Extreme warming and regime shift toward amplified variability in a far northern lake

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Abstract

Mean annual air temperatures in the High Arctic are rising rapidly, with extreme warming events becoming increasingly common. Little is known, however, about the consequences of such events on the ice-capped lakes that occur abundantly across this region. Here, we compared 2 years of high-frequency monitoring data in Ward Hunt Lake in the Canadian High Arctic. One of the years included a period of anomalously warm conditions that allowed us to address the question of how loss of multi-year ice cover affects the limnological properties of polar lakes. A mooring installed at the deepest point of the lake (9.7 m) recorded temperature, oxygen, chlorophyll a (Chl a) fluorescence, and underwater irradiance from July 2016 to July 2018, and an automated camera documented changes in ice cover. The complete loss of ice cover in summer 2016 resulted in full wind exposure and complete mixing of the water column. This mixing caused ventilation of lake water heat to the atmosphere and 4°C lower water temperatures than under ice-covered conditions. There were also high values of Chl a fluorescence and anoxic bottom waters. Extreme warming events are likely to shift polar lakes that were formerly capped by continuous thick ice to a regime of irregular ice loss and unstable limnological conditions that vary greatly from year to year.
between the water column and the atmosphere, and prevents direct wind-induced mixing, resulting in a stratified water column beneath the ice and the drawdown of oxygen over winter (Schindler et al. 1974). The ice cover reduces the penetration of solar radiation into the water column, especially when capped by reflective white ice or snow (Belzile et al. 2001). However, the solar energy penetrating the ice can slowly warm parts of the water column to well above ambient air temperatures. As an example, water temperatures reaching 8.5°C were observed in a High Arctic meromictic lake, and were likely the result of many decades of energy accumulation beneath the ice (Vincent et al. 2008). This solar heating can drive convective mixing cells (Kirillin et al. 2012; Pernica et al. 2017), and the photosynthetically available radiation (PAR) entering the water column can be sufficient to support photosynthesis below the ice, leading to oxygen supersaturation (Ludlam 1996). However, measurements are generally limited to summer and to regions where the ice cover melts out each year, and little is known about the seasonal variations in water temperature, oxygen, primary productivity, and light in perennally ice-covered Arctic lakes, especially in fall and spring when critical transitions are likely to occur (Hampton et al. 2017; Matveev et al. 2019). Annual under-ice records are lacking in most Arctic regions, and especially in the High Arctic due to logistical constraints.

Ward Hunt Lake, Canada’s northernmost lake, was characterized by 4-m-thick perennial ice cover over a 50-year record, followed by a period of rapid thinning and full loss of ice in summer 2011 and 2012 (Paquette et al. 2015). The aims of the present study were to evaluate the end-of-season dynamics during the new regime of intermittent ice-out and to obtain the first winter records for this lake. Two contrasting summers, with and without ice cover, allowed us to address the hypothesis that the shift in polar lakes from a continuous ice regime in the past to intermittent ice-out is accompanied by largescale variations in limnological properties such as water temperature, underwater PAR, phytoplankton variables (in this study, chlorophyll a [Chl a] fluorescence), and dissolved oxygen. Our results provide insight into how polar lakes elsewhere, for example, lakes in Antarctica that are projected to lose their ice covers in the decades ahead (Obryk et al. 2019), will respond to extreme warming events.

Methods
Study site
Ward Hunt Lake is located 26 m above sea level on Ward Hunt Island, 6 km off the northern coast of Ellesmere Island, within Quttinirpaaq National Park, Nunavut, Canada (Supporting Information Fig. S1). Its maximum known depth is 9.7 m, with a length of 990 m and an area of 0.37 km². The lake is mainly supplied by snow meltwater from the watershed via surface and subsurface water tracks, and drains to the sea by an outflow at its southern shore. The Ward Hunt Lake watershed and its water track hydrology are described in Paquette et al. (2017), and environmental features of the region are described in Vincent et al. (2011). The island experiences a polar desert climate, with a mean annual temperature of −17.4°C (CEN 2020) and mean annual precipitation likely similar to that recorded at Alert, 170 km to the southeast (mean of 155 mm for the period 1951–2017; Environment Canada, data available at http://climate.weather.gc.ca). A meteorological station in the SILA Network operated by the Centre for Northern Studies (CEN) is located 1 km north of Ward Hunt Lake, and during the period of study it recorded air temperature (thermistor HMP35CF, Vaisala, Helsinki, Finland, protected with a multiplate radiation shield model 41003, R.M. Young), incident solar radiation (radiometer LI-200, Li-Cor Biosciences), wind speed and direction (Wind Monitor 05103-10, R.M. Young), and snow height (Sonc Ranging Sensor SR50, Campbell Scientific) every hour; these data are archived in CEN (2020). Melting degree days (MDD) were calculated as the sum of mean daily air temperatures above 0°C each spring and summer (May to September). Freezing degree days (FDD) were calculated as the sum of mean daily air temperatures below 0°C from July of the previous year to June of the listed year, spanning the complete winter period.

