Limnological and planktonic studies in the Waterton Lakes, Alberta

by R. Stewart Anderson and
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Abstract

Limnological studies were conducted in the main lake system in Waterton Lakes National Park from 1969 to 1975 to provide baseline data for management purposes. During 1972–75, 19 crustacean and 12 rotiferan species of zooplankton and a total of 164 species and subspecies of phytoplankton were identified from the three main lakes. Comparison with earlier studies and samples indicated little change in zooplankton species composition, although numbers appeared to have increased. Changes in species composition and increases in abundance have occurred in the phytoplankton.

During the study period, water temperatures, light penetration, water renewal rates, and most chemical parameters have remained fairly constant. Although enrichment by sewage may have been responsible for increases in plankton abundance, chemical and biological indicators suggest that the oligotrophic status of the lakes has not been impaired. Longitudinal circulation in Upper Waterton Lake probably contributed to a greater retention of nutrients in that lake in 1972 and 1973 than in 1974 and 1975. The effects of enrichment on the phytoplankton in the downstream lakes appeared to be greater in the latter two years.

A monitoring program using at least four stations along the main lake system and involving sampling at two discrete depths, one in the upper 5 m and the other below the thermocline, would be more useful for total lake assessment than more detailed effort at one or two stations.

Résumé

Des études limnologiques ont été effectuées de 1969 à 1975 dans le réseau principal de lacs du Parc national des lacs Waterton afin d'obtenir des données de référence à des fins de gestion. Entre 1972 et 1975, on a repéré dans les trois principaux lacs 19 espèces de crustacés, 12 de rotifères zooplanctoniques et 164 espèces et sous-espèces de phytoplancter en tout. L'examen des études et échantillonnages antérieurs indique peu de changements dans la composition des espèces de zooplancton bien que les populations semblent avoir augmenté. Par contre, on a noté des changements dans la composition des espèces phytoplanctoniques ainsi qu'une augmentation de leurs effectifs.

La température de l'eau, la pénétration de la lumière, le taux de renouvellement de l'eau et la plupart des paramètres chimiques sont demeurés assez constants au cours de la période d'étude. Même si l'enrichissement du milieu par les eaux usées semble expliquer l'abondance du plancton, les paramètres chimiques et biologiques n'indiquent pas de détérioration de l'état oligotrophe des lacs. La circulation longitudinale dans le lac Upper Waterton a contribué à davantage de rétention des substances nutritives en 1972 et 1973 qu'en 1974 et 1975: l'effet sur le phytoplancton des lacs en aval semble en avoir été plus grand au cours de ces deux dernières années.

Le contrôle des paramètres à l'aide d'au moins quatre postes situés le long du réseau lacustre principal avec échantillonnage à deux profondeurs fixes, la première à moins de 5 m de la surface et l'autre sous la thermocline, serait plus utile à l'étude globale des lacs que des examens plus détaillés à un ou deux postes.

Introduction

Established in 1895, Waterton Lakes National Park is located in southwestern Alberta, Canada. It is adjacent to the Province of British Columbia to the west, and Glacier National Park in the State of Montana, USA, to the south. Waterton Lakes National Park is situated on the east slope of the Rocky Mountain continental divide between latitudes 49.00 and 49.12 north and longitudes 113.40 and 114.10 west. The park has an area of 526 km^2 (203 sq. mi). The main lakes and the townsite are approximately 1280 m (4198 ft) above sea level. The highest peak in the park is Mt. Blakiston at 2927 m (9600 ft).

Mountains, mostly of sedimentary origin, form most of Waterton Lakes National Park, which changes rather abruptly in the northeast to a prairie biome (see Baird 1964). The flora and fauna within the park are diverse for such a small area. The main lakes contain a number of "relict species" (see McAllister and Ward 1972, Ricker 1959, Wilson 1972).

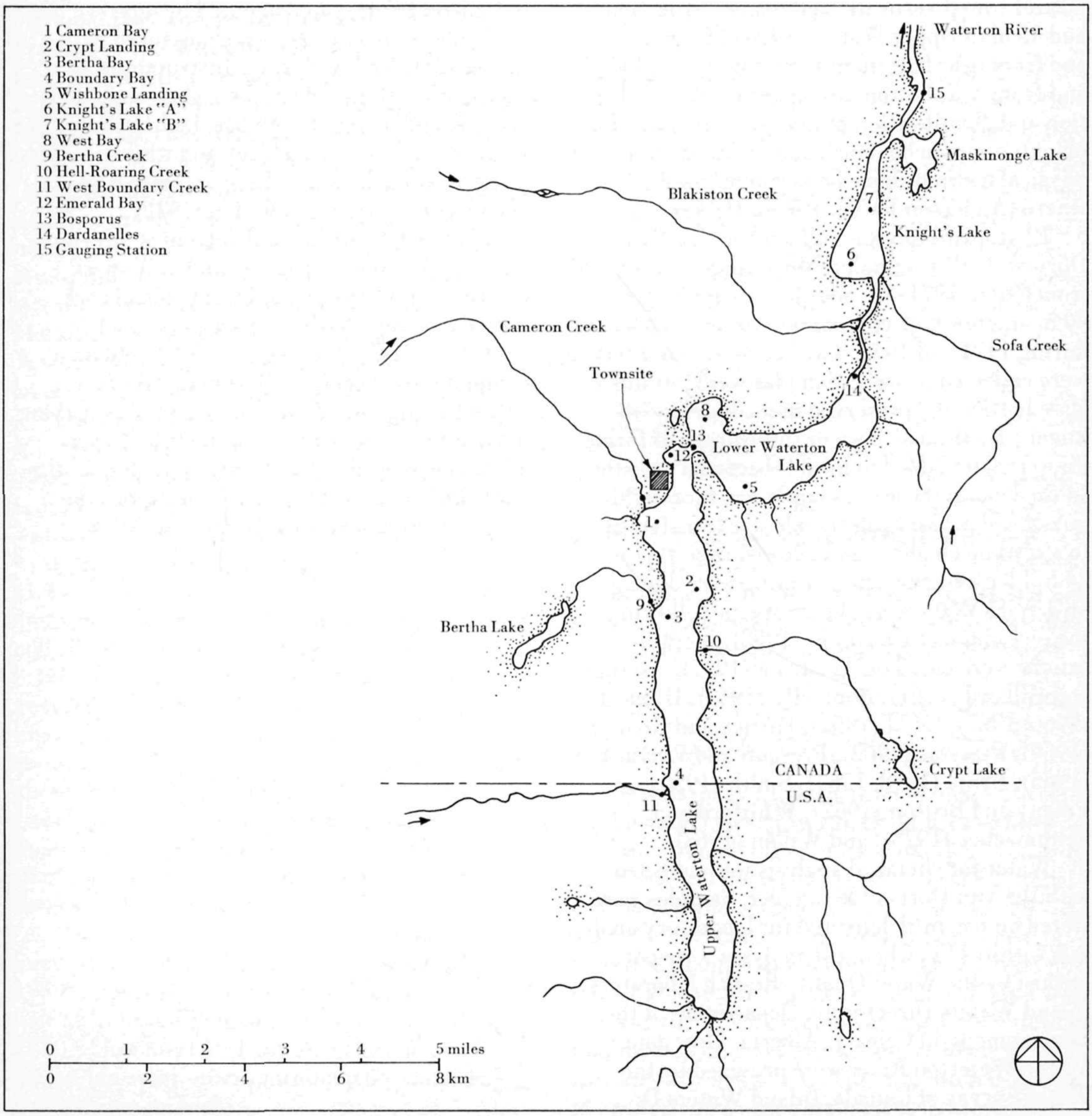
The park can be divided into two main watersheds drained by the Belly and Waterton rivers, tributaries of the Saskatchewan River which eventually flows into Hudson Bay. The main features of the park are the Waterton Lakes which give it its name (Fig. 1).

The townsite within the park is located on an alluvial fan, a blunt peninsula between Cameron Bay and Emerald Bay at the north end of Upper Waterton Lake where a shallow channel called the Bosporus connects Upper and Lower Waterton lakes. The townsite has had a permanent population of 120 in recent years. The mean number of annual visitors to the park during 1966–73 was 510 086 and the annual totals remained fairly constant. Until 1975, domestic sewage from the townsite and immediate vicinity was given partial primary treatment and chlorination before discharge into Upper Waterton Lake in Cameron Bay near the outlet of Cameron Creek (Fig. 1).

The purpose of the present study was to determine the nature and abundance of the plankton in the main lakes and to accumulate baseline data against which to assess changes. There have been few published studies of the communities and general limnology of the lakes, and most of these have been limited in time or scope (Anderson 1974a, Anderson and Dokulil 1976, Cuerrier and Schultz 1957, McAllister and Ward 1972, Rawson 1942, Ricker 1959, Thomasson 1962, Wilson 1972). Some unpublished studies have been conducted during one summer season (Anderson *et al.* 1972, Anderson and Krochak 1972, Donald 1975, Krishnaswami *et al.* 1968, Turner and Turner 1973).

Figure 1
Map of study area: main lake system, Waterton Lakes National Park, Alberta, showing main sampling sites and other dominant features

Figure 1



Methods

Zooplankton samples were collected with a plankton net (diameter 25 cm; mesh aperture 70 μm) towed vertically at 0.5 m·s^{-1} from 5 m and 45 m in Upper Waterton Lake, from 5 m and from near bottom in Lower Waterton Lake, and from near bottom in Knight's Lake. Collection and identification methods, corrections for plankton net inefficiency, and chemical and physical methods have been summarized elsewhere (Anderson 1970a, 1970b, 1974a).

Phytoplankton was collected with a Van Dorn-style PVC sampler. Most samples were from 5 m in 1971–73; additional samples from 30 m or a few metres from bottom were collected during 1974 and 1975. Two series at 5-m intervals were collected in 1974. Samples were put into glass bottles and preserved immediately with Lugol's-acetic acid. Two or three drops of formalin were later added to inhibit bacterial growth. In the laboratory, each sample was thoroughly mixed and a 25-ml sub-sample was transferred to a settling chamber and allowed to settle for 24 h. Identification and counting were done on a Wild M40 inverted microscope following the technique of Utermöhl (1958). Identifications were based on Ahlstrom (1937), Asmund and Hilliard (1961), Bourrelly (1968), Hilliard (1966, 1967), Lund (1962), Patrick and Reimer (1966), Prescott (1962), Prescott and Vinyard (1965), Skuja (1948, 1964), Smith (1950), Tiffany and Britton (1952), Whitford and Schumacher (1973), and Willén (1963).

Water for chemical analysis was collected with the Van Dorn-style sampler. Samples were stored on ice until delivered for laboratory analysis within 24 h. Chemical analyses were performed by the Water Quality Branch laboratory, Inland Waters Directorate, Department of the Environment, at Calgary, Alberta. Flow data for the Waterton River were provided by the Water Survey of Canada, Inland Waters Directorate, Department of the Environment, at Calgary, Alberta (see summary in Water Survey of Canada 1974), supplemented by our own data.

Water temperatures were measured with a model 42SC Yellow Springs Instrument Co. thermistor calibrated against a glass-stem mercury thermometer at each use. Light penetration was assessed by using a black and white Secchi disc, 20 cm in diameter. Lake volumes were calculated according to Welch (1948).

Air temperatures, wind velocities, precipitation data, freeze-up dates, and other park information were obtained from official park records or from diaries of park personnel.

Occasionally it was impossible to obtain a complete set of samples. The main lakes are subject to high winds and sudden storms making it hazardous to venture onto the lake and difficult to use equipment. Winter sampling is also hazardous because of poor ice conditions, but some sampling was done in 1973 and 1975.

Results

1. The lakes

The main lake chain in Waterton Lakes National Park consists of three lakes which are drained by the Waterton River (Fig. 1). The largest of the three lakes is Upper Waterton Lake, which is connected to Lower Waterton Lake by a narrow, shallow channel called the Bosporus. Water flows from the second lake through a short section of river called the Dardanelles to the third lake, Knight's Lake. Maskinonge Lake, a large and shallow body of water, lies to the east of the Waterton River downstream from Knight's Lake. No data from Maskinonge are included in this study. The Waterton River near the park boundary drains an area of approximately 616 km^2 (238 sq. mi).

The Upper Lake lies on a north-south axis: it is approximately 11.1 km (6.9 mi) long and 0.75 km (0.47 mi) wide. Lower Waterton Lake is 3.8 km (2.4 mi) long and has a maximum width of 1.33 km (0.83 mi); it lies on an east-west axis. Knight's Lake is about 2.2 km (1.4 mi) long, 1 km (0.62 mi) wide at the south end, and tapers to a narrow outlet at the north end. The volume of Lower Waterton Lake is 0.115 that of the Upper Lake and its surface area is 0.456 that of the Upper Lake. Approximately 19% of the volume of the Upper Lake is above the thermocline which usually occurs at about 16 m. The thermocline is usually only weakly defined in the Lower Lake, and approximately 58% of the lake volume is above the thermocline. A thermocline has not been detected in Knight's Lake.

The water level of Upper Waterton Lake fluctuates by about 1.5 m (5 ft — mean for 1959–72 period), reaching a peak in the latter half of June and remaining within about 0.3 m (1 ft) of low level for 8 months of each year. These and some other morphometric data are summarized in Table 1.

