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Temporal and Spatial Dynamics of Ice-Covered Upper Dumbell Lake (Ellesmere Island, Arctic Canada) during the Summer of 1959

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Abstract

We report on a limnological study of ice-covered Upper Dumbell Lake (Ellesmere Island, Canada) conducted during the summer of 1959. The lake was vertically profiled for physical (temperature, light), chemical (alkalinity, pH, oxygen, nutrients), and biological (chlorophyll *a*, gross and net primary productivity) variables on 21 dates spanning from early July to early September. Zooplankton density and age structure were also determined on four dates. Factors such as temperature, alkalinity, pH, and oxygen varied little with depth or over time, whereas nutrients (nitrate, dissolved silica, soluble reactive phosphorus), light, chlorophyll *a,* and gross and net photosynthesis varied substantially. Comparing July to August, nitrate and light intensity decreased while dissolved silica, chlorophyll *a*, and gross and net primary production increased, with two distinct peaks in algal biomass occurring over the month of August. Chlorophyll *a* in this lake was negatively correlated with nitrate concentrations, suggesting uptake of nitrogen as algal biomass increased. The copepod *Limnocalanus macrurus* was the dominant zooplankton taxon present; the age structure of the population advanced over the summer. This study reveals the dynamic nature of vertical habitat gradients even under the ice of Arctic lakes and provides important baseline data for conditions in an Arctic lake during the mid-20th century.

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Introduction

The sensitivity of lakes in the High Arctic to global environmental change is widely recognized (Rouse et al., 1997; Smol and Douglas, 2007; Adrian et al., 2009), with paleolimnological studies revealing rapid rates of ecological change in these lakes over the 20th century (as reviewed by Smol et al., 2005). Limnological surveys have been conducted across lakes in several regions of the High Arctic over the past 20 years (Douglas and Smol, 1994; Ellis-Evans et al., 2001; Michelutti et al., 2002; Antoniades et al., 2003), with the goal of establishing baseline conditions. Limnological data from earlier in the 20th century also provide key data to achieve this goal and play an important role in documenting changing conditions in these lakes, as they provide much higher spatial (i.e., vertical water column) and temporal (i.e., seasonal) resolution than is possible with paleolimnological records. These limnological data, however, are quite sparse.

Most Arctic limnological studies are synoptic surveys, with samples taken from one depth in the surface waters across a suite of lakes, typically once or twice during the summer (Lim et al., 2001; Michelutti et al., 2002; Antoniades et al., 2003). This approach provides key data on regional trends in water chemistry and species distributions. There are few detailed studies, however, on single lakes over the course of the summer (Schindler et al., 1974; Miller et al., 1986; MacIntyre et al., 2006). This approach provides a more comprehensive understanding of controls on algal production (Miller et al., 1986), patterns in nutrient cycling (MacIntyre et al., 2006), and linkages among physical, chemical, and biological processes. In particular, algal biomass can vary substantially with depth, with the concentration in surface waters not always being the most representative of lake trophic status.

Here we report on a limnological study of Upper Dumbell Lake (Ellesmere Island, Canada) conducted from early July to early September in 1959. The lake was vertically profiled for physical, chemical, and biological variables every 2 to 5 days during this period. We compare results of this 1959 survey to those of a comprehensive study of physical, chemical, and biological parameters throughout 1971 and over several years (1969–1972) in Char Lake on Cornwallis Island in the Canadian Arctic archipelago (Roff and Carter, 1972; Schindler et al., 1974; Kalff and Welch, 1974; Rigler et al., 1974). The Upper Dumbell study presented here contributes a detailed limnological study of a High Arctic lake more than a decade before Char Lake and is from a lake that had sustained ice cover over the summer (Char Lake, in comparison, was ice free for part of the summer of 1971 when detailed vertical profiles were collected). Paleolimnological approaches have revealed that Char Lake and Lower Dumbell Lake experienced changes during the 20th century, with Michelutti et al. (2002) finding changes in diatom community structure in Char Lake starting in the late 1980s, and Doubleday et al. (1995) finding increases in black carbon in the top 1.5 cm of a sediment core from Lower Dumbell Lake. The Upper Dumbell Lake and Char Lake limnological studies thus provide important context on the physical, chemical, and biological features of Arctic lakes at a relatively early time compared to the more recent survey studies conducted in the 21st century.

Site Description

Upper Dumbell Lake is one of two Dumbell Lakes near the northern coast of Ellesmere Island in the Canadian Arctic Archipelago (Fig. 1). The lake is about 1.8 km long and 1 km wide, with a surface area of about 100 ha. It is located at 82°29′N, 62°30′W, about 3 km south of Alert, the northernmost meteorological station in the world. The lakes lie about 21 m above sea level (Antoniades et al., 2003).

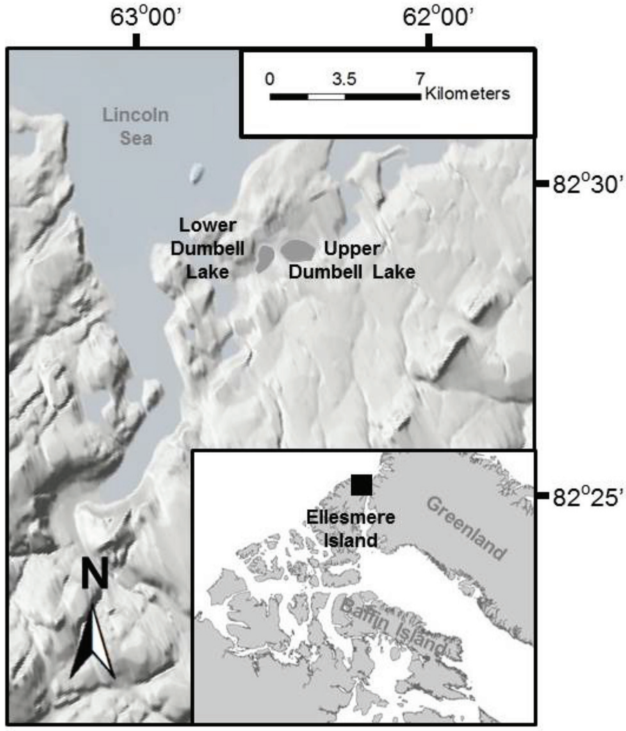

FIGURE 1. Location of the Dumbell Lakes, Ellesmere Island, Canada.

The Dumbell Lakes lie in what is known as the Cape Rawson group consisting of Ordovician to Silurian argillaceous limestone, shale, slate, graywacke, quartzite, chert, and calcareous sandstone (Blackadar, 1954). The group is strongly distorted and metamorphosed. The strata vary greatly in hardness and only the softer shales appear to disintegrate into stiff, fast-drying clays and silts (Bruggeman and Calder, 1953). A steep cliff, about 90 m high, rises abruptly from the southern shore of Upper Dumbell Lake. The cold, dry climate, short growing season, poorly developed soil, and sparse vegetation (a "polar desert") in terrain with low-lying mountains in the vicinity characterize Alert (Antoniades et al., 2003). There are landlocked char in Lower Dumbell Lake and Kirk Lake in the vicinity, but there are no fish in Upper Dumbell Lake (Antoniades et al., 2003).

Continuous daylight prevails at Alert from March through August. The first sunset occurs on September 5. Many foggy days occur in the summer, which is the season of greatest cloud cover. Average annual precipitation is ≈15 cm and falls mainly as snow. The monthly mean temperature for February, the coldest month, is about –34°C, and for July, the warmest month, is about 2°C. The annual mean is about –18°C. In the vicinity of the weather station, the general impression of a barren landscape prevails after the snow disappears. The tracts of very stony polygon soil support only scant vegetation, which moreover tends to congregate in the cracks. Only a few widely scattered and very small areas provide all the conditions necessary for the limited vegetation. Vegetation in the entire area is sparse, with 56 species reported from the area (Bruggeman and Calder, 1953). The most common species (*Saxifraga oppositifolia, S. caespitosa, Salix arctic,* and *Cerastium alpinum*) are the same as those reported from the vicinity of Char Lake (Schindler et al., 1974). Few plants are capable of surviving the harsh climate, lack of moisture, and poorly developed soils (Edlund and Alt, 1989).

