948, Rawson 1953, Ricker 1959, Henson 1954, Green 1968, Dadswell 1971) suggest that it is sensitive to water temperature in excess of 14.5 C. However, P. hoyi has been collected from shallow, warmer water - Barton and Hynes (1976) collected it in depth of less than 1 m on the shores of Lake Superior, in the shallows of Lake Huron, and occasionally from the shallows of Lakes Ontario and Erie. Duffy and Liston (1979) recorded its establishment in a reservoir (by being pumped up from L. Michigan) where summer water temperatures range from 20-23 C, while Henson (1970) reported small standing crops in waters <15 m deep in Lakes Huron and Michigan. Freitag et al. (1976) in a statistical analysis of the depth distribution of this species in Lake Superior showed that it preferred shallow water.

b) Dissolved Oxygen

Dissolved oxygen does not seem to affect the distribution of P. hoyi since though they are common in cold, deep northern lakes (Bousfield 1958), Juday and Birge (1927) recorded it in Green and Trout Lakes, in Wisconsin, from water containing <1 mg/L D.O., and Pennak (1953) recorded it from water of <7% saturation. Smith (1972) concluded that agitation of water with air bubbles, in the laboratory, interfered with the culture of P. hoyi.

c) Light

Light appears to control the vertical migration of P. hoyi since Wells (1968) recorded vertical migration of P. hoyi in Lake Michigan at night and during the day only at depths greater than 36.5 m. (the approximate depth of light extinction). Light is also involved in the reproduction of this species (see section on Life History) and may affect its temperature tolerance, since Marzolf (1965) collected them only at night in the shallow warm waters of Lake Michigan.

d) Depth

P. hoyi is typically most abundant at the depth of the junction of the sublittoral and profundal zones and then becomes less common, but is still present in large numbers, in the profundal (Cooper 1962, Alley 1968), where they were found at depths of almost 600 m (Great Slave Lake, Rawson 1953). They have rarely been collected at depths of <10 m. Other distributions recorded include: Great Slave Lake, maximum numbers at 0-5 m, a decline between 5 and 25 m, then an increase at 25-30 m (Rawson 1953); Lakes Huron and Michigan, maxima at 15-25 and 35-45 m, less at all other depths but still common in the profundal (Henson 1970). These and other minor variations from the typical distribution were attributed to the influences of temperature (Larkin 1948, Rawson 1953), changes in slope of the lake bottom (Henson 1970) and competition from shallow water amphipods (Juday and Birge 1927).

e) Substrate

Although in most lakes P. hoyi is most common in the profundal or at the sublittoral/profundal junction, many studies of its substrate/density distribution show that it has a preference for sandy or silty substrates, or at least does not select fine clay sediments. Adams and

Table 9. Life cycle lengths, biomass and production estimates, and turnover ratios for Pontoporeia spp.

Author	Water Body	Species	Production(P) (mg/m ² /yr, wet weight)	Mean Biomass (B)(mg/m ² wet weight)	Life Cycle	Turnover ratio (=P/B)
Green (1971)	Cayuga L.	<u>P. hoyi</u>	1810.3 ³	427.9	1+yr	4.23
Lubner (1979)	Michigan L.	<u>P. hoyi</u>	2890-5950	2560- 5236	1,2, and 3? yr.	-
Kužmenko (1969)	Krasnoe L.	<u>P. affinis</u>	3462 ¹ -2816 ²	917.15 ¹ -638.64 ²	1+yr	3.8 ¹ -4.4 ²
Cederwall (1977)	Baltic Sea	<u>P. affinis</u>	19393 ³	10206.8	2+yr	1.9
Bekman (1959)	L. Baikal	<u>P. affinis</u>	-	-	2+yr?	3.0
Greze (1951)	Yenisei R.	<u>P. affinis</u>	-	-	1+yr	3.44
Bekman (1959)	Angara R.	<u>P. affinis</u>	-	-	2+yr?	2.5

¹ 1964-65

² 1965-66

³ Converted from dry weight assuming dry weight = 16.5% wet weight (Baychorow and Semenchenko (1977)).

Kregear (1969), Henson (1970), Nalepa and Thomas (1970), Cook (1975), Barton and Hynes (1976), Kraft (1979) all found P. hoyi to be most abundant on sandy or silty substrates. Henson (1970), however, noted that clean 100% sand had few Pontoporeia. This is in agreement with Marzolf (1963) who, though he did not find a correlation between depth, sand or loss on ignition, did find a correlation between density of P. hoyi and bacteria counts. In contrast, Loveridge and Cook (1976), Freitag et al. (1976) and Dermott (1978) found little or no correlations with substrate type.

