

the benthic fauna of lower waterton lake, dardanelles, knights
lake, and the waterton river

waterton lakes national park

by

david b donald

1975



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7 March, 1975

Mr. W.C. Turnbull, Director
Western Region
Parks Canada
131 Customs Building
Calgary, Alberta T2G 0X5

Dear Mr. Turnbull:

I am pleased to transmit herewith a report entitled "The Benthic Fauna of Lower Waterton Lake, The Dardanelles, Knight's Lake, and the Waterton River in Waterton Lakes National Park" by David B. Donald^o (Limnos Associates, Calgary). This project was funded by your Branch and the work carried out in partial fulfilment of the requirements of Contract No. WRO 74/75-135 between the Contractor and the Canadian Wildlife Service. Supervision of the project was by Dr. R.S. Anderson, Research Scientist, Limnology Unit, Canadian Wildlife Service, Calgary.

The purpose of the study was to gather baseline data on the benthic flora and fauna of the two lower lakes of the main Waterton Lakes (i.e. Lower Waterton Lake and Knight's Lake), The Dardanelles, and the upper reaches of the Waterton River between Knight's Lake and the Park boundary. Some additional data were also gathered on shoreline communities.

We hope that the report meets your expectations, and we will welcome your comments and suggestions concerning the report contents and the approach taken in the study.

Yours sincerely,

W.J.D. Stephen, Director
Western Region
Canadian Wildlife Service

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THE BENTHIC FAUNA OF LOWER WATERTON LAKE, THE DARDANELLES,
KNIGHT'S LAKE, AND THE WATERTON RIVER IN
WATERTON LAKES NATIONAL PARK

by

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prepared for

Canadian Wildlife Service

and

National and Historic Parks Branch

Calgary, Alberta
January - 1975

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I would like to extend my thanks to the Superintendent, Mr. Tom Smith, and the Chief Warden, Mr. Max Winkler, and their staff in Waterton Lakes National Park for providing indispensable assistance and cooperation in the field and for helping with field accommodation. Stephen Anderson assisted with much of the field work; Rod B. Green identified and counted the periphyton; Mrs. B. Hallworth identified some of the macrophytes; and Ralph E. Smith helped with other aspects of the project. R.S. Anderson of the Canadian Wildlife Service designed the project, helped with much of the original organization, and made helpful criticisms and suggestions during the preparation of this report. The project was financed by the National and Historic Parks Branch. Laboratory facilities and field equipment were provided by the Canadian Wildlife Service and the Biology Department of the University of Calgary.

ABSTRACT

The benthic fauna of the lake-river system consisting of Lower Waterton Lake, the Dardanelles, Knight's Lake, and the Waterton River in Waterton Lakes National Park was described in detail. The number of taxa, standing crop, and biomass of fauna in Waterton Lake (12 species, 3732 individuals/m², and 4.25 grams/m² respectively) were only about half the values found for Knight's Lake (24 species, 7553 individuals/m², and 7.11 grams/m² respectively). The differences were attributed mainly to the shallower mean depth of Knight's Lake. The standing crop and biomass of fauna in the Dardanelles (308 individuals/m² and 1.39 grams/m²) were less than 1/3 that found for the Waterton River (1159 individuals/m² and 6.5 grams/m²). The higher standing crop and biomass of fauna in the Waterton River was attributed to the more stable substrate in this river. In comparison, the biomass, but not the numbers, of benthos in Lower Waterton and Knight's lakes was lower than in several other lakes from western Canada. The numbers of benthic animals in the Waterton River and the Dardanelles were comparable to other unproductive rivers and streams in western Canada and elsewhere. The average density of Pontoporeia affinis found in Waterton Lake was comparable to the highest average densities reported for this species in the literature. The low standing crops of benthic fauna and presence of Pontoporeia affinis, which is restricted to oligotrophic to mesotrophic lakes, indicates that the Waterton Lakes system has not been deleteriously affected by cultural development in recent years.

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INTRODUCTION

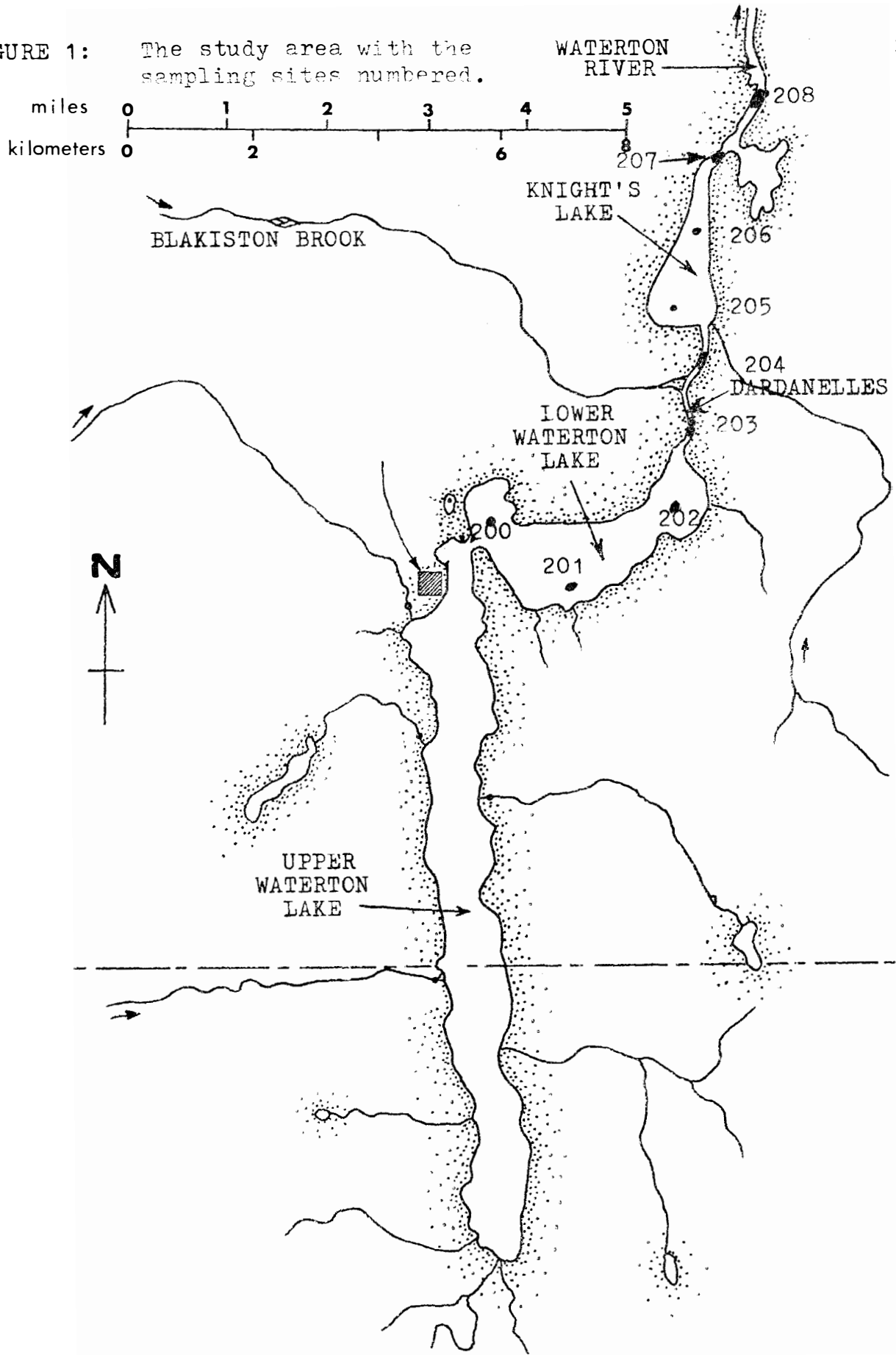
A detailed study of the benthic fauna of the lake-river system comprised of Lower Waterton Lake, the Dardanelles, Knight's Lake, and the Waterton River in Waterton Lakes National Park was carried out in the June-to-September period of 1974. This lake-river system is located in an area of the Park which is used intensively by park visitors, and therefore could be adversely affected by their activities. This study describes the benthic communities in enough detail to provide a baseline for assessment of human impact and suspected environmental changes in the system as determined by future monitoring studies. In addition to the benthic study, samples of periphyton, shoreline fauna, and macrophytic vegetation were also taken, and these data are presented in this report.