The Dumbell Lakes were ice-free in the summers of 1951 and 1957 and about 60% ice-free in 1958. During this study conducted in 1959, only the periphery of Upper Dumbell Lake became ice-free through the summer.

Methods

Lake bathymetry was determined by taking 41 soundings of lake depth through holes drilled through the ice on six transects across the lake, and using these measurements to estimate depth contours. Lake volume was calculated from the contours.

The lake was vertically profiled every 2 to 5 days, from 4 July to 2 September. All measurements in the lake, except for zooplankton collections, were made through a hole cut in the ice, which was covered when not in use. Light penetration into the lake was measured with a Whitney submarine photometer in µamps (4 µamps =1 f.c.) and converted to foot-candles (converted herein by 1 f.c. ≈ 2.031×10^{-1} µEin m^{-2} s^{-1}).

Water samples were collected in all-plastic Van Dorn samplers. Samples were routinely taken just under the ice at 2 m or at 1 m as the ice melted, and at 5, 10, 15, 20, and 23–24 m. Temperatures were measured by direct thermometer readings in the water samples as soon as they reached the surface. Between 24 July and 22 August, temperatures were instead measured with a temperature probe; however, this probe produced highly variable results, so these data are not reported, resulting in a gap in temperature data. Water samples were carried to the laboratory in polyethylene, dark brown bottles held in dark bags. The laboratory was at the Alert meteorological station, and most analyses (except chlorophyll and ^{14}C counts, see below) were done on the day of collection.

Alkalinity, pH, and oxygen were measured on whole water samples. A Beckman pH meter was used for pH measurement, while titration methods were used for alkalinity and oxygen. Alkalinity was measured by methyl-orange titration (Welch, 1948), and oxygen by the standard Winkler titration.

Nutrients were measured on unfiltered water samples, and optical densities were read with appropriate filters on a Klett-Summerson photoelectric colorimeter. Nitrate was measured by the method of Mullin and Riley (1955), phosphate by the standard Woods Hole Oceanographic Institution (WHOI) modification of the Harvey ammonium molybdate method, and dissolved silica by that of Armstrong (1951). All three analyses had a limit of quantification of 5 µg L^{-1} of the element. Because of initial problems with the reagent used in the dissolved silica analyses, only data measured after 19 July are reported.

Water for chlorophyll measures was filtered on 0.45 µm Millipore HA filter discs. The volume of water filtered was routinely 1.5–2.5 L. The filters were held in a dark desiccator under partial vacuum until extraction in October with 90% acetone and measurement at Yale University on a Beckman DU spectrophotometer. Values were estimated by the method of Richards with Thompson (1952) as modified by Creitz and Richards (1955), and the nomographs of Duxbury and Yentsch (1956).

Photosynthesis was measured by the oxygen (gross photosynthesis) method, with Winkler titration, using a photosynthetic quotient of 1.2 (Antia et al., 1963), and by the ^{14}C (net photosynthesis) method of Steeman-Nielsen (1952). The ^{14}C was prepared by, and the filter activities were counted at, WHOI. The ^{14}C had an activity of 5.4×10^{6} CPM mL^{-1}. The total carbonate content of lake water was estimated from alkalinity and pH by the equations and graphs of Vollenweider (1974). A glass-stoppered bottle wrapped in black electrical tape (a "dark" bottle) was suspended with a clear glass-stoppered bottle (a "light" bottle) in the oxygen and ^{14}C measurements for correction for respiration and for dark absorption of ^{14}C. The bottles were suspended in the lake at the depths from which their waters were taken. The oxygen bottles usually were suspended for 48–72 h, and the ^{14}C experiments ran for 24 h. It is assumed that the lower limit of measurable photosynthesis by oxygen evolution was about 0.05 mL L^{-1} or 15–20 mg C m^{-3}; for the ^{14}C method, the lower limit was assumed to be 1.3 mg C m^{-3} (Ryther and Vaccaro, 1954; Strickland, 1960). Because of technical problems in the field, net photosynthesis was not measured before the end of July.

Zooplankton were collected with a Clarke-Bumpus sampler (Clarke and Bumpus, 1940) with 158-μm mesh towed in the open-water perimeter of the lake. Tows captured zooplankton from 210–310 L of water. All the copepod stages were noted and counted under a binocular microscope (15×) at Yale University. Sizes of copepodite stages were estimated from measurements of the prosomes of 30–100 animals in the several tows.

To assess relationships between algal biomass (chlorophyll) and resources (nitrate, phosphate, and light) over the summer, Spearman's rank correlation analysis was used for dates with complete profiles for all four variables (with n = 94 across 20 sampling dates in this period).

Results

PHYSICAL DATA

Upper Dumbell Lake consists of a single basin, with an average depth of 12.5 m and a maximum depth of 33 m in the southeastern corner near the cliff that rises steeply from that shore (Fig. 2). Its volume is about 13×10^6 m^3. The lake is relatively shallow (8–10 m) in its northern and western sides.

In 1959, the lake surface was snow-free on 29 June and a shore lead began to develop on 1 July. It was about 6 m wide on 6 July; only the periphery of Upper Dumbell Lake became ice-free through the summer. Ice covered more than 80% of the lake and was 1.2–1.5 m thick on 24 July. The ice was still 38 cm thick on 10 August. New ice formed along the lakeshore by 20 August, and the lake surface was all frozen and covered by 10 cm of snow on 2 September. Although the lake remained largely ice-covered through the summer, the ice itself was continually changing in nature: thick, solid ice with melting snow cover in late June; snow-free and melting ice in early July; fragile, "candled," thin (38 cm) ice in mid-August and with infrequent small snow additions greatly reducing light penetration; refreezing by 22 August; and accumulating snow by early September.

Small variations in lake water temperature occurred under the ice over the course of the summer (Fig. 3; Table 1). Temperatures increased from an average of 2.5ºC in early July to 4.2ºC on 22 July, with the warmest measure of 5ºC at 2 m just under the ice on 9 July. The rest of the water column did not exceed 3.3°C on that date. Observed temperatures declined thereafter to averages around 3ºC in late August. On 4 July, the lowest temperature was at 2 m just under the ice and the highest was at 24 m. From 6 July to 22 July, the highest temperatures were at 2 m. From 25 August to 2 September the coolest temperatures were again just under the ice at 1 m.

Light intensity varied over the season and with depth (Fig. 4; Table 1). Light intensity was highest in early July, and then varied until mid-August, after which it declined substantially. The highest intensity at 2 m, where most net photosynthesis occurred, was 122 μEin m^{-2} s^{-1} on 11 July, and the lowest at 2m was 21 μEin m^{-2} s^{-1} on 13 August.