Adams and Kregear (1969) suggested that P. hoyi was most abundant on coarse substrates in Lake Superior because of its ability to exist in unstable environments. This, at first glance, appears to be an unusual ability for an animal that was regarded as a profundal species and has been so well studied in profundal situations. It is apparent, as more littoral studies are carried out and as more populations are studied (e.g. Lake Winnipeg), that P. hoyi is either a plastic species with several ecotypes or several species.

f) Production

Production estimates are available for two populations of P. hoyi and for five populations of P. affinis. These together with the mean standing crop and annual turnover ratios $\left(\frac{\text{production}}{\text{mean biomass}}\right)$ for each population are presented in Table 9. Production of P. hoyi varied widely from water body to water body, but turnover ratios, which are a better indicator of productivity, being measures of the rate at which biomass is replaced in a system, are relatively consistent at ≈ 2 for Pontoporeia with a 2 year life cycle and 3.5-4.5 for populations with a 1 yr cycle (Table 9). In a discussion of production of freshwater macrobenthos,

Waters (1969) suggested that animals with a one year cycle should have a turnover ratio of 3-4, while animals with a longer life cycle should have a smaller one. Obviously Pontoporeia spp. fit this prediction rather well. Pontoporeia spp. vary their life cycle lengths in relation to the day-degrees to which they are exposed, thus turnover ratio can also be expected to be related to the mean temperature of their environment. Johnson and Brinkhurst (1971) compared turnover ratios of benthic macroinvertebrates along a transect through the Bay of Quinte to Lake Ontario proper. They were able to show that turnover ratio approximately equalled one tenth of the mean temperature squared and thus that production (in K_{cals}) was equal to mean biomass times one tenth of the square of mean temperature. No attempt has been made to test this model against estimates of Pontoporeia spp. production.

Appendix II. Density ($\#/m^2 \pm S.D.$) of P. hoyi at the various stations and sampling times.

Station	Mean Depth(m)	June 4-12	July 4-17	July 24-Aug 1	Sept 2-10	Oct 3-13	Oct 27-31	Mean all Cruises	
South Basin	1	4.5	-	-	-	0	-	0	
	2	5.5	-	0	0	0	0	0	
	3	4.5	0	0	0	0	0	0	
	3c	5.0	-	-	0	0	0	0	
	4	7.5	0	0	0	0	0	0	
	5	10.5	-	44± 77	0	0	0	11± 39	
	6	11	-	-	0	0	0	0	
	7	6.5	0	30± 51	0	0	0	5± 21	
	8	8.0	0	0	0	0	0	0	
	9	8.0	0	0	0	-	-	0	
	10	13.5	0	0	0	0	0	0	
	11	10.5	-	-	-	0	-	0	
12	11	-	-	15 26	489± 847	0	0	126± 422	
Narrows	13b	13.5	-	0	0	-	-	0	
	14	9.0	1748±1130	2089± 126	1511±1232	815± 228	904± 447	504± 112	1262± 832
	16	9.5	-	3600±1615	4207± 607	3081±1169	1481± 515	2444± 511	2962±1284

...continued

Appendix II (continued)

North Basin	17	13.0	-	5588±3873	4620±3790	-	8547± 578	-	6252±3239
	18	16.0	2948±1259	1748± 454	2326± 26	1644± 267	1570± 848	-	2047± 813
	19	16.5	-	6± 11	844±1270	-	-	-	425± 925
	20	15.5	-	-	1355± 419	7644±3279	-	1077± 185	3335±3485
	21	16.5	-	-	3810±2447	89± 89	3065± 891	2000±2120	2241±2095
	22	15.0	-	25± 44	4812±1016	785±1137	-	-	1874±2369
	23c	16.0	-	0	0	74± 93	0	30± 51	21± 50
	23e	16.5	0	0	0	15± 26	44± 0	-	12± 20
	25	15.0	0	15± 26	15± 26	30± 26	0	30± 26	15± 22
	26	14.5	0	0	30± 51	0	0	-	6± 23
	27	7.0	3051±2742	4533±3164	5320±1004	-	2889±1244	-	3948±2187
	28	10.0	-	3148±2770	4482±2782	2237±3874	-	3199± 0	3267±2709
	31	11.0	-	2381± 520	3689±3962	7096±1713	3066±1712	-	4058±2692
	33	7.50	-	5066±3159	6484±2763	-	-	-	5775±2806
	35	16.5	-	0	0	0	0	-	0
	39	17.5	0	0	0	0	0	0	0
	41	14.5	0	30± 26	0	0	0	-	6± 16
	43	6.0	0	6± 11	533± 924	-	-	-	180± 533
	45	13.5	6± 11	557± 569	749± 505	0	-	-	328± 475
	48	17.0	0	0	0	0	0	0	0
50c	10.5	-	25± 22	0	0	0	-	6± 15	