Year-round lake observations
A mooring system was installed from 20 July 2016 to 19 July 2018 at the deepest point of Ward Hunt Lake (83°05.226’N; 74°08.721’W; WGS84 map datum). It was equipped with sensors to record: dissolved oxygen saturation and temperature (O₂ and T°); MiniDOT, PME; oxygen resolution: 0.01 mg L⁻¹, temperature resolution: 0.01°C); photosynthetically active radiation (PAR; ALW-CMP, JFE Advantec; PAR resolution: 0.1 μmol m⁻² s⁻¹); Chl a fluorescence (Chl a; ACLW-CMP, JFE Advantec; resolution: 0.01 μg L⁻¹) and additional temperature measurements (T°); Minilog-II-T, Vemco; DEFI-T, JFE Advantec; temperature resolution: 0.01°). The sensors were calibrated by the manufacturers, and maintenance and cleaning were performed each year at the time of data recovery and battery replacement. The Chl a optical sensor was equipped with a wiper that activated before each measurement, and the recorded concentrations were compared with extracted Chl a analyses of samples taken at the same depth during field visits each year. Water for these pigment extractions was filtered through 25 mm GF/F filters that were stored at −80°C until analysis. The pigments were extracted with 95% methanol and measured by high-pressure liquid chromatography (HPLC) as in Bonilla et al. (2005).

Sensors were installed at eight subsurface depths (relative to the piezometric water surface): 2.8 m (PAR, T°), 3.8 m (T°), 4.8 m (T°), 5.8 m (Chl a, T°), 6.9 m (T°), 7.9 m (T°), 8.5 m (O₂, PAR, T°), and 9.0 m (T°). In 2017, two oxygen sensors were installed at 3.8 and 5.8 m, the deep oxygen sensor was moved to 9.3 m and combined with a logging CTD (RBR420, RBR Ltd.), and all the other sensors were retained at the same depths. The logging frequency was set to 10 min for the
temperature loggers, 30 min for the PAR and Chl a loggers, and 60 min for the CTD. The logging frequency for the dissolved oxygen sensor was set to 1 min from 20 July 2016 to 22 January 2017 and to 1 h from 15 July 2017 to 19 July 2018. The loggers were installed along a chain held upright from an anchor on the sediments to a float at the top. The mooring was designed so that the float was always below the ice to prevent any displacement of the mooring by movements of the ice cover.

The Chl a fluorescence sensor was installed at 5.8 m. This depth was chosen because it was at the middle of a convective mixing zone from 4 to 8 m that had been detected in previous years of sampling (Mohit et al. 2017) as well as in the present study (Supporting Information Fig. S2), and was a stratum with supersaturated oxygen levels, indicative of active phytoplankton populations. Net oxygen gain or loss rates were calculated by fitting a linear regression model to oxygen concentrations and saturation values as a function of time during periods of linear change (identifiable visually from the time series plots) from mid-July to the end of October in each year. Differences in these slopes between 2016 and 2017 in the lower water column and between depths in 2017 were tested with a set of ANCOVA analyses.

Time-lapse images of Ward Hunt Lake were captured at hourly intervals from 04:00 to 19:00 h each day with an automated camera to couple the limnological measurements of change with ice and snow events. Details of this camera installation and the full data set of images are archived in NEIGE (2020). To compare incident solar radiation (in W m\(^{-2}\)) the irradiance recorded by the top sensor (\(z_1 = 2.8 \) m) and \(E_2\) was the irradiance recorded by the bottom sensor (\(z_2 = 8.5 \) m).

**Results**

**Thermal and ice regime**

The mean annual air temperature at Ward Hunt Island in 2016 was \(-15.6^\circ\)C, whereas the 2003–2017 mean was \(-17.4^\circ\)C (Supporting Information Table S1). This translated into 196 MDD in 2016, which was the highest value ever recorded at Ward Hunt Island, and 77% above the overall mean MDD for the period 2003–2017 (Fig. 1). At Alert, which has a much longer meteorological record, the mean annual temperature in 2016 was \(-13.8^\circ\)C whereas the 1951–2017 mean was \(-17.5^\circ\)C (Supporting Information Table S2). Since 1990, there has been a significant overall linear trend of increasing annual MDD (on average, by 40 per decade), but with large year-to-year fluctuations (Fig. 1; for 1990 to 2017, linear regression \(r^2 = 0.16\), \(F = 6.1\), df = 26, \(p = 0.02\)). The annual MDD in 2016 totaled 439, more than three standard deviations (108%) above the 1951–2017 mean which was 210 (Fig. 1). The mean annual air temperature value at Alert for 2016 was the maximum for the entire 67-year record (Supporting Information Table S2). For the period of overlap, these two MDD records were highly correlated (Pearson’s correlation test, \(r = 0.97\), df = 13, \(p < 0.001\)), with Ward Hunt values averaging 134 fewer MDD than Alert. FDD at Ward Hunt Island from July 2016 to June 2017 totaled 6054, which was more than one SD below the 2003–2017 mean (6470; Supporting Information Table S1). The FDD value at Alert was 5679, more than two SD below the mean of 6597 (Supporting Information Table S2).

