

A Review of the Research on the Benthos of Lake Winnipeg

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Central and Arctic Region Department of Fisheries and Oceans Winnipeg, Manitoba R3T 2N6

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ABSTRACT

Flannagan, J.F., D.G. Cobb, and P.M. Flannagan. 1994. A review of the research on the benthos of Lake Winnipeg. Can. Manuscr. Rep. Fish. Aquat. Sci. 2261: iv + 17 p.

A survey of the benthos of Lake Winnipeg in 1928-1930, established some baselines against which the results from a survey in 1969 by staff of the Freshwater Institute could be compared. Reports from the Manitoba Provincial Government provided some results intermediate in time between the former two surveys. Comparison of the results reported in all of these documents is complicated by the various methodologies used. The first survey used a very coarse mesh to sieve their samples, later surveys used finer mesh and captured more animals, thus it is considered that reductions from the initial 1928-1930 benthic invertebrate densities were more significant than increases.

The most obvious changes between the 1920's survey and 1969 were: <u>Diporeia brevicornis</u> was essentially eliminated from the South Basin; the original two species of Trichoptera were eliminated from the South Basin and their distribution was restricted elsewhere in the lake, a new pollution tolerant species of Trichoptera has colonized and become widespread and abundant in the South Basin and has become relatively common in the Narrows; there has been a loss of production and a change in the relative proportion of the two profundal species of Ephemeroptera. In general, it appears that changes are most drastic in the South Basin and moderate with latitude.

In light of the present knowledge of the benthic fauna of the Lake, the potential effects of climatic change and introduction of exotic species are discussed.

Key words: Benthos; Lake Winnipeg; Oligochaeta; Hirudinea; Crustacea; Ephemeroptera; Plecoptera; Trichoptera; Chironomidae; Mollusca.

RÉSUMÉ

Flannagan, J.F., D.G. Cobb, and P.M. Flannagan. 1994. A review of the research on the benthos of Lake Winnipeg. Can. Manuscr. Rep. Fish. Aquat. Sci. 2261: iv + 17 p.

Une étude sur le benthos du lac Winnipeg réalisée en 1928-1930 fournit des données de référence permettant de comparer les résultats obtenus en 1969 par une équipe de l'Institut des eaux douces, et certains rapports du gouvernement du Manitoba contiennent des données pour l'intervalle séparant ces études. Cependant, la diversité des méthodes employées complique la comparaison des résultats : pour les échantillons de la première étude, on a utilisé un tamis à mailles très grossières, alors que pour ceux des études ultérieures on a utilisé un tamis plus fin et capturé plus d'animaux. On peut donc considérer que les baisses de densité relevées chez les invertébrés benthiques depuis 1928-1930 sont plus significatives que les augmentations.

Les changements les plus évidents survenus entre les années 1920 et 1969 sont les suivants : le <u>Diporeia brevicornis</u> a presque disparu du South Basin; les deux espèces de trichoptères présentes en 1928-1930 ont aussi disparu du South Basin, et leur répartition s'est restreinte dans les autres secteurs du lac; une nouvelle espèce de trichoptère tolérant la pollution a envahi le South Basin, y est devenue abondante et répandue et est en outre devenue relativement commune dans le secteur des Narrows; on a observé une perte de production chez les deux espèces d'éphéméroptères de la zone profonde ainsi qu'une modification de la proportion relative de ces espèces. De manière générale, on constate que les changements sont très prononcés dans le South Basin et plus modérés dans les secteurs plus au nord.

Les auteurs examinent également les effets possibles du changement climatique et de l'introduction d'espèces exotiques, à la lumière des connaissances actuelles sur la faune benthique du lac Winnipeg.

Mots-clés: Benthos; lac Winnipeg; Oligochaeta; Hirudinea; Crustacea; Ephemeroptera; Plecoptera; Trichoptera; Chironomidae; Mollusca.

INTRODUCTION

Lake Winnipeg, a remnant of Glacial Lake Agassiz, is the eleventh largest (by area) freshwater lake in the world and the seventh largest in North America. Bordered on the north and east by the Precambrian Shield, and on the south and west by the Central Plains, the lake is the focal point of rivers draining its 953,250 km² watershed. It is extremely shallow relative to its area and does not stratify thermally during the open water season. This, together with the high nutrient load entering from the watershed, especially the south and western parts, have resulted in the lake being highly productive and supporting a very large commercial fishery. Compared to other Canadian Great Lakes. with the possible exception of Lake Erie, the offshore benthos of Lake Winnipeg are relatively well known. This knowledge results from three main sources: 1) a survey of the benthos of several large Manitoban lakes related to their capacity to support fish, carried out by Ferris Neave and Alexander Bajkov in the late 1920's and early 1930's (Bajkov 1930; Neave 1932, 1933, 1934); 2) a "baseline survey" of the physical, chemical and biological condition in the lake carried out by staff of the Freshwater Institute (FWI) in 1969, when it was thought that some major changes in the lake's drainage basin may have been influencing the lake (benthos papers include: Flannagan 1979; Flannagan and Cobb 1981, 1984, 1991, 1994; Chang et al. 1992, 1993, 1994); and 3) the continuing program on the lake carried out by biologists from the Fisheries Branch of the Manitoba Provincial government (many manuscript reports including Rybicki 1963, 1966; Stone and Cober 1965; Crowe 1969, 1972a, b, 1973a, b; Slack 1973: Kristofferson et al. 1975). These latter publications are unrefereed internal Departmental reports not generally available to the scientific community, thus reference will only be made to them when it is considered that the information they contain is not available elsewhere.

Ekman grabs of various sizes, and mesh sieves of 0.2-1.27 mm opening were used in all surveys, except for some Provincial government studies, where Ponar and Peterson grabs were used (Table 1). Comparisons using the latter two grabs or widely different mesh sizes must be carefully made, since the use of different grabs (Flannagan 1970) or different mesh sizes (Reish 1959) can affect species counts and abundance estimates.