CHEMICAL DATA

Across sample dates and depths, pH varied from 7.6 to 8.2 (Table 1). Alkalinity at 1 or 2 m just under the ice varied from 0.6

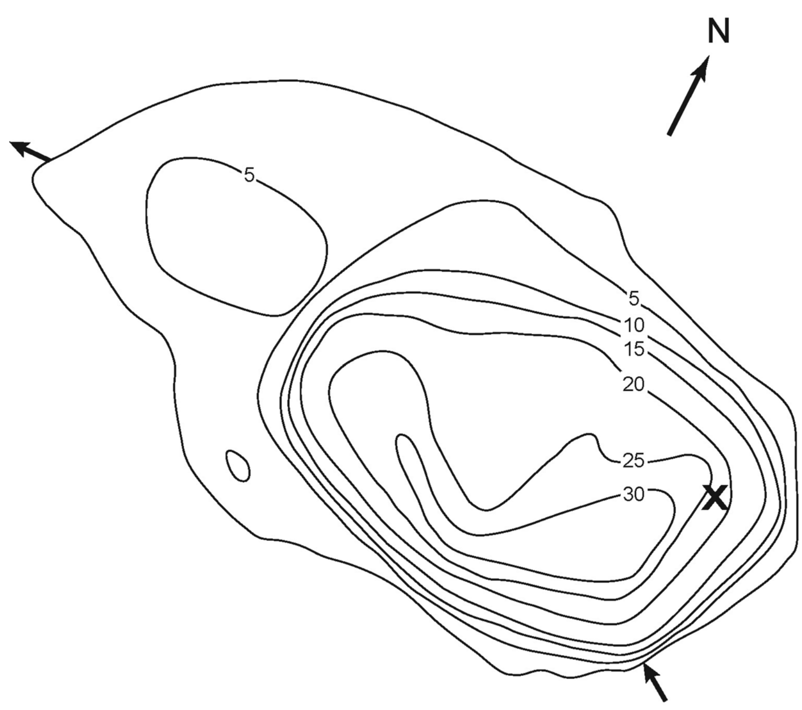

FIGURE 2. Bathymetry (in meters) of Upper Dumbell Lake. The inlet and outlet are indicated by arrows, and the sampling site is indicated by x.

TABLE 1

Physical, chemical, and biological metrics of the water column of Upper Dumbell Lake over the summer of 1959. Temp = temperature; PAR = photosynthetically active radiation; DO = dissolved oxygen; Alk = alkalinity; Chloro = chlorophyll; SRP = soluble reactive phosphorus; dSi = dissolved silica.

Date	Depth (m)	Temp (°C)	PAR (μE m^{-2} s^{-1})	DO (mg L^{-1})	Alk (meq L^{-1})	pH	Chloro (μg L^{-1})	Nitrate (μg L^{-1})	SRP (μg L^{-1})	dSi (μg L^{-1})
4 July	2	2.2	102	12.8			0	27	<5	
	5	2.2	61	13.3			0.20	12	<5	
	10	2.2	28	13.3			0.30	10	<5	
	15	2.5	14	13.8			0.45	13	<5	
	20	2.8	8	13.5			0	16	<5	
6 July	2	3.3	107				0.35	24	<5	
	5	2.8	56				0.40	24	<5	
	10	2.8	29				0.40	22	<5	
	15	2.8	14				0.40	20	<5	
9 July	2	5	107	11.9			0.80	14	<5	
	5	3.3	50	13.8			0.60	12	<5	
	10	3.3	26	13.8			0.65	12	<5	
	15	3.1	15	13.9			0.40	11	6	
	20	3.1	8	13.8			0.50	11	7	
	25	3.1	5							
11 July	2		122	12.2			0.25	27	22	
	5		71	13.7			0.10	18	16	
	10		39	13.7			0.10	18	25	
	15		20				0.10	24	11	
	20		11							
	25		7	11.6			0.85	50	25	
14 July	2		94	12.6			0.45	14	<5	
	5		39	13.8			0.60	13	<5	
	10		19	14.0				12	<5	
	15		10	14.0			0.70	12	<5	
	20		5							
	25		3	11.9			0.45	31	<5	
16 July	2	4.7	71	12.7			0.50	14	<5	
	5	3.9	69	14.0			0.10	15	<5	
	10	3.9	24	14.0			0.45	15	<5	
	15	3.9	13	14.1			0.55	15	<5	
	20	4.1	7							
	25	4.1	4	12.0			0.90	36	9	
19 July	2		39	12.8			0.40	13	<5	
	5		23	13.8			0.45	13	24	
	10		12	13.9			0.75	13	<5	
	15		6	13.9			0.60	12	<5	
	20		3							
	25		2	13.0			0.55	17	<5	
22 July	2	4.3	13	13.2				13	<5	<5
	5	4.3	7	14.2			0.95	13	<5	311
	10	4.2	3	14.0			0.70	13	<5	316
	15	4.2	2	14.1			0.75			316
	20	4.2	1							
	25	4.2	1	13.4			0.60	13	<5	342
24 July	2		81				0.35	13	<5	<5
	5		58	14.0			0.75	12	<5	322

TABLE 1
Continued.

Date	Depth (m)	Temp (°C)	PAR (μE m^{-2} s^{-1})	DO (mg L^{-1})	Alk (meq L^{-1})	pH	Chloro (μg L^{-1})	Nitrate (μg L^{-1})	SRP (μg L^{-1})	dSi (μg L^{-1})
	10		19	13.9				15	<5	328
	15		13	14.0			0.55	15	<5	342
	20		8							
	25		5	13.9			0.45	16	<5	342
29 July	2		50	12.9	0.80	7.7		7	<5	
	5		31	14.4	1.36	8.1		6	<5	
	10		15	14.3	1.36	8.1		6	<5	
	15		8	14.5		8.1		7	<5	
	20		4							
	25		3	14.5		8.1		7	<5	
1 Aug	2		86	13.2	0.75	7.6	0.35	<5	16	
	5		53	14.6	1.37	8.2	0.95	<5	16	
	10		28	14.5	1.37	7.9	1.22	<5	22	
	15		14	14.5	1.37	8.2	0.95	<5	28	
	20		8							
	25		4	14.4	1.37			<5	41	
4 Aug	1		43							
	2		28	12.7	0.60	7.7	0.65	<5	<5	<5
	5		23		1.34	8.2	0.85	<5	<5	260
	10		12	14.1	1.36	8.2	1.05	<5	<5	266
	15		6	14.1	1.34		0.80	<5	<5	272
	20		3							
	23		2	14.1	1.35		0.50	<5	<5	350
6 Aug	1		81							
	2		79	12.6	0.68	7.7	0.50	10	<5	
	5		39	14.4	1.36	8.2	0.70	28	<5	
	10		18	14.7	1.36	8.2	0.70	18	<5	
	15		9		1.36		0.75	18	<5	
	20		5							
	23		3		1.36		0.60	18	<5	
10 Aug	1		91							
	2		84	13.8	0.96	8.0	0.50	6	6	364
	5		58		1.35	8.2	0.75	6	<5	518
	10		31	13.8	1.38	8.2	0.85	11	<5	532
	15		17	13.9	1.38	8.2	1.00	7	<5	546
	20		9		1.37	8.2	0.75	10	<5	
	23		6							546
13 Aug	1		21	13.2						
	2		21	14.4	0.90	7.8	0	10	<5	
	5		14	14.3	1.35	8.2	0	10	<5	
	10		7		1.36	8.2	0.70	10	<5	
	15		3		1.38	8.2	0.65	10	<5	
	20		2							
	23		1		1.40	8.2	0.65	12	<5	
16 Aug	1		30							
	2		30	13.1	1.02	7.9		7	<5	
	5		13	13.6	1.20	8.2	0.80	8	<5	
	10		5	14.3	1.38	8.2	0.80	10	<5	
	15		2		1.38	8.2	0.55	10	<5	

TABLE 1

Continued.