Table 1
Summary of location and morphometric data from the main lakes, Waterton Lakes National Park. L — length of shoreline; $\overline{Z}$ — mean depth; Z_m — maximum depth

Parameter	Upper Waterton Lake	Lower Waterton Lake	Knight's Lake
Location: U.T.M. Grid Ref. No.	12U/TK880350	12U/TK900370	12U/TK918413
(Latitude–N/ Longitude–W)	(49.02/113.54)	(49.03/113.53)	(49.05/113.51)
Elevation above sea level: m (ft)	1278.3 (4193)	1278.0 (4192)	1276.5 (4187)
Length: km (mi)	11.1 (6.9)	3.8 (2.4)	2.2 (1.4)
Surface area: ha (acres)	941 (2325)	429 (1060)	143 (353)
Volume: m^3 (acre-ft)	645.2×10^6 (523 100)	74.2×10^6 (601 30)	3.97×10^6 (3215)
Maximum depth: m (ft)	135.3 (444)	27.4 (90)	7.3 (24)
Mean depth: m (ft)	68.6 (225)	17.3 (56.8)	2.8 (9)
Shoreline development: $\frac{L}{2\sqrt{\Pi A}}$	2.47	1.53	1.31
Volume development: $\frac{3\overline{Z}}{Z_m}$	1.52	1.89	1.14
Theoretical water renewal* rate (approx. per year)	0.8	7.1	161

*Based on mean flows, 1967–75.

2. Water temperatures and light penetration

Based on incomplete records, the usual times of spring ice breakup and autumn ice formation in the main lakes are summarized as follows:

	Upper Lake	Lower Lake	Knight's Lake
Ice formation	End of first wk in Jan. ± 1 wk	Nov. 20, ± 1 wk	Nov. 12, ± 1 wk
Spring breakup	Mid April, ± 1 wk	End March, ± 2 wk	End March, ± 2 wk

Winds delay the formation of an ice cover on the main lakes until two months or so after ice formation on other more sheltered lakes in the vicinity. This results in prolonged autumnal circulation and cooling. Although detailed winter water temperature data have not been collected, temperatures ranged from 3.2°C at the surface to 3.5°C at 20 m one month after ice breakup in 1971 (Anderson *et al.* 1972), indicating that mean winter temperatures are likely to be considerably below 4°C. This condition is known to occur in other mountain lakes in the vicinity which are subject to extensive wind action during autumn (Anderson 1970b).

The Upper Lake begins to stratify by mid June, and by July a thermocline usually develops at about 15 m, depending on wind velocities. Maximum surface water temperatures usually occur near mid August, rarely exceed 15°C (usually about 14°C), and tend to be 0.5°–1.0°C colder at the International Boundary than near the townsite at the north end of the lake. Cooling usually begins about the third week of August and may continue for five months.

The Lower Lake shows much weaker thermal stratification than the Upper Lake. A poorly developed thermocline occasionally develops at 10 to 15 m, but the temperature difference is rarely more than 3°C from surface to bottom. Surface waters in Lower Waterton Lake are usually 1.0°–2.0°C warmer than in the Upper Lake in summer (occasionally more, as discussed below), but are often slightly lower in the Lower Lake once the period of autumnal circulation begins.

Complete mixing is believed to occur at all times of the year in Knight's Lake. Summer surface temperatures range from 1.0°–3.0°C higher than those for the Lower Lake. Cooling occurs more quickly in this shallow lake, and it usually freezes before either Upper or Lower Waterton lakes.

Mean Secchi-disc transparency readings for both Upper and Lower Waterton lakes for 1972 and 1973 were 8.2 m. There was no significant difference between the means for the two years ($p < 0.01$). The most erratic readings occurred in the Lower Lake, ranging from 14.5–4.5 m in the two years ($\bar{x} = 8.38$ m; SD = 2.87 m), but there was no significant correlation between Secchi-disc transparency and cell counts ($p < 0.05$) in the Lower Lake during this period. Secchi-disc transparency was usually from 7 to 9 m in the Upper Lake during these two years ($\bar{x} = 8.08$; SD = 1.37). There was no significant correlation between algal counts and Secchi-disc readings in 1972, but the correlation was significant in 1973 ($p < 0.02$). Data for 1974 and 1975 were similar, except for the 1975 flood period discussed below.

3. Water chemistry and bacteriology

Samples for chemical analysis were usually collected from at least four stations down the main lake chain on sampling days during 1972 and 1973, although all samples were not collected by the same agency. Stations were close but not identical. On the basis of flow data, water renewal rates, and general morphometry (Table 1), it is unlikely that the differences in sampling would have contributed to significant differences in analytical results. Table 2 provides a summary of some parameters for the water analyses.

For all sets of samples collected on the same day along the lake chain, trends were usually very similar. Sum of constituents (mg/l), specific conductance (μS/cm), total alkalinity (as mg/l $CaCO_3$), bicarbonate (mg/l), total hardness (as mg/l $CaCO_3$), and calcium and magnesium (mg/l) all showed lowest mean concentrations near the International Boundary and highest mean concentrations in the Waterton River samples collected below the outlet of Knight's Lake (Fig. 1). The mean concentrations of the above constituents at the sampling sites in Upper and Lower Waterton lakes were not usually significantly different from one another, although mean concentrations were higher towards the Dardanelles. There were highly significant differences in the concentrations of all of the above constituents between the main lake stations and the Waterton River below Knight's Lake, and usually between the main lake stations and Knight's Lake.

Table 2
Summary of mean values of water analyses for sites on the main lakes and the Waterton River, Waterton Lakes National Park. 1973 river samples taken at 0.5 to 1.0 m; lake samples at 5.0 m. Mean values accompanied by standard deviations in parentheses. Dash indicates no data

	Sum of constituents mg/l	Specific conductance µS/cm	Total alkalinity as mg/l $CaCO_3$	Bicarbonate, mg/l calculated	Hardness, total, as mg/l $CaCO_3$	Calcium, dissolved mg/l (1973 only)	Silica, reactive SiO_2 mg/l	Sulfate, dissolved mg/l	Nitrogen (NO_2+NO_3) mg/l	Phosphate, mg/l $\frac{\text{dissolved ortho.}}{\text{dissolved inorg.}}$	Carbon, total organic mg/l
Upper Waterton L.											
Boundary Bay	63.6 (1.48)	121.3 (4.60)	60.2 (1.56)	70.8 (1.11)	64.8 (1.49)	18.5 (0.61)	2.4 (0.35)	3.8 (0.90)	0.12 (0.048)	$\frac{0.003}{0.003}$	4.7 (1.15)
Bertha Bay		—	57.7 (0.78)		62.6 (1.06)	—	2.1 (0.57)	3.4 (1.61)	0.13 (0.014)	$\frac{0.003}{0.003}$	
Crypt Lndg	63.8 (2.82)	116.5 (3.70)	58.0 (0.90)	70.8 (1.10)	63.2 (3.17)	—	2.1 (0.45)		0.16 (0.057)	$\frac{0.003}{0.003}$	4.0 (1.00)
Cameron Bay	64.4 (2.47)	116.8 (3.70)	58.0 (0.90)	71.1 (1.02)	61.6 (0.78)	—	2.1 (0.43)	3.8 (1.53)	0.15 (0.051)	$\frac{0.003}{0.003}$	3.3 (0.58)
Bosporus	—	121.5 (5.05)	60.7 (1.62)	—	64.5 (1.47)	18.8 (1.01)	2.4 (0.38)	3.4 (0.83)	0.14 (0.054)	$\frac{0.003}{0.003}$	—
Lower Waterton L. Wishbone	66.7 (2.30)	122.5 (3.70)	61.2 (0.75)	74.6 (0.92)	65.4 (1.54)	—	2.1 (0.46)	3.6 (1.59)	0.14 (0.031)	$\frac{0.003}{0.003}$	4.0 (1.00)
Dardanelles	—	126.4 (2.79)	62.9 (1.51)	—	68.8 (1.81)	—	2.7 (0.46)	4.0 (0.98)	0.11 (0.025)	$\frac{0.003}{0.003}$	—
Knight's Lake	73.6 (1.48)	—	68.0 (3.25)	82.9 (3.96)	73.2 (0.85)	—	2.2 (0.42)	2.9 —	0.14 (0.035)	$\frac{0.003}{0.003}$	3.5 (0.71)
Waterton River nr. gauging station	—	150.5 (14.12)	73.8 (5.03)	—	78.6 (4.77)	21.8 (1.53)	2.6 (0.32)	4.4 (0.86)	0.08 (0.031)	$\frac{0.003}{0.003}$	—

Certain other constituents showed no trend or the reverse of the above. Unfortunately, the sets of analyses for some of these constituents were incomplete, so interpretations of these data were made with reservations. Except for one May analysis of a Bosporus sample (0.006 mg/l), all analyses of 1972–73 samples throughout the main lake system produced results of 0.003 mg/l for both dissolved orthophosphate and dissolved inorganic phosphate. Because 0.003 mg/l represents the minimum level of detection in laboratory analyses, phosphate should probably be interpreted on the basis of "present-at-a-low-concentration" versus "absent".

Although the mean values for dissolved organic carbon at the various stations were not significantly different statistically (number of samples at each site was small), they were higher at the south end of the lake system. Mean sulfate concentrations showed a similar though very weak trend in the main lakes. Nitrite-plus-nitrate mean values were highest at Cameron Bay and Crypt Landing sites and were significantly higher ($p < 0.05$) in the main lakes than in the Waterton River below Knight's Lake. Mean silica concentrations were not significantly different from one part of the lake system to another and showed no clear trend.

In 1972, mainly in August, multiple-dilution total coliform determinations and standard plate counts indicated equally high or higher numbers of coliforms at the stations south and presumably "upstream" from Cameron Bay (i.e. Boundary, Crypt, and Bertha Bay sites — Fig. 1). Faecal coliform occurrences were recorded as frequently at these south stations during August as at Cameron Bay. Total counts were not especially high, but indicated the possibility of either a second source of contamination or a circulation pattern within the Upper Lake which could carry the Cameron Bay water in the opposite direction to both the prevailing winds and the direction of flow through the Waterton River system (Anderson and Dokulil 1976, Anderson and Green 1975).

4. Meteorological, stream flow and temperature data

The main lake system is subject to almost constant wind most years: it is a rare occasion when the Upper Lake remains glassy calm throughout the entire day. Wind records have not been kept consistently over the years (especially 1974–75), but it is possible to get a general picture from available data. Gusts in excess of 100 km/h (62 mph) are not uncommon, and mean daily windspeeds for July and August were estimated from park records to be approximately 10 km/h (6.2 mph) in 1972 and 14 km/h (8.7 mph) in 1971. The prevailing and strongest winds are southerly, and in some months northerly winds are seldom or rarely recorded. Because of the long fetch[1] on Upper Waterton Lake, waves on the lake near the townsite may reach 1 m or more in height.

If 10 cm of fallen snow is accepted as approximately equal to 1 cm of rain, then total "summer" and total "winter" precipitation are very similar most years. During 1967–75, there was a threefold variation in annual rainfall, but only a 1.5 fold variation in annual snowfall. Annual precipitation values for these years are summarized in Figure 2.

Mean daily air temperatures, mean-maximum and mean-minimum temperatures for the Waterton townsite area are summarized in Figure 3. Even though mean July 1973 air temperatures are about 4°C higher than in 1972, mean-maximum more than 5°C higher than 1972, mean-minimum about 3°C higher than 1972 (August air temperatures were similar both years), and total runoff as indicated by Waterton River flow data (Fig. 4) lower in 1973 than in 1972, surface water temperatures in the main lakes in 1973 were less than 1°C higher than in 1972. In 1971, air temperatures were only slightly cooler than in 1973, runoff in July 1971 was similar to 1972, and surface water temperatures in 1971 were only about 0.5°C higher than in 1972. Winds were considerably stronger in 1971 than in 1972, 1973 and 1975, and were probably lightest in 1974. Air temperatures were higher in 1971 and 1973 than in 1972, but the depth of the thermocline in the main lakes was not much different in the three years. The thermocline in the Upper Lake in August, 1975, was much shallower than usual (Anderson and Dokulil 1976) and reflects the coldest August air temperatures recorded at the townsite in the last nine years (Fig. 3).

Although winds, precipitation, and air temperatures do not seem to produce big differences in mid-summer surface temperatures from year to year, these factors do seem to cause considerable variation in break-up and freeze-up dates. The usual dates are summarized in section 2, (p. 9), but exceptions are common: for example, Upper Waterton Lake did not freeze over until 28 January 1974, and 31 January 1975, and

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[1] Distance that the wind blows across the lake surface.

