# Seasonal and Regional Controls of Phytoplankton Production along a Climate Gradient in South-West Greenland During Ice-Cover and Ice-Free Conditions

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# Seasonal and regional controls of phytoplankton production along a climate gradient in South–West Greenland during ice–cover and ice-free conditions

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ABSTRACT

Across a small geographic area (<180 km), the region of South–West Greenland covers a natural climate gradient. Variation in temperature and precipitation result in marked differences in limnology at three discrete locations: ice sheet margin, inland, and the coast. Replicate lakes from each location were sampled for physical (temperature, light), chemical (dissolved oxygen, pH, conductivity, nutrients), and biological (chlorophyll *a* [Chl *a*], photosynthetic pigments) variables on three occasions within a 12-month period: July–August 2010, April–May 2011, and June–July 2011 spanning ice cover. Variation in ice phenology was linked to the climate gradient; however, phytoplankton production and community composition did not differ regionally. Large-scale seasonal fluctuations in temperature and nutrient availability were the strongest predictors of phytoplankton production, with a shift from nitrate to phosphorus controlled production between ice-cover and ice-free conditions. Underlying seasonal drivers, variables predicting production were unique to each location—ice sheet margin (soluble reactive phosphorus), inland (temperature), and coast (silicate)—and reflect local differences in nutrient availability. Results from the current study have important consequences when controls over phytoplankton production in Arctic lakes are inferred from a limited number of sites, but up-scaled to represent pan-Arctic trends.

## INTRODUCTION

Lakes are a dominant feature of Arctic landscapes. They act as biodiversity hotspots as well as key sites for biogeochemical cycling and nutrient processing (Vincent et al., 2008). However, despite their abundance, ecological importance, and sensitivity to global environmental change (Adrian et al., 2009), the seasonal limnology (including physico–chemical changes and biological structure) of Arctic lakes

remains poorly understood. Sampling lakes in the Arctic is difficult for logistical reasons. As a result, information is typically derived from small-scale regional surveys and spot-sampling (e.g., Michelutti et al., 2002; Antoniades et al., 2003). There are only a few sites where detailed monitoring has occurred over several years, notably Zackenberg in North-East Greenland (Christoffersen et al., 2008), Toolik Lake in Alaska (Hobbie and Kling, 2014), Lake Torneträsk in northern Sweden (Jonasson et

al., 2012), and the Experimental Lakes Area in the Canadian High Arctic (Blanchfield et al., 2009). Moreover, the diversity of lake types across the Arctic is extensive: sites range from freshwater to hypersaline, isothermal to thermally stratified, and from perennially ice-covered to ice-free during the summer (Vincent et al., 2008). Finally, limnological sampling has typically focused on the pelagic zone during ice-free periods as this has traditionally been considered as the optimal conditions for biological activity (MacIntyre et al., 2006; Medeiros et al., 2012) and is least logistically challenging. Nonetheless, biological activity under ice (Rohde, 1955) and in benthic zones (Vadeboncoeur et al., 2003; Bonilla et al., 2005) in high–latitude lakes have been recognized for a long time. Phytoplankton production and standing stocks under ice cover can be as high or greater than during the open water during summer (Hampton et al., 2015).

Arctic lakes and the species that inhabit them have developed under a unique set of external pressures. As such, they are extremely sensitive to environmental change (Adrian et al., 2009). Any alteration to their physical environment (e.g., ice thickness and duration, light availability, water temperature, nutrient supply, mixing regime) can have a marked impact on overall structure and function. The Arctic is currently experiencing a period of unprecedented exposure to multiple global environmental stressors, including anthropogenically associated shifts in climate (temperature and precipitation), increased atmospheric pollutant deposition (e.g., nitrogen), and altered macronutrient cycling (in particular, carbon) (Kaufman et al., 2009; Schuur et al., 2009; Holtgrieve et al., 2011). Such impacts have been linked to rapid ecological change across a range of different Arctic ecosystems, including lakes (Smol et al., 2005; Wolfe et al., 2006). One of the most profound changes recently observed across many Arctic ecosystems is altered phenology (Post et al., 2009). For lakes that freeze annually, this is largely assumed to be driven by delayed ice formation in autumn and earlier ice-melt in spring (Duguay et al., 2006). A reduction in the duration of winter ice cover has been linked with several limnological changes in high latitude lakes: increased water temperature and light availability and altered mixing regimes, thermal structure, and nutrient cycling (Järvinen et al., 2002; Leppäranta et al., 2003).

It is widely reported that changes in the physical structure of Arctic lakes due to earlier ice-melt drives shifts in aquatic community composition (Sorvari et al., 2002; Smol et al., 2005) and results in significant production increases (Michelutti et al., 2005). However, these conclusions are generally inferred from lake sediments (which record an integrated measure of production over multiple years), and commonly, conclusions regarding enhanced production are drawn from aquatic community shifts, rather than direct measurements of biomass or productivity. Moreover, there is a vast range of biotic (e.g., grazing, resource-competition, microbial activity, niche partitioning) and abiotic (nutrients, light, mixing regime, morphometry, temperature) factors that act in various different combinations to determine total lake production in any lake at any given time. It is challenging to measure and account for all such variables, and given the number of lakes spread across the Arctic, it remains a challenge to establish causal drivers of lake production at any given site, let alone to up-scale to the regional or pan–Arctic level. Furthermore, when interpreting drivers of ecological change in the paleo-record, it is commonly assumed that relationships between variables measured today (water column or surface sediments) reflect identical conditions and community interactions as occurred in the past; yet, these remain to be determined (Seddon et al., 2014).

To date, there have been a limited number of process-based limnological studies and contemporary observations that attempt to address the relationship between duration of ice-free conditions, primary production, and aquatic community composition (Lotter and Bigler, 2000; Weyhenmeyer et al., 2008, 2013). In general, these studies conclude that variation in the timing of ice-melt can have broad ecological implications regarding seasonality, aquatic trophic structure, and in-lake production (Lotter and Bigler, 2000; Weyhenmeyer et al., 2008, 2013). The natural successional pattern of algal groups in Arctic lakes is tightly coupled to ice-cover, timing of melt, light regime, nutrient cycling, water temperature, and (in lakes that mix) duration of the mixed period and establishment of thermal stratification (Prowse et al., 2011). As such, any alterations to the physical structure of lakes as a result of shifts in ice-melt

dynamics can influence the competitive ability and growth of different algal groups and impact on the timing of peak abundances, thereby altering community structure and potentially generating trophic mismatches over longer timescales (Weyhenmeyer et al., 2013). Yet, despite a focus on phenological shifts, there still remains little contemporary evidence that supports the suggestion derived from paleolimnological studies that earlier ice-melt and an extension of the open water period are directly associated with an increase in total lake production. In subarctic Lake Saanajärvi during the 1990s, Forsström et al. (2005) reported higher algal biomass and Chl a associated with warmer air temperatures and a longer duration of the ice-free season; however, the authors acknowledge that both temperature and nutrients play a role in regulating algal biomass. Analysis of phytoplankton production in 205 small, oligotrophic Swedish lakes found that timing of ice melt (represented as the duration of the open water season) was most closely correlated with phytoplankton biomass, but that this encompassed changes in nutrients, light, and temperature (Weyhenmeyer et al., 2013). From this study, phytoplankton species richness and biomass were found to be controlled by different ecological conditions; phytoplankton production corresponded most closely to variation in nutrient availability (Weyhenmeyer et al., 2013). For Arctic lakes which thermally stratify, phytoplankton in the epilimnion can rapidly become nutrient limited (Levine and Whalen, 2001; Bonilla et al., 2005). As a result, regardless of the timing of ice-melt, it is unlikely that an increase in algal production will be supported throughout the entire open water period unless there is a simultaneous prolonged increase in nutrient availability or algal uptake efficiency (Kling et al., 1990).

In order to investigate differences in seasonal and regional controls over phytoplankton production and community composition in Arctic lakes, we undertook a survey of the biology, chemistry, and physical limnology of 18 freshwater lakes situated along a regional climate (temperature and precipitation) gradient in South-West (SW) Greenland spanning ice cover over a 12 month period. The gradient also represents variation in annual ice melt dates and permitted investigation of large-scale (regional) controls over phytoplank-ton production (Chl a) and community composition as well as any drivers unique to each location.

## REGION OF STUDY

The region between 66.5–67.2°N and 50–53.5°W is part of the widest ice-free margin of SW Greenland (Fig. 1) and forms a major lake district (ca. 20,000 lakes). Across the region there is a natural climate gradient from the warm, dry interior to the cooler, wetter coastal zone (Anderson et al., 2001). Annual precipitation increases from <150 mm yr$^{-1}$ close to the ice sheet margin to ca. 500 mm yr$^{-1}$ at the coast, with the largest proportion of this received as snow during winter. The strong precipitation gradient is a result of regional topography; there is a gradient of increasing altitude from the ice sheet margin (mean altitude ca. 500 m a.s.l.) to the coast (several peaks > 1200 m a.s.l.). The presence of the ice sheet (Fig. 1) also creates a unique and localized set of climatic conditions in the immediately adjacent ice-free areas. Strong katabatic winds blow off the ice sheet, and the presence of small glaciers and outcrops of ice act as topographical barriers to the prevailing movement of air, thereby creating a much drier and cooler climate close to the ice sheet margin (Nielsen, 2010). To date, very little research has been undertaken on lakes by the ice sheet margin and they are of interest as they most likely represent end members along the regional climate gradient. Although there is evidence that much of the Arctic experienced a warming trend during the 20th century (Kaufman et al., 2009), SW Greenland has only very recently (past ca. 15 yr) shown evidence of a significant warming trend (Hanna et al., 2012).