Water temperatures reached 6.6\(^\circ\)C at the bottom of Ward Hunt Lake at the end of July 2016 (Fig. 2a,b; Supporting Information Fig. S3), likely due to the warmest air temperatures

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**Fig. 1.** Melting degree days at Ward Hunt Island (bars) and Alert (black line and points). The arrows mark 2016, the year of extreme warming. The red lines are the overall average values for the two records.
At this time, combined with highest irradiances under the thinning ice (1.80 m of ice cover on 14 July 2016 vs. 2.18 m thickness on 14 July 2015). At the time of our visit in mid-July, there was already a distinct moat of open water along the northern and western edge of the lake, which subsequently widened (Fig. 3a). The water column showed an inverse thermal stratification by the end of summer 2016. The profiles in July 2016 were strongly influenced by salinity.

| Ice free period | Temperature (°C) | Air temperature (°C) | Photosynthetically active radiation (PAR) in the air | PAR in the upper water (2.8 m; red line) and lower water column (8.5 m; black line) | Chlorophyll a (Chl a) fluorescence (green line) and concentration measured by HPLC (black points) in the middle of the water column (5.8 m); and dissolved oxygen concentrations as % air-equilibrium in the lower (8.5 m) water column in 2016 and in the upper (3.8 m), middle (5.8 m), and lower (9.3 m) water column in 2017.

### Fig. 2.
Data collected by the mooring in Ward Hunt Lake from 20 July 2016 to 19 July 2018 and at the Ward Hunt Island climate station. (a) Water temperatures at eight depths (this is replotted as a heat map in Supporting Information Fig. S3); (b) air temperature; (c) photosynthetically active radiation (PAR) in the air; (d) PAR in the upper water (2.8 m; red line) and lower water column (8.5 m; black line); (e) chlorophyll a (Chl a) fluorescence (green line) and concentration measured by HPLC (black points) in the middle of the water column (5.8 m); and (f) dissolved oxygen concentrations as % air-equilibrium in the lower (8.5 m) water column in 2016 and in the upper (3.8 m), middle (5.8 m), and lower (9.3 m) water column in 2017. The blue shadow corresponds to the ice-free period (from ice break-up to new ice formation) in summer 2016. The gray shadows correspond to date intervals used to calculate the linear net oxygen change rates in the lower layer of the water column (Table 1).
gradients: water at 4°C with a lower conductivity was located above warmer, higher conductivity water toward the bottom (Supporting Information Fig. S2). This stratification persisted until 27 July when the camera showed that the ice cover had become detached from the edge of the lake and was moving northeastward due to strong winds from the southwest at that time (Supporting Information Fig. S4), which likely resulted in associated water movements beneath the ice cover. The water depth recorded via the pressure sensor on the logging CTD from July 2017 to July 2018 showed small-scale fluctuations (root-mean-square error of 0.097 m), with a mean increase of 0.284 m over this period (Supporting Information Fig. S5).

The automated camera recorded complete loss of the lake ice on 16 August 2016 (Fig. 3b). The water column was then exposed to wind and was mixed completely, with a subsequent drop in water temperatures to near 0°C in the whole water column. The lake returned to the pattern of inverse thermal stratification under the ice in November 2016, which persisted throughout winter. Water temperatures warmed during summer 2017, to around 6°C throughout much of the ice-covered water column by early August (Figs. 2, 3). The striking difference between ice-covered 2017 and ice-free 2016 is illustrated in the central panels of Fig. 3, showing that August–September bottom water temperatures were 2–4°C warmer in 2017.

**Light and chlorophyll fluorescence**

Ward Hunt Island experiences extreme polar winters with a total absence of solar radiation from mid-October to March (Fig. 2c,d). The lake was covered by ice for most of the period of observation, and the resultant effect on underwater light

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**Fig. 3.** Temperature (black) and oxygen (red) in the deep layer (8.5 m) of Ward Hunt Lake during four summers. The blue shadow corresponds to the ice-free period (from ice break-up to new ice formation) in summer 2016. Letters represent major events in ice phenology in 2016: (a) ice cover break-up, (b) ice-free conditions, (c) new ice formation, (d) thick ice formation. Corresponding dates in 2017: (e) ice cover thinning, (f) snow accumulation on ice cover, (g) new ice formation in the moat, and (h) thick ice formation.
was compound by snow cover in spring and intermittent snowfall over the ice in summer (Fig. 3f). As a result of the combined effects of snow, ice, and the seasonality of incident radiation, the main period of PAR availability in the water column was July–August (Fig. 4a–c).