Figure 2
Precipitation (cm), Waterton townsite: total snowfall for the winter ending in the indicated year; total rainfall for the indicated year

Figure 2

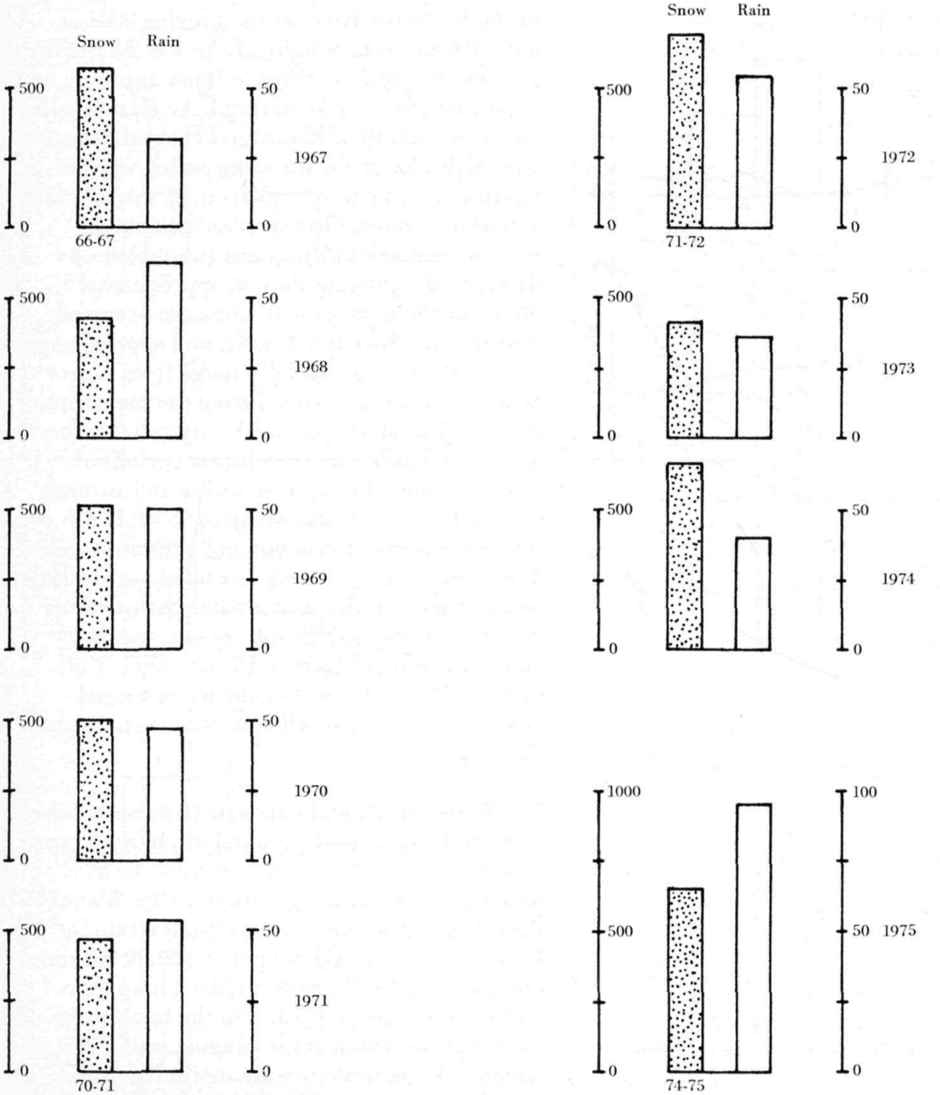
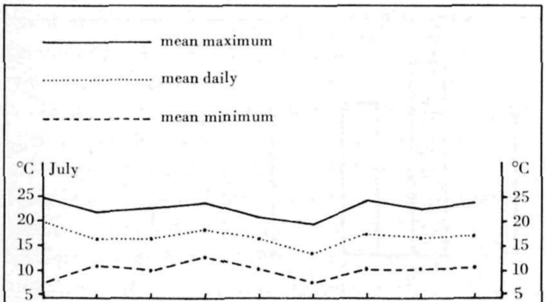


Figure 3
Air temperatures (°C), Waterton townsite: mean daily temperatures, and mean maximum and mean minimum temperatures for July and August, 1967–75

Figure 3



did not completely break up until 7 May 1974, and 16 May 1975.

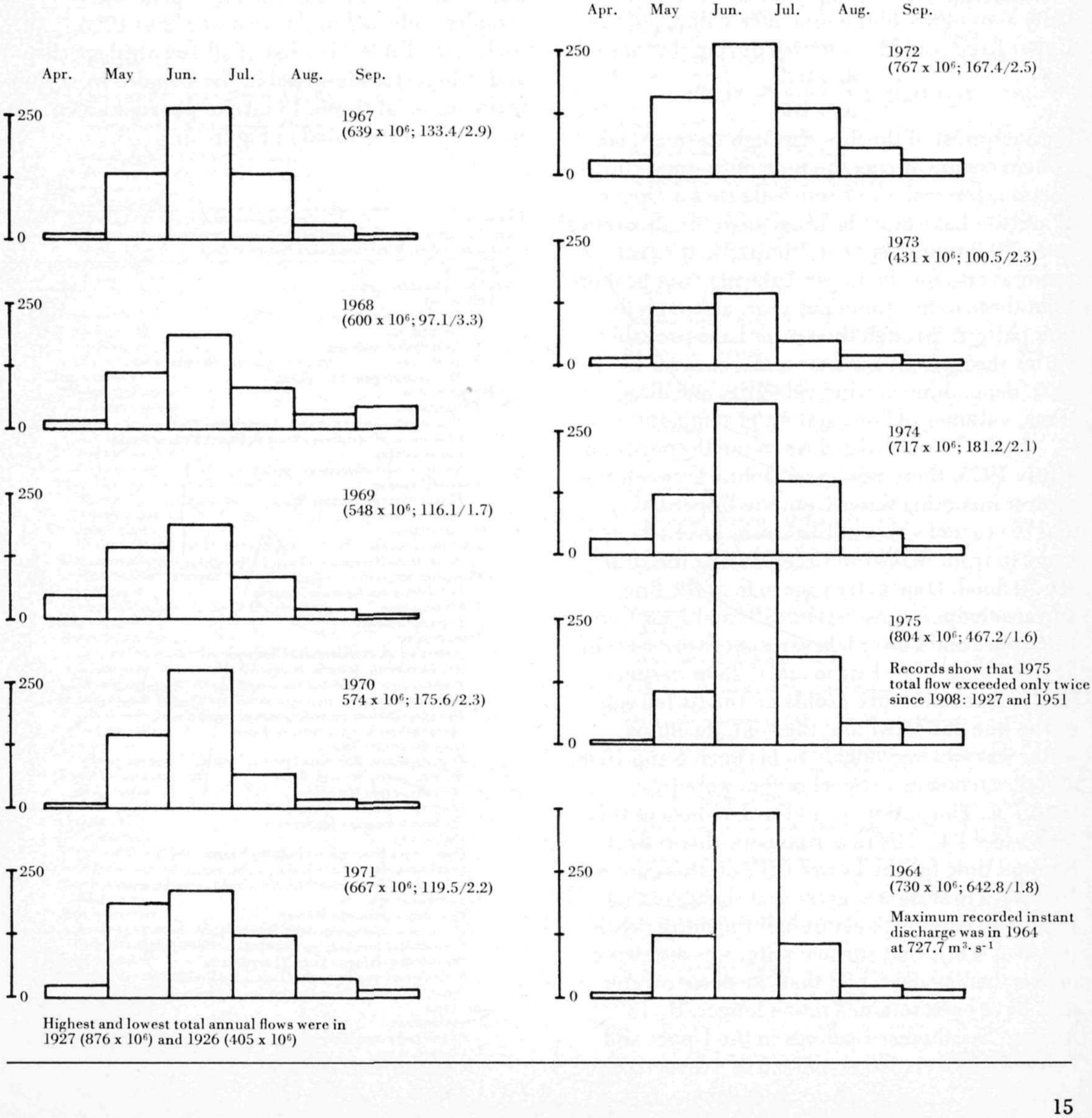
During 1967–75, the mean annual discharge in the Waterton River at the gauging station downstream from Knight's Lake was 20.2 $m^3 \cdot s^{-1}$ (713 cu. ft/s or 517 000 acre-ft per annum). At the outlet of Lower Waterton Lake (Dardanelles above the mouth of Blakiston Creek) the mean annual discharge for the same period was estimated to be 16.6 $m^3 \cdot s^{-1}$ (586 cu. ft/s or 424 500 acre-ft per annum) based on an estimate of 82% of total flow at this point (unpublished data). At the gauging station, approximately 56.5% of the total annual discharge occurred during June, July and August, and approximately 58% of the total annual discharge from Lower Waterton Lake occurred during the same three months. About 35% of the discharge from the Waterton Lakes occurred during periods of relative homeothermy (i.e. spring and autumn circulation). There can be up to 350-fold difference between maximum and minimum daily flow rates in one year (e.g. the flood year of 1964) in the Waterton River. A greater-than-twofold variation in the peak flow from one year to another is not uncommon (Water Survey of Canada 1974). Figure 4 summarizes annual flows and monthly discharges for the spring and summer.

5. Water-renewal rates in the main lakes

On the basis of the annual discharge from Lower Waterton Lake (considered to be 82% of total flow at the gauging station on the Waterton River), the theoretical water-renewal rate for Upper Waterton Lake is approximately 0.8 times per year, and for the Lower Lake it is approximately 7.1 times per year. On the basis of the discharge measured at the gauging station below Knight's Lake, the renewal rate for Knight's Lake is approximately 161 times per year.

Figure 4
Total monthly flow in the Waterton River at the gauging station below Knight's Lake during the months April to September, 1967–75, ($m^3 \times 10^6$). Total annual flow (m^3) and maximum and minimum daily flows ($m^3 \cdot s^{-1}$) are given in parentheses below the indicated year. Data from 1964, another recent flood year, are given for comparison

Figure 4



Records show that 1975 total flow exceeded only twice since 1908: 1927 and 1951

Maximum recorded instant discharge was in 1964 at 727.7 $m^3 \cdot s^{-1}$

Highest and lowest total annual flows were in 1927 (876×10^6) and 1926 (405×10^6)

Approximately 35% of the discharge from the Waterton lakes occurs during the period of homeothermy in the Upper and Lower lakes. Only about 28% of the total lake volume of the Upper Lake could be renewed during this period

$$(\text{i.e. } 0.35 \times \frac{424\ 000}{523\ 100} = 0.28).$$

Because most of the flow through the main lake system occurs during the time of thermal stratification, the real water-renewal rate for Upper Waterton Lake must be lower than the theoretical rate of 0.8 times per year. Similarly, the real renewal rate for the Lower Lake may not be more than three to five times per year, although the flow pattern through the Lower Lake probably varies throughout the year and from year to year, depending on wind velocities and directions, volumes of flow, and water temperatures.

In the Lower Lake close to the Bosporus on 4 July 1975, there was a visible line between the clearer incoming water from the Upper Lake and the turbid water in the Lower Lake which came in from Blakiston Creek during the June 19–20 flood. One metre each side of the line, surface temperatures were 7.5°C and 13.5°C in the Upper and Lower lakes, respectively. Secchi disc readings were 1.65 m and 0.25 m, respectively. A temperature profile on the turbid side of the line indicated that the cold, incoming water was sinking quickly to between 5 and 10 m, and that temperatures below 9 m were less than 7°C. The outlet river (Dardanelles) at this time was 14°C. The instantaneous theoretical renewal time for the Lower Lake on this date was 10 days. These data suggest that the incoming water was sinking to about half the mean depth (i.e. 8 or 9 m), that surface water was renewing in less than 10 days, and that the deeper water may have been retained much longer. By 13 August, Secchi disc readings in the Upper and Lower lakes were 7.5 m and 6.5 m, respectively.

6. Phytoplankton

A total of 164 species and subspecies of algae were identified in the phytoplankton samples collected in the years 1972 to 1975, inclusive. Table 3 is a list of all 164 algal species and subspecies identified in the samples from the main lakes. Of these, 13 rare or poorly known species are illustrated in Figure 5.

Table 3
Species of algae identified from phytoplankton samples collected in 1972—75 in the main lakes, Waterton Lakes National Park

- Chlorophyta
  - Euchlorophyceae
    - Volvocales
      - Chlamydomonadaceae
        - *Carteria* sp.
        - *Chlamydomonas* spp.
      - Volvocaceae
        - *Eudorina elegans* Ehrenberg
    - Tetrasporales
      - Palmellaceae
        - *Gloeocystis gigas* (Kutzing) Lagerheim
        - *Gloeocystis planctonica* (West & West) Lemmermann
        - *Gloeocystis* sp.
        - *Sphaerocystis schroeteria* Chodat
      - Coccomyxaceae
        - *Elakatothrix gelatinosa* Wille
        - *Elakatothrix* sp.
    - Chlorococcales
      - Hydrodictyaceae
        - *Pediastrum Boryanum* (Turp.) Meneghini
      - Coelastraceae
        - *Coelastrum microporum* Naegeli
      - Botryococceae
        - *Botryococcus* sp.
      - Oocystaceae
        - *Ankistrodesmus convolutus* Corda
        - *Ankistrodesmus falcatus* (Corda) Ralfs
        - *Ankistrodesmus falcatus* var. *acicularis* (A. Braun) G. S. West
        - *Ankistrodesmus falcatus* var. *mirabilis* (West & West) G. S. West
        - *Dictyosphaerium Ehrenbergianum* Naegeli
        - *Dictyosphaerium pulchellum* Wood
        - *Oocystis Borgei* Snow
        - *Oocystis crassa* Wittrock
        - *Oocystis parva* West & West
        - *Oocystis pusilla* Hansgirg
        - *Oocystis solitaria* Wittrock
        - *Oocystis submarina* Lagerheim
        - *Oocystis* sp.
        - *Quadrigula closteroides* (Bohlin) Printz
        - *Quadrigula lacustris* (Chodat) G. M. Smith
        - *Schroederuaderia setiger* (Schroeder) Lemmermann
      - Scenedesmaceae
        - *Crucigenia quadrata* Morren
        - *Crucigenia rectangularis* (A. Braun) Gay
        - *Scenedesmus arcuatus* var. *platydisca*. G. M. Smith
        - *Scenedesmus bijuga* (Turp.) Largerheim
        - *Scenedesmus quadricauda* (Turp.) De Brebisson
        - *Scenedesmus quadricauda* var. *longispina* G. M. Smith
    - Conjugales
      - Desmidiaceae
        - *Closterium venus* Kutzing
        - *Closterium* sp.
        - *Cosmarium bioculatum* Brebisson

Table 3, cont'd.