Vegetation across the study area is classed as dwarf shrub tundra, dominated by *Betula nana*, *Salix glauca*, *Empetrum* spp., and *Vaccinium* spp., with grasses and cryptogams also common (Nielsen, 2010). Close to the ice sheet margin, *Ledum palustre* heath, *S. glauca* heath, and *Carex stupina* steppe are more abundant, while toward the coast, *Empetrum* spp., bryophytes, and lichens are increasingly common (Anderson et al., 2001). The geology is relatively uniform, principally composed of granodioritic gneisses, and the region is at the southernmost zone of continuous permafrost in Greenland (Nielsen, 2010).
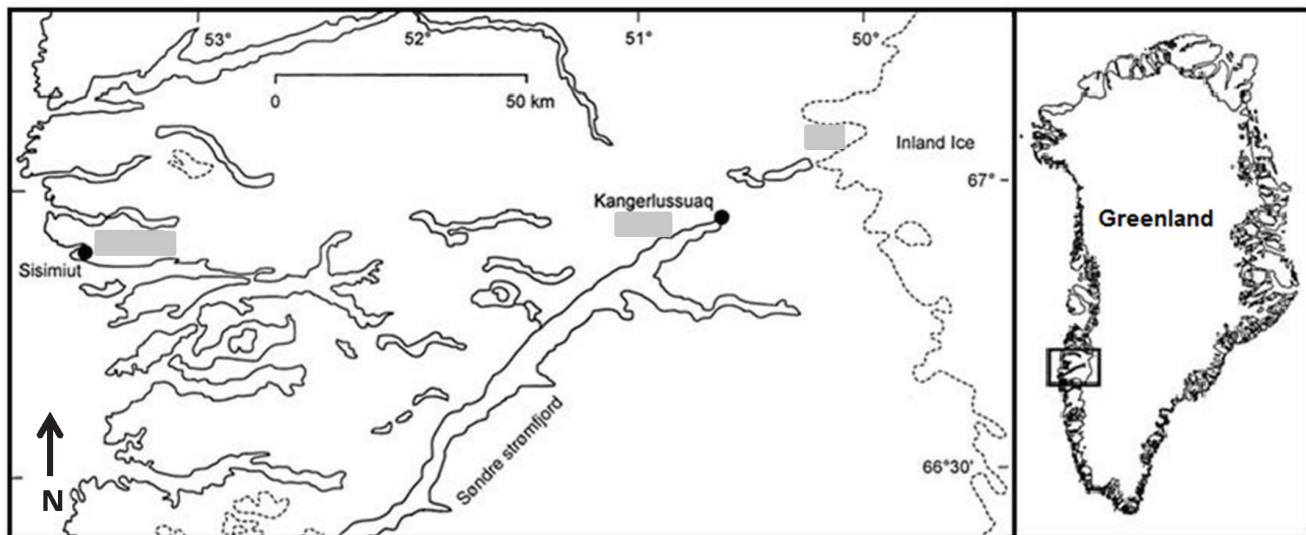
**FIGURE 1.** Map of study area in South–West Greenland showing three study locations: ice sheet margin, inland (close to Kangerlussuaq), and coast (close to Sisimiut) shaded by gray rectangles.

## STUDY LAKES

Study lakes ($n = 18$) were selected from three locations across the region: ice sheet margin ($n = 6$), inland ($n = 6$), and the coast ($n = 6$) (Fig. 1). During under-ice sampling in April–May, sampling at lake SS906 by the ice sheet margin was not possible. The three locations formed a transect along the climate gradient corresponding to distinct local differences in the timing of ice melt. Ice-off generally occurs first in lakes inland, which are typically ice-free by mid-June. Field observations over the past decade confirm that ice-melt dates are delayed by up to three weeks at the coast (Anderson and Brodersen, 2001), with a slight degree of interannual variation. After ice melt, all lakes stratify rapidly before regional cooling results in a deepening of the thermocline and water column mixing in mid to late August. Ice formation typically begins late September to mid-October (Kettle et al., 2004).

Study lakes are glacially scoured basins, and lakes at the coast are smaller in area (7.8 ± 1.3 ha) than lakes at the ice sheet margin (20.5 ± 5.5 ha) or inland (21.5 ± 4.1 ha) (Table 1). Mean maximum depth is similar across the region (coast: 16.2 ± 2 m, inland: 15 ± 1.7 m, ice sheet margin: 19.9 ± 4.4 m, Table 1). Although the lakes are oligotrophic and chemically dilute (<425 µS cm$^{-1}$; ca. 5–10 µg TP L$^{-1}$; Anderson et al., 2001), the regional climate gradient directly affects the local precipitation/evaporation balance, hydrological connectivity, and lake water residence times, in turn influencing water chemistry (especially conductivity), which varies systematically across the region (Anderson et al., 2001).

## METHODS

### Limnological Sampling

Study lakes were visited on three occasions during a 12 month period spanning winter ice cover: July–August 2010 (summer, open water conditions; 25 July to 12 August 2010), April–May 2011 (under ice, 26 April to 23 May 2011) and June–July 2011 (after ice melt, 19 June to 29 July 2011). This approach was dictated by logistical constraints, but nonetheless, enables comparisons of limnology during ice cover and periods of open water preceding and following ice. We have collated meteorological data from both years and long-term 2000–2012 averages (Table 2), and consideration of interannual variability on observed trends is provided in the discussion.

During each sampling occasion, all lakes were visited within a three-week period. Water samples were generally taken at the deepest part of the lake using a van Dorn sampler from a depth of 2 m, accessing the water using a motorized ice borer during ice cover

and from an inflatable boat during ice-free conditions. After collection, samples were stored cool in the dark until they were returned to the laboratory in Greenland (typically within 8 hours of collection) and were stored at 4 °C in the dark until analysis of water chemistry parameters. This was within three days for analyses undertaken in the laboratory in Greenland, or 14 days for samples transported in cool, dark conditions to the U.K. or U.S.A.

In 2011, colder winter temperatures (Table 2) led to extended ice cover on lakes across the whole region; at the coast, this prevented safe access of the water column at the deepest point of most lakes. For logistical reasons, limnological sampling at this location and time was undertaken on lake outflows, which were just establishing. Access to lake outflows provided the safest and closest environmental and limnological conditions for ecological comparisons, as upon ice melt, newly released colder water from ice and snow melt is less dense than the lake water below and remains at the top of the water column within the upper few meters (as sampled inland and at the ice sheet margin) and will exit via outflows (sampled at the coast) where available (Forsström et al., 2005).

Depth profiles of temperature, dissolved oxygen, conductivity, and pH were measured at ca. 1 m intervals using a YSI 6600V2 Sonde (YSI Incorporated, Yellow Springs, Ohio, U.S.A.). Secchi disk readings were taken at all study lakes during ice-free periods, with euphotic depth ($Z_{eu}$: 1% percentage surface irradiance remaining) estimated as twice Secchi disk depth (Preisendorfer, 1986). Photosynthetically active radiation (PAR) was measured at 1 m intervals down the water column at two lakes under snow and ice cover (inland: SS2 and ice sheet margin: SS903) using a Li-cor LI-192SA underwater quantum sensor attached to an LI-1400 data logger (LI-COR Biosciences, Lincoln, Nebraska, U.S.A.), with values of $Z_{eu}$ calculated as 1% surface irradiance levels. During April–May 2011, the thickness of snow cover on lakes was measured using a tape measure at five random locations on the lake surface, with ice thickness measured through the drilled hole.

Without thermistor data or high intensity monitoring, it is difficult to report the exact timing of ice melt for each lake. Given known regional variation in ice phenology, we sampled lakes in the order inland > ice sheet margin > coast. In June–July 2011 at the coast, remaining ice-cover prevented safe access and sampling of lakes. Only AT8 was completely ice-free (weak thermal profile suggests ice melt was only a few days previously). For all other lakes at the coast, samples were taken from the lake outflow at 0.5 m depth to provide an integrated water sample. This provided the closest possible replication of mixed surface waters in the pelagic zone. Although differences in timing between final ice melt and sampling cannot be excluded from our interpretations, we are confident that regional trends can be drawn from samples taken at a comparable time period (close as possible to ice melt) as best as is possible given logistical constraints of sampling remote Arctic lakes across a 180 km distance.