Previously, Rawson (1942) studied the benthic fauna of Upper Waterton Lake, Anderson, Donald, and Krochak (1972) surveyed the benthic fauna of some of the lakes and streams in the Park, including a few sites in Lower Waterton Lake and the Waterton River system, and Turner and Turner (1973) studied the benthic and shoreline fauna at some sites in Lower Waterton Lake and Knight's Lake.

METHODS

A total of 167 benthic samples were taken from 9 stations in the study area (Figure 1) between June 20 and July 13, and between August 20 and September 9, 1974. Usually 10 samples were taken at each station. The samples from each station were combined, and therefore

FIGURE 1: The study area with the sampling sites numbered.



the data presented are composite values. In Lower Waterton and Knight's lakes, the samples were taken with a 6 X 6 inch (15 X 15 cm) Ekman dredge, and were then washed through a sieve with aperture size 0.36 mm X 0.52 mm. The river stations were sampled using a kick-sample technique, where the flat side of a 12-inch (30.5 cm) D-mouth pond net was placed on the bottom of the river after which the river bed was agitated vigorously with one foot immediately upstream of the net for three minutes. A standard area of approximately one square foot (929 sq.cm) was kicked on each occasion. During June and July, the samples were taken in water up to 1 meter deep while wearing chest waders and with the aid of a boat. This method was preferred over the Surber method because it permitted samples to be taken from mid-stream during the high water period from May to July. Organisms from the lake and river benthic samples were picked from debris in white enamel trays in the field. All of the macro-invertebrates (length greater than 2 to 3 mm) were removed from the debris and were preserved in 70% alcohol. The biomass of invertebrates from each station was determined as the wet weight. The samples were carefully blotted to remove excess moisture from the surface of the organisms, and were then weighed to the nearest hundredth of a gram. Care was taken to ensure that the organisms were not crushed or distorted during this procedure. The trichopterans were weighed without their cases, and the mollusks were weighed with their shells.

The organic content of the benthic mud of lower Waterton and Knight's lakes was determined by drying the mud samples from these lakes for 24h at 105 C and then ashing the sample for 2h at 650 C. The organic content was taken as the percentage weight loss of the dry

sample. The details of this method will be described elsewhere (D. R. Mudry and R. S. Anderson, 1975, report in preparation).

The inshore fauna was collected by sweeping a pond net through the water column over an area which was being stirred up vigorously by kicking the near-shore substrate. Several small areas were sampled during a standard 5-minute shoreline sample. The net used for collecting the shoreline fauna was the same as the one used for sampling the river benthos. The 5-minute sampling period was used to provide a rough standard of comparison for the different sites sampled.

Samples of periphyton were collected by removing 5 rocks at random from the river bottom or lake shoreline and then scraping 1 cm^2 from the upper surface of each rock (i.e. the surface which had been exposed to the flowing water and light). The periphyton was preserved in Transeau's solution.

Based on random collections and observations made on the lakes, the distribution of aquatic macrophytes was mapped in Lower Waterton and Knight's lakes.

The invertebrates from each sample were counted and identified with the aid of keys in Davies (1971), Edmondson (1959), Gaufin et al. (1966), Jewett (1959), Needham et al. (1935), Ricker (1943), and Usinger (1956). The periphyton was identified with the aid of keys in Cleve-Euler (1951-1955), Patrick and Reimer (1966), Tiffany and Britton (1951), and Prescott (1962).

RESULTS

Lower Waterton Lake and Knight's Lake

Table 1 shows the percentage composition by species of the benthic community of Lower Waterton Lake. The average number of animals and biomass (weight) per square meter were 3732 indiv. and 4.25 g respectively. The dominant benthic organisms were species of Chironomidae ($2096/m^2$). Procladius was the dominant genus in the group. Different genera of Chironomidae become either more or less prominent in the benthic community depending on their life cycles. Some species of benthos develop from the egg stage to the aerial adult stage in a relatively short period of time. These species will be absent from the benthic communities of lakes or rivers for at least part of the year. This probably accounts for the absence of the genera Heterotrissocladius and Psectrocladius in late August.

In general, Pontoporeia affinis Lindstrom was the second most abundant organism in the benthos ($1211/m^2$) of Lower Waterton Lake. It was the dominant organism at two of three stations. The size distribution of this amphipod in the two sampling periods suggested that there was one generation of Pontoporeia per year.

No macrophytic vegetation was found in Lower Waterton Lake except for a small, shallow, mid-lake area which supported the Horned Pondweed, Zannichellia palustris L. (Figure 2). This species is usually found in saline, alkaline or, rarely, fresh water pools, (Stewart, Dennis, and Gikey, 1963) and is often associated with organic enrichment (personal communication to R. S. Anderson from R. Schröder, Bodensee, Germany).

TABLE 1: Percentage composition by number and weight, and standing crop (numbers) and biomass (weight) of the benthic fauna from three stations in Lower Waterton Lake.