Date	Depth (m)	Temp (°C)	PAR ($\mu E\ m^{-2}\ s^{-1}$)	DO ($mg\ L^{-1}$)	Alk ($meq\ L^{-1}$)	pH	Chloro ($\mu g\ L^{-1}$)	Nitrate ($\mu g\ L^{-1}$)	SRP ($\mu g\ L^{-1}$)	dSi ($\mu g\ L^{-1}$)
	20		1			8.2	0.55	10	<5	
	23		1		1.38	8.2	0.25			
20 Aug	1		30	14.0	0.72		0.05	<5	9	
	2		23			8.0				<5
	5		6	15.2	1.17	8.2	1.10	<5	<5	336
	10		4	16.6	1.39	8.2	0.90	<5	<5	840
	15		2		1.39	8.2	0.55	<5	<5	868
	20		1					<5		
	23		1	13.5	1.39	8.2	0.40	<5	6	868
22 Aug	1		38	15.0	0.62	8.1	0.65	7	5	
	5		13	15.7	1.12	8.2	1.30	10	<5	
	10		4		1.32	8.2	0.80	10	<5	
	15		2		1.33	8.2	0.20	11	<5	
	23		1	13.2	1.34	8.2	0.40	13	<5	
25 Aug	1	1.4	29	13.2			0.95	6	<5	364
	5	3.2	8	13.5			1.50	6	<5	420
	10	3.3	3	14.2			0.40	10	<5	532
	15	3.4	1				0.60	10	<5	532
	23	3.4	0					11	<5	532
27 Aug	1	1.7	36	13.1	0.92	8.1	1.60	<5	<5	
	5	3.4	8	13.9	1.17	8.2	1.25	6	<5	
	10	3.5	3	14.4	1.36	8.2	0.45	10	<5	
	15	3.5	1		1.36	8.2	1.10	10	<5	
	23	3.4	0		1.34	8.2	0.40	10	<5	
2 Sept	1	1.3	23		1.05	8.2	1.65	<5	<5	392
	5	2.2	2	13.8	1.15	8.2	1.25	6	<5	426
	10	3.6	1	14.3	1.34		0.45	6	<5	532
	15	3.4	0		1.36	8.2	1.10	10	<5	532
	23	3.4	0		1.36	8.2	0.40	13	<5	532

meq L^{-1} in early August to 1.05 meq L^{-1}, increasing toward the end of the season (Table 1). Alkalinity from 5 to 24 m depth varied little with depth or time, ranging from 1.1–1.4 meq L^{-1}.

Oxygen was generally high throughout the water column and over time (Table 1). The lowest observed value was 11.6 mg L^{-1} at 5 m on 11 July, and the highest value was 16.6 mg L^{-1} at 10 m on 20 August. July values averaged about 13.5 mg L^{-1}, and August values averaged 14.5 mg L^{-1}. Two patterns of distribution with depth are apparent. On many, but not all, sampling dates, maximum values were at mid depth, 10–15 m, and on most dates in July and August, minimum values were found at 2 or 1 m, just under the ice.

NUTRIENTS

Dissolved silica (Fig. 5; Table 1) increased at 5–24 m from about 300 µg L^{-1} on 22 July to over 800 µg L^{-1} at deeper depths on 20 August. On each sampling date it was highest at the bottom. It was lowest at 1 or 2 m, increasing from undetectable from 22 July to 4 August, to about 500 µg L^{-1} at the end of August. The lowest values throughout the water column (about 265 µg L^{-1}) occurred on 4 August when lower values of nitrate and phosphate also were found. Other than the values below detection on some dates at 2 m just under the ice, all other dissolved silica values are considered ample to support algal growth.

Nitrate was detectable on all sampling dates and depths except August 1, 4, and 20. It varied with depth and over the summer (Fig 6, part a; Table 1), with the highest values (31–50 µg L^{-1}) found at 25 m on sampling dates in the first half of July. The average nitrate concentration across dates and depths for the first half of July was 19 µg L^{-1}. After mid-July, nitrate concentrations were generally lower and relatively even throughout the water column, with an average across all dates and depths of 9 µg L^{-1}.

Phosphate was not detectable at any depths on 13 sampling dates through the season (July 4, 6, 14, 22, 24, 29, August 4, 6, 13, 16, 25, 27, September 2; Table 1). On both July 11 and August 1, phosphate concentrations averaged across the water column were 20 µg L^{-1}.

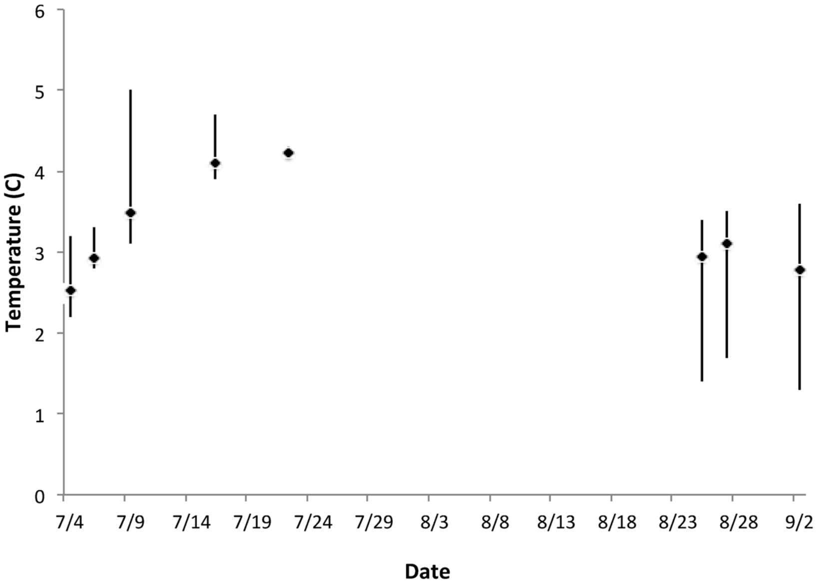

FIGURE 3. Average water column temperature under the ice over the summer. Vertical bars indicate the range of temperatures on each date. Missing dates are due to malfunctioning equipment (see Methods for description).

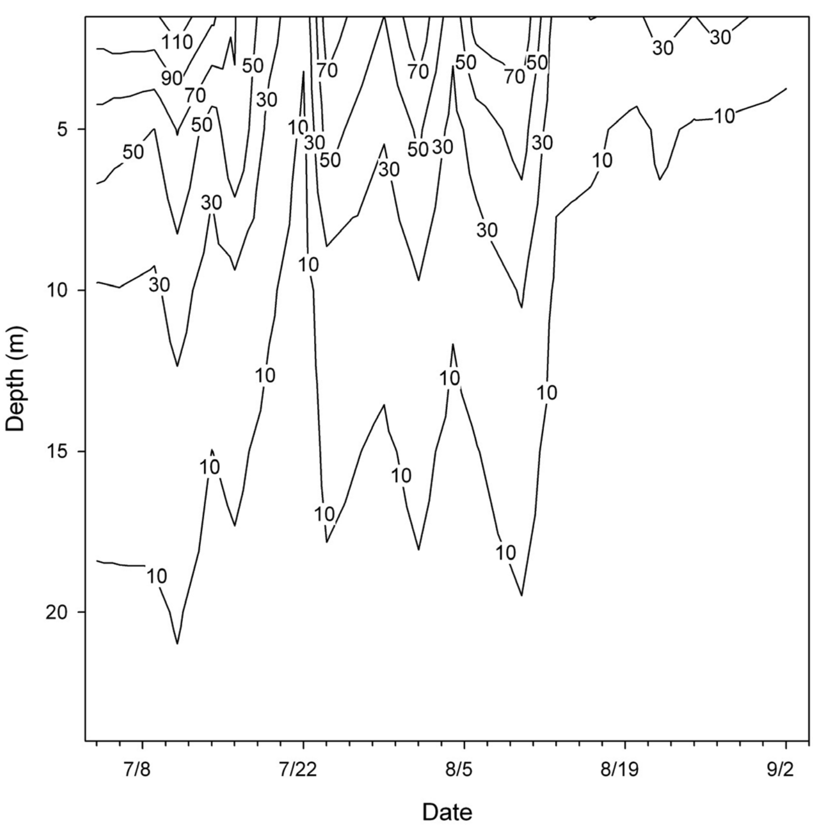

FIGURE 4. Subsurface irradiation (µEin m^{-2} s^{-1}) with depth, spanning from early July to early September.

CHLOROPHYLL

Chlorophyll varied substantially with depth and over the season (Fig. 6, part b; Table 1). Chlorophyll was very low throughout the water column during most of July. On 22 July, a bloom began at 5 m and, by early August, increased and was distributed between 5 to 15 m. Between 6 and 20 August, chlorophyll concentrations declined but remained higher than those found in early July. The highest concentrations of chlorophyll were found at the surface depths between 20 August and 2 September. Chlorophyll integrated to the bottom (Fig. 7) varied from 6 to 18 mg m^{-2}, increasing through July, and generally higher but somewhat variable in August.