This report attempts to collate the existing knowledge of the species composition, distribution, life history, production and changes in the benthos of Lake Winnipeg. As a result, it will be possible to better understand changes to the lake ecosystem. Potential threats to the present lake biota include: 1) direct introduction of undesirable species (e.g. zebra mussels) via inter-basin transfer of boats; 2) diversion of water originating Mississippi/Missouri watershed into the Lake Winnipeg watershed (e.g. Garrison Dam and diversion in the north-central United States) perhaps providing the necessary water routes required for the introduction of exotic species (Flannagan and Flannagan 1982); and 3) predictions of climate warming, and its effect on water temperature and water supply.

RESULTS AND DISCUSSION

The reported physical and chemical characteristics of Lake Winnipeg (Table 2) vary widely, partly because of seasonal and annual variation in water supply to and discharge from the lake and their attendant effects on physical and biological characteristics of the lake, and partly because the various studies often did not include the whole lake.

In addition to the offshore collections of benthos, shore collection of adults by Neave (1934), light trap samples collected in 1969 and 1971 by FWI staff (Chang et al. 1994), and occasional samples from the FWI collection have provided a reasonably good species list of the inshore benthos. In total, 413 benthic invertebrate species have been recorded or collected from the lake (Table 3).

OLIGOCHAETA

Bajkov (1930) did not identify to species the oligochaetes he recorded from the Lake. He collected two oligochaetes m² (0.4% of the fauna) in the South Basin, and a mean of 18.2 m² (3% of the fauna) from the whole lake (Table 4). Crowe (1972b), in a summary of the changes in the South Basin of the lake from 1962-1969, recorded three species: Limnodrilus hoffmeisteri, L. sp. and Tubifex tubifex as accounting for 95-98% of the oligochaetes. She recorded densities of oligochaetes varying from >1400 ·m² in the south part of the South Basin to 275 m² in the north. On

average, these animals represented 15% of the fauna.

In a study in the Narrows area, Slack (1973) found the oligochaetes represented 2.9-35.8% of the macroinvertebrate fauna. He did not report actual numbers.

Rybicki (1966) found that oligochaetes accounted for 30 and 20% of all macrobenthos collected from the North Basin of the Lake in 1963 and 1964. In a survey of the same areas in 1974, Kristofferson et al. (1975) recorded oligochaetes to represent only about 2% of the macrobenthos.

Chang et al. (1992) reported 29 taxa of oligochaetes from areas of the lake deeper than 4 m. Of these, 10 species occurred throughout the lake, one species was collected only from the South Basin, no species were restricted to the Narrows basin and seven species were restricted to the North Basin. The remaining species occurred in two basins. The densities of oligochaetes were 461, 160 and 566 m⁻² and they represented 25.8, 4.7 and 17.9% of the fauna in the South, Narrows and North Basins, respectively (Table 4). Use of Saether's (1980) Oligochaete indicator communities lake classification system, developed from the Okanagan lakes on the data of Chang et al. (1992), indicated that the South Basin was eutrophic and the North Basin more oligotrophic, but provided no clear classification of Lake Winnipeg or its basins. For example, Limnodrilus profundicola, which in the Okanagan lakes was part of the oligotrophic community, was most common in the South Basin of Lake Winnipeg, off the mouth of the Red River and the Winnipeg River. The varying methodologies used in the studies referred to above could account for what appears to be a large increase in the oligochaetes, especially in the South basin. For example, the collections of only a few Oligochaetes by Bajkov (1930) can be attributed to his use of a sieve of mesh size openings in excess of 1 mm (Reish 1959). Similarly, the apparent temporary decline of oligochaetes in the North Basin recorded by Kristofferson et al. (1975) may be due to their use of a coarse mesh screen. Even if there was an increase in the density of oligochaetes from the 1920's to 1970's, it is not comparable with the increases from 6,000 to 154,000 oligochaetes m² attributed to increased sedimentation resulting from hydroelectric development in Lake Randsfjorden, Norway (Sloried 1994) or the increases up to 40,000⋅m⁻² attributed to organic pollution in the Detroit River area of Lake Erie (Carr and Hiltunen

1965). Thus, increasing eutrophication in the South Basin, if present, appears to be minor.

HIRUDINEA

Eight species of leeches have been recorded from the offshore areas of Lake Winnipeg (Table 3). Bajkov (1930) did not identify his leeches beyond Order. He recorded 1.9 leeches-m⁻² (≈0.4% of the fauna) in the South Basin and about 2.3 m⁻² (<0.4% of the fauna) in "the mud bottom areas" of the lake. The provincial reports generally do not separate leeches from "others". Freshwater Institute survey collected eiaht species, however, with the exception of Helobdella stagnalis and Moorebdella fervida, they were collected only sporadically and in very low numbers (Table 5). The FWI survey recorded approximately the same densities of leeches in each of the three basins and never exceeded 0.6% of the benthos (Table 4). Since only the Freshwater Institute survey identified leeches to species, and since there appears to be little change in the density of leeches from 1930's to 1969, we are unable to say if there have been changes in the leech fauna since the 1930's.

CRUSTACEA

Six benthic crustacean species have been collected from Lake Winnipeg (Table 3). Other than their presence, no further information on the three littoral species in Lake Winnipeg, <u>Hyallela azteca</u>, <u>Gammarus lacustris</u> and <u>Orconectes virilis</u>, is available. <u>Mysis relicta</u> is profundal and was collected in all three basins during the FWI survey (Flannagan and Cobb 1994), but, probably because of its vertical migratory behaviour, it was collected only rarely (Table 4). Bajkov (1930) also collected it in all three basins and only rarely.

<u>Caenestheriella setosa</u> was collected in all three basins by Flannagan and Cobb (1994), but was only common in the Narrows Basin where it averaged 13 individuals m² and 0.4% of the fauna (Table 4). Bajkov (1930) collected it (as <u>Esteria mexicana</u>) in about twice the densities recorded during the FWI survey (Table 4). In his survey, they represented almost 1% of the total fauna. Generally the Provincial government reports do not separate this species.