## Water Chemistry

Total nitrogen (TN), total phosphorus (TP), and total alkalinity were measured on unfiltered water and soluble reactive phosphorus (SRP), ammonium ($NH_4^+$), nitrate ($NO_3^-$), silicate ($SiO_3$), major ions ($K^+$, $SO_4^{2-}$), and dissolved organic carbon (DOC) from precombusted Whatman 1.2 μm GF/C glass-fiber filtered water (GE Healthcare, Buckinghamshire, U.K.). Water chemistry was measured by standard methods following Mackereth et al. (1989) (TP, SRP, $NH_4^+$, $NO_3^-$, and $SiO_3$), Koroleff (1983) modified by Qualls (1989) (TN, analyzed by the Environment Agency, U.K., and J. Saros, University of Maine, U.S.A.) and Golterman et al. (1978) (total alkalinity). Samples for DOC analysis were preserved with $H_3PO_4$ and measured by Pt-catalyzed combustion at 680 °C following removal of inorganic C by sparging with $CO_2$ free air and were measured using a Shimadzu TOC-V$_{CSN}$ (Shimadzu Scientific Instruments, Japan). Analysis of major ions was undertaken in the U.K. using an ion chromatograph (anions: 761 compact IC, cations: 792 Basic IC, Metrohm, Switzerland).

## Algal Photosynthetic Pigments

Chlorophyll *a* (Chl *a*) and photosynthetic pigments were measured by filtering a known volume of water through a Whatman 1.2 μm GF/C glass-fiber filter. Filters were immediately wrapped in aluminum foil and stored at −20 °C until analysis. Chlorophyll *a* was measured trichromatically

on a spectrophotometer following Jeffrey and Humphrey (1975). Phytoplankton pigments were measured with standard high–performance liquid chromatography (HPLC) following Leavitt and Hodgson (2001) as described in McGowan et al. (2012). Briefly, filters were extracted in a mixture of acetone:methanol:water (80:15:5) by sonicating for 15 min and leaving in the dark at 4 °C overnight. Extracts were filtered through 13 mm PTFE syringe filters (pore size 0.4 μm), evaporated under $N_2$ gas until dry, and redissolved in a 70:25:5 mixture of acetone:ion pairing reagent (IPR, 0.75 g tetrabutyl ammonium acetate and 7.7 g ammonium acetate in 100 ml water):methanol before they were injected into the HPLC. Analysis of phytoplankton groups was based on HPLC separations of photosynthetic chlorophylls and carotenoids from chlorophytes (Chl *b*, lutein–zeaxanthin), cryptophytes (alloxanthin), cyanobacteria (canthaxanthin), dinoflagellates (peridinin), and siliceous algae including diatoms and chrysophytes (fucoxanthin). Pigment concentrations are expressed as nmol pigment $L^{-1}$. Photosynthetic pigment analysis was undertaken to provide an indication of phytoplankton community structure on samples with low biomass where it can be challenging to concentrate up samples via settling for taxonomic counts when standing stocks are low (especially during ice cover).

## Statistical Analysis

All data were initially checked for equal variance using Levene's homogeneity of variance test (SPSS 22.0 IBM, New York, U.S.A.). Values for all variables (Table 3) were $\log_{10}$-transformed and used to explore relationships among locations and sampling occasions and to identify the strongest predictors of phytoplankton production (Chl *a*). Regional patterns in limnological variables were explored for each sampling occasion using principal components analysis (PCA) following detrended correspondence analysis (DCA) to establish the axis 1 gradient lengths < 2 SD. Principal components analysis was performed and ordination biplots created with CANOCO version 4.5 (ter Braak and Smilauer, 2002). To identify drivers of variation in phytoplankton Chl *a* (predictor variable), all variables were used in regression tree analyses for the entire data set for all lakes at all times. Data was subdivided into under–ice and ice–free (June–July

2011 and July–August 2010) and also by location (ice sheet, inland, coast) for regression tree analysis to determine the strongest significant predictors of phytoplankton Chl *a*. Under ice, snow depth was used as a proxy for light availability. SPSS v. 22.0 (IBM, New York, U.S.A.) was used to perform all regression tree analyses with minimum outputs of $n = 4$ in parent and $n = 2$ in child nodes. All regression tests undertook multiple tests of data for significance; therefore Bonferroni corrections were applied, lowering significance thresholds on each occasion. Two–tailed *t*–tests were used to determine statistically significant differences in annual meteorological conditions, while two–way ANOVA determined statistically significant differences ($P < 0.05$) in phytoplankton pigment assemblages among locations and sampling occasions, with least-squares difference post–hoc analyses (Table 4). SPSS v. 22.0 was used for all *t*–tests and ANOVA.

## RESULTS

### Regional Ice Phenology

In March 2011, mean snow depth on the study lakes was 624 ± 462 mm (coast), 222 ± 125 mm (inland), and 178 ± 142 mm (ice sheet margin) (C. Curtis, personal communication). By April–May 2011, when we sampled, snow cover had decreased to 100 ± 50 mm (coast), 46 ± 22 mm (inland), and 23 ± 19 mm (ice sheet margin). Ice thickness was 1.4 ± 0.06 m (coast), 1.2 ± 0.04 m (inland), and 1.3 ± 0.09 m (ice sheet margin). In June–July 2011, inland lakes were all ice-free on the first day of sampling (19 June 2011), whereas the final stage of ice melt at SS902 (ice sheet margin) was recorded on 25 June 2011, and substantial ice cover was still present on lakes at the coast on 4 July 2011.

### Regional and Seasonal Limnology

The physical, chemical, and biological structure of lakes varied seasonally and regionally (Figs. 2–4, Table 3). On each sampling occasion, replicate lakes within each location clustered together showing similar limnological properties (Fig. 3, Table 3). Typically, inland lakes were characterized by warmer surface water temperatures, while temperatures were low at the coast and intermediate at the ice sheet margin (Figs. 2–3, Table 3). In July–August
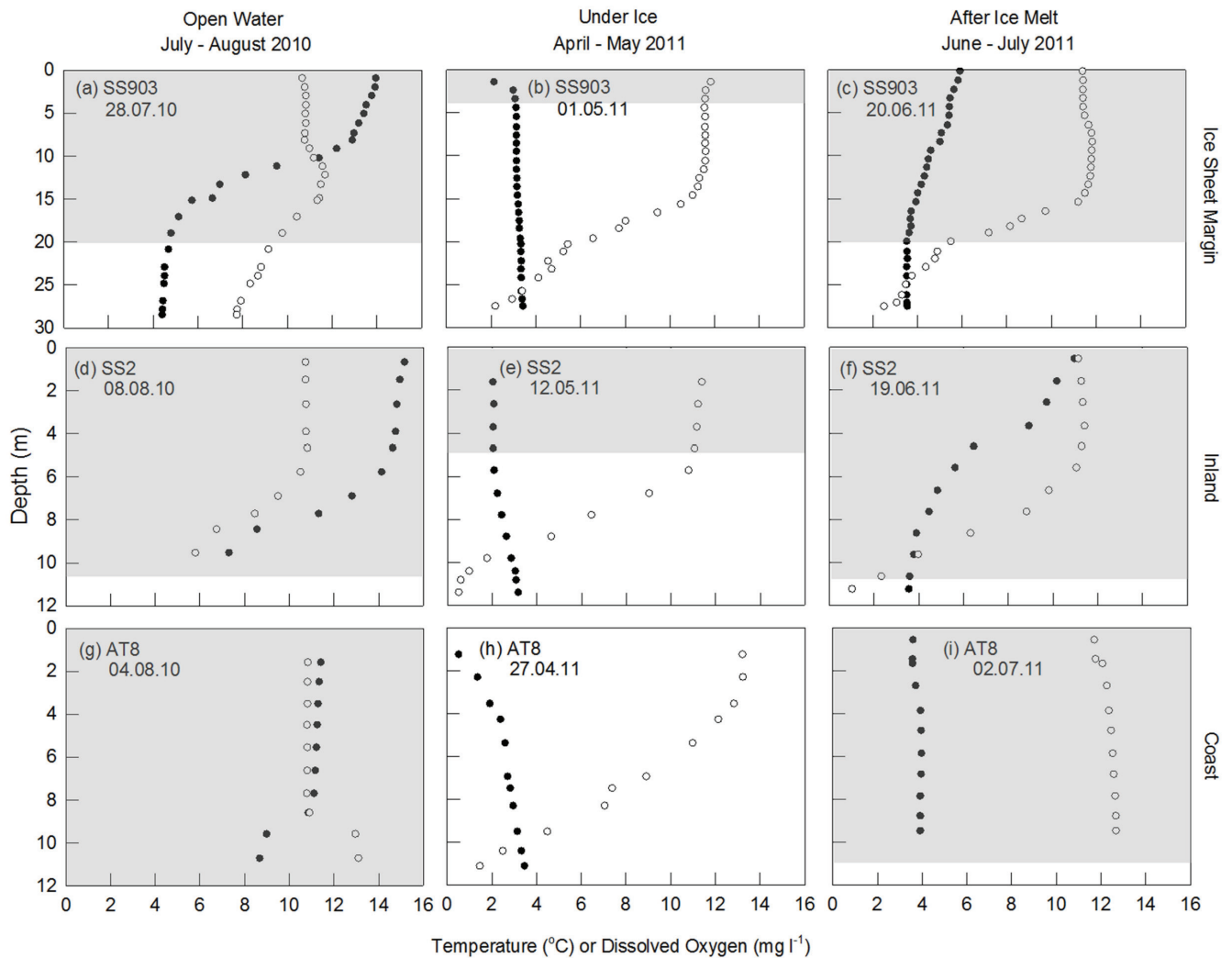
**FIGURE 2.** Regional representative depth profiles of temperature (●) and dissolved oxygen (○) in lakes SS903 (ice sheet margin, a–c), SS2 (inland, d–f), and AT8 (coast, g–i). The euphotic zone depth (1% surface irradiance) is shaded in gray. Profiles were taken on three sampling occasions: open water (July–August 2010), under ice (April–May 2011), and immediately following ice melt (June–July 2011).