...continued

Appendix II (continued)

Narrows	50b	6.5	-	123 63	0	-	-	-	62 79
	51	4.0	0*	11243 2375	15 26	3096 5362	0	-	4785 5818 (excluding June sample)
	52	10.0	4910 717	7788 1396	10490 1806	6666 5887	3066 664	-	6584 3391
	54	12.0	-	-	-	-	-	3126 4311	3126 4311
South Basin	57	11.0	0	0	0	0	0	-	0
	59	11.0	15 26	0	0	0	0	0	3 10
	60	9.5	0	0	0	0	0	0	0
	60b	8.5	-	0	0	0	0	-	0
	60c	8.5	-	-	0	0	0	-	0
	61	9.0	0	0	0	0	0	0	0
	62	6.0	-	-	0	-	0	-	0
63	6.5	0	0	0	0	0	0	0	
Narrows	64	15.5	-	0	15 26	0	0	0	3 11
	65	8.0	-	764 171	6 11	-	-	-	385 429
	66b	4.5	-	-	15 26	-	-	-	16 26
	68	13.0	-	455 498	4124 2361	-	1066 423	109 153	1438 1961
	69	10.5	-	1540 1431	3033 1633	1215 810	-	-	1929 1496

* Station location different during this cruise

Appendix III. Data used in multi-linear regression analyses.

Station	Mean(ln #/m ² +1)	Max. bottom Temperature	Depth	% Loss on Ignition	Arcsin % Sand	Arcsin % Silt	Arcsin % Clay	Conductivity	Secchi
2	0	21.4	5.5	12.5	6.8	49.2	39.89	480	0.3
3	0	21.9	4.9	14.6	13.31	44.60	42.36	600	0.35
3c	0	22.3	5.2	13.7	7.49	55.37	33.58	550	0.20
4	0	20.6	7.5	10.8	26.28	37.23	41.44	400	0.3
5	0.95	20.2	10.5	11.9	3.63	39.52	50.24	275	0.6
6	0	20.0	9.5	12	11.83	50.3	37.23	155	0.8
7	0.57	20.0	6.2	15.1	25.33	55.80	21.39	99	0.75
8	0	20.2	8.2	13.2	5.13	44.78	44.78	110	0.85
10	0	19.6	11.5	12.1	5.44	32.01	57.42	175	0.9
12	2.24	19.6	10.9	2.7	61	21.97	17.05	220	1.0
57	0	18.9	10.3	9.5	4.055	40.34	49.37	240	0.9
59	0.46	19.8	10.3	9.4	7.71	33.52	55.37	260	0.95
60	0	20.2	9.5	9.2	4.44	33.90	55.73	355	0.9
60b	0	20.2	8	15.8	8.33	34.33	54.39	340	0.35
60c	0	19.9	8.2	13.5	5.44	42.48	47	460	0.25
61	0	20.0	8.8	9.6	5.13	41.67	47.87	370	0.75
14	7.03	20.3	9.1	8.8	27.73	49.08	31.11	205	0.7
51	6.71	20.8	6.5	15.4	25.33	45.34	33.9	48	0.85
52	8.71	18.5	10.3	7.4	17.56	28.59	55.92	118	0.6

...continued

Appendix III (continued)

Narrows	.54	8.83	20.1	12	12.2	10.14	44.43	43.80	163	0.7
	64	0.55	19.2	16.5	10.4	4.28	33.02	55.37	310	0.5
	68	6.53	21.3	13.1	9.3	43.45	32.71	29	163	0.4
	17	8.71	17.0	13.3	5.2	44.66	29.13	31.24	250	1.3
	18	7.59	17.8	16	10.8	10.78	56.6	31.18	245	1.1
	21	7.09	17.3	17	4.6	39.64	29.4	36.39	290	1.8
	23c	1.55	17.3	16.3	8.5	4.44	41.21	48.45	300	1.8
	27	8.25	17.5	7	21.2	11.09	59.54	27.97	335	1.2
	31	8.22	16.2	11	10.3	63.22	23.97	11.24	315	1.9
	35	0	17.0	16	8.8	4.05	55.3	34.39	290	2.1
North Basin	39	0	17.5	17.3	11.6	38.65	36.99	29.87	310	2.6
	41	0.684	17.6	15	10	5.74	49.84	39.58	318	2.4
	48	0	17.7	16.5	9.5	7.71	30.66	58.18	207	1.0