<u>Diporeia</u> <u>brevicornis</u> is by far the most common single offshore benthic species in the

lake, both historically and now. Bajkov (1930) calculated that these animals (as Pontoporeia hoyi) varied from 320-500·m⁻² ($\bar{x} = 455.5$) in 1928 and 1929 in the various basins and the lake itself (Table 4). Total Amphipoda accounted for an average (1928, 1929) standing crop of 20,517 kg per square mile ($\bar{x} = 7.9 \text{ g} \cdot \text{m}^{-2}$ wet weight), 63% by number, of the benthos (Bajkov 1930). Flannagan and Cobb (1994) recorded a mean of 1378·m⁻², 0.4-72% of the fauna in 1969 (Table 4), while Flannagan (1982) estimated a mean annual standing crop of 2.2 and 0.99 g·m⁻² in the Narrows and North Basins, respectively. The differences in weight of individual animals (standing crop/density) and of density between 1920's and 1969 can be explained by Bajkov's use of a coarse mesh which would perhaps eliminate the smaller animals and by the fact that Bajkov's data included Gammarus and Hyallela, which are larger than Diporeia. However, the almost complete elimination of the species from the South Basin (Flannagan and Cobb 1994) cannot be attributed to methodological differences, since a smaller mesh size should have resulted in increased numbers. The cause(s) of this elimination, although unknown, are probably the same as those causing the changes in Ephemeroptera and Trichoptera discussed below.

Flannagan (1982) estimated that production of this species (as P. hovi) in the Lake was about 7.4 and 2.3 g·m² yr¹ in the North and Narrows Basins, respectively, giving an annual production for the lake of 67,000 tonnes. The importance of D. brevicornis as a food source for the fishes of Lake Winnipeg was documented by Bajkov (1930). Any changes in the lake which impact on the population of this species could have a catastrophic effect on the fishery. The elimination of this species from the South Basin (Flannagan and Cobb 1994) means a production loss in the area of 20,000 tonnes [basin area about the same as the Narrows and Bajkov's population in the South Basin about three quarters that of the Narrows (Table 4)].

Flannagan (1982) showed that the life history of <u>D</u>. <u>brevicornis</u> in the lake extended over 2+ years, the young being released in mid-May to early June, maturity being achieved in the winter of the second year, and only a few senescent females surviving into a third summer. Growth did not occur in any cohort of this species from July to October, the warmest part of the year. This diapause probably allows this cold stenothermic species to survive in such a warm lake and undoubtedly accounts for the apparent

contradiction of haustoriids exhibiting a one year life cycle in cold water and a two year cycle in warm waters.

EPHEMEROPTERA

In total, 18 species of Ephemeroptera have been recorded from the lake (Table 3). Of these, two species extend into the offshore areas and were considered to be so important to the feeding of the commercial fishes of the lake by Bajkov (1930) that their life history, distribution and relative abundance were investigated by Neave (1932). Flannagan (1979) and Flannagan and Cobb (1984) also studied their life cycle, distribution and production. The offshore species, Hexagenia limbata and H. rigida together (Bajkov did not separate them), represented 1.33-24.33% (\bar{x} = 7.9%) of the benthic fauna in 1928-1929 (Bajkov 1930). Neave (1932), in a more extensive and intensive study carried out in July and August of 1929 and 1930, collected 4.5 H. rigida·m⁻² and 62 H. limbata ·m² in the South Basin, 44 and 94·m² in the Narrows, and 0 and 10·m⁻² in the North Basin of these two species, respectively. The two species together represented 0.8-6.0% ($\bar{x} = 2.0\%$) of the fauna in 1969, with densities varying from 108·m⁻² in the South Basin, 162·m⁻² in the Narrows to 25 ·m⁻² in the North Basin (Table 4). The large mesh size used by Bajkov and Neave should have resulted in the earlier surveys producing densities lower than those found by Flannagan (1979). In fact, this latter author recorded higher densities in the North Basin, similar densities in the Narrows, and about a 20% decrease in the South Basin, perhaps suggesting some South to North impact. Flannagan and Cobb (1984) calculated the annual production of these two species in each basin and in the whole lake. In order to make Neave's (1932) data comparable with theirs, they used the relative proportion of Hexagenia in their July and August samples to calculate changes in production of Hexagenia from 1929-1930 to 1969. showed a whole lake reduction in production of 28%, from 1932 to 1969 (121,291 to 86,902 tonnes). The South and Narrows Basins showed 27 and 46% reduction while the North Basin increased by 257%. If the reduction in Diporeia is added to the estimated reduction in Hexagenia, a total reduction of over 44,000 tonnes of annual production of the two most important fish food species has occurred in the period 1928-1930 to 1969.

Neave (1932) suggested a two-year life cycle for both <u>Hexagenia</u> species throughout the lake. Flannagan (1979) clearly showed that both species have a 14-month alternating with a 22-month life history in the South Basin, a two-year life history in the North Basin, and a mixture of both life history types in the Narrows Basin, the changes caused by the decreasing day-degree availability with increasing latitude. This flexibility in life history and its relationship with temperature suggest that global warming could have a large positive effect on the production of <u>Hexagenia</u> in Lake Winnipeg.

Flannagan (1979) also noted that the relative proportions of <u>H</u>. <u>limbata</u> to <u>H</u>. <u>rigida</u> had changed from 7:1 in Neave (1932) to 4:1 in 1969. He offered no explanation for this change, but as <u>H</u>. <u>rigida</u> has completely replaced <u>H</u>. <u>limbata</u> in the Red River in Winnipeg over the last 30 years, it suggests that causative factor(s) of this change originate in the Red River, in or above the City of Winnipeg.

PLECOPTERA

Only two species of Plecoptera, <u>Isoperla bilineata</u> and <u>Acroneuria lycorias</u>, have been recorded from the lake (Table 3). Both species are associated with the rocky shorelines common in some areas of the lake. No investigation of these stoneflies has been made.