2010, all lakes showed evidence of stratification; mixed depth was greatest at the ice sheet margin (7.6 ± 0.6 m) compared with lakes at the coast (6.8 ± 0.6 m) or inland (5.8 ± 0.3 m) (Table 3). Under ice, all lakes were inversely stratified: water immediately beneath the ice was <2.5 °C, increasing to ca. 4 °C toward the deepest point (e.g., Fig. 2). Surface water temperature increased rapidly after ice melt (e.g., by 7 °C within 5 days at SS903 at the ice sheet margin) with the onset of thermal stratification developing first in lakes inland, followed by those at the ice sheet margin. Mean euphotic zone depth ($Z_{eu}$) during open water periods was greatest in lakes at the ice sheet margin (16.7 ± 1.1 m) compared with the coast (13.7 ± 1.7 m)

and inland lakes (14.2 ± 1.8 m), while similar $Z_{eu}$ values were recorded for two lakes sampled under ice (SS2 and SS903; 4.5 m, Fig. 2). During ice cover, maximum dissolved oxygen was recorded in the upper water column. The depth to which maximum oxygen concentrations were recorded under ice differed across the region: 4.3 ± 0.2 m (coast), 6.1 ± 0.3 m (inland), and 13.6 ± 1.8 m (ice sheet margin) (e.g., Fig. 2). Below these depths, dissolved oxygen decreased rapidly in all lakes to <3 mg L$^{-1}$ at the deepest point. Profiles were similar under ice and following ice melt at inland and ice sheet lakes (e.g., Fig. 2). However, at AT8 (coast), dissolved oxygen concentrations were uniform (ca. 12.5 mg L$^{-1}$) throughout the water column (Fig. 2).
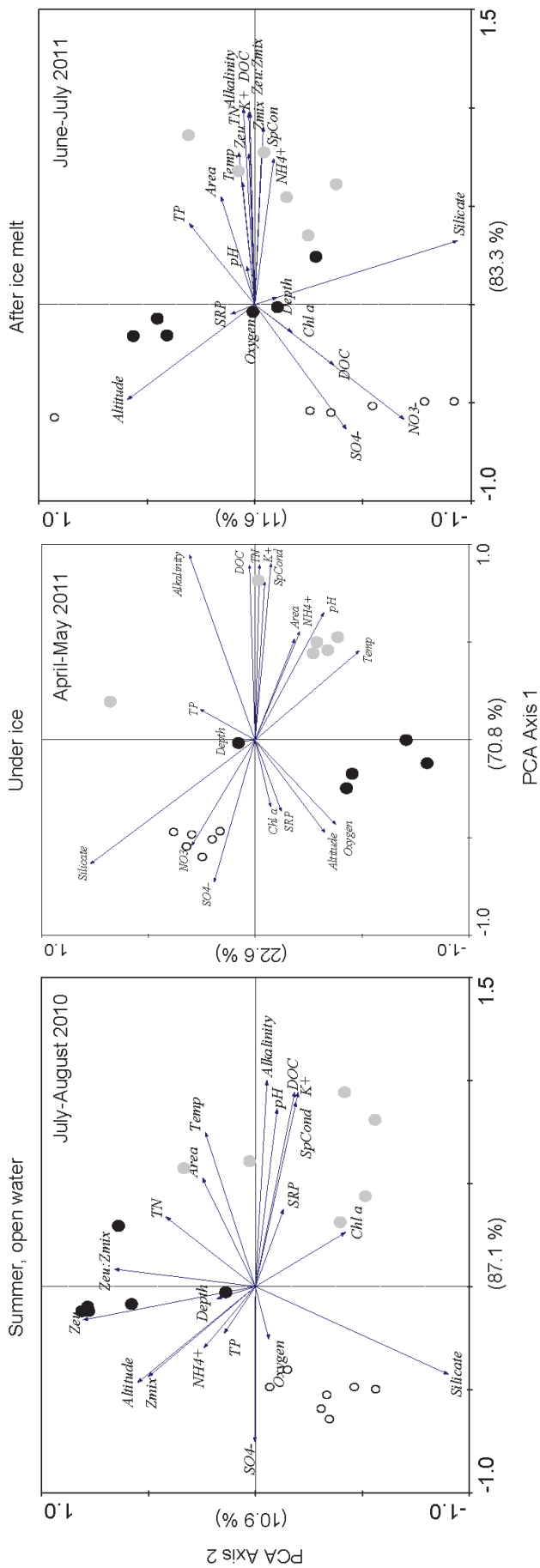
FIGURE 3. Principal components analysis (PCA) biplots of all physical, chemical, and biological (Chl *a*) variables measured at study lakes (*n* = 18) on three sampling occasions: (left) July–August 2010 (open water period), (center) April–May 2011 (under ice), and (right) June–July 2011 (immediately following ice melt). Individual lakes are plotted as circles and shaded to represent sampling location: (○) coast, (●) inland, (●) ice sheet margin. The amount of variance (%) captured by axes 1 and 2 is shown for each sampling occasion.

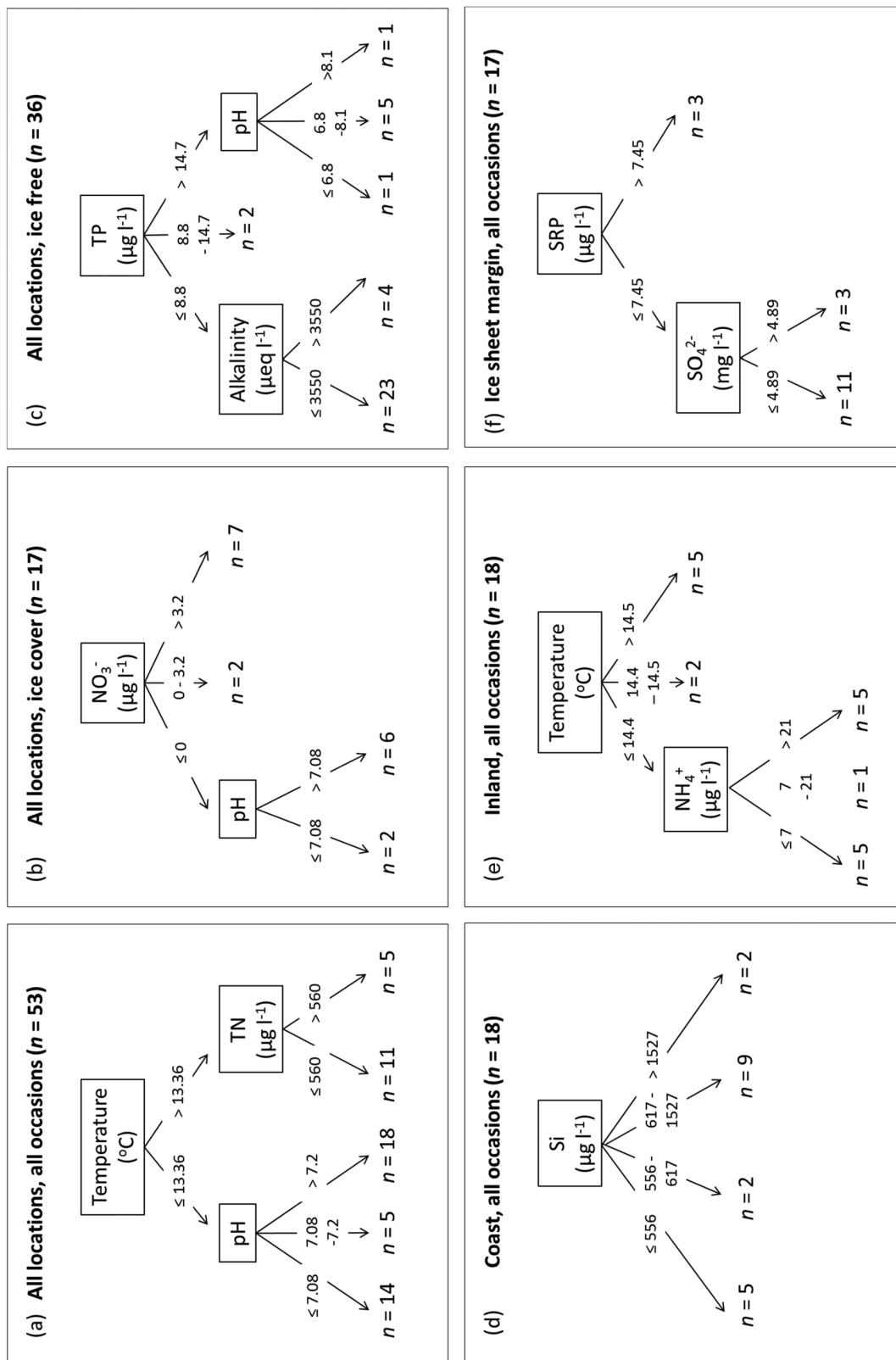FIGURE 4. Regression tree analyses of controls over phytoplankton Chl *a* in South–West Greenland lakes. All variables (Table 3) were added to regression analyses and were split by both sampling occasion (ice cover: April–May 2011 or ice free: July–August 2010, and June–July 2011) and location (ice sheet margin, inland, and coast) to reveal differences in controls over phytoplankton Chl *a* production. Analysis of all survey data is shown for all locations and (a) sampling occasions, (b) ice cover, and (c) ice free conditions. To determine unique controls over phytoplankton Chl *a* by location, analyses were also run for all occasions and (d) coast lakes, (e) inland lakes, and (f) ice sheet margin lakes. Variances explained by the model are given in the manuscript, with analyses run for a minimum of 2 samples in every branch. Abbreviations: TN (total nitrogen), TP (total phosphorus), $NO_3^-$ (nitrate), $NH_4^+$ (ammonium), Si (silica), SRP (soluble reactive phosphorus), and $SO_4^{2-}$ (sulfate).