Chlorophyll was negatively correlated with nitrate concentrations ($\rho = -0.37$, $p = 0.0002$), suggesting that nitrate was drawn down as chlorophyll concentrations increased. Correlations with chlorophyll were not significant for light ($\rho = -0.18$, $p = 0.09$) or phosphate ($\rho = -0.12$, $p = 0.24$). There was no relationship between nitrate and phosphate concentrations ($\rho = -0.004$, $p = 0.97$).

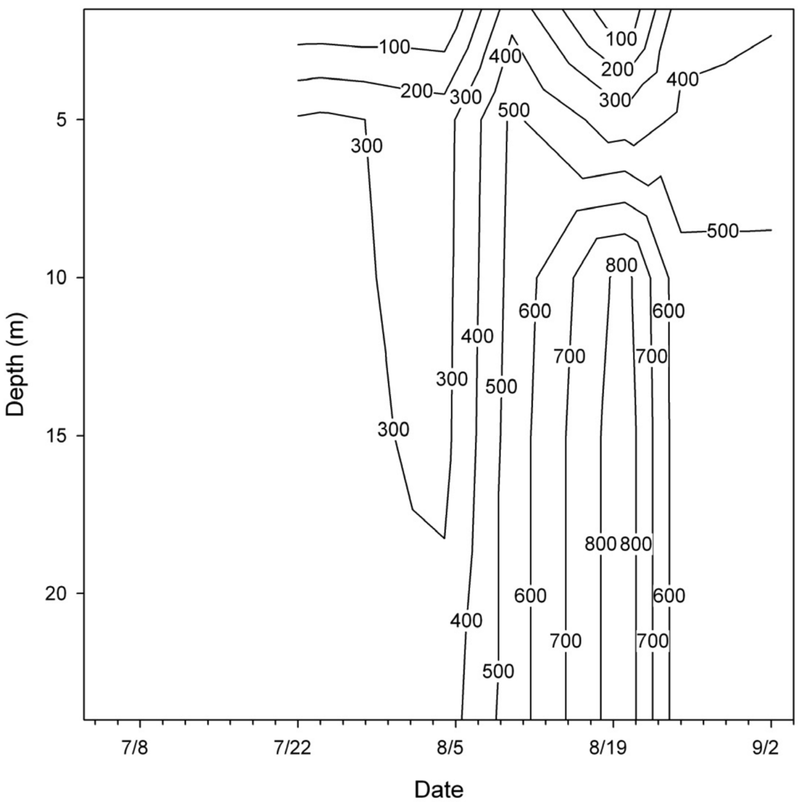

FIGURE 5. Dissolved silica concentrations (μg L⁻¹) with depth over the sampling period.

PRIMARY PRODUCTIVITY

Gross photosynthesis was detectable at very low levels on 16 of 19 dates (Table 2) and was usually limited to 2 m. The highest observed value was 40 mg C m^{-3} d^{-1} at 2 m on 22 August. Integrated (Fig. 8) to 5 m, the greatest depth of detectable gross photosynthesis, gross photosynthesis varied from 15 to 122 mg C m^{-2} d^{-1} and averaged 34 mg C m^{-2} d^{-1}. The average for July was 22 mg C m^{-2} d^{-1} and for August it was 46 mg C m^{-2} d^{-1}. The average value of measureable integrated gross photosynthesis was 33.3 mg C m^{-2} d^{-1}. The combined total for the sampling period was about 715 mg C m^{-2}. Gross photosynthesis normalized to chlorophyll varied between 0.25 and 6 mg C m^{-3} h^{-1} mg^{-1} chl. The average normalized number was 1.6. The highest numbers occurred in July. Removing the two highest numbers (5, 6) from the July totals, the average normalized numbers for July were still higher than those for August (1.22 vs. 1.12 mg C m^{-3} h^{-1} mg^{-1} chl).

Net (^{14}C) photosynthesis was detectable to 10 m and once to 15 m (10 August, Table 2). It averaged 2.3 mg C m^{-3} d^{-1} from 29 July to 3 September and ranged from 1.3 to 4.6 mg C m^{-3} d^{-1}, the highest value was found at 1 m on 2 September. The next highest values—3.3–3.9 mg C m^{-3} d^{-1}—were all found after mid-August. Maximum net photosynthesis on each sampling date was found at 5 m (or 10 m, 10 August) except on the last two sampling dates (27 August, 2 September) when it was found at 1 m. Net photosynthesis integrated to 10 m (Fig. 8) ranged from 7.5 to 19.9 mg C m^{-2} d^{-1}. The highest values occurred in the last half of August. The average of measurable integrated net photosynthesis was 12.7 mg C m^{-2} d^{-1} and the combined total of measured net production, 29 July–2 September, was 128 mg C m^{-2}. The net numbers normalized to chlorophyll ranged from 0.04 to 1.73 mg C m^{-3} h^{-1} mg^{-1} chl, with an average of 0.24. The highest gross and net photosynthesis and chlorophyll values all occurred at the end of August and first week of September when the lake was covered with new ice and 10 cm of snow. This was true also in the marine waters of nearby Dumbell Bay (Apollonio, 1980).

ZOOPLANKTON

Limnocalanus macrurus showed the transition from a population dominated by stage 3 and 4 and younger copepodites, including nauplii, at the end of July, when the ice-free lake perimeter permitted sampling, to a population of only stage 4 and 5 and adults at the end of August (Table 3). The number of females was about 10 to 50 times the number of males until the end of August, when they became roughly equal. The density of animals varied between 4.9 and 6.6 animals L^{-1}. The prosome lengths (mm) of the copepod stages were as follows: I—0.49, II—0.6, III—0.77, IV—0.91, V—1.05, adults—1.2.

On 4 August, 7 cyclopoid copepods (*Cyclops scutifer*?) were found in the sample. Because it is typically a hypolimnetic copepod, and our tows were made only in the peripheral shallow (5–10 m) waters of the lake, its single appearance in small numbers is not surprising.

Discussion

Our study depicts the variation in physical, chemical, and biological variables that occurred under the ice over the course of the 1959 summer in this oligotrophic, cold monomictic Arctic lake.

TABLE 2

Gross and net photosynthesis (GP and NP, respectively) in Upper Dumbell Lake.

Date	Depth (m)	GP (mg C m^{-3} d^{-1})	NP (mg C m^{-3} d^{-1})
4 July	2	26.5	—
9 July	2	26.5	—
11 July	2	12	—
	5	15	—
16 July	2	10.7	—
19 July	2	13.3	—
22 July	2	0	—
24 July	2	0	—
29 July	2	0	1.9
	5	7.7	0
	10	—	1.9
1 Aug	2	21	0
4 Aug	2	20	1.7
	5	23	2.7
6 Aug	2	0	1.7
	5	—	2.0
	10	—	0
10 Aug	2	23	0
	5	9	1.6
	10	—	2.6
	15	—	2.3
13 Aug	2	0	0
16 Aug	2	—	2.7
	5	5.6	3.3
	10	—	1.5
20 Aug	2	29	1.8
	5	—	2.0
	10	—	0
22 Aug	2	40	1.6
	5	—	3.3
	10	—	0
25 Aug	1	20	1.9
	5	—	2.3
27 Aug	1	6	3.9
	5	6	1.3
	10	—	0
2 Sept	1	0	4.6
	5	—	0

From early July to early September, vertical gradients of light, nutrients, algal biomass, and rates of photosynthesis changed substantially under the sustained ice cover. The changing nature of the ice cover, together with declining incident radiation, greatly affected light penetration, which was higher in early July and substantially diminished by mid-August. Subsequently, the first chlorophyll maximum (in late July/early August) was deeper in the water column (at approximately 10 m) than the second chlorophyll