Station Depth Month	200 20m		201 26m		202 16m		Mean Number per m ²
	June	August	June	August	June	August	
Oligochaeta	2.03(8.99) ¹	24.90(10.03)	.53(20.71)	8.99(5.54)	7.66(3.73)	7.14(2.95)	350
Amphipoda							
Pontoporeia affinis	44.33(34.63)	57.26(71.49)	34.46(8.01)	73.20(75.84)	0.15(0.16)	6.06(12.08)	1211
Diptera							
Chironomidae	51.05(51.97)	17.06(17.62)	51.37(70.55)	16.36(17.55)	90.03(92.42)	83.76(81.67)	2096
Brillia	--	2.90	0.21	5.03	--	0.86	
Chironomus	0.08	0.25	1.05	0.71	1.22	4.65	
Heterotrissocladius	9.48	--	12.05	--	1.22	--	
Procladius	3.81	7.33	1.47	5.03	39.11	37.33	
Psectrocladius	30.71	--	3.38	--	6.59	--	
Sergentia	0.41	1.89	5.07	2.87	2.76	4.65	
Tanytarsini spp.	0.89	--	24.73	0.53	35.73	34.41	
Other	5.67	4.67	3.38	2.15	3.37	1.83	
Heleidae	--	--	--	--	0.15	0.11	
Pelecypoda							
Pisidium	--	0.25(0.41)	--	--	0.30(0.43)	2.48(2.89)	20
Other	2.59(4.41)	0.50(0.43)	0.63(0.71)	1.43(1.04)	1.84(3.23)	0.43(0.38)	53
Total							
Number (m ²)	5904	3405	2036	2393	4677	3978	3732
Weight (m ²)g	2.693g	5.255g	1.997g	4.322g	5.736g	5.514g	4.253g
Substrate organic content (%)	5.92		6.95		6.16		

¹Values in parentheses are percentage composition by weight in grams.

FIGURE 2: Lower Waterton lake shown with the area known to support the growth of Zannichellia palustris crosshatched. Depths in meters.

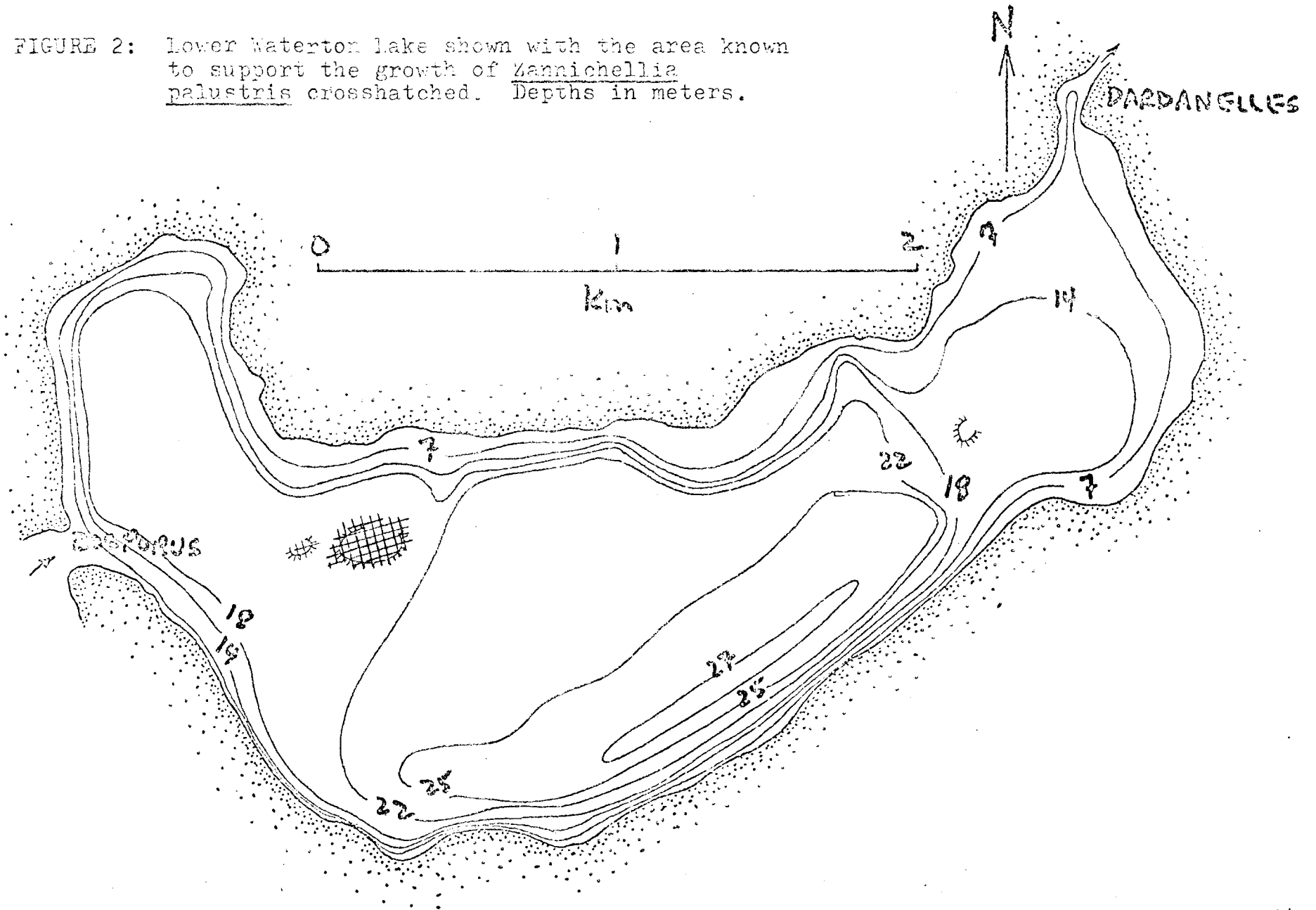


Table 2 shows the percentage composition of the benthic community of Knight's Lake. The average standing crop and biomass of organisms per square meter was 7,553 indiv. and 7.11 g respectively. In numbers and biomass, the Chironomidae were the dominant benthic organisms. The Oligochaeta were numerically second in importance to the Chironomidae, but their biomass was much less than the Hirudinoidea and Pelecypoda.

Knight's Lake supported a dense growth of pondweed over most of its area (Figure 3). Potamogeton richardsonii (Benn.) Rydb. was by far the dominant species, although Potamogeton vaginatus Turcz. was present. The distribution of these species in Knight's Lake agrees with the distribution described by Turner and Turner (1973), although these plants are perhaps somewhat more widespread than their report indicates.

Chi square tests indicated that there were statistically significant differences in the proportions of the different taxa at the three stations in Lower Waterton Lake and the two stations in Knight's Lake. This indicated that the benthic communities at these stations were different, although it is obvious that the communities were similar in some respects, such as in the species composition.