ARCTIC, ANTARCTIC, AND ALPINE RESEARCH / ERIKA J. WHITEFORD ET AL. / 147

TABLE 1

**TABLE 1**

**Physical parameters of study lakes.**

| Region | Lake | Latitude (°N) | Longitude (°W) | Lake area (ha) | Altitude (m a.s.l.) | Maximum depth (m) |
|---|---|---|---|---|---|---|
| Ice sheet margin | SS901 | 67.131 | 50.234 | 12 | 375 | 14.5 |
| | SS902 | 67.129 | 50.219 | 37.3 | 375 | 37 |
| | SS903 | 67.130 | 50.172 | 38 | 350 | 30 |
| | SS904 | 67.157 | 50.278 | 12.4 | 425 | 11.4 |
| | SS905 | 67.163 | 50.285 | 14.2 | 450 | 11.2 |
| | SS906 | 67.120 | 50.255 | 9.3 | 450 | 15 |
| Inland | SS2 | 66.997 | 50.970 | 36.8 | 185 | 11.2 |
| | SS8 | 67.013 | 51.082 | 14.6 | 190 | 10.4 |
| | SS85 | 66.983 | 51.057 | 24.6 | 178 | 13 |
| | SS1333 | 67.001 | 51.146 | 13.8 | 350 | 2.9 |
| | SS1341 | 66.991 | 51.143 | 7.0 | 350 | 16 |
| | SS1381 | 67.016 | 51.119 | 21.5 | 200 | 18.5 |
| | SS1590 | 67.010 | 50.982 | 24.6 | 200 | 21 |
| Coast | AT1 | 66.966 | 53.411 | 8 | 500 | 13.7 |
| | AT2 | 67.082 | 53.607 | 12 | 500 | 11 |
| | AT4 | 66.964 | 53.501 | 5.6 | 125 | 18 |
| | AT6 | 66.969 | 53.494 | 11.1 | 150 | 23 |
| | AT7 | 66.973 | 53.586 | 6.5 | 450 | 20 |
| | AT8 | 66.968 | 53.588 | 3.8 | 425 | 11.4 |

In July–August 2010, there was a distinct regional difference in dissolved oxygen concentrations with depth; this decreased across the metalimnion in inland lakes (Fig. 2, part d), increased by up to 13% across the metalimnion, before decreasing to ca. 8 mg L$^{-1}$ in ice sheet margin lakes and increased by

**TABLE 2**

**Summary of climate conditions of the three study locations: coast, inland, and ice sheet margin in South-West Greenland. Data are presented for 2010 and 2011. Mean 2000–2010 data are provided as long-term averages.**

| | Location | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Coast[*] | | | Inland[*] | | | Ice sheet margin[**] | | |
| | 2010 | 2011 | 2000–2012 | 2010 | 2011 | 2000–2012 | 2010 | 2011 | 2000–2012 |
| Annual precipitation (mm) | 663 | N/A | 410 | 166 | 112 | 183 | N/A | N/A | N/A |
| March Snow depth (mm) | N/A | 624 | N/A | N/A | 222 | N/A | N/A | 178 | N/A |
| July precipitation (mm) | 27 | N/A | 36 | 14 | 16 | 24 | N/A | 17 | N/A |
| Mean annual temperature (°C) | 1.4 | −2.1 | −1.5 | −0.2 | −5.6 | −3.8 | N/A | −5 | N/A |
| Mean March temperature (°C) | −6.4 | −11.3 | −10.2 | −12.9 | −17.8 | −14.8 | N/A | −20‡ | N/A |
| Mean July air temperature (°C) | 8.7 | 9.1 | 8.2 | 11.6 | 12.5 | 11.2 | N/A | 9 | N/A |

Data from [*]DMI (http://www.dmi.dk) and [**]PROMICE (http://www.promice.dk).
Data ‡supplemented by 2012 where 2010 and 2011 are not available.

**TABLE 3**

**Mean regional (coast, inland, ice sheet margin) limnology of study lakes sampled on three occasions spanning ice cover (July–August 2010, April–May 2011, June–July 2011). Data are given as means (n = 6) ± 1 SEM. See Methods section for full details of analyses undertaken.**

| | Location / Sampling Occasion | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Coast | | | Inland | | | Ice Sheet Margin | | |
| Parameter | Jul–Aug 2010 | April–May 2011 | Jun–Jul 2011 | Jul–Aug 2010 | April–May 2011 | Jun–Jul 2011 | Jul–Aug 2010 | April–May 2011 | Jun–Jul 2011 |
| $Z_{eu}$ (m) | 13.7 ± 1.7 | N/A | 16 | 14.2 ± 1.7 | 4.5 | 15.3 ± 1.5 | 16.7 ± 1.1 | 4.5 | 17.2 ± 1.7 |
| $Z_{mix}$ (m) | 6.8 ± 0.6 | N/A | N/A | 5.8 ± 0.3 | N/A | N/A | 7.6 ± 0.6 | N/A | N/A |
| Temperature (°C) | 12.7 ± 0.4 | 1.3 ± 0.2 | 5.2 ± 0.4 | 15.1 ± 0.2 | 2.4 ± 0.1 | 13.7 ± 0.7 | 14.2 ± 0.3 | 3.2 ± 0.2 | 7.8 ± 1.2 |
| $O_2$ (mg L$^{-1}$) | 10.6 ± 0.1 | 12.4 ± 0.6 | 12.0 ± 0.2 | 10.8 ± 0.2 | 8.4 ± 1.6 | 11.0 ± 0.1 | 10.6 ± 0.1 | 12.3 ± 0.4 | 11.1 ± 0.2 |
| pH | 7.2 ± 0.1 | 6.3 ± 0.3 | 6.6 ± 0.1 | 8.5 ± 0.2 | 7.4 ± 0.1 | 8.2 ± 0.1 | 7.8 ± 0.2 | 7.2 ± 0.1 | 7.5 ± 0.1 |
| Conductivity (µS cm$^{-1}$) | 38.8 ± 3.0 | 43.1 ± 3.6 | 31.7 ± 4.3 | 403.5 ± 55.5 | 414 ± 52.5 | 371 ± 49 | 103.7 ± 21.5 | 104.4 ± 21.3 | 106 ± 29 |
| Alkalinity (µeq L$^{-1}$) | 529 ± 86.5 | 517 ± 28 | 100 | 9057 ± 1114 | 5421 ± 1424 | 2593 ± 260 | 2650 ± 530 | 880 ± 214 | 758 ± 130 |
| TN (mg L$^{-1}$) | 0.3 ± 0.1 | 0.1 ± 0.04 | 0.1 ± 0.01 | 0.5 ± 0.09 | 1.5 ± 0.1 | 0.8 ± 0.1 | 0.6 ± 0.1 | 0.42 ± 0.1 | 0.3 ± 0.1 |
| NH$_4^+$ (µg L$^{-1}$) | 0.6 ± 0.4 | 9.7 ± 6.3 | 0.2 ± 0.2 | 1.3 ± 1.3 | 37.0 ± 11.5 | 5.2 ± 1.4 | 1.3 ± 1.1 | 12.8 ± 5.9 | 0.3 ± 0.3 |
| NO$_3^-$ (µg L$^{-1}$) | 0 | 56.7 ± 36.6 | 12.2 ± 4.6 | 0 | 2.9 ± 1.6 | 0 | 0 | 1.3 ± 0.04 | 0 |
| TP (µg L$^{-1}$) | 15.9 ± 6.1 | 8.5 ± 1.5 | N/A | 5.5 ± 2.3 | 11.9 ± 1.6 | 3.5 ± 1.6 | 10.7 ± 4.6 | 9.2 ± 1.7 | 7.2 ± 1.9 |
| SRP (µg L$^{-1}$) | 1.2 ± 0.8 | 3.0 ± 1.0 | 1.8 ± 0.5 | 3.4 ± 1.1 | 1.2 ± 1.2 | 1.9 ± 0.5 | 1.3 ± 0.6 | 3.9 ± 1.9 | 6.8 ± 2.4 |
| SiO$_3$ (mg L$^{-1}$) | 0.9 ± 0.1 | 1.5 ± 0.1 | 0.3 ± 0.1 | 0.3 ± 0.1 | 0.5 ± 0.2 | 0.4 ± 0.04 | 0.04 ± 0.04 | 0.2 ± 0.1 | 0.2 ± 0.1 |
| DOC (mg L$^{-1}$) | 1.5 ± 0.2 | 1.5 ± 0.1 | 3.6 ± 0.4 | 25.9 ± 2.6 | 34.4 ± 3.8 | 24.1 ± 2.3 | 5.8 ± 0.7 | 6.1 ± 1.1 | 6.1 ± 1.0 |
| K$^+$ (mg L$^{-1}$) | 1.2 ± 0.7 | 0.4 ± 0.02 | 0.4 ± 0.03 | 13.2 ± 2.0 | 16.0 ± 2.8 | 11.4 ± 1.8 | 3.2 ± 0.6 | 3.2 ± 0.7 | 2.7 ± 0.5 |
| SO$_4^{3-}$ (mg L$^{-1}$) | 6.5 ± 0.9 | 8.1 ± 1.9 | 5.1 ± 0.7 | 1.4 ± 0.2 | 1.6 ± 0.2 | 1.6 ± 0.3 | 4.0 ± 0.4 | 3.3 ± 0.4 | 4.0 ± 0.4 |
| Chl $a$ (µg L$^{-1}$) | 0.9 ± 0.3 | 0.3 ± 0.1 | 0.4 ± 0.1 | 0.9 ± 0.1 | 0.2 ± 0.1 | 0.3 ± 0.05 | 0.4 ± 0.04 | 0.4 ± 0.1 | 0.5 ± 0.3 |