- Zygnematales
  - Zygnemataceae
    - *Mougeotia* sp.

- Cyanophyta
  - Myxophyceae
    - Chroococcales
      - Chroococcaceae
        - *Chroococcus dispersus* (v. Keiss) Lemmermann
        - *Chroococcus Prescottii* Drouet & Daily
        - *Chroococcus* spp.
        - *Coelosphaerium Kuetzingianum* Naegeli
        - *Gloeocapsa* sp.?
        - *Gomphosphaeria lacustris* Chodat
        - *Merismopedia* sp.
    - Hormogonales
      - Oscillatoriaceae
        - *Lyngbya perelegans* Lemmermann
        - *Oscillatoria amphibia?* C. A. Agardh
        - *Oscillatoria* sp.
      - Nostocaceae
        - *Anabaena* sp.

- Chrysophyta
  - Chrysophyceae
    - Chrysocapsales
      - Bitrichiaceae
        - *Bitrichia chodatii* (Reverdin.) Chodat
    - Chromulinales
      - Euchromulinaceae
        - *Chromulina* sp.
        - *Kephyrion littorale* Lund
        - *Kephyrion planctonicum* Hilliard
        - *Kephyrion* spp.
        - *Kephyriopsis globosa* Hilliard
        - *Kephyriopsis crassa* Hilliard
        - *Kephyriopsis* nr. *sphaerica*
        - *Kephyriopsis* sp.
        - *Stenocqlyx* sp.
      - Chromulinales (unident. species)
      - Mallomonadaceae
        - *Mallomonas tonsurata* Teiling var. *alpina* (Pascher & Ruttner) Krieger
        - *Mallomonas pseudocoronata* Prescott
    - Isochrysidales
      - Isochrysidaceae
        - *Chrysoikos skujae* (Nauwerck) Willen
        - *Chysolykos planctonicus* Mack
        - *Dinobryon bavaricum* Imhof.
        - *Dinobryon cylindricum* Imhof.
        - *Dinobryon sociale* Ehrenberg
        - *Ochromonas* sp.
      - Synuraceae
        - *Spiniferomonas bourellii* Takahashi
      - Lepochromonadaceae
        - *Epipyxis* sp.
        - *Pseudokephyrion* sp.
    - Prymesiales
      - Prymesiaceae
        - *Chrysochromulina parva* Lackey
    - Craspedomonadales
      - Bicoecaceae
        - *Bicoeca* sp.
      - Monosigaceae
        - *Monosiga varians* var. *vagans* Skuja
        - *Stelexomonas dichotoma* Lackey
    - Mischococcales
      - Pleurochloridaceae
        - *Nephrodiella* sp.
  - Bacillariophyceae
    - Centrales
      - Coscinodiscaceae
        - *Cyclotella comta* (Ehrenberg) Kutzing
        - *Cyclotella ocellata* Pantocsek
        - *Cyclotella* sp.
        - *Melosira italica* (Ehrenberg) Kutzing var. *subarctica* O. Mueller
        - *Melosira* nr. *ambigua*
        - *Melosira* sp.
        - *Stephanodiscus astrea* (Ehrenberg) Grunow
        - *Stephanodiscus niagarae*
      - Rhizosoleniaceae
        - *Rhizosolenia eriensis* H. L. Smith
    - Pennales
      - Fragilariaceae
        - *Asterionella formosa* Hassall.
        - *Diatoma hiemale* (Roth.) Hieberg
        - *Diatoma hiemale* var. *mesodon* (Ehrenberg) Grunow
        - *Diatoma tenue* var. *elongatum* Lyngbya
        - *Diatoma tenue* Agardh
        - *Fragilaria brevistriata* Grunow
        - *Fragilaria capucina* Desmarziers
        - *Fragilaria construens* (Ehrenberg) Grunow
        - *Fragilaria crotonensis* Kitton
        - *Fragilaria pinnata* Ehrenberg
        - *Fragilaria virescens* Ralfs
        - *Fragilaria* spp.
        - *Hannea arcus* Patrick
        - *Meridion circulare* (Grev.) Agardh
        - *Synedra acus* Kutzing
        - *Synedra amphicephala* var. *austriaca* (Grunow) Hustedt
        - *Synedra cyclopum* Brutschy
        - *Synedra delicatissima* Wm. Smith
        - *Synedra radians* Kutzing
        - *Synedra ulna* (Nitzsch.) Ehrenberg
        - *Synedra ulna* var. *chasena* Thomas
        - *Synedra* sp.
        - *Tabellaria fenestrata* (Lyngbya) Kutzing
      - Achnanthaceae
        - *Achnanthes flexella* (Kutzing) Brunnthaler
        - *Achnanthes linearis* (G. M. Smith) Grunow
        - *Achnanthes microcephala* (Kutzing) Grunow
        - *Achnanthes minutissima* (Kutzing) Grunow
        - *Achnanthes* nr. *curvirostrum*
        - *Achnanthes* sp.
        - *Cocconeis placentula* Ehrenberg
        - *Cocconeis pediculus* Ehrenberg
      - Naviculaceae
        - *Amphipleura pellucida* Kutzing
        - *Diploneis elliptica* (Kutzing) Cleve
        - *Diploneis* sp.
        - *Gyrosigma acuminatum* (Kutzing) Cleve
        - *Gyrosigma* sp.
        - *Navicula elginensis* var. *rostrata* (A. Mayer) Patrick
        - *Navicula elginensis* (Greg.) Ralfs
        - *Navicula menisculus* var. *upsaliensis* (Grunow) Grunow
        - *Navicula peregrina* (Ehrenberg) Kutzing
        - *Navicula pupula* var. *capitata* Skv. & Meyer
        - *Navicula radiosa* Kutzing
        - *Navicula* spp.
        - *Neidium dubium* var. *constrictum* Hustedt
        - *Neidium binode* (Ehrenberg) Hustedt
        - *Pinnularia mesolepta* (Ehrenberg) W. Smith
        - *Pinnularia* sp.
        - *Stauroneis* sp.
      - Gomphonemaceae
        - *Gomphonema intricatum* Kutzing
        - *Gomphonema* spp.
      - Cymbellaceae
        - *Amphora ovalis* Kutzing
      - *Cymbella amphicephala* Naegeli

continued next page

Table 3, cont'd.

      - *Cymbella cymbiformis* (Kutzing) Brebisson
        - *Cymbella lanceolata* (Ehrenberg) Van Heurck
        - *Cymbella microcephala* Grunow
        - *Cymbella ventricosa* Kutzing
        - *Cymbella* spp.
      - Epithemiaceae
        - *Denticula* sp.
        - *Epithemia turgida* (Ehrenberg) Kutzing
      - Nitzschiaceae
        - *Nitzschia acicularis* (Kutzing) Wm. Smith
        - *Nitzschia suecica* (Grunow) A. Cleve
        - *Nitzschia vermicularis* (Kutzing) Hantzsch
        - *Nitzschia* spp.
      - Surirellaceae
        - *Surirella linearis* Wm. Smith

- Pyrrophyta
  - Peridineae
    - Gymnodiniales
      - Gymnodiniaceae
        - *Gymnodinium helveticum* Penard
        - *Gymnodinium* sp.
    - Peridinales
      - Glenodiniaceae
        - *Glenodinium pulviscus* (Ehrenberg) Stein
        - nr. *Wolosynzkia* sp.
      - Peridiniaceae
        - *Peridinium cinctum* (Mueller) Ehrenberg
        - *Peridinium pusillum* (Penard) Lemmermann
        - *Peridinium* sp.

- Cryptophyta
  - Cryptophyceae
    - Cryptomonadales
      - Cryptomonadaceae
        - *Cryptomonas* spp.
        - *Rhodomonas minuta* Skuja

Phytoplankton samples were collected at five or six stations on the main lakes three or four times a year in 1972 and 1973, from seven stations on five dates in 1974, and from two stations on seven dates in 1975. Figure 6 summarizes total cell counts of 5-m samples to the end of 1973 by major taxa. The few counts available for two previous years are also included (data from Krishnaswami *et al.* 1968, and Anderson *et al.* 1972). Total cell counts for 5-m and deeper samples for 1974 and 1975 are summarized by major taxa in Figure 7. Summary tables of detailed counts can be provided by the authors on request.

On four dates in 1972 (Cameron Bay, 1 and 25 August, 27 September; Crypt Landing, 27 September), 25-m or 30-m samples were collected in addition to the 5-m samples. Total cell counts and species composition for both depths on 25 August for Cameron Bay and on 27 September for Crypt Landing were virtually identical. Cameron Bay total counts were higher at the surface on 1 August and higher at 25 m on 27 September. Differences were almost entirely due to variations in *Dictyosphaerium ehrenbergianum* numbers.

Most of the differences between 1972 and 1973 samples were differences in magnitude. The small pulse of *Melosira* in the Lower Lake in late 1972, the small pulses of *Oocystis* in mid summer in 1973 in the Upper Lake, the much greater relative contribution of *Coelosphaerium* to total cell counts in the Upper Lake in 1973 (especially at the three more southerly stations), and the relatively larger numbers of *Rhodomonas* in 1972 in the more southerly stations were among the more obvious differences. Extending the sampling program in 1974–75 to include earlier and later dates and more deep sampling provided interesting contrasts to the 1972–73 data. The extended time revealed peaks in phyto-

Figure 5
Some of the rare or poorly known phytoplankton species occurring in the Waterton Lakes:
A, *Bicoeca* sp.; B, *Chrysochromulina parva* Lackey; C, *Chrysoikos skujae* (Nauwerck) Willén; D, *Chrysolykos planctonicus* Mack; E, *Kephyrion planctonicum* Hilliard; F, *Kephyriopsis crassa* Hilliard; G, *Bitrichia chodatii* (Reverdin.) Chodat; H, *Monosiga varians* var. *vagans* Skuja; I, *Stelexomonas dichotoma* Lackey; J, *Spiniferomonas bourrellii* Takahashi; K, *Mallomonas tonsurata* Teiling var. *alpina* (Pascher & Ruttner) Krieger; L, *Kephyrion littorale* Lund; M, *Kephyriopsis globosa* Hilliard;

A–J all to same scale; K–M to scale as shown. Scales in micrometres

Figure 5

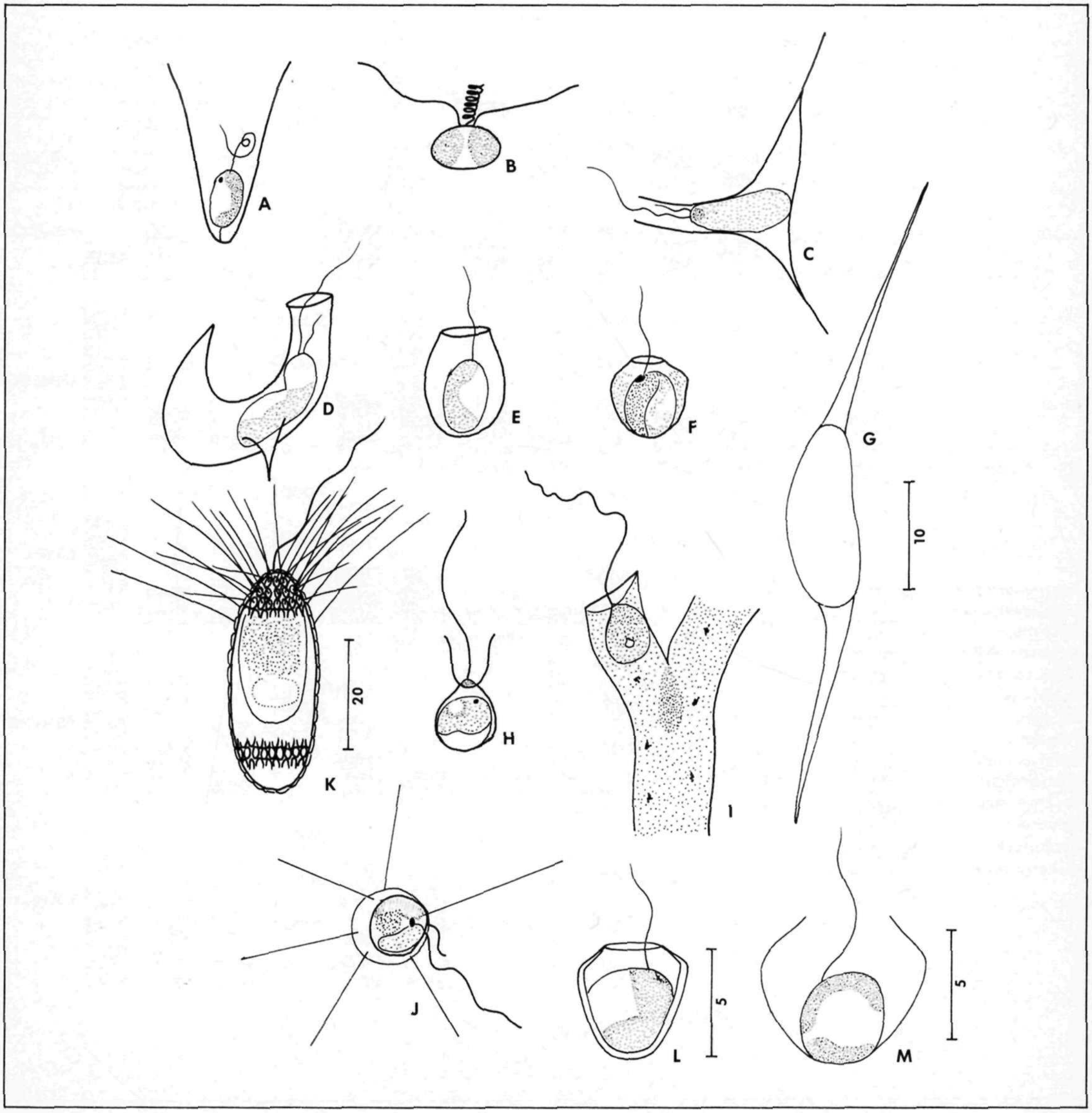


Figure 6
Phytoplankton counts (cells/ml) by dominant taxa for the sampling stations on the main lake system, Waterton Lakes National Park, for the years 1967 and 1971–73