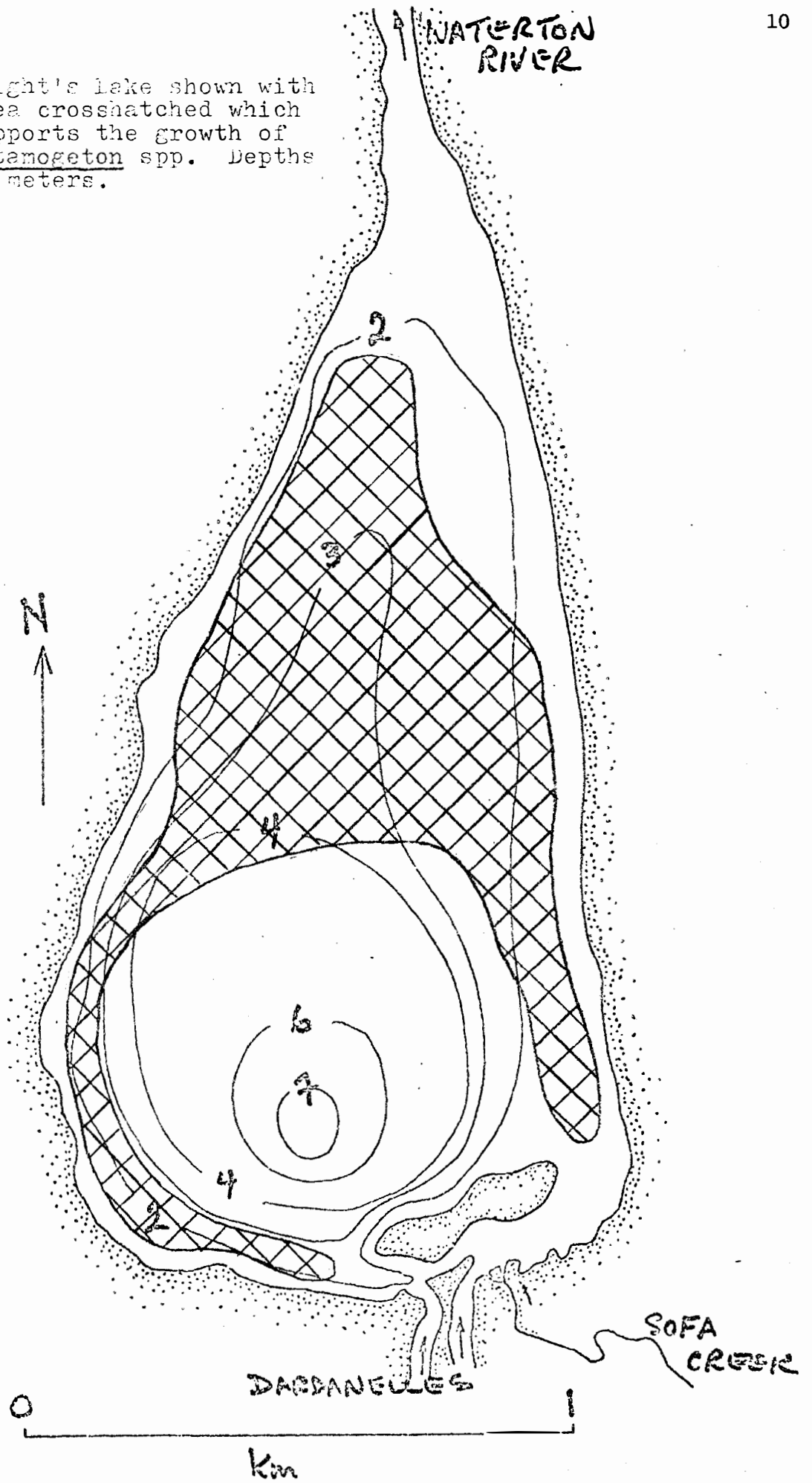
The organic content of the mud substrate at all stations in Lower Waterton Lake and Knight's Lake was similar (Tables 1 and 2). At the 5 stations it varied from 5.84% to 6.95% by weight of the dry substrate. Therefore, the organic content was unlikely to influence the distribution in numbers and biomass of organisms in this system. The organic content of the substrate can vary considerably from lake to lake. For example in Linnet Lake in Waterton Lakes National Park, it was 32.09% by weight of the dry substrate. Low organic content is

TABLE 2: Percentage composition by number and weight, and standing crop (numbers) and biomass (weight) of the benthic fauna from two stations in Knight's Lake.

Station	205		206		Mean No. per m ²
Depth	8m		4.5m		
Month	June	August	June	August	
Nematoda	5.01(0.36)	8.73(0.19)	--	17.47(1.08)	597
Oligochaeta	3.93(3.45)	19.97(16.16)	6.33(5.35)	27.05(17.94)	877
Hirudinoidea	0.67(5.34)	2.07(48.56)	2.69(29.06)	0.05(0.30)	69
Erpobdella punctata	--	0.59	0.58	--	
Glossophonia complanata	0.07	0.15	0.82	--	
Helobdella stagnalis	0.60	1.04	0.46	0.05	
Nephelopsis obscura	--	0.30	0.82	--	
Amphipoda	--	1.04(1.41)	1.75(2.25)	0.11(0.44)	26
Hyalella azteca	--	1.04	1.52	--	
Pontoporeia affinis	--	--	0.23	0.11	
Trichoptera	0.06(0.13)	0.29(0.73)	0.93(1.49)	0.05(0.94)	14
Leptoceridae	--	--	0.23	--	
Molannidae	0.06	0.29	0.46	0.05	
Phryganeidae	--	--	0.23	--	
Diptera					
Chironomidae	82.94(74.74)	30.92(3.04)	63.42(27.83)	23.90(38.36)	4580
Chironomus	0.70	--	--	--	
Cryptochironomus	0.10	--	1.05	--	
Cryptotendipes	9.52	--	--	--	
Endochironomus	--	0.15	1.75	--	
Parachironomus	0.03	3.40	0.93	0.62	
Procladius	15.61	1.04	28.01	13.75	
Psectrocladius	3.06	--	0.23	--	
Tanytarsini spp.	52.69	18.79	21.57	9.35	
Other	1.21	7.54	9.84	0.16	
Geratopogonidae	2.32(0.94)	23.52(2.20)	17.23(3.93)	16.51(5.27)	737
Pelecypoda Pisidium & Sphaerium	4.60(13.86)	11.69(25.34)	6.33(28.34)	12.11(31.32)	558
Gastropoda	0.13(0.70)	0.74(1.89)	0.35(0.74)	0.11(0.90)	16
Gyraulus parvus	0.10	--	0.12	0.05	
Valvata sincera helicoidea	0.03	0.74	0.23	0.05	
Other	0.30(0.43)	1.03(0.43)	0.70(0.38)	2.59(3.51)	75
Total					
Number (m ²)	15,995	2910	3672	7637	7,553
Weight (m ²)	10.189g	5.533g	7.554g	5.162g	7.109g
Substrate organic content (%)	5.84		6.48		

1 Values in parentheses are percentage composition by weight in grams.

FIGURE 3: Knight's Lake shown with area crosshatched which supports the growth of Potamogeton spp. Depths in meters.



usually associated with oligotrophy (low production and/or geological youth) or high water renewal rates, or both.

Table 3 shows the percentage composition by number of the shoreline fauna from one station in each of Knight's and Lower Waterton lakes on September 10, 1974. The communities of both lakes were dominated by the amphipod Gammarus lacustris Sars. Corixids, primarily immature nymphs, were second in importance in Knight's Lake and the elmid, Heterlimnius, was second in importance in Lower Waterton Lake. There was a substantial shoreline community of epiphytic chrysophytes at the stations where the benthic fauna collections were made (Appendices 1 and 2).