ca. 20% across the metalimnion at the coast where concentrations remained high to the bottom of each lake (e.g., Fig. 2, part g).

There were marked regional differences in water chemistry (Fig. 3, Table 3). Inland lakes were characterized by high conductivity, pH, alkalinity, major ions, DOC, TN, and $NH_4^+$ (Fig. 3, Table 3), and compared with other sampling locations, inland lakes were the most diverse in terms of chemical composition. Coastal lake waters had lower major ion concentrations, alkalinity, pH, DOC, and conductivity, but much higher concentrations of $NO_3^-$, $SiO_3$, and $SO_4^{2-}$ (Fig. 3, Table 3). Very low $SiO_3$ concentrations ($<0.3$ mg $L^{-1}$) were recorded in ice sheet margin lakes; typically lakes in this location were chemically intermediate between the other locations but, in general, had more in common with coastal lakes (Fig. 3, Table 3). There were strong seasonal differences in water chemistry (Table 3). Under ice and immediately following ice melt, TN was up to 2.5 times higher in lakes inland compared with other locations (Table 3). Consistent with this, maximum $NH_4^+$ under ice was measured inland (Fig. 3, Table 3) and a decrease in $NH_4^+$ concentration was recorded in all study lakes following ice-melt (Table 3). In contrast, $NO_3^-$ concentration was ca. 20 times higher ($57 \pm 5$ μg $L^{-1}$) in lakes at the coast under ice; following ice melt, $NO_3^-$ was only detected in this location ($12 \pm 5$ μg $L^{-1}$) (Table 3). No $NO_3^-$ was measured in any lake during July–August 2010 and $NH_4^+$ concentrations remained low ($<1.3$ μg $L^{-1}$). In July–August 2010, TN was $<0.6$ mg $L^{-1}$ in all study lakes. Across the region, the seasonal pattern of P availability was variable (Table 3). Under ice, TP was highest in inland lakes ($11.9 \pm 1.6$ μg $L^{-1}$), while during ice-free conditions, TP was lowest in this region. A decrease in TP was observed in all locations following ice melt, and during June–July 2011, bioavailable SRP was highest in lakes at the ice sheet margin (Fig. 3, Table 3). Across all sampling occasions, dissolved organic C was greatest in inland lakes (ca. 22–38 mg $L^{-1}$), followed by ice sheet margin lakes (ca. 6 mg $L^{-1}$), and was lowest in lakes at the coast ($<4$ mg $L^{-1}$). The availability of dissolved Si was greatest in lakes at the coast under ice cover (1.5 mg $L^{-1}$) and at all times was lowest in ice sheet margin lakes (Table 3).

## Phytoplankton Production and Community Composition

Regression tree analysis of limnological variables from all seasons and regions showed temperature was the most significant predictor of variation in phytoplankton production ($R^2 = 0.518$, $F = 13.654$, df = 1, $P = 0.001$, Fig. 4, part a) with a positive correlation between temperature and Chl *a* (Fig. 4). The high temperature lake group ($>13.4$ °C) contained lakes sampled during open water conditions (inland lakes from June–July 2011, all locations during July–August 2010) and corresponded to the highest phytoplankton Chl *a* values (Figs. 4–5). Across all locations, maximum Chl *a* values were recorded during July–August 2010, in particular at lakes at the coast and inland where values were 2–3 times higher than at the ice sheet margin and significantly greater than recorded on other sampling occasions (Fig. 5, parts a–c). For all lakes, under high temperature conditions ($>13.4$ °C), TN was the second most significant predictor of Chl *a* ($R^2 = 0.840$, $F = 5.769$, df = 1, $P = 0.031$) and reflected phytoplankton production in inland lakes sampled during June–July 2011. Lakes grouped by temperature $<13.4$ °C (containing all samples taken under ice and some following ice melt) showed a secondary control over Chl *a* by pH ($R^2 = 0.386$, $F = 7.464$, df = 2, $P = 0.002$; Fig. 4, part a).

Seasonal predictors of phytoplankton Chl *a* were significant ($P = 0.05$) compared to regional predictors ($P = 0.671$) (Table 4). Regression tree analysis on all lakes on different sampling occasions revealed variable predictors of Chl *a*. Under ice, low surface water temperatures were associated with low Chl *a* ($>0.1$ μg $L^{-1}$), but at this time, $NO_3^-$ was the most significant variable selected to explain Chl *a* concentrations ($R^2 = 0.321$, $F = 11.397$, df = 2, $P = 0.001$; Fig. 4, part b). Lakes with $NO_3^- > 3.2$ μg $L^{-1}$ under ice included all sites sampled at the coast. Where no $NO_3^-$ was detected under ice, pH was the secondary significant control over phytoplankton Chl *a* ($R^2 = 0.279$, $F = 25.769$, df = 1, $P = 0.002$; Fig. 4, part b); this group included all lakes from the ice sheet margin (Fig. 4, part b). Following ice melt, Chl *a* increased in all regions (Fig. 4);
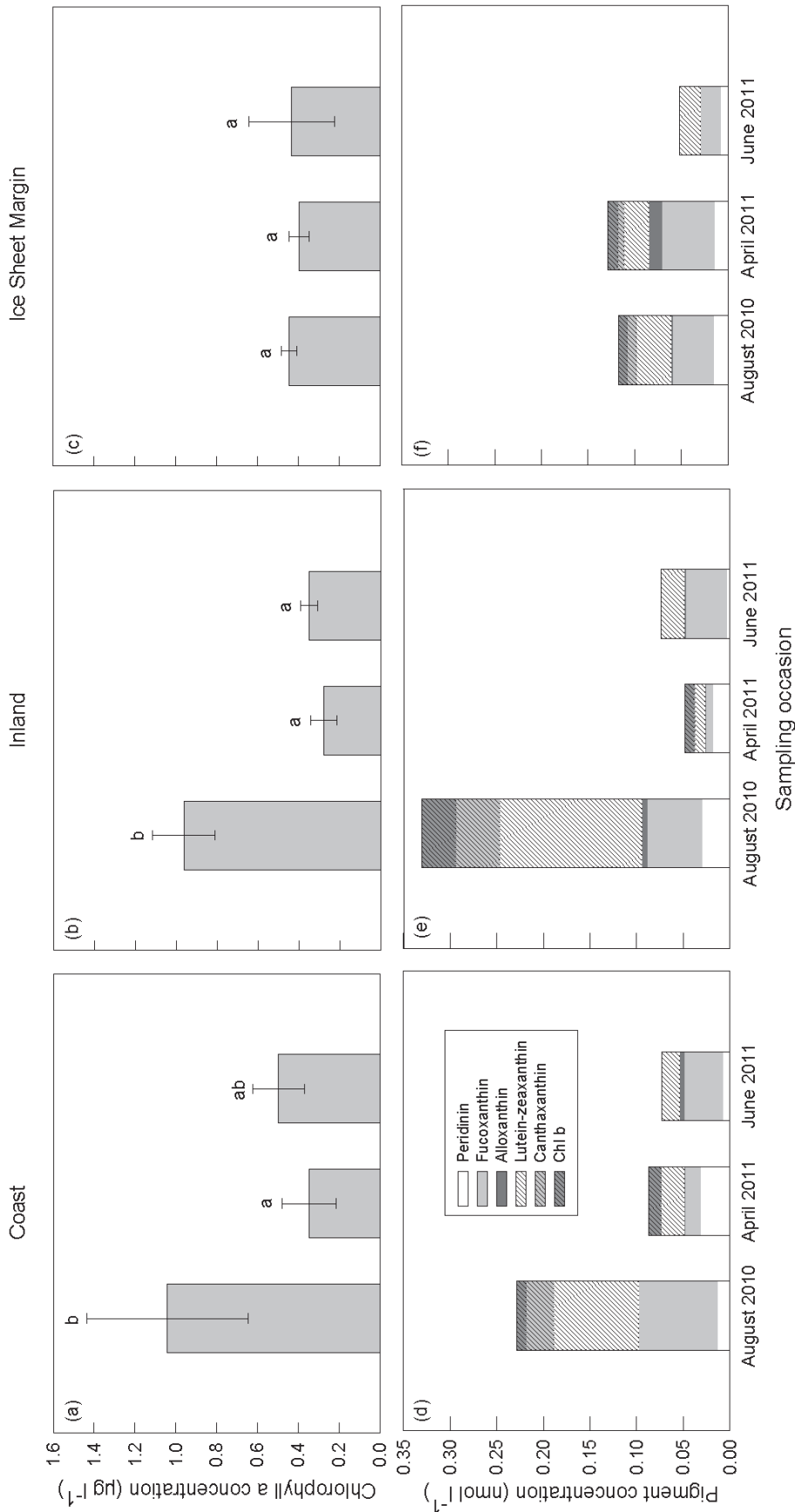
**FIGURE 5.** Mean regional phytoplankton Chl *a* and photosynthetic pigment concentrations from three study locations (coast, inland, and ice sheet margin) on three sampling occasions: July–August 2010 (open water), April–May 2011(under ice), and June–July 2011 (immediately following ice melt). Error bars represent means ($n$ = 5–6) ± 1 SEM, and bars assigned the same letter are not significantly different at the $P \leq 0.05$ level following post-hoc tests on two-way ANOVA. Algal pigment concentrations are shown in white (peridinin, dinoflagellates), light gray (fucoxanthin, siliceous algae), dark grey (alloxanthin, cryptophytes), white stripe (lutein-zeaxanthin, green algae, and cyanobacteria), light gray stripe (canthaxanthin, cyanobacteria), and dark gray stripe (Chl *b*, green algae).