TRICHOPTERA

Eighty-seven species of caddisflies have been recorded from the lake (Table 3). Bajkov (1930) recorded 2-39 ($\bar{x} = 8.2$) Tricoptera·m⁻², comparable to the 5-19·m⁻² ($\bar{x} = 8.5$) recorded in 1969 (Table 4). Neave (1933) showed that the two offshore species. Phryganea cinerea and Molanna flavicornis, differed in their ability to colonize the offshore areas. P. cinerea was distributed throughout the whole lake while M. flavicornis was apparently limited to areas with coarse sand for case buildina. Neave (1933) found 2.4 and 4.7 P. cinerea m⁻² in the South and North Basins, respectively and 10-15 M. flavicornis m2 throughout the lake. By 1969, both species had disappeared from the South Basin, and M. flavicornis, and perhaps both species, were much reduced in the North Basin and even more in the Narrows (Flannagan and Cobb 1981), suggesting a south to north impact. Flannagan and Cobb (1981) also noted that a species new to the offshore areas of the Lake since the earlier surveys, <u>Oecetis inconspicua</u> was widespread in the South Basin (up to 180·m⁻²), common in the Narrows (1-25·m⁻²) and absent from most of the North Basin in 1969. They pointed out the apparent South to North density gradient, and suggest that this species was pollution tolerant and in the process of replacing the other two species. It is perhaps relevant in view of the mercury contamination problem in Lake Winnipeg at the time of the 1969 survey, that <u>O. inconspicua</u> was the only insect species present in an acid strip mine effluent, heavily contaminated with heavy metals in Southern Illinois (Zullo and Bates 1983).

CHIRONOMIDAE

Two hundred and twenty-two species of chironomids have been recorded from the Lake (Table 3), mostly by Chang et al. (1993, 1994). Bajkov (1930) did not generally identify his specimens beyond family, and the Provincial reports mention only a few species by name. Bajkov collected 18-54 ($\overline{x}=24$), chironomids m^2 during his whole lake survey. The much larger densities recorded for the whole lake during the FWI survey (Table 4, 346-628· m^2 , $\overline{x}=519$) undoubtedly are a result of the use of fine mesh sieves in this later survey. Similarly, the variation in proportional representation (Table 4) between Bajkov's and the FWI survey can be attributed to the selectivity of the methods used.

No published information exists on the life history or production of any of the chironomid species within Lake Winnipeg, although from the literature the species present have life cycles varying in length from a few weeks to one year; this, together with the large size of some of the faster growing species, suggests that the production could be very high.

Saether (1979) analyzed the chironomid communities in the lake and its basins, and concluded that the South Basin was moderately eutrophic, the Narrows mesotrophic and the North Basin moderately oligotrophic to mesotrophic. He cautioned that because of polymixis and light limitation by turbidity, a relationship between total phosphorus to mean depth and the trophic levels could not be expected. It is, however, interesting that the trophic level indicated show marked increasing oligotrophy from South to North (Saether 1979, Fig. 3).

As in several of the other groups reviewed, a few species dominate the chironomid fauna, e.g. Polypedilum simulans and Cryptotendipes casuarius account for almost half the density of the chironomid fauna of the South Basin (Chang et al. 1993).

MOLLUSCA

Fifty species of molluscs have been recorded from the lake: 21 snails, 9 unionids, and 20 fingernail clams (Table 3). The densities of offshore molluscs in 1969 appear to have increased over the 1920-1930's by about 10x, although their frequency in the samples over the same period have just doubled (Table 4). Kristofferson et al. (1975) sampling in the North Basin, Crowe (1971) the South Basin, and Stone and Cober (1965) the North and South Basins, all used mesh sizes intermediate between those of the FWI survey and those used by Bajkov (1930) and collected intermediate densities of molluscs (200-300·m⁻²). It seems likely that the apparent increase in Molluscs shown in Table 4 can again be attributed to differences in methodology.

In the shallow South Basin of Lake Winnipeg, gastropods accounted for almost half of the molluscan fauna (266 of 554·m²), while they represented only about 25% in the deeper Narrows and North basins (Flannagan and Cobb 1991). In this study, three species, <u>Pisidium casertanum</u>, <u>P. lillieborgi</u> and <u>Probythinella lacustris</u> accounted for more than half of the molluscs in the South and North Basins, and almost half in the Narrows. Thus, as in the Ephemeroptera, Chironomidae and Crustacea, this, the second most common benthic group, is largely dominated by a few species.

SUMMARY OF RESEARCH AND POTENTIAL SOURCES OF FUTURE CHANGE

1. Changes from the 1928-1930 surveys to the 1969 survey

In general, increases in number over these two time periods could result from the different mesh sizes used. Decreases in densities, however, are likely to be real, as are changes in species or species composition, since both surveys relied on the best taxonomists available. Therefore, we conclude that there have been quite large changes in the lake bottom fauna over the above time period, and that these changes are largest in the South Basin and least in the North Basin.

Relative changes in the two species of <u>Hexagenia</u> in the Red River and Lake Winnipeg suggest that the cause may originate in the Red River in or above the City of Winnipeg. Since there have been no demonstrable large increases in oligochaetes, it seems likely that the changes are not the result of organic enrichment. Elimination of the original two species of Trichoptera, and their replacement by a species tolerant to heavy metals suggests that toxicity rather than eutrophication is the cause of the changes.

2. Potential effects of climatic warming

Global climate change (e.g. warming from increased greenhouse gas emissions), if in fact it is occurring, could have implications for water temperatures and water supply in central Canada (see review by Hengeveld, 1990). Advanced seasonal warming of water temperature, and higher mean temperature, as well as reduction of water supplies to Lake Winnipeg could significantly alter thermal and chemical conditions of the lake.

Three species of invertebrates have been identified as being particularly important as food for the commercial fishes of the lake: D. brevicornis and the two Hexagenia species. D. brevicornis, the single most abundant benthic species in the lake, is a cold stenotherm which appears to have its growth and reproduction limited to the cooler or cold times of the year. Increase in water temperature and especially in length of warm water season may further restrict the growth or perhaps interfere with the reproduction of this species. Hexagenia species and perhaps most of the species in the lake may be able to take advantage of both an increase in water temperature and extension of the season to increase their growth rates and thus, their production. However, changes in water temperature and season may also allow invasion of warm water species which could change the present communities with unknown effects on the fishery.