Dardanelles and Waterton River

Table 4 shows the percentage composition by number and weight of the benthic fauna of the Dardanelles and the Waterton River. The species composition in these two sections was similar. Trichoptera and Chironomidae were in general the numerically dominant organisms in both sections, although there was considerable variability in the fauna between the two sampling dates and from station to station. The overall standing crop and biomass of organisms in the Dardanelles (308 indiv./m² and 1.39 g/m²) approached 1/4 of that determined for the Waterton River (1159 indiv./m² and 6.5 g/m²).

TABLE 3 : Percentage composition by number of the shoreline fauna of Knight's and Lower Waterton Lakes on September 10, 1974.

	Knight's	Lower Waterton
Amphipoda		
<i>Gammarus lacustris</i>	35	62
<i>Hyalella azteca</i>	5	+
Oligochaeta	2	-
Hirudinoidea		
<i>Helobdella stagnalis</i>	1	-
<i>Nepheleopsis obscura</i>	3	+
Ephemeroptera		
<i>Paraleptophlebia</i>	+	4
Other	1	+
Plecoptera		
Perlodidae	4	-
<i>Alloperla</i>	-	2
Trichoptera		
Limnephilidae	9	+
Diptera		
Tipulidae	-	1
Heteroptera		
Corixidae	34	15
Notonectidae	1	-
Coleoptera		
<i>Heterolimnius</i>	-	40
Dytiscidae	2	-
Pelecypoda		
<i>Pisidium</i>	1	-
Gastropoda		
Lymnaea	-	+
Physa	3	-
Total number	255	502

TABLE 4: Percentage composition by number and weight, and standing crop (numbers) and biomass (weight) of the benthic fauna from the Dardanelles and Waterton River.

Station	203		204		Mean Number	207		208		Mean Number	
Month	July	August	July	August	per m ²	July	September	July	September	per m ²	
Amphipoda											
<i>Hyalella arteca</i>	---	---	---	---		4.79(1.70)	0.30(0.11)	---	0.16(0.17)	9	
Oligochaeta	---	0.37	---	---		3.14(0.27)	1.82(0.13)	---	---	9	
Mirudinoidea	---	0.37(2.97)	---	---	1	3.64(57.46)	0.91(4.35)	0.15(1.04)	0.04(1.38)	8	
<i>Glossiphonia complanata</i>	---	0.37	---	---		0.82	0.30	0.15	---		
<i>Helobdella stagnalis</i>	---	---	---	---		0.66	0.30	---	---		
<i>Nepheleopsis obscura</i>	---	---	---	---		2.14	0.30	---	0.04		
Ephemeroptera	7.54(3.01) ¹	8.37(5.29)	71.76(56.51)	17.26(16.52)	53	17.35(14.79)	5.30(2.71)	59.39(38.68)	4.85(2.46)	166	
<i>Baetis</i>	---	0.55	2.35	1.19		0.99	---	10.53	1.89		
<i>Cinygmula</i>	---	1.48	18.82	0.95		4.79	---	6.26	---		
<i>Ephemerella</i>	7.54	3.91	2.35	---		10.58	---	17.71	0.08		
<i>Ephemerella coloradensis</i>	---	---	12.94	1.19		---	0.91	0.15	0.98		
<i>Ephemerella doddsi</i>	---	---	---	4.31		---	---	---	---		
Iron	---	---	---	---		---	---	2.44	---		
<i>Paraleptophlebia</i> sp.A	---	0.93	---	0.23		---	2.42	---	0.37		
<i>Paraleptophlebia</i> sp.B	---	0.55	---	---		0.83	1.67	6.41	0.66		
<i>Pseudocloeon</i>	---	0.93	---	1.43		0.17	---	12.67	0.33		
<i>Rithrogenia</i>	---	---	35.29	7.91		---	---	0.15	---		
Other	---	---	---	---		---	0.30	3.05	0.53		
Plecoptera	3.14(0.85)	4.09(2.74)	8.23(4.35)	7.19(7.09)	17	0.99(1.81)	4.55(25.87)	2.75(7.89)	1.93(8.46)	29	
<i>Acroneuria pacifica</i>	---	0.18	---	---		0.16	4.24	0.76	1.39		
Alloperia & Paraperia	3.14	0.92	7.06	1.67		0.83	---	1.53	---		
<i>Arcynopteryx</i>	---	2.60	---	4.79		---	0.30	---	0.37		
<i>Nemoura cinctipes</i>	---	0.37	---	---		---	---	---	0.16		
<i>Nemoura oregonensis</i>	---	---	1.18	0.23		---	---	---	---		
Other	---	---	---	0.47		---	---	0.46	---		
Trichoptera	1.25(0.29)	32.77(6.92)	3.53(4.77)	38.12(26.51)	85	3.30(11.45)	25.00(20.15)	11.30(21.50)	75.88(40.35)	544	
Glossosomidae	1.25	2.04	---	6.71		---	---	---	0.04		
Hydropsychidae	---	24.95	1.18	28.53		0.16	20.00	4.12	74.40		
Hydroptilidae	---	---	---	---		---	---	0.46	0.57		
Leptoceridae	---	3.91	---	---		2.15	3.48	1.53	0.53		
Leptostomatidae	---	1.86	1.18	1.19		---	1.06	---	0.33		
Limnephilidae	---	---	1.18	1.67		0.99	0.45	---	---		
Rhyacophilidae	---	---	---	---		---	---	5.19	---		
Diptera											
Tendipedidae	66.66(14.97)	20.67(1.99)	11.76(0.88)	28.05(2.20)	86	48.76(1.74)	48.33(2.74)	8.85(0.66)	5.75(0.65)	237	
<i>Ablabesmyia</i>	0.62	0.18	---	---		0.99	1.82	0.31	0.86		
<i>Dicrotendipes</i>	---	---	---	---		0.33	---	---	---		
<i>Endochironomus</i>	---	---	---	---		0.49	---	---	---		
<i>Microtendipes</i>	61.00	---	---	---		1.49	37.72	---	0.74		
<i>Orthocladius</i>	---	5.02	---	11.51		1.65	---	1.83	1.03		
<i>Parachironomus</i>	---	0.74	---	---		---	---	0.15	0.04		
<i>Tanytarsini</i> spp.	2.51	2.42	3.53	1.67		35.70	---	4.43	0.86		
Other	2.52	12.29	8.23	14.86		8.10	8.79	2.14	2.21		
Empididae	---	---	---	1.19(0.25)	1	---	---	---	---		
Rhagionidae	---	---	---	---		---	---	---	0.57(5.09)	4	
Simuliidae	---	5.21(0.48)	---	1.91(0.17)	9	0.99(0.19)	---	8.24(1.37)	0.45(0.14)	18	
Tipulidae	3.77(70.22)	8.75(63.93)	2.35(1.30)	3.35(46.53)	17	2.64(5.80)	2.42(32.00)	0.30(1.46)	0.86(25.34)	15	
Pelecypoda	1.25(0.21)	0.55(0.20)	---	---	1	0.99(0.67)	0.61(0.39)	0.61(0.34)	4.02(8.77)	28	
<i>Pisidium</i> & <i>Sphaerium</i>	1.25(0.21)	0.55	---	---		0.99	0.61	0.61	4.02		
Gastropoda	11.32(8.70)	13.40(12.74)	1.18(32.02)	---	23	0.82(3.41)	5.91(9.98)	4.73(22.89)	3.04(6.58)	41	
<i>Cyraulus parvus</i>	---	5.66	0.74	---		---	0.61	2.90	2.30		
<i>Lymnaea</i>	---	5.66	1.18	---		---	---	1.35	0.53		
<i>Physa</i>	---	1.86	---	---		0.82	5.15	0.46	0.20		
<i>Valvata sincera</i>	---	1.86	---	---		---	0.15	---	---		
<i>helicoidea</i>	---	---	---	---		---	---	---	---		
Other	5.03(1.71)	5.76(2.75)	1.18(0.16)	2.87(0.68)	13	12.56(2.62)	4.85(1.55)	3.66(4.16)	2.42(0.06)	51	
Total	Number (m ²)	155	537	121	417	308	605	943	655	2434	1159
	Weight (m ²)g	1.271	2.113	0.712	1.456	1.388	5.132	7.521	4.741	8.597	6.497