Figure 6

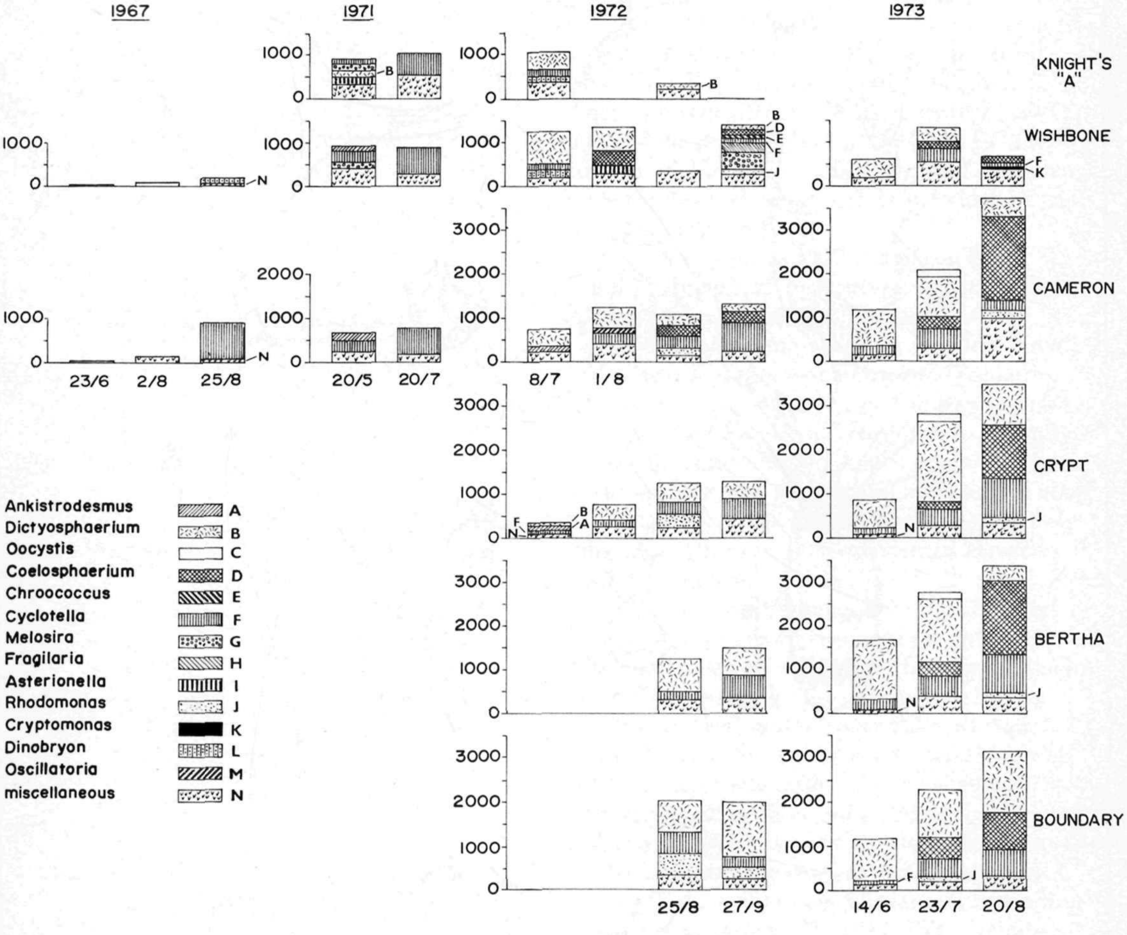


Figure 7
Phytoplankton counts (cells/ml) by dominant taxa for the sampling stations on the main lakes system, Waterton Lakes National Park, for the years 1974 and 1975. In the paired histograms, the left side is the 5-m sample, right side is the 30-m or near-bottom sample. Single histograms are shallow depths only. Legend is for genera new to 1974–75: others as in Fig. 6

Figure 7

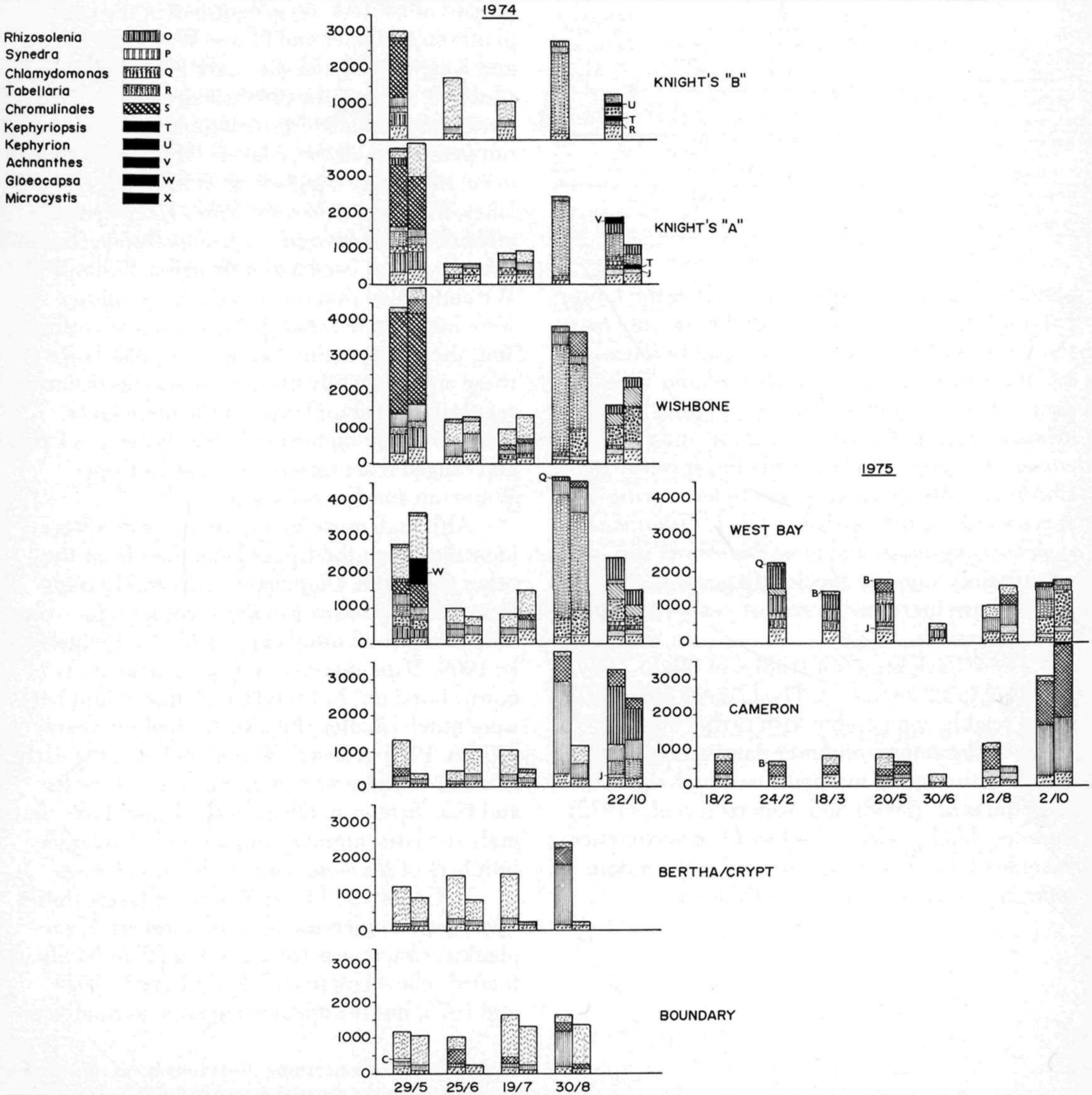


Table 4
Comparison of methodology and results in this and previous studies

Author	Total no. sampling dates	No. sampling sites per date	No. species reported	No. species not found in present study
Thomasson (1962)	1	1	9	2
Krishnaswami *et al.* (1968)	3	2	27	6
Anderson *et al.* (1972)	2	3	32	7
Anderson and Green, (1972–1973) (this study)	7	4–6	107	—
Anderson and Green, (1974–1975) (this study)	12	2–7	164	—

plankton numbers in spring and fall in the Lower Lake and Knight's Lake and a fall peak only in the Upper Lake. Some species, notably *Rhizosolenia eriensis* and *Asterionella formosa*, appear primarily in fall and winter; others such as *Rhodomonas minuta*, *Cyclotella ocellata*, and *Fragilaria crotonensis*, appear to be mainly fall species; a Chromulinales species appears to be a spring species only in the two lower lakes. *Coelosphaerium kuetzingianum* and most *Dinobryon* spp. were mainly summer species. In general, the cell counts have increased in recent years throughout the lake system.

There have been few studies of phytoplankton in these waters. The present analysis is not readily comparable with earlier studies which took samples on fewer dates and at fewer sites. Furthermore, methods used by Krishnaswami *et al.* (1968) and Anderson *et al.* (1972) were less likely to have disclosed the occurrence of some of the smaller species and may contain some errors in identification (Table 4).

7. Zooplankton

A total of 19 species of crustaceans and 12 species of rotifers were identified in the zooplankton of Upper and Lower Waterton lakes and Knight's Lake in the years 1969–75 inclusive (Table 5). Ten of the crustacean species occurred irregularly, usually in small numbers, and were not present in all three lakes. Of the nine species occurring fairly regularly in at least one of the lakes, five (*Senecella calanoides*, *Macrocyclops albidus*, *Eucyclops agilis*, *Chydorus sphaericus*, and *Alona guttata*) occurred only in small numbers. We concluded that our sampling techniques were inadequate for accurate counts of rotifers and, therefore, estimated relative abundance of these animals. Only five rotifer species occurred regularly and abundantly in the main lakes. Numbers were highest in Lower Waterton Lake, and ranged from zero to very low in Upper Waterton and Knight's lakes.

Although more zooplankton species were identified from the Upper Lake than from the other two lakes, *Diaptomus sicilis* and *Cyclops bicuspidatus thomasi* usually accounted for over 98% of the total numbers in 1970–75 inclusive. In 1969, *Daphnia rosea*[2] was proportionately more abundant, but total zooplankton numbers were much smaller (Fig. 8). In the four years 1972 to 1975 in Lower Waterton Lake, the early summer samples were dominated by *D. sicilis* and *C.b. thomasi* much as in the Upper Lake, but mid- and late-summer samples included larger numbers of *Bosmina longirostris* and *D. rosea*.

In Upper and Lower Waterton lakes, there was a general increase in total numbers of zooplankters each year from 1969 to 1973. Numbers tended to level off in the Lower Lake in 1974 and 1975, but the apparent decline in numbers

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[2] Some comments concerning the taxonomy of this species are included in the discussion and in Table 5.

in the Upper Lake was due mainly to a drastic drop in numbers of *C.b. thomasi* in 1974 and 1975. In Upper Waterton Lake, there was a trend toward higher counts at the south end of the lake, especially in 1973 (Fig. 8). An examination of some samples collected by D. S. Rawson in 1937 in the Upper Lake indicated the presence of *D. sicilis* and *C.b. thomasi* at fairly low numbers, no other crustaceans, and no rotifers. Knight's Lake zooplankton was not sampled regularly in the present study, but available data suggest that abundance is erratic.