There was a pronounced difference in the underwater light regime between the 2 years. The 1-year ice derived from freeze-up in winter 2016/2017 allowed light to penetrate into the water column in April 2017, whereas the 2-year ice derived from the winters of 2016/2017 and 2017/2018 (and associated snow cover) delayed the rise in underwater PAR to June 2018 (Fig. 4b,c). Comparing with the algal physiological and growth thresholds identified by Gosselin et al. (1985), PAR in the upper water column reached 7.6 μmol m$^{-2}$ s$^{-1}$ (photosynthetic activity threshold) on 18 May 2017 and 20 μmol m$^{-2}$ s$^{-1}$ (biomass accrual threshold) on 7 June 2017. In contrast, the spring 2018 irradiance in the upper water column was less than 0.5 μmol m$^{-2}$ s$^{-1}$ through May, the photosynthetic activity threshold value was not achieved until 29 June, and the biomass accrual threshold not until 3 July, about 1 month later than in 2017.

The lower irradiance conditions at the bottom of the lake during the mixing period of August 2016 were not associated with lower irradiance at the surface (Fig. 4b,c), but were the result of increased attenuation through the water column, as measured by the sharply increased $K_{d}$ values relative to August 2017 (Fig. 5a), Chl $a$ fluorescence values increased during this period (Fig. 4d), and were positively correlated with $K_{d}$ (Pearson’s correlation test $r = 0.37$, df = 1396, $p < 0.001$). In contrast, the large difference in bottom PAR between the May–July period in 2017 and 2018 (Fig. 4b,c) was at a time of similar incident irradiance and $K_{d}$ attenuation coefficients (Fig. 5b). However, snow accumulation on the ice cover was 12–20 cm thick in mid-July 2018 but absent in the other years of sampling, and the resultant differences in reflection and attenuation likely produced this 2017 vs. 2018 divergence in underwater PAR.

Two peaks in in vivo Chl $a$ fluorescence in the mid water column occurred in both years, with one in spring and the second in late summer. The maximum (Fig. 2e) and mean daily (Fig. 4d) fluorescence values in September 2016 were around 50% higher than in the subsequent ice-covered year, and occurred earlier in 2016, near the end of the period of ice-out and full water column mixing. The spring rise in Chl $a$ fluorescence began much earlier in 2017 (mid-April) than in 2018 (mid-June), reflecting the earlier rise in PAR beneath the 1- vs. 2-yr ice cover; this was also indicated by the earlier rise in water column $K_{d}$ values in 2017 (Fig. 5b). Peak fluorescence was timed at least 2 weeks earlier in 2017 than in 2018 (Figs. 2e, 4d), and corresponded to a period of sharply reduced under-ice irradiance (Fig. 4b,c) associated with a period of snowfall over the ice at that time (Supporting Information Fig. S6). The high PAR penetration in the water column in late June and early July 2017 was likely associated with the melting and loss of snow over the ice. Comparison of Chl $a$ concentrations as measured by the fluorescence sensor with those obtained by HPLC analysis of sample extracts showed a close match on all three dates, with a small mean difference of 0.17 μg L$^{-1}$ (Fig. 2e), and no evidence of sensor drift.

Dissolved oxygen

Oxygen rose in concentration in the lower water column of Ward Hunt Lake during the summer ice-covered period, to a maximum of 140% saturation (% air-equilibrium value at the measured water temperature) in both years. However, there was a faster rate of increase above saturation at the end of July 2016 (5.31% d$^{-1}$) than in the period late July to mid-August 2017 (2.48% d$^{-1}$; Table 1; Fig. 3, in red). There were high-frequency oscillations in temperature and dissolved oxygen at the bottom of the lake during the 2016 ice-covered period, indicative of internal waves with a period of 110 min (Supporting Information Fig. S7). With the movement and break-up of the ice cover in late July–August 2016, and water column mixing and ventilation under the influence of strong winds (Supporting Information Fig. S4), dissolved oxygen saturation dropped at a rate of ~2.30% d$^{-1}$. Oxygen values subsequently remained around 100% saturation (change rate of 0.08% d$^{-1}$) until freeze-up and the reinstatement of ice cover in September.

After a 2-week delay, dissolved oxygen then decreased (~3.03% d$^{-1}$) to undetectable levels by late November 2016. Fluctuations in oxygen were observed over the subsequent 2 months until the logger reached its memory capacity in late January and ceased recording. In 2017, water oxygen concentrations at 9.3 m followed a contrasting pattern, with values above 100% through most of August and a maximum value that was higher and later than in the previous year (Fig. 3, right panel). From mid-August 2017 onward, oxygen concentrations in the lower water column steadily decreased, and then much more rapidly in early September (Table 1). The lower water column became anoxic by the end of September, 2 months earlier than in 2016. It remained anoxic while the middle of the water column remained at 50% saturation and the upper water column at 100% saturation for the rest of the record until July 2018, when oxygen saturation increased in the middle water column (5.10% d$^{-1}$) in tandem with increasing Chl $a$ fluorescence.