**TABLE 4**

Results of two-way ANOVA to compare phytoplankton pigments measured in study lakes (n = 18) regionally among different study locations (coast, inland, ice sheet margin) and seasonally among sampling occasions (July–August 2010, April–May 2011, June–July 2011). See Methods section for full details of analyses undertaken.

| Parameter | Regionally | | | LSD Post Hoc / P-value | | | Seasonally | | | LSD Post Hoc / P-value | | | Regional–Seasonal |
| | df | F-ratio | P-value | Ice Sheet–Inland | Ice Sheet–Coast | Inland–Coast | df | F-ratio | P-value | Aug 10–Apr 11 | Aug 10–Jul 11 | Apr 11–Jun 11 | Interaction P-value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Chl $a$ | 2 | 0.402 | 0.671 | 0.584 | 0.344 | 0.674 | 2 | 6.026 | 0.005* | 0.001* | 0.007* | 0.479 | 0.230 |
| Total pigments | 2 | 0.808 | 0.452 | 0.168 | 0.433 | 0.553 | 2 | 0.456 | 0.016* | 0.005* | 0.008* | 0.873 | 0.006* |
| Peridinin | 2 | 0.385 | 0.683 | 0.813 | 0.469 | 0.604 | 2 | 2.294 | 0.112 | 0.785 | 0.100 | 0.063 | 0.431 |
| Fucoxanthin | 2 | 0.418 | 0.661 | 0.396 | 0.592 | 0.759 | 2 | 1.972 | 0.151 | 0.026* | 0.485 | 0.122 | 0.027* |
| Alloxanthin | 2 | 2.123 | 0.131 | 0.093 | 0.143 | 0.849 | 2 | 1.591 | 0.215 | 0.150 | 0.485 | 0.456 | 0.101 |
| Lutein–zeaxanthin | 2 | 2.759 | 0.074 | 0.034* | 0.909 | 0.042* | 2 | 9.407 | <0.001* | <0.001* | <0.001* | <0.001* | 0.001* |
| Canthaxanthin | 2 | 4.773 | 0.013* | 0.005* | 0.719 | 0.012* | 2 | 15.274 | <0.001* | <0.001* | <0.001* | 0.995 | 0.001* |
| Chl $b$ | 2 | 6.363 | 0.004* | 0.001* | 0.440 | 0.006* | 2 | 26.586 | <0.001* | <0.001* | <0.001* | 0.004* | <0.001* |

Values indicated by (*) are significant at P <0.05 level.

the greatest increase (20%) was recorded in lakes at the coast, and these changes were closely matched by changes in nutrient (TP and $NO_3^-$) availability (Table 3). During all ice-free conditions (June–July 2011 and July–August 2010), TP was selected by regression tree analysis as the most significant predictor of phytoplankton Chl $a$ ($R^2$ = 0.606, $F$ = 14.940, df = 2, $P$ < 0.001; Fig. 4, part c); TP was positively related to Chl $a$.

Across all sampling occasions, individual lakes clustered together regionally in terms of limnology (Fig. 3, Table 3) and production (Figs. 4–5). Regression tree analyses revealed different variable predictors of phytoplankton Chl $a$ for each location (Fig. 4, d–f). For lakes at the coast, $SiO_3$ was the best predictor selected to explain variation in Chl $a$ ($R^2$ = 0.575, $F$ = 13.467, df = 3, $P$ = 0.01; Fig. 4, part d). Low $SiO_3$ values corresponded to sampling post ice melt, contrasting with the highest $SiO_3$ availability recorded under ice. Inland lake regression tree analysis showed a split with temperature ($R^2$ = 0.519, $F$ = 46.550, df = 2, $P$ < 0.001; Fig. 4, part e). The higher temperature groups (>14.4 °C) contained lakes sampled during July–August 2010 (Fig. 4, Table 3), correlating to the highest recorded Chl $a$ values. For under ice and ice-melt sampling occasions in 2011 (<14.4 °C), the main branching factor for inland lakes was $NH_4^+$, with branch points of ≤7, 7–21, and >21 µg $L^{-1}$ (Fig. 4, part e). Higher $NH_4^+$ availability (>16 µg $L^{-1}$) corresponded to samples taken under ice with a negative relationship between $NH_4^+$ and phytoplankton Chl $a$. At lakes by the ice sheet margin, SRP was selected as the best predictor for Chl $a$ ($R^2$ = 0.451, $F$ = 124.912, df = 1, $P$ < 0.001; Fig. 4, part f) with a positive relationship between this parameter and phytoplankton biomass. The branch point at 7.45 µg $L^{-1}$ accounted for a subset of three lake samples during June–July 2011 sampling (Fig. 4, part f) and a secondary control by $SO_4^{2-}$ was revealed to explain further variation in Chl $a$ ($R^2$ = 0.361, $F$ = 15.167, df = 1, $P$ = 0.002) across all seasons (Fig. 4, part f).

Seasonal and regional variation in phytoplankton pigment concentrations typically matched patterns in Chl $a$ (Fig. 5). Seasonal differences were more significant than regional differences (Table 4). A decrease in peridinin (dinoflagellates) by 42%–86% in all lakes was recorded following ice melt; values measured in July–August 2010 were generally comparable to those recorded under ice (0.01–0.03

nmol L$^{-1}$, Fig. 5, parts d–f). Under ice, maximum fucoxanthin (siliceous algae) was recorded in ice sheet margin lakes (0.06 ± 0.02 nmol L$^{-1}$); this decreased markedly following ice melt (Fig. 5, part f). In contrast, fucoxanthin increased markedly in coastal and inland lakes following ice melt (Fig. 5, parts d–e) and in July–August 2010, it accounted for 20%–40% total pigment concentration in all lakes (Fig. 5, parts d–f). Lutein-zeaxanthin (chlorophytes and cyanobacteria) differed significantly among sampling occasions ($P < 0.001$, Table 4) and accounted for a large proportion of total pigment concentration at all times (22%–46%), in particular during July–August 2010 (Fig. 5, parts d–f). Chlorophyll $b$ (chlorophytes) differed significantly seasonally ($P < 0.001$, Table 4) as maximum values were recorded in July–August 2010, with low values under ice and none detected following ice-melt (Fig. 4, parts d–f). Canthaxanthin (cyanobacteria) varied significantly seasonally ($P < 0.001$) and regionally ($P = 0.013$); the highest concentrations were recorded in inland lakes (0.05 ± 0.01 nmol L$^{-1}$), with seasonal maxima in all locations during July–August 2010 (Fig. 5, parts d–f, Table 4).