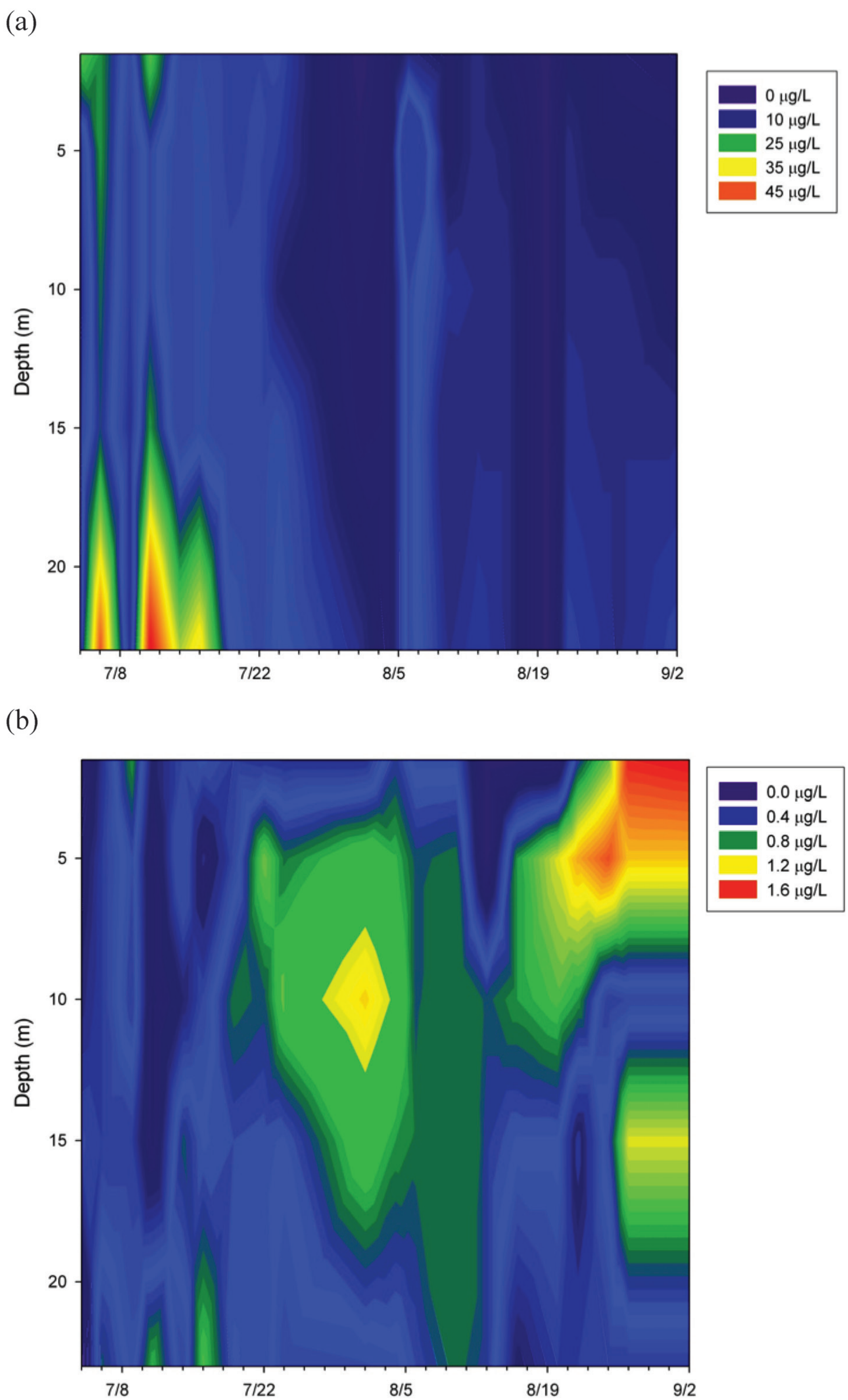

FIGURE 6. Concentrations of (a) nitrate (µg L^{-1}), and (b) chlorophyll (µg L^{-1}) with depth over the sampling period.

maximum (late August, in the top 5 m). Vertical distributions of nutrients, when detectable, were similar in that the highest values were found in the deeper waters and usually at the deepest at 24–25 m. This pattern was also found with temperatures, except for those at 2 m which in mid-July were the highest. The density of copepods remained fairly stable during this time, but the age structure shifted, with the population aging to adulthood by the end of the period. The high spatial and temporal resolution of this study provides an important perspective of the dynamic vertical gradients that can occur under ice.

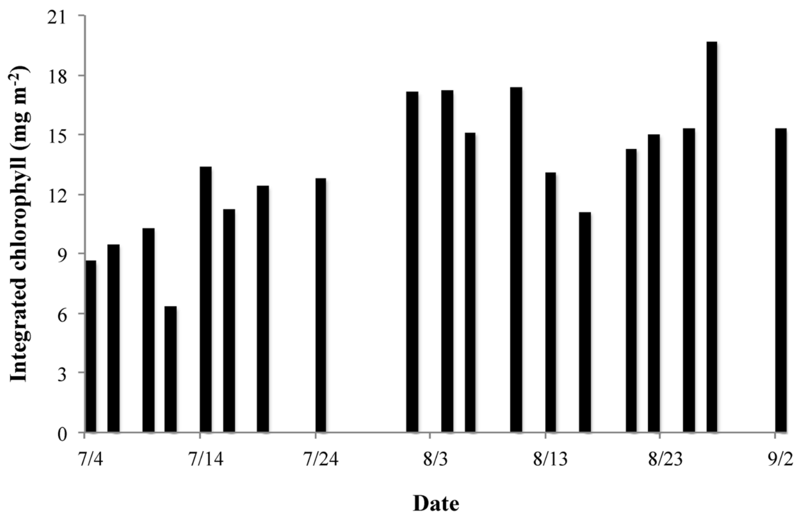

FIGURE 7. Integrated chlorophyll (through whole water column) in Upper Dumbell Lake.

This study also improves our understanding of the factors controlling algal biomass in this High Arctic lake, because we sampled chlorophyll at multiple depths over time rather than one surface sampling. Even under the ice, water transparency was relatively high over the course of the summer. In low-productivity, clear waters such as these, the chlorophyll maximum can occur deeper in the water column (Saros et al., 2005), so sampling in the top 1–2 meters alone provides an incomplete assessment of algal biomass compared to the full water column profile. With chlorophyll data from multiple depths and dates, we found two peaks in algal biomass occurring over time under the ice, with one in late July and the second starting at the end of August. This is in contrast to patterns observed in some other polar lakes, which have a single peak in biomass over the summer (as reviewed by De Senerpont Domis et al., 2012). The frequency of these blooms is certainly dependent, in part, on the conditions of ice cover if the blooms are autotrophic species, so the number of blooms per summer may vary.

The data presented here provide an assessment of limnological conditions in the High Arctic during the mid-20th century, and may be compared with those of a survey from late July to early August in 2000 by Antoniades et al. (2003) as well as those of Keatley et al. (2007), who reported data from ponds and lakes across northernmost Ellesmere Island but not near Alert.

Freshwaters in the vicinity of Alert are strongly alkaline, ranging from pH 8.1 to 8.9 (mean 8.4; Antoniades et al., 2003). Their values for Upper Dumbell Lake were pH 8.2–8.35. Our data were similar, and for late July–early August, ranged from 7.7–8.2 throughout the water column. The values of ≈7.7 were confined to water just under the ice until mid-August, after which all values were >8. Antoniades et al. (2003) noted that pH in ponds may be raised by photosynthesis, as apparently were ours, slightly, from July into September.