Comparison of the net oxygen change rates in absolute units indicated a period of high variability from 20 July to the end of September in both years (Table 2). However, the timing of the shift from positive to negative oxygen balance differed between years: this was late August in 2017, but around 1 month later (late September) in 2016. The installation of the additional two oxygen sensors for the second year showed that net oxygen change rates were of larger amplitude and more variable in the lower water column relative to the shallower depths. Highest rates of net oxygen accumulation in
Fig. 4. Mean daily values of photosynthetically active radiation (PAR) and chlorophyll a (Chl a) fluorescence. PAR (a) in air; (b) in the upper (2.8 m) and (c) lower water column (8.5 m); and (d) Chl a fluorescence in the middle water column (5.8 m) of Ward Hunt Lake. The blue shadow corresponds to the ice-free period (from ice break-up to new ice formation) in summer 2016.

Fig. 5. Comparison of attenuation coefficients ($K_d$) between years. Hourly data are shown for the periods: (a) from 30 July to 30 August and (b) from 5 June to 15 July. The coefficients were calculated from the in situ irradiance measurements at 2.8 and 8.5 m.
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Arctic lake responses to extreme warming

Table 1. Linear oxygen change rates in Ward Hunt Lake. The values are expressed in terms of net increase or decrease in oxygen saturation (% air-equilibrium) per unit time. The numbers refer to the periods identified by gray shadows in Fig. 2f.

| Time period     | Net oxygen change rate (% d\(^{-1}\)) | 3.8 m | 5.8 m | Bottom* |
|-----------------|--------------------------------------|-------|-------|---------|
| 2016            |                                      |       |       |         |
| 1 21–25 Jul     |                                      | —     | —     | +5.31   |
| 2 30 Jul–07 Aug |                                      | —     | —     | −2.30   |
| 3 07 Aug–17 Sep |                                      | —     | —     | +0.08   |
| 4 17 Sep–03 Oct |                                      | —     | —     | −3.03   |
| 2017            |                                      |       |       |         |
| 5 23 Jul–14 Aug | −1.44−0.17                           |       |       | +2.48   |
| 6 15 Aug–05 Sep | −2.86°−7.89°−1.85                    |       |       |         |
| 7 05–09 Sep     | +0.09−0.05                           |       |       | −14.57  |
| 8 09–20 Oct     | +0.03−1.80                           |       |       | <0.01   |
| 2018            |                                      |       |       |         |
| 9 29 Jun–10 Jul | +0.62+5.10                           |       |       | <0.01   |
| 10 10–20 Jul    | +1.17+0.81                           |       |       | <0.01   |

—, no data.

*a5 m in 2016 and 9.3 m in 2017.
†15 to 18 Aug 2017.
‡15 to 19 Aug 2017.

Table 2. Net oxygen change rates in Ward Hunt Lake for equivalent 2-week time periods in 2016 and 2017.

| Time period | Net oxygen change rate (mg O\(_2\) m\(^{-3}\) d\(^{-1}\)) | 3.8 m | 5.8 m | 9.3 m | 8.5 m |
|-------------|----------------------------------------------------------|-------|-------|-------|-------|
| 20–31 Jul   | −4.1+16.5+240.9                                          |       |       |       |       |
| 01–15 Aug   | −100.8−32.1+236.7                                         |       |       |       |       |
| 16–31 Aug   | −18.2−144.3−192.5                                         |       |       |       |       |
| 01–15 Sep   | +7.4−7.2−1067.4                                          |       |       |       |       |
| 16–30 Sep   | −3.2−7.6−60.0                                            |       |       |       |       |
| 01–15 Oct   | +6.8−102.2+0.1                                          |       |       |       |       |
| 16–31 Oct   | +5.0−31.3+0.1                                          |       |       |       |       |

The northern coastline of Ellesmere Island experienced extreme warming in 2016, with record maximum air temperatures and an unusually high number of MDD at Ward Hunt Island and Alert. These elevated temperatures appear to be part of a broader pattern of warming that extended across the central Arctic earlier that year (Overland et al. 2019). The following year, the northern Ellesmere Island region returned to much cooler conditions that persisted throughout summer. These contrasting temperature regimes resulted in striking differences in the ice cover of Ward Hunt Lake, and consistent with the hypothesis that an unstable ice regime results in largescale variations in limnological properties, we recorded major differences between the two summers in temperature and mixing, underwater light, Chl \(a\) fluorescence, and oxygen dynamics. Some of these differences continued into fall and winter, for example, net oxygen depletion rates, indicating that intermittent ice-out causes limnological effects that extend beyond the open water period. Extreme warming events are likely to increase in intensity and duration with ongoing global climate change (Meredith et al. 2019), and our 2-yr comparison of high-frequency observations from Ward Hunt Lake provides insights into the future state of polar aquatic ecosystems.