¹Values in parentheses are percentage composition by weight in grams.

DISCUSSION

The benthic communities of Lower Waterton and Knight's lakes were quite different. In Knight's Lake both the number of species and the standing crop and biomass of the organisms in the benthic community were greater than in Lower Waterton Lake. In all, 24 taxa were identified from Knight's Lake, while only 12 were identified from Lower Waterton Lake. The higher benthic productivity and greater species diversity of Knight's Lake is undoubtedly related to the much shallower mean depth of this lake (Figures 1 and 2). In general, smaller and shallower lakes are known to be more productive than deep large lakes (Ryder *et al.* 1974), although in Knight's Lake the potential productivity may be somewhat offset by the high water renewal rate of the water in this lake. The shallowness of Knight's Lake permits the development of extensive beds of Potamogeton spp. (Figure 3)¹. The presence of Potamogeton could contribute to the higher levels of secondary productivity by providing additional food sources, shelter, and surface areas for the benthos.

The average number of organisms in Lower Waterton ($3732/m^2$) and Knight's ($7753/m^2$) lakes were generally greater than a number of other lakes in western Canada for which data exist. The benthic fauna of 11 lakes in central Alberta averaged $1047/m^2$ (Smith, 1970a and 1970b); 11 lakes in southern Saskatchewan averaged $1612/m^2$ (Rawson, 1944); 5 lakes in northern Saskatchewan averaged $2014/m^2$ (Rawson, 1957); and 6 large alpine lakes in the Rocky Mountains averaged $791/m^2$ (Rawson,

¹Development of rooted macrophytes is limited to the zone of effective light penetration which is often less than 5 m in much of the Waterton Lakes area.

1942). The average biomass (wet weight) of benthic fauna in Lower Waterton (4.2 g/m^2) and Knight's (7.1 g/m^2) lakes was less than the average of the lakes in southern (19.9 g/m^2) and northern (21.4 g/m^2) Saskatchewan, and was similar to the lakes in the Rocky Mountains (4.2 g/m^2). The sampling techniques, particularly with regard to sieve mesh size, were different for most of these studies. This, of course, could account for a part of the differences between the various lakes, but in general the comparisons are valid.

A preliminary survey of the benthic fauna in Waterton Lakes National Park was carried out in 1971 (Anderson *et al.*, 1972). The densities of benthic organisms on July 20 and 21, 1971 in Lower Waterton and Knight's lakes were 3872 and 6051 indiv./m², respectively. The numbers and the species composition then were very similar to those obtained during the present study. This suggested that there has been no major change in these benthic communities from 1971 to 1974.

Previously, the shoreline fauna of Knight's and Lower Waterton lakes had been investigated by Anderson *et al.*, (1972) and Turner and Turner (1973). The sampling technique, and usually the sampling times and stations for these studies, were different from the present study. Nevertheless, many of the taxa found along the shoreline of the two lakes were common to all three studies. Differences in the abundance of the various taxa among the three studies could probably be attributed to differences in sampling techniques and sampling locations, and seasonal changes in the abundance of the specific organisms due to patterns of development in life cycles.

The Dardanelles delta, situated at the south end of Knight's Lake, graduates from gravel at the mouth of the Dardanelles to sand

at the far edge of the delta. Most of the delta was above water by the end of September in 1974. Five Ekman samples taken from this delta on July 12, indicated that the fauna was extremely sparse, as might be expected in a gravel and sand substrate. The avifauna often observed on the delta probably use this location more as a resting place rather than a feeding area, although Turner and Turner (1973) suggested that it might be used as a feeding area.

Pontoporeia affinis is restricted in its North American distribution to limited coastal areas and to oligotrophic-to-mesotrophic proglacial lake systems (Ricker, 1959; Dadswell, 1973) and is usually resident in fairly deep lakes. At present, this species is only known to occur in a few other lakes in Alberta - Lake Athabasca (Ricker, 1959), Tulip Lake, Leland Lakes, and Bocquene Lake (McDonald, 1966a,b,c), and Cold and Lesser Slave lakes (Paetz and Zelt, 1974). Pontoporeia is an important food source in many Canadian lakes for young lake trout, Salvelinus namaycush, (Scott and Crossman, 1973), and is probably an important food of young trout in the Waterton Lakes as well.

Table 5 gives a comparison of the abundance of Pontoporeia in several lakes in Canada, U.S.A., and Sweden. This table indicates that the average density of this crustacean in Lower Waterton Lake ($1211/m^2$) was close to the highest mean values reported in the literature, although the maximum site density recorded for Lower Waterton Lake ($2615/m^2$) was less than the maximum reported for some other lakes. For example, the maximum density reported for Lake Michigan is $14,000/m^2$ (Marzolf, 1965).

The large differences in the number and biomass of organisms found in the Dardanelles and Waterton River below Knight's Lake

TABLE 5:

Comparative densities of Pontoporeia affinis in lakes in Canada, U.S.A., and Sweden.

Lake	Number/m ²		Reference
	Station or Zone Maximum	Approximate Lake Mean	
Waterton Lake-Lower(Alberta)	2615	1211	This study
Big Peter Pond(Saskatchewan)	--	1071	Rawson (1957)
Wollaston Lake(Saskatchewan)	--	614	Rawson (1959)
Lake Huron(Michigan)	--	1119	Teter (1960)
Lake Michigan(Michigan)	6565	821	Robertson & Alley (1966)
Lake Vättern(Sweden)	--	1001	Grimås (1969)
Lake Mälaren(Sweden)	4920	--	Willén (1972)
Lake Athabasca (N W Territories)	1450	--	Larkin (1948)
Great Slave lake (N W Territories)	3476	--	Larkin (1948)

(Table 4) is undoubtedly related to the substrate differences in these two sections of the river. The Dardanelles has extensive gravel bars where the maximum rock diameter is approximately 15 cm. There are only a few deep holes in this section, characterized by a stable, large-boulder substrate. The Dardanelles passes along the active edge of the Blakiston Brook delta which consists of relatively unstable material and, therefore, some of the river bed material would move during high water in May, June, and July. In most locations there was no obvious periphyton in this river. Samples collected at one station in the Dardanelles indicated that there was no periphyton in July, although by September a substantial growth of epiphytic chrysophytes had developed (Appendices 1 and 2). This supports the conclusion that the substrate is relatively unstable. This sort of river bed does not generally support a dense population of river fauna.