3. Potential for the introduction of exotic species

Many species recorded from the upper Mississippi and Missouri systems are not present in the Churchill/Nelson system. The reasons for this are mostly unknown but those which have been suggested range from there not being the correct environmental condition present to the physical lack of opportunity, such as a direct water route, said to be important for cross basin introductions (Flannagan and Flannagan 1982). In

many of the well known and well documented cases of introduction of exotic species catastrophic (at least from an anthropocentric point of view) effects have occurred, e.g. dandelions in North America, rabbits in Australia, zebra mussels in the Great Lakes, carp in North America, etc. However, although it seems reasonable to assume it has happened many times, we know little about those exotics which have been introduced and failed to establish. In the case of Lake Winnipeg where almost all groups are numerically dominated by only one or two species and where at least the commercial fishery appears to be reliant on only a few of species, it would seem prudent to avoid situations which would threaten to unbalance these few species.

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Table 1. Mesh sizes and grab types used by the various benthic workers on Lake Winnipeg.

Author	Mesh Size	Grab Used
Bajkov 1930	1.3 mm	Ekman ¹
Crowe 1969; 1972a, b; 1973a, b	1962-1967, 0.6 mm 1967-1970, 0.245 mm	1962-1970, Ekman ¹ , except Petersen (Sept. 1964) Ponar (Sept. 1967)
FWI, 1969 survey	Generally 0.2 mm except 0.4 on sand	Ekman²; Ponar on sand
Rybicki 1966	0.6 mm	Ekman ¹ (1963); Petersen (1964)
Slack 1973	0.2 mm	Ekman ³
Stone and Cober 1965	0.6 mm	Ekman ¹ (1962-1964) Petersen (1964)
Neave 1932, 1933, 1934	1.3 mm	Ekman ⁴

Sample area = 523 cm².
 Sample area = 225 cm².
 Sample area = 1000 cm².
 Sample area = 413 cm².

Table 2. Summary of published physical and chemical characteristcs of Lake Winnipeg.

Characteristic	Value	Source		
Maximum length	436 km	а		
Maximum width	111 km	а		
Surface area (km²)	23,750 24,200 24,530	a b, c d		
Maximum depth (m)	36 32 20 18 19	a e f b d		
Mean depth (m)	10.6 12.0 13.0	e a d		
Water level (m above sea level) 1927-1964	216.2-218.5	а		
Water residence time whole lake South basin	2.9-4.6 y 0.1-0.5 y	a, e a		
Secchi depth (m) whole lake North basin South basin	1-1.75 0.05-3.5 0.05-1.0	b g, e e		
Nutrient loading (t/y, 1969-1974) Total P Total N	2,980-10,570 47,020-108,260	a a		
Dissolved oxygen	near saturation, all year, all depths	g		
pH Whole lake range Whole lake range	6.8-8.4 6.8-8.8	b g		
Salinity, range (ppm)	220-560	С		
Sedimentation rate south basin	1 mm·y ⁻¹ 5 mm·y ⁻¹	h i		

a = Brunskill et al. 1980; b = Neave 1934; c = Bajkov 1930; d = Hutchinson 1957;

e = Brunskill 1973; f = Neave 1933; g = Brunskill et al. 1979; h = Brunskill and Graham 1979;

i = Kushnir 1971.

Table 3. List of benthic invertebrate taxa known from Lake Winnipeg.

Phylum Annelida
Superclass Clitellata
Order Lumbriculida
Family Lumbriculidae
Lumbriculus variegatus Muller

Order Tubificida

Family Enchytraeidae sp.

Family Tubificidae

<u>Tubifex</u> <u>tubifex</u> (Muller)

Limnodrilus angustipenis Brinkhurst and

Cook

L. <u>claparedianus</u> Ratzel
L. <u>claparedianus</u> var

L. <u>hoffmeisteri</u> Claparede

L. hoffmeisteri var

L. prufundicola (Verrill)

L. <u>udekemianus</u> Claparede <u>Isochaetides freyi</u> Brinkhurst

Ilyodrilus sp. var 1

1. sp. var 2

Rhyacodrilus sodalis (Eisen)

R. coccineus (Vejdovsky)

R. montana (Brinkhurst)

Aulodrilus americanus Brinkhurst and Cook

A. <u>limnobius</u> Bretscher A. <u>pigueti</u> Kowalewski

Family Naididae

Uncinais uncinata (Orsted)

Nais communis Piquet

N. variabilis Piquet

Slavina appendiculatata (d'Udekem)

Vejdovskyella comata (Vejdovsky)

Arcteonais lomondi (Martin)

Stylaria lacustris (L.)

Dero digitata (Muller)

Naididae sp.

Family Glossoscolecidae

Sparaganaophilus tamesis Benham

Class Hirudinaidea
Order Hirudinea

Sub-Order Rhynchobdellae

Family Glossiphoniidae

Placobdella montifera (Moore)

Helobdella nephiloidea (Graf)

H. stagnalis (L.)

H. papillata Moore

Glossophina complanata (L.)

Family Piscicolidae

Piscicola milneri (Verrill)

Sub-Order Pharyngobdellae

Family Erpobdellidae

Mooreobdella fervida (Verrill)

Mysobdella moorei (Meyer)

Phylum Arthropoda

Class Crustacea

Subclass Branchiopoda

Order Conchostraca

Family Cyzicidae

Caenestheriella setosa (Pearse)

Subclass Malacostraca

Order Amphipoda

Family Talitridae

Hyalella azteca (Saussure)

Family Haustoriidae

Diporeia brevicornis (Serg.)

Family Gammaridae

Gammarus lacustris Sars

Order Mysidacea

Mysis relicta Loven

Order Decapoda

Family Astacidae

Orconectes virilis Hagen

O. Ephemeroptera

F. Baetidae

Baetis cf. flavistriga McDunnough

Callibaetis pallidus Banks

F. Heptageniidae

Ecdyonurus hebe (McDunnough)

Heptagenia elegantula (Eaton)

H. pulla (Clemens)

Stenacron interpunctatum (Say)

Stenonema femoratum (Say)

Stenonema terminatum (Walsh)

F. Leptophlebiidae

Leptophlebia cupida (Say)

F. Ephemerellidae

Ephemerella sp.