Patterns in nutrient concentrations in 1959 and 2000 are somewhat difficult to compare, owing to differences in sampling frequency in the two studies and possibly interannual variation that alters conditions on the same day across years. Antoniades et al. (2003) reported 31–39 µg L^{-1} nitrate, 1 µg L^{-1} phosphate, 32–38 µg L^{-1} total phosphorus, and 920 µg L^{-1} dissolved silica in Upper Dumbell Lake in 2000, which we assume was at a sampling depth of 0.5 m (based on references to previous work). The average nitrate concentration (across dates and depths) in Upper Dumbell Lake after mid-July in 1959 was 9 µg L^{-1}, suggesting that nitrate concentrations have increased in the lake since 1959.

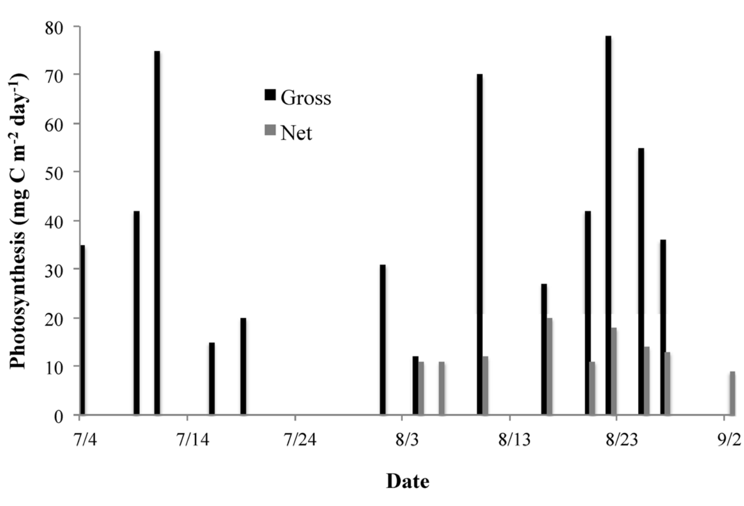

FIGURE 8. Gross (O_2) and net (^{14}C) primary production, integrated from the surface to 5 m for gross and to 10 m for net production.

TABLE 3

Age structure and numbers of *Limnocalanus macrurus* in Upper Dumbell Lake. Copepodite stages are indicated by C1 through C5; adults are separated by sex. Numbers are the count in the total number of liters filtered (L).

Date	L	Nauplii	C1	C2	C3	C4	C5	Male	Female	Total
28 July	307	166	42	98	667	686	169	1	49	1878
4 Aug	307	80	12	56	412	704	104	4	152	1524
11 Aug	210	44	0	16	88	440	320	40	432	1380
28 Aug	219	0	228	20	0	52	228	308	332	1168

We note, though, that in early July 1959, nitrate concentrations reached 44–50 µg L^{-1} in the bottom waters of the lake, suggesting that changes in internal nutrient cycling may also explain the difference in nitrate between 1959 and 2000; a future study similar to this 1959 one would help to resolve whether nitrate concentrations have increased in this lake. In terms of phosphate, the 1959 data vary substantially and with no apparent regularity with depth and date, ranging from below quantification to 41 µg L^{-1} during the late July–early August period. Dissolved silica concentrations in 1959 were below quantification in surface waters until August 10, and then ranged from 364 to 546 µg L^{-1} from 5 m down through the water column. By 20 August, dissolved silica was more than 800 µg L^{-1} from 10 m down through the water column.

The 1959 chlorophyll values are comparable to those in more recent years. Antoniades et al. (2003) reported chlorophyll values of 0.5 and 0.9 mg m^{-3} in Upper Dumbell Lake on one day between 27 July and 7 August 2000. Those authors found a range from undetectable to a maximum of 2.6 mg m^{-3} (median 1.0 mg m^{-3}) in the lakes and ponds in the vicinity of Upper Dumbell Lake. Chlorophyll concentrations in this work ranged from below detection limit at 0.1 to a maximum of 1.65 mg m^{-3}. Keatley et al. (2007) found a chlorophyll mean of 0.5 mg m^{-3} in 31 ponds and lakes sampled in July 2003 in northern Ellesmere Island in habitats similar to that of Upper Dumbell Lake. These values compare to the average value of 0.52 mg m^{-3} found in July 1959 of this work. Markager et al. (1999) found chlorophyll from 0.04 to 1.24 mg m^3 in seven lakes of various types (including Char Lake) on Cornwallis and Little Cornwallis islands in the Arctic archipelago in the first half of August 1995. Our data for that period 36 years earlier in Upper Dumbell Lake range from undetectable to 1.22 mg m^{-3}.

We found a correlation between chlorophyll and nitrate over the summer of 1959, suggesting the importance of nitrogen availability for algal production in this lake. This is consistent with experimental results from more than 50 lakes in the Arctic Foothills region of Alaska (Levine and Whalen, 2001), where N limitation or colimitation by N and P was found for most lakes. While we cannot directly compare patterns from one lake (Upper Dumbell) to those from a survey across several lakes in the area (Antoniades et al., 2003), we simply note that the 2000 survey across lakes did not find any relationships between Chl-*a* and N or P and suggested that other factors may be regulating phytoplankton in this area.

For lakes in the High Arctic, Markager et al. (1999) found that the maximum photosynthetic rate normalized to chlorophyll varied sevenfold from 0.16 to 1.12 g C g^{-1} Chl-*a* h^{-1}, but most values were below 0.5 g C g^{-1} Chl-*a* h^{-1}. The Dumbell Lake data from 1959 lie within the lower part of that range.

Our data may be compared with those from Char Lake, an ultra-oligotrophic lake on Cornwallis Island, Arctic Canada (74°42′N, 94°50′W), which was studied throughout the year of 1971 and over several seasons (Schindler et al., 1974; Kalff and Welch, 1974; Rigler et al., 1974). Both lakes lie in similar frost-shattered limestone rubble (Blackadar, 1954; Schindler et al., 1974). Char Lake has about half the surface area (52 vs. 100 ha) of Upper Dumbell Lake. Its maximum depth is 27.5 m compared to 33 m, and a mean depth of 10.2 m compared to 12.5 m in Upper Dumbell Lake. Char Lake "in most years" (Schindler et al., 1974) is a cold monomictic lake, as is Upper Dumbell Lake. Both lakes may be ice-free for about six weeks from late July to early September in some years and in other years may remain largely ice-covered with only peripheral, shallow, ice-free water throughout the summer. In the 1971 Char Lake study (Schindler et al., 1974), the lake was ice free in August and September, in contrast to the sustained ice conditions on Upper Dumbell in this study.

Values for pH were very similar (≥8) at all depths in the two lakes, but at 2 m in Upper Dumbell Lake, pH was 7.7–7.9 until mid-August when it increased to above 8. Oxygen and nutrients showed similar patterns through the summer in both lakes. Oxygen varied between 13.3 and 14.7 mg L^{-1} in the upper 15 m of both lakes. Dissolved inorganic phosphate was consistently undetectable in Char Lake. Upper Dumbell Lake showed both undetectable and low values of phosphate with no apparent pattern. Dissolved silica in both lakes declined in early August, apparently because of melt-water dilution (Schindler et al., 1974). Dissolved silica remained low for several months in Char Lake, but in Upper Dumbell Lake it quickly returned to higher values, and by early September it was about double the values of early July. Presumably this difference between the lakes was due to greater diatom demands in Char Lake. Nitrate showed the greatest differences between the two lakes. In Char Lake, nitrate was high in June in surface waters, and then very low throughout late July and August when the lake was ice-free. Nitrate was quite variable in Upper Dumbell Lake, ranging from 50 µg L^{-1} at 25 m in mid-July to undetectable at any depth on August 20. Differences in nitrate between the two lakes may have been related to length of ice cover, with the period of ice-free conditions on Char Lake providing greater light availability and possibly promoting greater primary production and hence nutrient uptake. These differences in nitrate may have also been the result of variations in local disturbances. Schindler et al. (1974) cited disturbance at Char Lake from construction of a nearby airstrip, while Doubleday et al. (1995) used paleolimnological evidence of black carbon deposition to suggest possible pollution to Lower Dumbell Lake sometime during the 20th century from the development of a military base in nearby Alert.