Ice cover

A major transition in the lake ice regime of Ward Hunt Lake has taken place over the last two decades, with the rapid thinning of its summer ice cap from a thickness around 4 m in 2003 to the first loss of ice and open water conditions in 2011 (Paquette et al. 2015). The thinner summer ice has contributed to an enhanced sensitivity to climate warming, with full ice-out occurring subsequently in 2012 and 2016. These changes are consistent with the general contraction of the cryosphere, including a shorter duration of lake ice cover in the Arctic (Du et al. 2017) and more generally throughout the Northern Hemisphere (Sharma et al. 2019).

The transition from perennial to annual lake ice cover implies not only less ice, but also a greater degree of interannual variability in ice conditions. This effect has been observed and modeled for Arctic sea ice, where the replacement of thick multiyear ice by annual ice results in a greater response to year-to-year variations in climate forcing (Serreze and Meier 2019). This is because less energy is required to completely melt the ice, and also because wider expanses of open water result in positive feedback effects that amplify the interannual variations in ice melt (Mioduszewski et al. 2019). For Ward Hunt Lake, the transition to a more extensive moat each year not only increases the solar heating of the lake, but also allows the central ice pan to detach from the shore and

the bottom waters occurred in late July in both years, but in 2017 this high positive rate continued into mid-August and then became strongly negative, with a net depletion rate exceeding 1000 mg O\(_2\) m\(^{-3}\) d\(^{-1}\). This depletion rate was around twice the maximum oxygen loss rate measured in 2016, and occurred while the ice cover remained in the first half of September, whereas in 2016 maximum depletion rates occurred while the ice cover was gradually reforming in the second half of September (Fig. 2). The ANCOVA analyses of the linear regression slopes showed that the bottom water oxygen change

rates were significantly different \((p < 0.05)\) between 2016 and 2017 for every equivalent 14-d period in Table 2.
move around, as seen in the late summer images in both years (NEIGE 2020). This movement of the ice cover increases its likelihood of mechanical break-up of the ice, and allows greater exposure of ice surfaces to warmer littoral water. The thinning of the ice combined with more rapid loss of overlying snow also results in a greater penetration of solar energy to warm the underlying water column.

Projections of temperature and ice changes in permanently ice-covered Lake Bonney, Antarctica, indicate that this lake will lose its 3–5 m ice cap within one to four decades, with an abrupt shift from multiyear to annual ice cover (Obryk et al. 2019). The results from Ward Hunt Lake show that such changes in polar lakes may not be a simple transition from always ice-covered to annually ice-free, but rather may be a new regime, as observed here, of alternating periods of multiyear and annual ice conditions due to the amplified sensitivity of thin ice to interannual variability in climate. This type of year-to-year variation was also noted during the IBP study of High Arctic Char Lake (Schindler et al. 1974), which lies 1000 km to the south of Ward Hunt Island. In three of the four study years, the lake experienced open water conditions in late August, but during a cold cloudy summer the lake remained ice-covered, and the 2-yr ice accumulated to 2.9 m thickness by May the next year. Even lakes that are continuously overlaid by thick ice are known to respond to climate signals (Fountain et al. 2016), however the transition to thin ice that can completely melt out in warmer years results in a new regime of amplified sensitivity to climate fluctuations.

Mixing and stratification

Consistent with our hypothesis, the ice-out conditions in Ward Hunt Lake induced by extreme warming during August–September 2016 resulted in a completely different thermal regime than in the subsequent year of sustained ice cover. The exposure of the water column to convective cooling as well as direct wind-induced mixing in 2016 resulted in uniform temperatures throughout the water column and loss of energy to the overlying atmosphere. This effect was observed at Char Lake when a fall period of open water and strong winds resulted in rapid cooling of the entire water column to just above 0°C (Schindler et al. 1974), as in Ward Hunt Lake. Simulation of heat storage in Lake A, a meromictic lake near Ward Hunt Island, indicated that the loss of its perennial ice cover and exposure of its water column to the atmosphere could induce the loss of heat accumulated over more than 50 yr, with eventual disappearance of its mid water column temperature maximum (Vincent et al. 2008). In Ward Hunt Lake in 2017, the persistence of lake ice in late summer allowed inverse stratification to be maintained, with warmer bottom water temperatures that continued into winter and spring. Similarly, in Colour Lake on Axel Heiberg Island, the persistence of late summer ice resulted in warmer temperatures beneath the ice in the subsequent spring than in years that followed a summer with ice-out, mixing, and heat loss to the atmosphere (Doran et al. 1996).