F. Tricorythidae

Tricorythodes minutus Traver

F. Caenidae

Brachycercus prudens (McDunnough)

Caenis amica Hagen

C. latipennis Banks

F. Ephemeridae

Ephemera simulans Walker

Hexagenia limbata Serville

H. rigida McDunnough

F. Polymitarcidae

Ephoron album (Say)

Order Plecoptera

Family Perlodidae

Isoperla bilineata (Say)

Family Perlidae

Acroneuria lycorias (Newman)

Order Trichoptera

F. Psychomyiidae

Psychomyia flavida Hagen

F. Polycentropodidae

Neureclipsis bimacualta (L.)

N. crepuscularis (Walker)

N. validus (Walker)

Nyctiophylax affinis (Banks)

Phylocentropus placidus (Banks)

Polycentropus aureolus (Banks)

P. cinereus Hagen

P. flavus (Banks)

P. interruptus (Banks)

P. remotus Banks

F. Hydropsychidae

Cheumatopsyche campyla Ross

C. miniscula (Banks)

C. pettiti (Banks)

Hydropsyche alternans (Walker)

H. confusa (Walker)

H. morosa Hagen

H. scalaris Hagen

F. Hydroptilidae

Agraylea multipunctata Curtis

Hydroptila albicornis Hagen

H. armata Ross

H. consimilis Morton

H. hamata Morton

H. spatulata Morton

H. vala Ross

H. waubesiana Betten

H. wyomia Denning

Ithytrichia clavata Morton

Neotrichia sp.

Orthotrichia cristata Morton

Oxyethira serrata Ross

O. zeronia Ross

F. Phryganeidae

Agrypnia glacialis (Hagen)

A. improba (Hagen)

A. straminea Hagen

Banksiola crotchi Banks

Phryganea cinerea Walker

Ptilostomis ocellifera (Walker)

P. semifasciata (Say)

F. Limnephilidae

Anabolia consocia (Walker)

Asynarchus rossi (Leonard & Leonard)

Limnephilus canadensis Banks

L. externus Hagen

L. femoralis Kolenati

L. hyalinus Hagen

L. infernalis (Banks)

L. kennicotti (Banks)

L. minisculus (Banks)

L. moestus Banks

L. nimmoi Roy and Harper

L. ornatus Banks

L. parvulus (Banks)

L. secludens Banks

L. sericeus (Say)

L. thorus Ross

Nemotaulius hostilis (Hagen)

Pycnopsyche subfasciata (Say)

F. Lepidostomatidae

Lepidostoma togatum (Hagen)

F. Molannidae

Molanna flavicornis Banks

M. uniophila Vorhies

F. Helicopsychidae

Helicopsyche borealis (Hagen)

F. Leptoceridae

Ceraclea alagma (Ross)

C. ancylus (Vorhies)

C. annulicornis (Stephens)

C. arielles (Denning)

C. cancellata (Betten)

C. diluta (Hagen)

C. erratica (Milne)

C. resurgens (Walker)

C. tarsi-punctata (Vorhies)

C. transversa (Hagen)

Mystacides interjecta (Banks)

M. sepulchralis (Walker)

Nectopsyche albida (Walker)

N. candida (Hagen)

N. diarina Ross

Table 3, cont'd.

N. exquisita (Walker)

Oecetis avara (Banks)

O. cinerascens (Hagen)

O. immobilis (Hagen)

O. inconspicua (Walker)

O. ochracea (Curtis)

Trianodes aba Milne

T. baris Ross

T. frontalis (Banks)

T. tarda (Milne)

F. Brachycentridae

Micrasema scissum McLachlan

Order Diptera

F. Chironomidae

S.F. Tanypodinae

Tribe Coleotanypodini

Clinoptanypus (Clinotanypus) pinguis (Loew)

Coelotanypus scapularis (Loew)

Tribe Macropelpiini

Psectrotanypus dyari (Coquillett)

Tribe Procladiini

Procladius bellus (Loew)

P. (Holotanypus) culiciformis (L.)

P. (H.) denticulatus Sublette

P. (H.) freemani Sublette

P. (H.) paragretis Roback

P. (H.) sublettei Roback

Tribe Tanypodini

Tanypus (Tanypus) punctipennis Meigen

T. (T.) vilipennis (Keiffer)

Tribe Pentaneurini

Ablabesmyia (Karelia) illinoensis (Malloch)

A. (K.) pulchripennis (Lundb.)

A. (Ablablesmyia) aspera Roback

A. (A.) mallochi (Walley)

A. (A.) monilis (L.)

A. (Asyia) annulata (Say)

Conchapelopia currani (Walley)

C. telema Roback

Thelopelopia okoboji (Walloch)

Hayesomyia senata (Walley)

Thienemannimyia norena (Roback)

Guttipelopia guttipennis (v.d. Wulp)

Helopelopia sp. n.

Labrundinia pilosella (Loew)

Larsia sp.

Paramerina smithae (Sublette)

Subfamily Diamesinae

Tribe Diamesini

Potthastia longimanus Kieffer

Subfamily Prodiamesinae

Monodiamesa depectinata Saether

M. tuberculata Saether

Subfamily Orthocladiinae

Acricotopus nitidellus (Malloch)

Baeoctenus bicolor Saether

Brilla flavifrons (Johannsen)

Camptocladius stercornarius (De Geer)

Corynoneura lobata Edwards

C. scutellata Winnertz

Corynoneura n. sp.

Cricotopus (Cricotopus) annulator

Goetghebuer

C. (C.) abanus Curran

C. (C.) bicinctus (Meigen)

C. (C.) coronatus Hirvenoja

C. (C.) festivellus (Kieffer)

C. (C.) pilosellus Brundia

C. (C.) triannulatus Macguart

C. (C.) trifascia Edwards

C. (C.) varipes Coquillett

C. (C.) vierriensis Goetghebuer

C. (Isocladius) intersectus (Staeger)

C. (I.) ornatus (Meigen)

C. (I.) pilitarsis (Zetterstedt)

C. (I.) sylvestris (Fabricius)

Epoicocladius flavens (Malloch)

Heterotanytarsus sp. n.