Annual primary production in Char Lake was estimated at 4.1 g C m^{-2} y^{-1} from early April to early October (Kalff and Welch, 1974). Our estimate of annual gross photosynthesis was for 2 months. If we assume that production started in Dumbell Lake in early April, as it did in Char Lake, then total annual gross production in Dumbell Lake might be estimated at ≈3 g C m^{-2} y^{-1}, making it less productive than Char Lake, considered to be one of the most oligotrophic lakes on record. The maximum monthly mean net production in Char Lake over four years was about 0.74 g C m^{-2}. The net production in August in Upper Dumbell Lake was about 0.37 g C m^{-2}

Some net ^{14}C production experiments for extended periods in the temperate zone have been criticized as being affected by a bottle effect. Kalff and Welch (1974) found that in Char Lake, there was no significant difference between 24-h exposures and the sum of a series of short-term exposures totaling 24 h. We are confident, therefore, that our net photosynthesis estimates of 24 h are reasonable and not affected by a bottle effect.

Kalff and Welch (1974) noted that their estimates of annual production were not corrected for possible loss of organic carbon during filtration. They suggested that if so corrected, their production estimates for Char Lake would be increased fivefold. We note that the ratio of mean gross (47.7 mg C m^{-2} d^{-1}) and net (12.7 mg C m^{-2} d^{-1}) integrated production estimates in Upper Dumbell Lake is ≈3.7. This discrepancy between gross and net production has been noted in Arctic marine phytoplankton in two locations previously (Apollonio, 1980; Apollonio and Matrai, 2011), and is not a loss during filtration but likely a natural characteristic loss of photosynthetic products in nutrient deficiency and perhaps in low light and temperatures (Fisher and Schwarzenbach, 1978).

Because of ice conditions on the lake in 1959 with open water only in the shallow perimeter, the Clarke-Bumpus sampler was not an appropriate zooplankton sampling device. *L. macrurus*, which is often hypolimnetic in other waters (Vanderploeg et al., 1998), might be expected to prefer darker waters under the ice cover, which could not be sampled by this sampler.

Lakes of the Canadian Arctic Archipelago support low densities of crustacean zooplankton, often <1 individual L^{-1} (Chètelat and Amyot, 2009). The densities reported here—4–6 animals L^{-1} from Upper Dumbell Lake—compare with the maximum (5.9 animals L^{-1}) reported by Hirche et al. (2003) from the Kara Sea where *L. macrurus* was feeding on phytoplankton blooms, and appear to be above the average density of High Arctic lakes in spite of the lake's very low productivity. This might be explained by the observation of Schindler and Smol (2006) that under such ice conditions as prevailed in Upper Dumbell Lake in 1959 much of the primary production is shifted to the ice-free littoral zone, perhaps attracting zooplankton to the periphery of the lake. This might also explain the occurrence of hypolimnetic cyclopoid copepods in the littoral zone of the lake in August. Unfortunately, production in the perimeter of Upper Dumbell Lake was not measured in 1959. There is a suggestion of this "littoral effect" in limited gross (O_2) photosynthesis data in mid-July 1958 from the ice-free edge of Lake Hazen, Ellesmere Island (McLaren, 1964).

The low ratio of *L. macrurus* males to females found here was also found in Char Lake (Roff and Carter, 1972) and with *Calanus hyperboreus* in the central Arctic Ocean by Dawson (1978), who suggested that in waters of restricted food supply, that ratio would provide a selective advantage from greater fecundity by supporting a larger number of females.

The low productivity of our lake may be the cause of the small sizes recorded for *L. macrurus*, 1.2 mm for adults, which is comparable to that noted (≈1 mm length) by Chètelat and Amyot (2009), who found that Arctic copepods have the smallest adult body size.

The reproductive season of *L. macrurus* in Upper Dumbell Lake appears to be similar to that in Immerk Lake, Devon Island (Apollonio and Saros, 2013), and apparently differs from that of *L. macrurus* in Lake A near northernmost Ellesmere Island (Van Hove et al., 2001) in which no nauplii and only adults were found on the one sampling date, 8 June 1999. Such variability of reproductive seasons was found in adjacent Char and Resolute Lakes on Cornwallis Island, Arctic Canada, by Roff and Carter (1972), who also noted that the season of reproduction may change from year to year.

The effects of ever-changing ice cover on the parameters reported here are variable and not always obvious, and comparisons with the other studies considered here do not contribute to that issue. Antoniades et al. (2003) did not indicate whether Upper Dumbell Lake was ice covered at the time of their study. In Char Lake, light penetration data are given, averaged for 1971 and 1972 in which the lake was ice-free and ice-covered, respectively. Kalff and Welch (1974) make no direct reference to effects of ice on primary production, but they estimated production in ice-free 1971 was slightly higher than in 1972.

The percentage of incident radiation reaching the underside of the ice of Upper Dumbell Lake varied with the season and particularly with even small amounts of new snow on the ice. In the first half of July, with no snow cover and the ice melting, the percentage of incident radiation was 59% (51%–64%). In the first half of August, 52% (30%–68%) of incident radiation was measured under the ice (the ice was 38 cm thick on 10 August but was refreezing on 20 August). In the latter half of August it was 37% (22%–66%). In September (three days only) it was 14%. On three occasions (22 July, 4 August, 16 August), when ≤8 cm of new snow fell, sub-ice radiation fell to 36%–50% of the previous measures.

The effect of ice cover on Upper Dumbell Lake in 1959 on light penetration is suggested by the fact that photosynthesis normalized to chlorophyll falls within the lower range of values reported by Markager et al. (1999). But no restraints upon melt-water inputs would be expected from ice cover because of the narrow, ice-free perimeter from early July to mid-August. In fact, melt-water enrichment of nitrate on each date from 4 to 14 July is suggested by higher values at 2 m, with lower values at mid-depths and highest values at 24 m. After 14 July, nitrate values were equivalent at all depths, or increased from 2 or 1 m to highest values at 24 m.

While Upper Dumbell Lake is an ultra-oligotrophic lake, its extensive but not complete ice cover, at least in 1959, does not appear to be the major contributor to that status. The poverty of the lake may primarily be a consequence of the limited nitrate resources, to the extent of nitrate exhaustion on 22 August; chlorophyll mass and nitrate were negatively correlated. Neither phosphate nor dissolved silica showed variations related to algal biomass, nor to ice cover, nor to nitrate variations. A slight increase in pH was shown in the latter half of the season, perhaps as a result of photosynthesis. Oxygen reached its highest values (15.2–16.6 mg L^{-1}) at mid-depths on 20 August, the date of nitrate exhaustion, and at the time (16–23 August) of maximum net productivity at 5 m (2.0–3.3 mg C m^{-3} 24 h^{-1}). Five centimeters of new snow had covered the ice on 16 August when radiation at 1 m was 25% of surface incident radiation, the second lowest percentage in July and August.

Conclusions

This study reveals the dynamic nature of vertical habitat gradients even under the ice of Arctic lakes, and provides important baseline data for conditions in an Arctic lake during the mid-20th century. We found substantial variation in nutrients (nitrate, dissolved silica, soluble reactive phosphorus), light, and chlorophyll *a* with depth and over the course of the summer in this ice-covered lake. Comparing July to August, nitrate and light intensity decreased while dissolved silica, chlorophyll *a,* and gross and net primary production increased, with two distinct peaks in algal biomass occurring over the month of August. While some contemporary studies of Arctic lakes have found no relationship between nutrients and algal biomass, chlorophyll *a* in this lake in 1959 was negatively correlated with nitrate concentrations, suggesting uptake of nitrogen as algal biomass increased. Our study provides detailed limnological data from an Arctic lake during the mid-20th century that can be used for comparison to present and future changes. It also raises questions about how changing ice cover on Arctic lakes over the summer will alter productivity and vertical habitat gradients in these systems.

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