Table 5
Species of rotifers and crustaceans identified in zooplankton samples, 1969–75 inclusive. Species present in 3 or more years in the lakes indicated "x", otherwise presence is specified by years. Absence in samples indicated by a dash

	Upper Waterton L.*	Lower Waterton L.	Knight's Lake
Senecella calanoides Juday 1923	x	x	74
Diaptomus sicilis S.A. Forbes 1882	x	x	x
Diacyclops bicuspidatus thomasi S. A. Forbes 1882	x	x	x
Acanthocyclops vernalis Fischer 1853	74	x	71
Macrocyclops albidus (Jurine) 1820	—	—	x
Eucyclops agilis (Koch) 1838	—	—	x
Bryocamptus sp.	71, 69	75	—
Polyphemus pediculus (Linné) 1761	72	—	—
†*Daphnia rosea* (?) Sars 1862 emend. Rich	x	x	x
Ceriodaphnia reticulata (Jurine) 1820	73, 71	71	—
Acroperus harpae Baird 1843	72	—	—
Eurycercus lamellatus (O. F. Müller)	—	—	73
Chydorus sphaericus (O. F. Müller)	x	x	x
Bosmina longirostris (O. F. Müller)	73, 72	x	x
Alona guttata Sars 1862	x	71	—
Alona affinis (Leydig) 1860	70	70	—
Alonella excisa Fischer 1854	—	—	72
‡*Mysis relicta* Lovén 1861	x	—	—
Cyclocypris ampla Furtos 1933	—	71	73, 72
Asplanchna priodonta Gosse 1850	69	x	x
Synchaeta oblonga Ehrenberg 1832	71, 74	x	x
Keratella cochlearis (Gosse 1851)	x	x	x
Keratella quadrata (Müller 1786)	—	74	72
Kellicottia longispina (Kellicott 1879)	x	x	x
Polyarthra vulgaris Carlin 1943	x	x	x
Brachionus sp.	73, 71	71	72
Notholca sp.	71	—	—
Monostyla lunaris Ehrenberg 1832	71, 69	—	—
Lecane (*depressa?*)	71	—	71
Euchlanis sp.	71	—	—
Lepadella ovalis	74	—	—

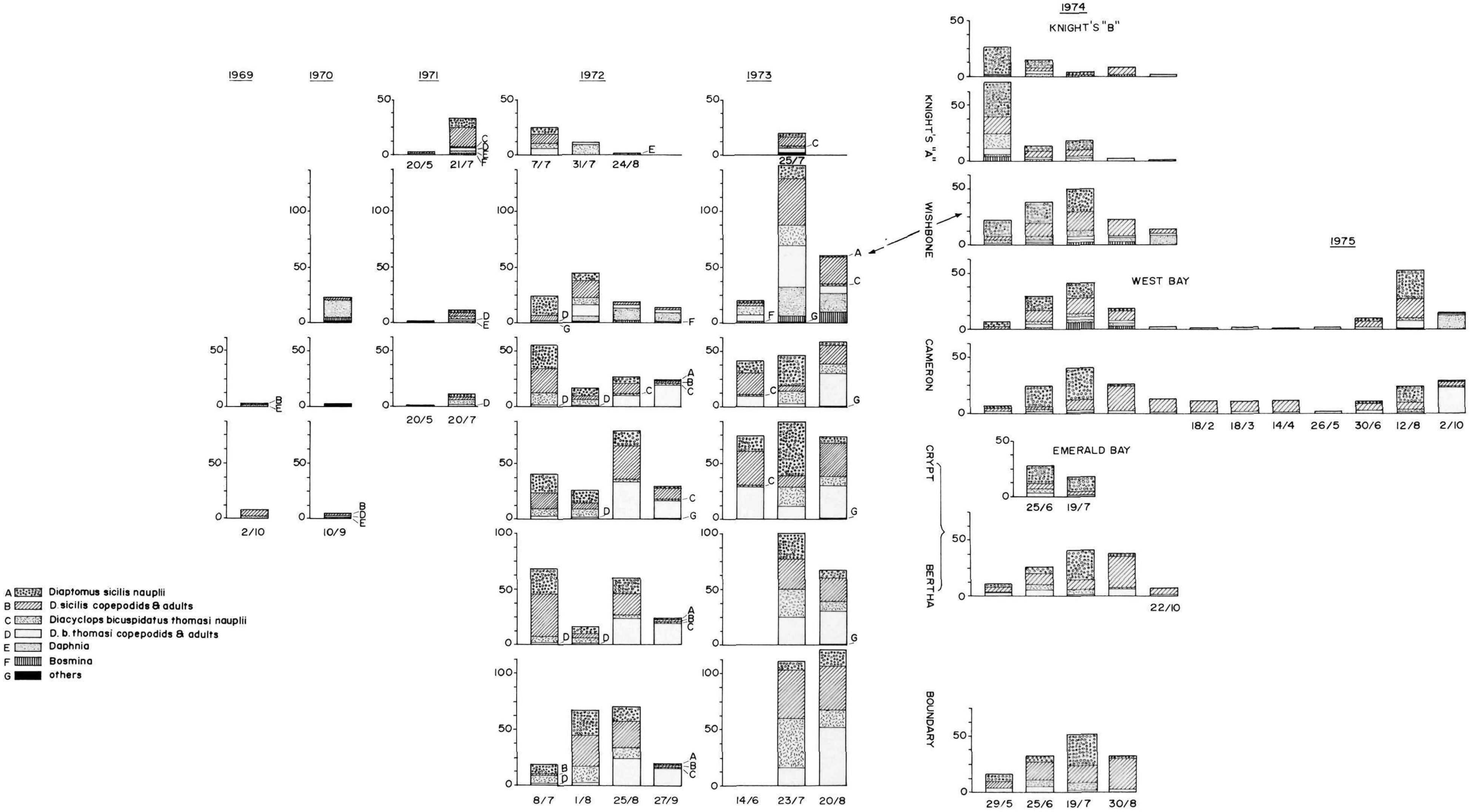
*Rotifers rare; seldom more than one sparsely represented species at any one time.

†Species has features of both *D. rosea* and *D. galeata mendotae* as described by Brooks (1957), but bears some resemblance to *D. longispina* as noted by Rawson and Bajkov in earlier accounts.

‡Only occasionally collected in plankton samples from the Upper Lake, but known to be present in large numbers in the Upper Lake and smaller numbers in the Lower Lake.

Figure 8
Crustacean zooplankton counts (animals/litre) for the main lake system sampling stations, Waterton Lakes National Park, for the years 1969–75

Figure 8



Discussion

The volume development factor (Table 1) for a lake indicates the extent to which a lake basin differs in shape from a cone of equal base area and height, but the factor becomes less meaningful limnologically when a lake is extremely deep or shallow relative to surface area (see Hutchinson 1957). For Knight's Lake, the coefficient of 1.14 indicates a regular increase in depth from shore to lake centre, but the maximum depth is not great compared to the area. The height coefficient for the Lower Lake reflects the sharp drop-off along much of the shoreline: the littoral zone is very restricted in extent. The coefficient for the Upper Lake is intermediate in value but, because of the lake's great depth, there is virtually no littoral zone. A more useful descriptive factor is shoreline development, which is the ratio of lake shoreline length to the perimeter of a circle having the same area as the lake. A high shoreline development coefficient usually indicates an irregular shoreline, along which productivity is often higher than in the open water. Of the three lakes, Upper Waterton Lake has the highest shoreline development factor (Table 1), but it is a reflection of the long and narrow shape of the lake rather than shoreline irregularity.

Chemical analyses of water samples in 1972 and 1973 showed that the inorganic constituents comprising the dominant ions became significantly more concentrated from south to north in the Waterton Lakes – Waterton River system (i.e. "downstream"). On the other hand, constituents most likely to be associated with human activities (nitrate-plus-nitrite nitrogen, orthophosphate, organic carbon, sulfate) tended to be uniform throughout the system or showed the reverse trend — higher concentrations toward the south end (i.e. "upstream"). Examinations for the presence of coliform bacteria in 1972 showed a trend similar to that for nitrogen, phosphorus, carbon, and sulfur.

Water temperatures above the thermocline have been fairly constant in Upper Waterton Lake from year to year despite considerable variations in mean and maximum air temperatures, in annual flow through the lake system, and in summer precipitation. Because prevailing winds are southerly and fairly constant, the warmer surface layer is usually moved toward the outlet, the Bosporus. The Lower Lake, less exposed to winds, not so deep, and receiving the warmer surface waters from the Upper Lake, has higher summer water temperatures. The trend continues into Knight's Lake which remains homoethermic as a result of the combined effects of winds and high rate of water renewal (Table 1).

The greater depth of the thermocline at the north end of the Upper Lake, especially during July and August 1973, the direction of flow through the main lake system northward to the Waterton River, and prevailing southerly winds of relatively high velocity suggested the existence of a circulation pattern within the Upper Lake. This probability is strengthened on consideration of the water renewal rate, water volume moved by the wind, and the shallow lake outlet. At a windspeed of 27 to 32 $\text{km}\cdot\text{h}^{-1}$ from the south, assuming the current velocity in the upper 2 m to be 0.2% of wind velocity,[3] a minimum water volume of 2.47×10^6 $\text{m}^3\cdot\text{day}^{-1}$ could be moved northward down the lake by the wind. This volume is close to the mean daily water renewal for July, about half the mean daily renewal for June, and about four times the mean daily renewal for August. The estimate of water volumes moved by the wind may be too small by a factor of 10 (see Hutchinson 1957, p. 278). Noble (1966) noted that a water current velocity near 0.5% of wind velocity was generated at a depth of

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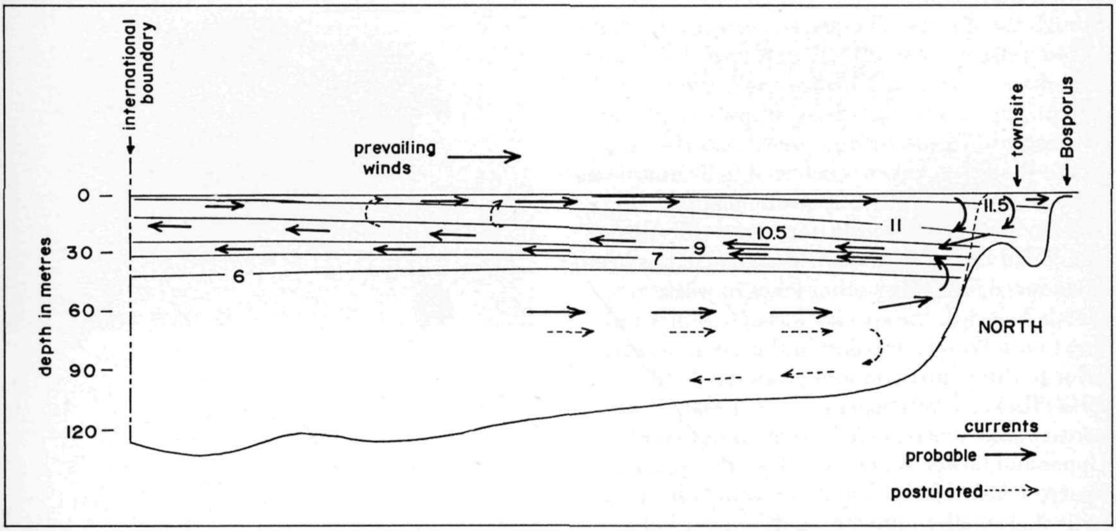
[3] Based on estimates using Hellström's theoretical treatment (see Hutchinson 1957, p. 277).

Figure 9
Profile of circulation pattern for Upper Waterton Lake, 23 July 1973, showing probable and postulated currents. Isotherms, °C; depths, m

Figure 9



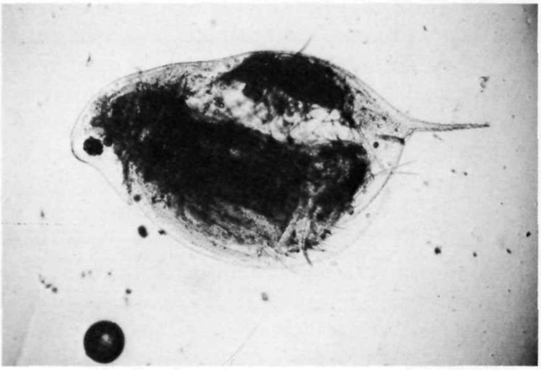
180 m in Lake Michigan in 2 h at a wind velocity of 60 km·h^{-1}. Therefore, it is likely that the wind can move from 5 to 40 times the actual renewal volume in the Upper Lake, depending on the month, the actual wind velocities, and the duration of the blow. Certain data suggest that wind-generated circulation within the Upper Lake was greatly reduced in 1974 and 1975.

A circulation pattern like that indicated in Figure 9 probably occurs in the lake in years of consistently strong southerly winds. This would explain why certain nutrient concentrations and faecal bacteria counts are sometimes higher towards the south end of the lake. Sewage plant effluent (until 1975) and flow from Cameron Creek would tend to circulate downward with the surface waters. To some extent, the Upper Lake may be acting as a nutrient reservoir. Although the concentration of nutrients is low compared to more eutrophic lakes, gradual increases in nutrients may have contributed to increases in phytoplankton numbers in recent years (Figs. 6 and 7).

Deep, slow-moving currents to the south in the Upper Lake in 1972–73 could have contributed to higher copepod numbers toward the south end of the lake (Fig. 8). In many large lakes, both *Diaptomus sicilis* and *Cyclops bicuspidatus thomasi* tend to be more abundant in deeper waters (Patalas 1972). Higher numbers of crustacean plankters at the south end were not evident in 1974.