Heterotrissocladius changi Saether

Hydrobaenus johannseni (Sublette)

Limnophyes brachytomus (Kieffer)

L. margaretae Saether

L. minimus (Meigen)

L. natalensis (Kieffer)

L. ninae Saether

L. pilicistulus Saether

L. pumilio (Holmgren)

Mesocricotopus thienimanni (Goetghebuer)

Metriocnemus sp.n.

Nanocladius anderseni Saether

N. cf. balticus (Palmen)

N. distinctus (Malloch)

N. cf. parvulus (Kieffer)

N. rectinervis (Kieffer)

Orthocladius (Eudactylocladius) dubitatus

Johannsen

O. (E.) mixtus (Holmgren)

O. (Orthocladius) dentifer Brundin

O. (O.) manitobensis Saether

O. (O.) nigritus Malloch

O. (O.) obumbratus Johannsen

Table 3, cont'd.

O. (Symposiocladius) lignicola Kieffer

Parakiefferella bathophila Kieffer

P. coronata Edwards

P. subaterrima (Malloch)

Parakiefferella sp.n.

Paraphaenocladius exagitans (Johannsen)

P. masthecus Saether

Psectrocladius (Allopsectocladius) flavus

(Johannsen)

P. (A.) nigrus Roback

P. (Psectrocladius) barbimanus (Edwards)

P. (P.) limbatellus (Holmgren)

P. (P.) simulans (Johannsen)

<u>P</u>. <u>(P.)</u> sp.n. A

P. (P.) sp.n. B

P. (P.) sp.n. C

Rheocricotopus (Psilocotopus) glabricollis

(Meigen)

Smittia aterrima (Meigen)

<u>S</u>. sp.n.A

S. sp.n.B

S. sp.n.C

Synorthocladius semivirens (Keiffer)

Thienimanniella xena (Roback)

Subfamily Chironominae

Tribe Tanytarsini

Subtribe Zavreliina

Stempellina sp.n. A

S. sp.n. B

S. sp.n. C

Subtribe Tanytarsina

Cladotanytarsus amandus Hirvenoja

C. atridorsum Kieffer

C. mancus (Walker)

C. viridiventris (Malloch)

Cladotanytarsus sp.n. (6 new species)

Micropsectra sp.

Neozavrelia sp.n.

Paratanytarsus laccophilus (Edwards)

Paratanytarsus sp.n. (6 new species)

Rheotanytarsus exiguus (Johannsen)

Tanytarsus allicis Sublette

T. confusus Malloch

T. curticornis Kieffer

T. dendyi Sublette

T. fimbriatus Reiss & Fittkau

T. inaequalis Goetghebuer

T. medius Reiss & Fittkau

T. mendax Kieffer

T. nemorosus Edwards

T. neoflavellus Malloch

T. norvegicus Kieffer

T. recens Sublette

T. usmaensis Pagast

Tanytarsus sp.n. (9 new species)

Tribe Pseudochironomini

Pseudochironomus articaudus Saether

P. badius Saether

P. crassus Townes

P. fulviventris (Johannsen)

P. middlekauvfi Townes

P. rex Hauber

Tribe Chironomini

Axarus scopula (Townes)

Chironomus (Camptochironomus)

pallidivittatus Malloch

C. (C.) tentans Fabricius

C. (Chaetolabis) atroviridis (Townes)

C. (Chironomus) anthracinus (Zetterstedt)

C. (C.) atrella Townes

C. (C.) atritibia Malloch

C. (C.) crassicaudatus Malloch

C. (C.) decorus Johannsen

C. (C.) maturus Johannsen

C. (C.) muratensis Ryser, Scholl & Wulker

C. (C.) plumosus (L.)

C. (C.) riparius Meigen

C. (C.) staegeroi Lundbeck

C. (C.) tuxis Curran

Cladopelma viridula (L.)

Cryptochironomus blarina Townes

C. digitatus (Malloch)

C. psittacinus (Meigen)

Cryptochironomus sp.n. A

<u>C</u>. sp.n. B

<u>C</u>. sp.n. C

<u>C</u>. sp.n. D

<u>Cryptotendipes</u> <u>casuarius</u> (Townes)

C. darbyi (Sublette)

C. emorsus (Townes)

C. pilicuspis Saether

Demicryptochironomus cuneatus (Townes)

Dicrotendipes botaurus (Townes)

D. leucoscelis (Townes)

D. milleri (Townes)

D. modestus (Say)

D. neomodestus (Malloch)

D. nervosus (Staeger)

Endochironomus nigricans (Johannsen)

E. subtendens (Townes)

Einfeldia synchrona Oliver

<u>E</u>. sp. A

<u>E</u>. sp. B

Harnischia curtilamellata (Malloch)

Microchironomus nigrovittatus (Malloch)

Microtendipes caducus Townes

M. pedullus pedullus (DeGeer)

Nilothauma sp. n.

Pagastiella ostanso (Webb)

Paracladopelma galaptera (Townes)

P. undine (Townes)

Parachironomus abortivus (Malloch)

P. digitalis Edwards

P. elodeae (Townes)

P. frequens (Johannsen)

P. parilis (Walker)

P. potamogeti (Townes)

P. tenuicaudatus (Malloch)

P. vitiosus (Goetghebuer)

P. sp. n. A

P. sp. n. B

Paralauterborniella nigrohalterale (Malloch)

Paratendipes albimanus (Meigen)

Phaenopsectra flavipes (Meigen)

P. obediens (Johannsen)

P. punctipes (Wiedemann)

Polypedilum (Pentapedilum) sordens

(v.d. Wulp)

P. (P.) tritum (Walker)

P. (P.) sp. n.

P. (Polypedilum) braseniae (Leathers)

P. (P.) fallax Johannsen

P. (P.) illinoense (Malloch)

P. (P.) laetum (Meigen)

P. (P.) nubeculosum (Meigen)

P. (Tripodura) albinodus Townes

P. (T.) digitifer Townes

P. (T.) griseopunctatum (Malloch)

P. (T.) halterale (Coquillett)

P. (T.) scalaneum (Schrank)

P. (T.) simulans (Townes)

Saetheria tylus (Townes)

Stenochironomus (Stenochironomus) hilaris

(Walker)

Stictochironomus devinctus (Say)