The high-frequency temperature record from summer 2016 indicated that the stratified waters beneath the ice contained strata of movement and mixing, including homogenous midwater column temperatures that were suggestive of a sub-ice convection cell (as described in Pernica et al. 2017) and internal waves (Kirillin et al. 2012). After the period of cooling in the end of summer 2016, the bottom waters of the lake then rose in temperature during the period of early winter ice formation. This may be due to heat transfer from the sediments, but may also result from density flows of warmer water from the littoral zone that are enriched in ions due to salt exclusion by the forming moat ice or by sediment decomposition and mineralization processes (Cortés and MacIntyre 2020).

PAR and Chl a fluorescence

The PAR regime of High Arctic lakes is constrained by the extreme seasonality of incident solar radiation, the persistence of thick ice throughout most of the year and the presence of overlying snow. The continuous in situ records from Ward Hunt Lake showed signs of combined effects of all three factors, which limited the period of under-ice PAR exposure to mostly July–August. The incident energy supply was almost identical for the 2 yr, however the water column PAR differed sharply, with much lower irradiances in the lower water layer in August 2017 associated with the 2-yr ice and its associated snow cover. The sharp increase in $K_d$ during the late summer period of 2016 with strong winds and mixing suggests that this increased turbidity was due in large part to sediment resuspension, in combination with a rise in phytoplankton. The underwater PAR sensor at 9.0 m recorded values in the range 10 to 35 $\mu$mol photons m$^{-2}$ s$^{-1}$ from July to August in both years, which are above the thresholds for photosynthetic activity and biomass accrual (Gosselin et al. 1985). These values were at or above the PAR fluxes recorded under thick ice in McMurdo Dry Valley lakes; for example, 3.5 $\mu$mol photons m$^{-2}$ s$^{-1}$ at 9.2 m depth in Lake Hoare when the ice cover was less than 4 m thick (Vopel and Hawes 2006), and 4 to 45 $\mu$mol photons m$^{-2}$ s$^{-1}$ at 10 m in Lake Bonney under 2 to 4 m of ice cover (Doran et al. 1996).

Two annual maxima in phytoplankton communities, one during spring mixing and the other during late summer–fall, are common in many northern temperate lakes, although the pattern is often muted in oligotrophic waters (Kalf 2003). This bimodal pattern was also a feature of Ward Hunt Lake in both years. A spring peak in chlorophyll that developed beneath the ice followed by a late summer peak during and immediately after the open water period was also observed in Char Lake each year (Kalf and Welch 1974). The initial peak likely results from the use of nutrients released by mineralization over winter, while the second peak may be stimulated by nutrient inflows to the lake in late summer. Two periods of maximum phytoplankton densities have also been observed.
in Antarctic oligotrophic lakes, with the highest Chl a fluorescence recorded in fall (Tanabe et al. 2008).

The greater maximum Chl a fluorescence in the late summer of 2016 vs. 2017 may be the result of nutrient entrainment from the bottom waters and exposure to near surface light for photosynthesis during wind-induced mixing, in the absence of ice cover. Bioassays performed on samples from Ward Hunt Lake in summer indicated that the phytoplankton communities are highly responsive to nutrient input (Bonilla et al. 2005). The higher phytoplankton biomass suggested by the late summer fluorescence values in 2016 may also have influenced the subsequent nutrient and production regime in spring 2017, when higher fluorescence maxima were detected than in spring 2018. However, this potential legacy effect (Hampton et al. 2017) would require direct sampling and nutrient measurements to confirm.

The spring maximum in Ward Hunt Lake was delayed in 2017, likely because of the reduced light availability under the ice that year. Similarly in Char Lake, the spring increase was delayed during years of high snow cover (Kalff and Welch 1974). Snowfall is also a factor that is becoming more variable with climate warming in the Arctic, with extreme precipitation events observed recently (Schmidt et al. 2019). Along with variable ice conditions, this will amplify the magnitude of interannual variability in energy supply for primary production.

The variations in Chl a fluorescence measured in the mid water column provided an overall guide to the seasonal dynamics of phytoplankton biomass in Ward Hunt Lake, however this signal was almost certainly influenced by processes other than population growth. Large (up to 3 mm) visible colonies of the chrysophyte *Uroglena* along with other motile chrysophytes have been detected in this lake (Charvet et al. 2012). Some of the variations, and especially the sharp spikes observed in the high-frequency record, may be due to large chrysophytes moving past the fluorescence sensor actively, given their known ability to actively migrate over the 24-h cycle (Paterson et al. 2008), or passively via vertical mixing. Changes in pigment concentrations per unit biomass are likely to take place over hours to days during physiological acclimation to changes in the ambient light regime, and over the longer term through photoadaptation (Moore et al. 2006), potentially leading to an overestimation of biomass from Chl a under low light. Finally, in vivo Chl a fluorescence is a complex physiological variable that is subject to multiple photoregulation processes at timescales from seconds to hours (Huot and Babin 2011). The rapid increase in signal during the snowfall event in late June 2017 may be the result of lower nonphotochemical quenching of excitation energy in the dimmer light regime at that time, combined with upward migration of motile algal species from greater depths in the lake. The highest episodic peaks of Chl a fluorescence, notably on 29 June 2017, thus have to be interpreted with caution, as they co-occurred with significantly lower irradiances (Fig. 2e).