Much of the river bed of the Waterton River (stations 207 and 208, Figure 1) consists of a stable boulder-substrate, which has an obvious growth of periphyton covering most rocks. This type of substrate usually supports a substantial benthic community. The abundance and genera of periphyton found at station 208 are shown in Appendices 1 and 2.

The limited data available from two sampling periods and the extreme variability in benthos from station to station do not permit a detailed discussion of the life histories or the seasonal changes in the fauna of the Waterton River. However, one trend is evident: the total numbers and biomass of fauna increased from July to August at all stations, especially at station 208. Increases were mainly due to the Trichoptera (Hydropsychidae) and, to a lesser extent, the Plecoptera.

As might be expected in a mountain stream associated with oligotrophic lakes and relatively cold waters, the number of organisms in the Waterton River and Dardanelles was generally less than other comparable streams and rivers reported in the literature. For example, the mean annual numbers of organisms from the upper and lower rapids on the Montreal River in Saskatchewan were $1146/m^2$ and $8748/m^2$ respectively (Cushing, 1963); from Bridger Creek in Montana it was $2254/m^2$ (Logan, 1963); and from Lusk Creek in Alberta it was $417/m^2$ (Radford, 1971). The abundance of organisms from several different substrate types from rivers in England varied from 3,316 to $243,972/m^2$ (Percival and Whitehead, 1929).

The abundance of benthic fauna in streams and rivers is dependent on substrate type, silt load, current, the sampling methods used in obtaining the abundance estimates, and other factors (Hynes, 1970). These factors alone could account for much of the variability in the numbers and quantities compared above.

Robinson and Smith (1974) recently conducted an intensive study of the Bow River near Lake Louise in Banff National Park. The Bow River at this location is similar in size to the Dardanelles and Waterton River. The mean annual standing crop in numbers and the biomass of organisms from stations upstream and downstream of Lake Louise was 407 indiv./m^2 and 0.86 g/m^2 , and 2925 indiv./m^2 and 7.63 g/m^2 , respectively. These differences were attributed to eutrophication due to human influence from the Lake Louise townsite area. The above values were similar to values for the Dardanelles (308 indiv./m^2 and 1.39 g/m^2) and Waterton River (1159 indiv./m^2 and 6.5 g/m^2). This

comparison suggests the importance of both the natural substrate and cultural enrichment in determining the numerical standing crop and biomass of benthic organisms in mountain streams.

In the Dardanelles and Waterton River 20% and 18% respectively of the kick samples which were taken yielded large numbers of fish eggs. The appearance of the eggs and the nature of the spawning locations indicated that these eggs were probably deposited by the longnose sucker (Catostomus catostomus). This fish is apparently common in Knight's Lake (Turner and Turner, 1973).

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GLOSSARY OF TERMS

- Amphipoda - an order of Crustacea; various species commonly occur in freshwater and marine environments, and are often important food sources for fish; one of many groups called "freshwater shrimps" or "scuds".
- Benthos - the association of species of plants and animals that live in or on the bottom sediments of a body of water.
- Chironomidae - midges; a family of insects which is widely distributed in freshwater habitats. The larval stages are aquatic, while the adult stage is aerial. These insects are important as food for many species of fish.
- Chrysophytes - algae which are golden-brown in colour, and generally have cell walls composed of two overlapping halves which are frequently impregnated with silica.
- Corixidae - water boatmen; a family of insects in which both nymphs and adult stages are aquatic, although the adults can fly (i.e. for dispersal). They are commonly inhabitants of shallow-water habitats.
- Eutrophication - enrichment of waters by nutrients, either through man's activities or by natural means. Phosphorus and nitrogen are the most important elements responsible for eutrophication.
- Hirudinoidea - leeches; primarily freshwater organisms which comprise part of the phylum Annelida, - the segmented worms.

- Macrophytes - vascular aquatic plants which may grow either free floating, submerged, or emergent.
- Nymphs - immature stages of insects which resemble the adults in many structural features. In such insect species, metamorphosis consists of a series of gradual differentiation stages or instars from nymph to adult, rather than a series of radical morphological changes such as occurs in complete metamorphosis (i.e. larva to pupa to adult).
- Oligochaeta - a class of annelids (the segmented worms) similar in structure to the earthworms. The freshwater species occur in all types of aquatic habitats, but the greatest abundances are usually associated with organically rich substrates.
- Oligotrophic - descriptive term for lakes which are characteristically deep, rich in oxygen, have little macrophytic vegetation around their margins, are poor in dissolved nutrients such as phosphorus and nitrogen, and have low rates of production.
- Pelecypoda - bivalved mollusks (freshwater clams) which are found in both marine and freshwater environments. They are most commonly inhabitants of relatively stable substrates which are free from pollution and high silt-turbidity.
- Periphyton - minute organisms (both plant and animal) attached to submerged substrates (such as plants and other objects) which project above the bottom sediments.

- Plecoptera - the stoneflies; insect nymphs which are common inhabitants of swift, cool streams, and the shores of oligotrophic temperate lakes.
- Primary production - the rate at which energy is stored (or the amount of organic matter produced) by the photosynthetic activity of plants.
- Secondary production - the net production or formation of animal tissue or matter after respiration and excretion.
- Taxon (pl. taxa) - a taxonomic division such as a family, order, or species; in discussion, usually refers to the highest level of identification employed in the study at hand.
- Transeau's solution - made up from six parts of water, three parts of 95% ethanol, and one part formalin.
- Trichoptera - caddisflies; the larval stages of these insects are common in running and standing waters. Many of the larval forms build cases for protection, and some spin webs for trapping their food.
- Water renewal rate (or flushing rate) - the theoretical time required for the total volume of water in a lake or its equivalent to be discharged via the outlet stream or river.

APPENDIX 1: Numbers of cells and filaments of periphyton $\times 10^3$ per 5 square centimeters from the river beds of the Dardanelles and Waterton River, and from the shoreline of Knight's lake and lower Waterton lake.

Number per 5 cm ²	Dardanelles		Waterton River		Knight's Lake		Waterton Lake	
	12/07/74	10/09/74	13/07/74	10/09/74	11/07/74	10/09/74	13/09/74	10/09/74
Cells	0	2101	895	1512	2866	2219	1494	3660
Filaments	0	18	526	163	0	54	0	0
Total	0	2119	1422	1675	2866	2274	1494	3660

APPENDIX 2: Relative abundance of genera or species of periphyton at one station in each of the Dardanelles, Waterton River, Knight's Lake, and Lower Waterton Lake.