S. pictulus (Meigen)

S. rosenschoeldi (Zetterstadt)

Synendotendipes impar (Walker)

Tribelos jucundum (Walker)

Xenochironomus xenolabis (Kieffer)

Phylum Mollusca

Class Pelecypoda

Order Eulamellibranchia

Family Unionidae

Anodonta grandis grandis Say

Anodonta grandis simpsoniana Lea

Anodontoides ferussacius (Lea)

Fusconia flava (Rafinesque)

Lampsilis radiata siliquoidea (Barnes)

Lampsilis ventricosa (Barnes)

Lasmigona complanata (Barnes)

Ligumia recta (Lamark)

Strophites undulatus (Say)

Order Heterodonta

Family Pisidiidae

Subfamily Sphaeriinae

Sphaerium lacustre (Muller)

S. nitidum Clessin

S. partumeium (Say)

S. rhomboideum (Say)

S. simile (Say)

S. striatinum (Lamarck)

S. transversum (Say)

Subfamily Pisidiinae

Pisidium casertanum (Poli)

P. compressum Prime

P. conventus Clessin

P. ferrugineum Prime

P. idahoense Roper

P. lilljeborgi Clessin

P. milium Held

P. nitidum Held

P. obtusale Pfeiffer

P. punctiferum Guppy

P. subtruncatum Malm

P. variable Prime

P. walkeri Sterki

Class Gastropoda

Subclass Prosobranchia

Order Mesogastropoda

Family Viviparidae

Campeloma decisum (Say)

Family Valvatidae

Valvata sincera sincera Say

V. tricarinata (Say)

Cincinnatia cincinnatiensis (Anthony)

Probythinella lacustris (Baker)

Amnicola limosa (Say)

Amnicola walkeri Pilsbry

Subclass Pulmonata

Table 3, cont'd.

Order Basommatophora

Family Lymnaeidae

Fossaria exigua (Lea)

F. parva (Lea)

Pseudosuccinea columella (Say)1

Lymnaea stagnalis jugularis Say²

Stagnicola catascopium (Say)

S. elodes (Say)

Bulimnea megasoma (Say)3

Family Physidae

Physa jennessi skinneri Taylor

P. gyrina gyrina Say⁴

Family Planorbidae

Gyraulus parvus (Say)5

Promentus exacuous exacuous (Say)6

Planorbula armigora (Say)

Helisoma trivolvis subcrenatum (Carpenter)

H. pilsbryi infracarcinatum Baker

- 1. Probably as Succinea ovalis Say by Bajkov (1930).
- 2. As Lymnaea stagnalis appressa (Say).
- 3. As Lymnaea megasoma (Say).
- 4. Physa integra (Haldeman) recorded by Bajkov (1930) is an ecophenotype.
- 5. As Planorbulus parvus (Say) by Bajkov (1930).
- 6. As Planorbulus exacuous (Say) by Bajkov (1930).
- * Source of material (Bajkov 1930; Chang et al. 1991, 1993; Clarke 1973, 1981; Flannagan and Cobb 1991, 1994; Neave 1932a,b, 1934).

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Table 4. Comparison of density (number of animals·m⁻²) and % frequency (in parenthesis) of each taxon in the samples collected in each basin and the whole lake during the surveys of Bajkov (1930) and the FWI (1969).

	South Basin		Narrows Basin		North Basin		Whole lake	
	1928/29	1969	1928/29	1969	1928/29	1969	1928/29	1969
Oligochaeta	2 (0.4)	461 (25.8)	3 (0.4)	160 (4.7)	25 (4.2)	566 (17.9)	18.2 (2.9)	485.2 (16.1)
Hirudinea	1.9 (0.4)	10.7 (0.6)	6.6 (0.8)	9.3 (0.3)	1.9 (0.3)	8.2 (0.3)	2.7 (0.4)	8.7 (0.3)
Crustacea <u>Mysis relicta</u> <u>Caenestheriella setosa</u> <u>Diporeia brevicornis</u>	0.8 (0.2) 3.9 (0.8) 320 (62.8)	0.2 (0.01) 1.0 (0.06) 6.5 (0.4)	13.7 (1.7) 27.5 (3.5) 454 (57.4)	0.6 (0.02) 13 (0.4) 2457 (71.9)	0.7 (0.1) 0 (0) 483 (80.3)	0.2 (0.01) 0.3 (0.01) 1397 (44.3)	2.8 (0.45) 5 (0.8) 456 (73.5)	0.3 (0.01) 2.5 (0.08) 1378 (45.8)
Ephemeroptera	124 (24.3)	108 (6.0)	158 (19.9)	162 (4.7)	8 (1.3)	25 (0.8)	48.8 (7.9)	60 (2.0)
Trichoptera	3.3 (0.7)	18.7 (1.1)	39 (4.9)	13 (0.4)	2 (0.3)	5.4 (0.2)	8.2 (1.3)	8.5 (0.3)
Chironomidae	20.7 (4.1)	628 (35.1)	53.4 (6.8)	346 (10.1)	17.9 (2.9)	538 (17.1)	24.1 (3.9)	519 (17.3)
Mollusca	33 (6.5)	554 (30.9)	36 (4.6)	257 (7.5)	63 (10.5)	611 (19.4)	54.4 (8.8)	545 (18.1)
Total (number·m ⁻²)	510	1789	791	3418	601	3151	620	3008
Total number of grabs	200	285	44	141	165	261	409	687

Table 5. Distribution of leeches¹ collected during the FWI 1969 Lake Winnipeg survey.

Species	South Basin	Narrows	North Basin	Whole Lake
Helobdella stagnalis (L.)	6.6	5.2	9.4	7.3
H. nepheloidea (Graf)	0	0.2	0	0.04
H. papillata Moore	0.3	0.5	0	0.2
Moorebdella fervida (Verril)	1.1	2.1	1.0	1.3
Mysobdella moorei (Meyer)	0	0.3	0.1	0.1
Glossophina complanata (L.)	0.1	1.0	0.1	0.3
Placobdella montifera (Moore)	0	0	0	0.1
Piscicola milneri (Verrill)	0	0	0.2	0.1

¹ indentifications by Dr. R. Davies, University of Calgary.