Excluding these sharp episodic peaks, and given the concordance between the fluorescence and HPLC values for Chl a concentrations, the generally higher fluorescence values observed in late summer 2016 and the differences in timing of fluorescence maxima between years imply that the interannual variation in ice-cover translated into effects on phytoplankton dynamics.

**Oxygen dynamics**

Despite the oligotrophic status of Ward Hunt Lake, its bottom waters showed marked seasonal variations in oxygen saturation, from anoxia to 140% of air-equilibrium. Oxygen accumulation below the ice is a common feature among ice-covered lakes (Craig et al. 1992). In addition to oxygen production by phytoplankton, cyanobacterial mats coat the bottom of Ward Hunt Lake and likely contribute to these seasonal variations (Mohit et al. 2017). Cyanobacteria-dominated mats in other systems have shown the potential to induce oxygen supersaturation in bottom waters (Vopel and Hawes 2006), and the microbial heterotrophs that occur abundantly in such mats (Mohit et al. 2017) may contribute to the oxygen draw-down in winter. Schindler et al. (1974) observed in Char Lake that even despite its extreme oligotrophic status, oxygen concentrations in its bottom waters fell to 2.5 mg L⁻¹ (ca. 18% saturation) by the end of stratification, and attributed this to benthic respiration processes.

There were pronounced differences in the pattern of change in dissolved oxygen between the years with and without ice cover, as for the other limnological variables. During ice-off and mixing in 2016, the excess oxygen was ventilated to the atmosphere, but the water column remained oxic well into the early winter period. In 2017, the oxygen concentrations were rapidly depleted below air-equilibrium, and became anoxic in early winter, possibly because of higher sediment temperatures in 2017 vs. the sediments in 2016 that had been cooled by water column mixing. The timing of switching from net oxygen accumulation to net depletion differed between years by a month. The oxygen sensor located at 8.5 m in 2016 was relocated at 9.3 m in 2017, which may have influenced the values recorded. However, this large difference in timing implies that the phytoplankton community was active longer in the absence of ice.

The observed rates of oxygen change expressed in absolute units of mg O₂ m⁻³ d⁻¹ allow comparison with other waterbodies, and show that Ward Hunt Lake has sustained periods of net production or loss as a consequence of its active microbial communities under prolonged ice cover, and the annual light/dark cycle at high polar latitudes. The fastest net gains of 240–360 mg O₂ m⁻³ d⁻¹ are comparable with rates over summer in Lake Hoare, Antarctica (e.g., net gain of 216 mg O₂ m⁻³ d⁻¹ in the upper water column beneath 5 m of ice between 15 November 1980 and 22 January 1981; Wharton et al. 1986), where physical as well as biological processes have a controlling influence (Craig et al. 1992). These
rates are well above net daily changes in the surface waters of lakes at temperate latitudes, where the gains from photosynthetic production over each 24 h cycle may be approximately balanced by respiratory losses during the nighttime hours of darkness, as well as by daily equilibration with the atmosphere (e.g., fig. 2 in Staehr et al. 2010). The highest depletion rate observed in the lower water column of Ward Hunt Lake in 2017 (1067 mg O₂ m⁻³ d⁻¹) was similar to the most rapid losses recorded at the bottom of subarctic shallow thermokarst ponds in early winter (1060 mg O₂ m⁻³ d⁻¹; Deshpande et al. 2015). Application of a numerical model such as MyLake (Couture et al. 2015) to the high-frequency data set from Ward Hunt Lake, once its morphometric, hydrological, and biogeochemical parameters are better defined, may allow further identification of biogeochemical processes controlling the large seasonal and interannual variability in oxygen concentrations, and the potential responses to ongoing change.

Conclusions
The High Arctic is moving into a new climate regime of not only warmer average air temperatures, but also an increasing amplitude of extreme weather. The long-term climate observations at Canada’s far northern coast indicate a trend of increasing MDD since the 1990s, with 2016 as an anomalous year of extreme warming. The recent transition of Ward Hunt Lake from a regime of continuously thick multiannual ice to thinner ice that is vulnerable to full melt-out has made the lake especially sensitive to such extreme events. The complete loss of ice in 2016 resulted in a major disruption of the physical and biogeochemical dynamics of the lake. The lake became fully exposed to wind-induced mixing, which caused a rapid temperature decline, high turbidity, and a longer period of oxygen depletion year-to-year variability.

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Conflict of interest

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