	Dardanelles		Waterton River		Knight's Lake		Lower Waterton Lake	
	10/09/74	13/07/74	10/09/74	11/07/74	10/09/74	13/07/74	10/09/74	
Chlorophyta								
<i>Ulothrix zonata</i> (Weber + Monr.) Kuetzing	-	-	-	-	-	-	+	
<i>Zygnema</i> sp.	-	+	-	-	-	-	-	
<i>Bulbochaeta</i> sp.	-	++	-	-	+	-	-	
Cyanophyta								
<i>Chroococcus</i> spp.	-	++	-	-	-	-	-	
<i>Gleocapsa</i> spp.	-	+++	-	-	-	-	-	
<i>Lyngbya Diguettii</i> Comont	-	-	-	-	+	-	-	
<i>Oscillatoria</i> spp.	-	++	-	-	-	-	-	
<i>Calothrix</i> sp.	-	+++	+	-	-	-	-	
Chrysophyta								
<i>Dinobryon bavaricum</i> Imhof.	+	-	-	-	-	-	-	
<i>D. sociale</i> Ehrenberg	+	-	+	-	-	-	+	
<i>Cyclotella comta</i> (Ehrenberg) Kuetzing	+	-	-	-	-	-	-	
<i>C. ocellata</i> Pantocsek	+	-	+	+	+	+	+	
<i>Melosira</i> spp.	+	-	+	+	+	-	+	
<i>Diatoma tenue</i> var. <i>elongatum</i> Lyngb.	+	-	-	+	-	-	-	
<i>D. hiemale</i> var. <i>mesodon</i> (Ehrenberg) Grun.	-	-	-	+	-	-	-	
<i>Diatoma</i> spp.	-	+	-	+	+	+	+	
<i>Fragilaria brevistriata</i> Grun.	-	-	+	-	-	-	-	
<i>F. crotonensis</i> Kitton	-	-	-	-	-	-	+	
<i>F. leptostauron</i> (Ehrenberg) Hust.	-	-	+	-	+	-	-	
<i>F. pinnata</i> Ehrenberg	+	-	-	-	+	-	-	
<i>F. virescens</i> Ralfs	+	-	+	-	-	-	-	
<i>Fragilaria</i> spp.	-	+	++	-	+	+	++	
<i>Synedra acus</i> Kuetzing	-	-	-	+	+	-	+	
<i>S. amphicephala</i> Kuetzing	-	-	-	+	-	-	-	
<i>S. delicatissima</i> Wm. Smith	-	-	-	-	-	-	+	
<i>S. delicatissima</i> var. <i>angustissima</i> Grun.	+	-	-	+	-	-	-	
<i>S. radians</i> Kuetzing	-	-	-	+	-	+	++	
<i>S. ulna</i> (Nitzsch.) Ehrenberg	+	-	+	+	+	-	+	
<i>Synedra</i> spp.	++	+	+	+++	+	+++	++	
<i>Tabellaria fenestrata</i> (Lyngb.) Kuetzing	+	-	-	-	+	-	-	
<i>Achnanthes flexella</i> (Kutz.) Brun.	+	+	+	+	+	+	+	
<i>A. lanceolata</i> var. <i>dubia</i> Grun.	-	-	-	-	+	-	-	
<i>A. microcephala</i> (Kutz.) Grun.	+	+	+	+	+	+	+	
<i>A. minutissima</i> (Kutz.) Grun.	+	-	+	-	+	-	+	
<i>A. nodosa</i> A. Cleve.	-	-	+	-	-	-	-	
<i>Achnanthes</i> spp.	++++	+	++	++++	++++	++	+++	
<i>Cocconeis placentula</i> Ehrenberg	+	-	+	-	-	-	-	
<i>Diploneis elliptica</i> (Kutz.) Cleve.	-	-	-	-	-	+	+	
<i>Navicula aurora</i> Sov.	-	-	-	-	+	-	-	
<i>N. gottlandica</i> Grun.	-	-	-	-	-	-	+	
<i>N. graciloides</i> A. Mayer	-	+	-	-	-	-	-	
<i>N. radiosa</i> Kuetzing	+	-	+	-	+	-	+	
<i>N. radiosa</i> var. <i>tenella</i> (Breb. & Kutz.) Grun.	-	-	+	-	+	-	-	
<i>N. vulpina</i> Kuetzing	-	-	-	-	-	-	+	
<i>Navicula</i> spp.	++	+	++	+++	++	++	+++	
<i>Neidium dubium</i> (Ehrenberg) Cleve.	-	-	+	-	-	-	-	
<i>Pinnularia</i> sp.	-	-	-	-	-	-	+	
<i>Stauroneis anceps</i> Ehrenberg	-	-	+	+	+	-	-	
<i>Stauroneis</i> sp.	-	-	-	+	-	-	-	
<i>Gomphonema constrictum</i> Ehrenberg	-	-	-	+	+	+	+	
<i>G. intricatum</i> Kuetzing	-	-	+	-	+	-	-	
<i>G. intricatum</i> var. <i>pumilum</i> Grun.	-	-	+	-	-	-	-	
<i>G. olivaceum</i> (Lyng.) Kuetzing	-	-	-	-	+	-	-	
<i>G. quadrangulatum</i> (Ostr.) Wislouch	-	-	-	-	-	-	+	
<i>Gomphonema</i> spp.	+	+	+	+	+	++	+	
<i>Amphora ovalis</i> Kuetzing	-	-	+	-	-	-	-	
<i>Cymbella affinis</i> Kuetzing	+	+	-	+	-	+	+	
<i>C. distula</i> (Hemp.) Grun.	+	-	+	-	+	+	++	
<i>C. cymbiformis</i> (Kutz.) Brebisson	-	-	-	-	+	-	++	
<i>C. microcephala</i>	+	+	+	++++	+++	-	+++	
<i>C. ehrenbergii</i> Kuetzing	+	-	-	-	-	-	-	
<i>C. ehrenbergii</i> var. <i>hungarica</i> (Kutz.) Pautocsek	-	-	-	-	-	-	+	
<i>C. perpusilla</i> var. <i>genuina</i> A. Cleve	-	-	-	-	+	-	+	
<i>C. ventricosa</i> Agardh.	+	+	+	+	+	+	+	
<i>Cymbella</i> spp.	+	+	+	++	++	+++	+++	
<i>Denticula</i> spp.	+	-	-	-	-	-	-	
<i>Nitzschia amphibia</i> Grun.	-	+	+	+	+	-	-	
<i>N. angustata</i> var. <i>acuta</i> Grun.	-	-	-	-	-	-	+	
<i>Nitzschia</i> spp.	-	+	+	-	+	+	+	
<i>Cymatopleura solea</i> (Breb.) W. Smith	-	-	+	-	-	-	-	