The occurrence of three "relict" species of crustaceans and two fish species, whose distribution and occurrence appear linked to refugia in deep, cold-water proglacial lakes, makes the fauna of the Waterton Lakes unique on this part of the continent. The occurrence of the pygmy whitefish *Prosopium coulteri* Eigenmann and Eigenmann in the Waterton Lakes is the only

Figure 10
Daphnia longispina/hyalina (hybrid?) from Lake Sevan, Armenian S.S.R., 9 August 1971



known occurrence of this species in the Hudson Bay drainage (Lindsey and Franzin 1972), although the species is known to occur in the State of Montana to the south (Weisel *et al.* 1973) and in Yoho National Park (Mudry and Anderson 1975). The occurrence of the deepwater sculpin *Myoxocephalus quadricornis thompsoni* (Girard) in the Waterton Lakes is believed to be unique in Alberta, the next nearest known location being 725 km (450 miles) to the northwest (McAllister and Ward 1972). Although *Mysis relicta* has been introduced into many other lakes in western North America, the species was apparently unique to the Waterton Lakes in this general region prior to these introductions (Rawson 1938, 1942; Ricker 1959; Sparrow *et al.* 1964). *Pontoporeia affinis* was reported as common to both Upper and Lower Waterton lakes (Rawson 1938, Sparrow *et al.* 1964) although recent collections indicated smaller numbers in the Upper Lake (Donald 1975). Although not reported by Rawson in his earlier reports on the Waterton Lakes, *Senecella calanoides* was present in samples collected at that time (Wilson 1972). Our deep vertical plankton tows usually produced a few *S. calanoides* in each sample.

On the basis of previous reports and re-examination of samples collected in 1937 from the Waterton Lakes, no change in the composition of zooplankton in the main lakes seems to have occurred, although total numbers of copepods have apparently increased over the years, roughly paralleling increases in phytoplankton abundance. Patalas (1972) suggests that *D. sicilis* abundance has decreased with increasing eutrophication in the Great Lakes. Such a decrease has not occurred so far in the Waterton Lakes, suggesting that the oligotrophic character of the lakes has not been seriously impaired.

Although Brooks (1957) and Reed (1959) reported the occurrence of *Daphnia middendorffiana* Fischer 1851 in the Waterton Lakes, and Reed (1959) noted the occurrence of *D. schoedleri* Sars 1862 as an inshore species in the Waterton Lakes, no specimens of these two species occurred in the 1937 samples which were re-examined, and none has been found in the samples collected since 1937. Although *Daphnia* have occurred consistently in the zooplankton of Lower Waterton Lake since 1967, most samples from the Upper Lake contained no specimens.

There is some question concerning the identity of the *Daphnia* sp. present in the lakes. Rawson (1938) referred to the species as *D. longispina*, and Bajkov (1929) also referred to this species as occurring in many of the lakes of the mountain national parks. This form has been referred to *D. rosea* by Brooks (1957) and Reed (1959), although J. Hrbáček (pers. comm.) has indicated that specimens which he has examined

Figure 11
Daphnia rosea (?) female with embryos, Upper Waterton Lake, 2 October 1969

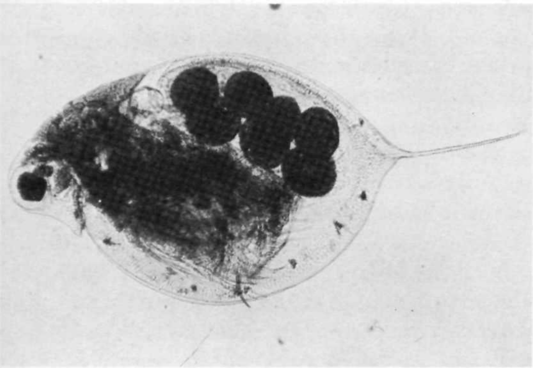
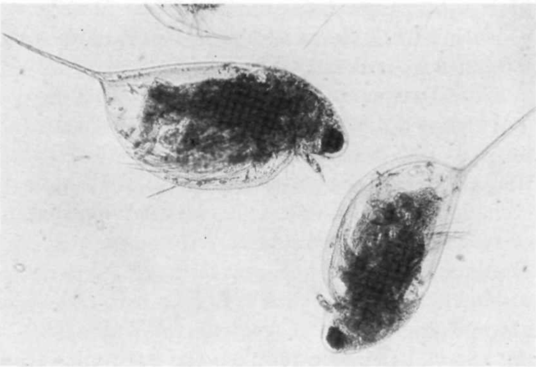


Figure 12
Daphnia rosea (?) males from Upper Waterton Lake, 2 October 1969



are very close to European *Daphnia*, intermediate between *D. hyalina* and *D. longispina* and similar in form to the species occurring in Lake Sevan, a large, high mountain lake in the Armenian S.S.R. Lake Sevan specimens (Fig. 10) do not resemble closely the diagram of Manuilova (1964, p. 127, Figs. 24–26). The Lake Sevan *Daphnia* have longer rostra, heavier shell spines, and smaller eyes than the Waterton Lake specimens, although the general body form is similar (Fig. 11). In general body form, the *Daphnia* from the Waterton Lakes most closely resemble the form (included with *D. galeata mendotae*) figured by Brooks (1957, p. 135, Plate 46-C) or the *D. longispina typica* figured by Šrámek-Hušek *et al.* (1962, p. 215, Plate 76-A). We did not observe the toothed crest noted by Brooks (1957) as characteristic of male and immature *D. rosea* on the Waterton Lakes *Daphnia* (Fig. 12), nor did we observe helmets on this form. Furthermore, the heads are usually considerably smaller than indicated for *D. rosea* by Brooks. In the plankton communities of the lakes of the mountain national parks, most *Daphnia* without the coarse mid-pecten on the post-abdominal claw are of the type found in the Waterton Lakes. There are very few populations of "typical" *D.g. mendotae* and "typical" *D. rosea* as described by Brooks. Until more studies are done, we will consider the *Daphnia* of the Waterton Lakes as *D. rosea* of questionable status.

Seasonal changes in zooplankton species composition and abundance were greater in Lower Waterton Lake and Knight's Lake than in Upper Waterton Lake, especially in 1973. Zooplankton abundance in Knight's Lake probably depends to a great extent on animals drifting from the main lakes upstream. The changes in abundance and species composition in Knight's Lake are undoubtedly related to the high water renewal rate in this lake and to the predation by the large numbers of sucker and whitefish fry present in the lake.

The reasons for the changes in abundance and composition in the Lower Lake are obscure, but they may reflect selective predation early in the summer on the copepod populations which come in from the Upper Lake during the period of peak flow. Small and relatively sparse, the dominant copepod species in the main lakes are unlikely to be heavily preyed on by fish, although young lake whitefish, *Coregonis clupeaformis*, are known to feed on zooplankton in the Lower Lake (unpubl.). *Cyclops bicuspidatus thomasi* is known to prey heavily on *Diaptomus sicilis* in other lakes (Anderson 1970a, 1970c), and this cyclopoid copepod may be the chief predator on the diaptomid copepod.

The erratic zooplankton abundance in the Upper Lake in 1972 compared to 1973 levels (Fig. 8) was probably caused by a combination of biological factors and the wind-induced circulation pattern in the lake (Fig. 9). Distribution is probably complicated by the tendency of both *D. sicilis* and *C.b. thomasi* to remain fairly deep in the water column. Although we have no evidence of vertical migration by *D. sicilis* in the Waterton Lakes, vertical movement to the deeper waters may be extensive, especially on bright days. Patalas (1969, 1972) reports migration below 50 m by this species during daylight hours in the Great Lakes. Towards the end of summer 1972 and 1973 at most Waterton Lake sampling sites, *D. sicilis* numbers often declined, whereas *C.b. thomasi* numbers showed a smaller decline or, in some cases, an increase (Fig. 8). Numbers of *C.b. thomasi* declined in 1974 and 1975, recovering somewhat in late 1975. *Mysis relicta* appeared to be especially abundant in the summer and fall of 1974, and stomach contents indicated heavy feeding on copepods of both species (D. B. Donald, pers. comm.). *Mysis relicta* probably has a 2-year or 3-year life cycle in this lake, and its annual abundance may be cyclic. Other studies have also shown that *Mysis relicta* can be a voracious predator (Lasenby and Langford 1973), so periodic declines in zooplankton numbers in the Upper Lake may be due in part to *Mysis* feeding.

Of the 164 algal species and subspecies in the phytoplankton of this study only 27 spp. of 23 genera reached or exceeded densities of 100 cells/ml. An annotated list of these species follows:

Ankistrodesmus convolutus — seldom over 100 cells/ml, usually occurring in late spring or early summer. The genus is sometimes abundant in small eutrophic waters, but is usually considered a "clean-water" species (Palmer 1962, Prescott 1962).

Chlamydomonas sp. — only occasionally exceeded 100 cells/ml. Some species of the genus known to tolerate organic enrichment (Palmer 1962).

Dictyosphaerium ehrenbergianum — a sudden increase in abundance in 1972 continued into 1973–74, but dropped off in 1975; widespread in the plankton of lakes, permanent and semipermanent ponds (West 1904, Smith 1950); *Dictyosphaerium* spp. are rather insensitive to mild inorganic pollution (Round 1965).

Oocystis spp. — five species present, of which *O. parva* was most common; moderate numbers only in mid summer 1973. The genus tends to be more common in shallow, soft-water, nutrient-rich lakes, but may be the dominant phytoplankter in deep, unproductive lakes (Hutchinson 1967, Prescott 1962); may form part of the summer pulse in large lakes (Lake Mendota, Wisconsin; Lake Ohrid, southern Yugoslavia).

Chroococcus spp. — two species present; moderately abundant only once in Lower Waterton Lake in late summer.

Coelosphaerium Kuetzingianum — consistently one of the dominant summer species in the Waterton Lakes, 1972 to 1975, but not noted before 1972; often forms "blooms" in fresh water (Smith 1950); the genus becomes very abundant in late summer and early autumn in certain lakes and is usually considered a "polythermic-oligotrophic" species (Findenegg 1943, Hutchinson 1967).

Gloeocapsa sp. — single occurrence; not usually planktonic.

Microcystis sp. — abundant only for a short time during August 1974 in Cameron Bay.

Oscillatoria amphibia — moderately abundant once in mid summer in Cameron Bay; one other low count from Bertha Bay; blooms in presence of organic pollution (Palmer 1962).

Asterionella formosa — highest counts recorded from October to May in this lake system; usually a spring and summer species (Feuillade 1969, Round 1965); capable of attaining high densities at very low phosphate concentrations (i.e. <0.002 mg/l, Lund 1950, Mackereth 1953, Round 1965, Vollenweider 1970) but appears to show optimal growth at about 0.02 mg/l (Vollenweider 1970).

Cyclotella ocellata — usually increased in abundance throughout the summer and fall, reaching maxima in September or October; often abundant in lake plankton (West 1904) and tolerant of high turbidity (Hutchinson 1967).

Fragilaria crotonensis — occasionally abundant in Lower Waterton Lake in fall and winter, 1972, 1974, 1975; year-round in Lac de Venzins, France, especially in July (Feuillade 1969); considered an indicator of early stages of eutrophication (Vollenweider 1970).

Tabellaria fenestrata — occurrence pattern similar to *Asterionella*, but less abundant.

Melosira italica — var. *subarctica* — small numbers throughout the summer in the Lower Lake and Knight's Lake, reaching high numbers in fall and early winter; occurrence pattern similar to *Asterionella formosa;* meroplanktonic and requires turbulence to remain suspended (Hutchinson 1967, Round 1965); growth in some species of this genus stimulated by mild organic pollution (Round 1965).

Rhizosolenia eriensis — a winter and early spring species in Lower Waterton Lake, an autumn species in the English Lake District (Hutchinson 1967); benefits from slight organic enrichment (Round 1965).

Cryptomonas spp. — only moderately abundant once in the Lower Lake; generally present throughout the open-water season at low numbers in samples from all stations.

Chromulinales sp? — occurred only in May 1974 samples from the Lower Lake and Knight's Lake where it dominated the counts.

Dinobryon divergens — usually rather sparse and confined to Lower Waterton Lake and Knight's Lake, reaching peaks in mid summer; considered a spring species in many lakes (Hutchinson 1967); tends to be sensitive to high phosphate, but tolerant of high nitrate (Round 1965, Stewart and Rohlich 1967, Vollenweider 1970).

Dinobryon sociale — dominant in the Lower Lake in August 1974, but virtually absent other years and at other sites.

Dinobryon cylindricum — moderately abundant in October 1974 in Cameron Bay; known to occur at high densities under ice cover (Hilliard 1966).

Kephyrion spp. — (Figs. 5-E, 5-L) abundant in Knight's Lake in fall 1974; little known of the ecology of this genus.

Table 6
Pollution indices based on the presence of a minimum abundance of 50 cells/ml per indicator species of algal species tolerating organic pollution (Palmer 1969). Numbers in brackets are indices based on a minimum abundance of 25 cells/ml

	1972				1973		
Site	July 8	Aug. 1	Aug. 25	Sept. 27	June 14	July 23	Aug. 20
Boundary Bay	—	—	1 (5)	7 (7)	1 (1)	1 (3)	1 (1)
Bertha Bay	—	3 (3)	—	1 (7)	1 (1)	1 (8)	1 (5)
Crypt Landing	3 (3)	3 (3)	1 (5)	5 (7)	1 (1)	3 (3)	1 (5)
Cameron Bay	3 (3)	8 (8)	1 (5)	1 (3)	1 (3)	1 (3)	5 (5)
Wishbone Landing	3 (3)	1 (1)	2 (2)	2 (5)	1 (1)	5 (9)	2 (2)
Knight's Lake	4 (7)	—	1 (4)	—	—	—	—

	1974					1975						
Site	May 29	June 25	July 19	Aug. 30	Oct. 22	Feb. 18	Feb. 24	Mar. 18	May 20	June 30	Aug. 12	Oct. 2
Boundary Bay	3 (3)	3 (3)	3 (3)	1 (1)	—	—	—	—	—	—	—	—
Crypt/Bertha midlake site	1 (3)	3 (3)	3 (3)	1 (1)	—	—	—	—	—	—	—	—
Cameron Bay	3 (3)	1 (3)	3 (3)	1 (1)	1 (3)	3 (3)	3 (3)	2 (3)	3 (8)	0 (0)	0 (4)	5 (5)
West Bay	4 (4)	3 (3)	1 (4)	6 (6)	4 (4)	—	7 (11)	0 (6)	2 (7)	0 (0)	5 (7)	2 (2)
Wishbone Landing	4 (4)	3 (4)	2 (2)	6 (6)	3 (4)	—	—	—	—	—	—	—
Knight's Lake "A"	4 (8)	3 (4)	2 (4)	6 (6)	7 (7)	—	—	—	—	—	—	—
Knight's Lake "B"	2 (4)	3 (3)	1 (8)	5 (6)	3 (13)	—	—	—	—	—	—	—

Kephyriopsis globosa — (Fig. 5-M) abundant only in fall in Knight's Lake, 1974; little known of the ecology of this species.

Rhodomonas minuta — consistently occurring in moderate numbers at most stations in late summer or early fall; genus often occurs in spring at optimum temperatures of 8°–12° C (Hutchinson 1967).

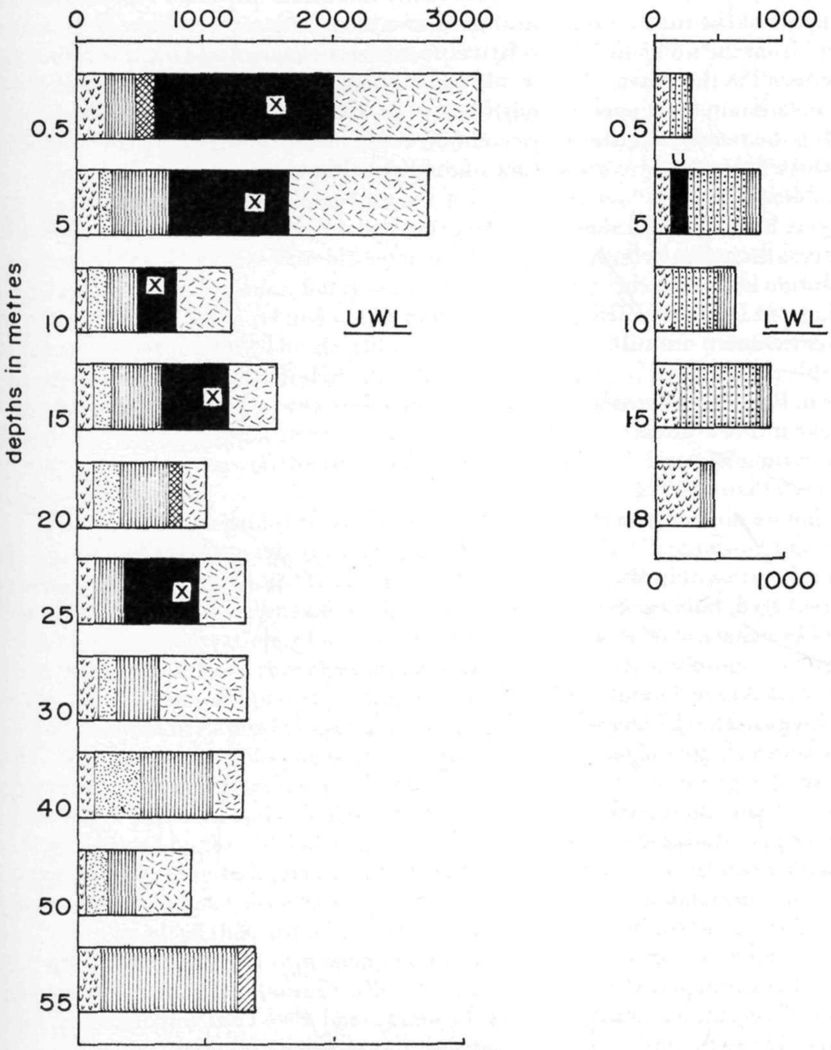
The presence of some of the above species and their increase in abundance in recent years may reflect nutrient enrichment resulting from the addition of sewage effluent to the Upper Lake. The occurrence of low numbers of certain other species known to form nuisance blooms under conditions of enrichment indicates the importance of keeping nutrient levels as natural as possible in this lake system (note short-lived *Microcystis* peak, Fig. 13).

Palmer (1969) devised a pollution index based on the occurrence of algal species tolerating organic pollution. Algal species significantly associated with pollution were given point values. In determining the pollution index for a lake, species were deemed "present" and assigned points only if they numbered at least 50 cells/ml. A score of 20 or more was considered an indication of high organic pollution; a score of 15 to 19 was considered probable evidence of organic pollution. Using Palmer's index, the highest score for any station in this study was 8 (Cameron Bay, August 1972). By reducing the abundance requirements to 25 cells/ml for "present", scores up to 13 were calculated, with higher numbers generally in the Upper Lake in 1972–73 and in the Lower Lake and Knight's Lake in 1974–75. In spite of higher cell counts in 1973, pollution indices were lower than in 1972 (Table 6). The low indices in both years indicated that pollution was at a low level. However, general increases in plankton counts in recent years suggest that enrichment may have been increasing or cumulative.

In 1972 and 1973, plankton counts in the three lakes tended to be inversely proportional to flow rates in the lake system. Although flow could have been an important reason for low

Figure 13
Analyses of phytoplankton samples (cells/ml) from discrete depths for Upper (UWL) and Lower (LWL) Waterton Lakes on 3–4 August 1974. Legend for phytoplankton genera as in Figs. 6 and 7

Figure 13



counts in Knight's Lake, it was less likely to be the reason for smaller numbers in the Lower Lake compared to the Upper Lake. Counts in the Upper Lake were usually higher at the south end, apparently "upstream" from the nutrient source, and lower "downstream" in the other two lakes. Longitudinal circulation in the Upper Lake would cause nutrients to be retained in the lake long enough to allow them to become incorporated into plankton biomass.

A levelling-off of numbers in the Upper Lake in 1974 and 1975 and the great increases in both numbers and Palmer's pollution indices in the Lower Lake and Knight's Lake in 1974 and 1975 indicate that the effects of enrichment are still increasing, but that these effects have been shifted down the lake system. Reduced internal circulation in the Upper Lake in 1974–75, as noted earlier, and a greater volume of flow through the system in 1974–75 than in 1973 (Fig. 4), could have allowed more nutrients to reach the lower lakes.

The number of algal species present in the main lakes seems to have increased, but because the earlier methods may not be comparable, it is uncertain whether the increase in numbers of species is real. However, increases in cell numbers are undoubtedly real. Zooplankton numbers have also increased and, therefore, higher algal cell counts cannot be attributed to decreases in grazing. Algal numbers have actually increased in spite of a greater number of potential grazers.

Water temperatures in the main lakes (especially the Upper Lake) have been fairly consistent from year to year during the study. Therefore, it is unlikely that temperature differences are responsible for changes in plankton numbers. The concentration of certain nutrients detected by chemical analyses seems to have remained fairly constant, but a nutrient build-up in the Upper Lake may have contributed to the larger numbers of plankters. A larger plankton biomass could account for some accumulated nutrients, and some have probably accumulated in the sediments as particulate matter. The relatively low water-renewal rate for this lake would contribute to such an accumulation of nutrients, especially in years when internal circulation could have prolonged the retention time of nutrient-rich water.

Conclusions

There have been changes in both phytoplankton species composition and abundance in the main lakes, Waterton Lakes National Park, in recent years. Although some species now present are indicative of a low level of enrichment, both the species changes and numerical increases could be due to the cumulative effects of nutrient addition over a period of years.

The species composition of the zooplankton has remained virtually unchanged since 1937, although numbers of organisms have increased in recent years. The most variable component of the zooplankton is *Daphnia*, but its erratic occurrence is not likely related to the addition of nutrients to the lakes. The stability of species composition is an indication that there has been no serious deterioration of environmental conditions within the lakes. The quantitative changes, however, may be the result of a low level of enrichment.

According to available records, temperatures, sum of constituents, turbidity, and water renewal rates have remained fairly constant. Chemical analyses of water samples have not shown high concentrations of nutrients, but in some years the nutrient concentration gradient in the lake system was opposite to the concentration gradient of natural dissolved inorganic salts. Temperature profiles, dissolved nutrient gradients, coliform bacteria and plankton distribution patterns, and calculated water volumes moved by the wind all suggested the probability of a longitudinal circulation within Upper Waterton Lake, especially in 1972 and 1973. As a result of this circulation, it is likely that most of the nutrient load coming into the lake these 2 years was retained within the lake with little reaching the Lower Lake. Some of the nutrients were undoubtedly incorporated into biomass in the Upper Lake, and a considerable proportion probably precipitated to the bottom as particulate matter. Based on some analyses of bottom mud for organic matter, the cumulative total is still very low (i.e. about 4% of dry weight in the Upper Lake; about 5% in the Lower Lake and Knight's Lake).

As a result of a combination of several factors, mainly high total volumes of flow through the lakes and fewer periods of sustained high-velocity southerly winds in summer, longitudinal circulation in the main lakes was less pronounced in 1974 and 1975. Consequently, the effects of enrichment of the phytoplankton were greater in the downstream lakes than in the previous 2 years. An apparent reduction in zooplankton numbers in the Upper Lake in 1974 and 1975 was mainly due to the greatly reduced numbers of *Cyclops bicuspidatus thomasi*, a reduction probably related to changes in numbers of *Mysis relicta*, a species which has been shown recently to be a predator on zooplankton. A limited sampling program for *Mysis* in 1974 and 1975 indicated that 1974 was a year of high abundance.

As indicated by the vertical distribution of phytoplankton species in Figure 13 and by the horizontal series in 1972, 1973 and 1974 (Figs. 6 and 7), a sampling program involving the two discrete depths and at least four stations spaced along the system would be more useful for total lake assessment than more detailed effort at one or two stations (i.e. 5- and 30-m samples from two Upper Lake sites, 5- and 20-m samples from one Lower Lake site, and 2-m samples from one Knight's Lake site).

Summary

(1) The principal purpose of this study was to investigate and describe the main lake system of Waterton Lakes National Park, in southwestern Alberta. The Waterton Lakes are susceptible to cultural influence because of their central location in the park and the townsite and main campground facilities on their shores. Until recently, few baseline data had been gathered against which to assess change or around which to formulate management policies and practices.

(2) The main lake system comprises a chain of three large lakes, each different morphometrically, at an elevation of approximately 1280 m. Extending across the International Boundary into the United States, Upper Waterton Lake has an area of 941 ha, a maximum depth of 135.3 m, and a water-renewal rate of less than once per year. The second and third lakes in the chain have areas of 429 and 143 ha, maximum depths of 27.4 and 7.3 m, and water-renewal rates of 7.1 and 161 times per year, respectively.

(3) Most concentrated sampling was done during the open-water seasons of 1972, 1973, and 1974. Less intense sampling was done in 1969–71 and 1975 for zooplankton and in 1971 and 1975 for phytoplankton. A few earlier studies and samples dating back to 1937 were available for comparison.

(4) A total of 164 species and subspecies of algae were identified from the main lakes in the years 1972 to 1975. In the zooplankton, 19 crustacean and 12 rotiferan species were identified, of which at least four are meroplanktonic.

(5) The species composition of the zooplankton appears to have remained unchanged since 1937, although abundance has increased. Both total abundance and numbers of species appear to have increased for the phytoplankton.

(6) Physical conditions have been fairly constant in recent years: in the Upper Lake the maximum surface temperature is usually about 14°C and mean Secchi disc readings are usually about 8 m. Chemical analyses for inorganic constituents have indicated little change in recent years, although there is some evidence of nutrient enrichment.

(7) The distribution of phytoplankton, zooplankton, coliform bacteria, and certain nutrients in 1972 and 1973 suggests longitudinal circulation within Upper Waterton Lake. This concept was supported by temperature profiles and calculations of water volumes moved by the wind.

(8) Three main factors indicated greatly reduced longitudinal circulation in the Upper Lake in 1974 and 1975: changes in the distribution pattern of phytoplankton, less sustained high-velocity southerly wind, and a greater flushing due to higher flows through the lake system in June and July.

(9) The level of organic enrichment in the main lake system is low according to Palmer's (1969) pollution index, which is based on the occurrence and abundance of certain algal species.

(10) New domestic sewage treatment facilities at the townsite will virtually eliminate the unnatural contribution of nutrients to the lake system. This nutrient source, although small relative to the volume of the lakes, may have been responsible for recent increases in plankton abundance.

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