## Discussion

### Controls over Regional and Seasonal Phytoplankton Production

Variation in climate along a small geographic area in SW Greenland from the inland ice sheet margin to coast results in marked differences in the biogeochemical structure and function of lakes. Study lakes all exhibited strong seasonality, characteristic of dimictic Arctic lakes which freeze annually and thermally stratify during summer months (Vincent et al., 2008). Phytoplankton production was most tightly linked to seasonal changes in physical and chemical limnology, in particular, a shift from $NO_3^-$-N to TP linked production between ice-cover and ice-free conditions. However, underlying strong seasonal trends, predictors of phytoplankton production varied regionally and were unique to groups of lakes in three discrete locations at the ice sheet margin, inland, and coast.

On a regional scale, phytoplankton production was principally regulated by temperature, with a positive relationship between this parameter and Chl $a$. However, this analysis appears to be driven largely by strong seasonal fluctuations in temperature associated with winter ice cover and open water conditions. After temperature, nutrients (TN) and chemical conditions (pH) were found to be the strongest correlates with phytoplankton production in SW Greenland lakes. This is consistent with other Arctic lakes, where phytoplankton biomass is driven by strong seasonality patterns in ice cover, temperature, and nutrient availability (Medeiros et al., 2012; Weyhenmeyer et al., 2013).

Under ice cover, $NO_3^-$ availability was the strongest predictor of phytoplankton production, although this relationship was negative. During winter, $NO_3^-$ is recycled within lakes and supplied from catchment melt and run-off via fissures and cracks in the ice (Forsström et al., 2007). However, in all lakes, production was supported only where sufficient light penetrated snow and ice cover and density currents mixed water, remobilizing nutrients (Lotter and Bigler, 2000). Although the highest $NO_3^-$ availability was recorded in lakes at the coast under ice (due to a regional atmospheric N-$NO_3^-$ deposition gradient), this corresponded to lowest (although not significant) regional phytoplankton Chl $a$ values. Despite high bioavailable N supply, deep winter snowpack accumulation is likely to restrict phototrophic uptake by plankton in lakes at the coast as a result of light limitation. Although limited measurements of PAR availability under ice were taken, regression tree analyses included a value of snow depth as a proxy for light availability under ice, but this was secondary to strong regional nutrient ($NO_3^-$) and chemical (pH) gradients.

During ice-free conditions, TP was the best predictor of phytoplankton production in SW Greenland lakes. The shift from $NO_3^-$-N to P-control between ice-cover and ice-free conditions reflects differences in the delivery and availability of these essential macronutrients. Whereas $NO_3^-$ is delivered via wet deposition and subsurface flow (maximal during winter and spring snow thaw), P is supplied primarily via dry deposition processes. In SW Greenland, this is by eolian transport and deposition of glacially derived dust from outwash plains (Nielsen, 2010; Bullard and Austin, 2011). In ultraoligotrophic Arctic lakes, phytoplankton growth is tightly controlled by N and P availability (Lev-

ine and Whalen, 2001, Symons et al., 2012). During open water conditions, the positive relationship between TP and Chl *a* suggests that phytoplankton production might be growth-limited by P availability. Brutemark et al. (2006) suggested that phytoplankton growth in lakes in SW Greenland was limited by P following significant increase in Chl *a* after P enrichment. In the current study, the majority of lakes recorded high atomic TN:TP values (28–600), exceeding the Redfield (1958) ratio of 16:1. However, it is important to consider that variation in these ratio scores reflects regional differences in the form and availability of both nutrients, N and P, and that phytoplankton nutrient limitation may vary across the region, as demonstrated for benthic algae (Hogan et al., 2014).

Underlying broad-scale seasonal trends, controls over phytoplankton production were unique to each location. Phytoplankton production in lakes at the ice sheet margin, inland, and coast was found to be controlled by SRP, temperature, and $SiO_3$, respectively, with positive relationships between these parameters and Chl *a*. The regional climate gradient has a marked effect on nutrient form, delivery, and availability in each location. At the coast, higher precipitation results in greater delivery of nutrients (including Si) weathered from the catchment compared to other locations where low precipitation results in restricted hydrological connectivity and limited wet nutrient inputs. Higher Si availability in lakes at the coast supports the growth of siliceous algae. Siliceous algae benefit from high accumulation of $SiO_3$ under ice cover, utilizing this resource to support growth into the open water period. Fucoxanthin concentration was greatest in lakes at the coast during open water conditions suggesting increased abundance of diatoms and chrysophytes. High precipitation combined with coastal fog banks and dew deposits increases delivery of macronutrients (N, P, and Si) to lakes at the coast, supporting phytoplankton growth throughout the open water season and accounting for high production recorded in this location in late summer, despite later ice melt dates.

For inland lakes, phytoplankton Chl *a* was controlled by temperature, followed by $NH_4^+$ availability. Lakes inland are exposed to a warm continental climate and are exposed to the largest fluctuations in temperature over an annual cycle. Although in-

creased water temperature is associated with higher phytoplankton production in high latitude lakes (Vincent et al., 2008), there is still a requirement for nutrient addition to support growth. For inland lakes, this appears to be controlled by N as bioavailable $NH_4^+$; although this is not a straightforward positive relationship. Maximum $NH_4^+$ was recorded under ice cover in inland lakes, which might be associated with subsurface delivery (R. Northington, personal communication) and high organic matter mineralization (Anderson and Stedmon, 2007). Inorganic N as $NH_4^+$ is often preferentially taken up by phytoplankton due to lower energy costs associated with diffusive (rather than active) transport across the electrochemical cell membrane gradient (Dortch, 1990).

At the ice sheet margin, SRP was the best predictor of Chl *a*. Water with elevated SRP supported much higher phytoplankton Chl *a*, supporting the suggestion that lakes in this region are nutrient limited by P. Phosphorus is delivered to lakes close to the ice sheet margin principally via eolian deposition of glacially derived dust. The dust supplies organically bound nutrients, which require enzymatic hydrolysis by bacteria and phytoplankton (Reche et al., 2009) as well as bioavailable nutrients, including SRP which rapidly leach from particles once in water. Desorption of SRP from dust has been shown to promote phytoplankton and bacterial growth in mountain lakes (Pulido-Villena et al., 2008). Nonetheless, regionally restricted Chl *a* recorded in lakes at the ice sheet margin during summer most likely reflects ultraoligotrophic conditions, with scarce bioavailable nutrients. Nutrient inputs from dust deposits will depend on local weather (e.g., wind speed and direction) patterns and is likely to be sporadic. In addition, organic nutrient inputs associated with dust require high energy investment in their acquisition (via enzyme activity), which may not be physiologically beneficial for phytoplankton in such a low nutrient environment.

Regional variation in climate and associated ice phenology had no effect on phytoplankton production. In July–August 2010, phytoplankton production was highest in lakes at the coast and inland, despite these locations representing end-members of the ice-melt gradient. Interpretations from recent paleo-records commonly suggest that algal production in Arctic lakes is related to the timing of ice-

melt and length of the open-water period (Sorvari et al., 2002; Smol et al., 2005). However, this interpretation is often drawn from shifts in algal community composition (e.g., increases in % abundance of planktonic diatoms), rather than direct evidence of changes in algal production. It is important to consider that community turnover and production are two distinct algal responses to environmental stressors and they can respond in different manners to different external controls (Weyhenmeyer et al., 2013). To date, little evidence exists to unequivocally link extended ice-free period and temperature alone with increased lake production, either in the paleo-record or in contemporary limnological studies. As our study shows, lengthening the open water period is unlikely to support increased phytoplankton production and/or biomass alone unless there is a marked shift to heterotrophic production or a concurrent increase in nutrient supply (Kling et al., 1990; Weyhenmeyer et al., 2013).

We cannot discount interannual variation in regional climate for the higher phytoplankton Chl *a* values recorded in coastal and inland lakes during the open water periods in 2010 versus 2011. Statistical analysis (*t*-tests) revealed no significant difference in temperature between study years for either spring (March–May: $P > 0.31$) or summer (June–August, $P > 0.64$) months at both coast and inland locations. However, we cannot discount that higher spring temperatures in 2010 may have resulted in earlier onset of snow and ice thaw, potentially increasing nutrient inputs into lakes at this time while extending the open water period and raising surface water temperatures. Yet, potentially earlier ice melt would extend the period of open water conditions and, as shown in the current study, would require sustained and/or increased nutrient additions to maintain or promote phytoplankton production measured late in the summer season. In addition, should interannual differences in environmental conditions (e.g., temperature–associated warming) be acting to override local signals and control phytoplankton production during this time, we might expect this to act across the whole region, stimulating production in all three locations; yet no significant difference in Chl *a* values were reported for lakes at the ice sheet margin between any sampling occasion during 2010–2011. Further, unpublished survey data from late July 1997 (N. J.

Anderson, unpublished) reports mean surface Chl *a* from freshwater inland lakes ($n = 17$) as $1.8 \pm 0.4$ µg L$^{-1}$ consistent with late summer values for 2010 reported in the current study ($1 \pm 0.1$ µg L$^{-1}$). We also cannot account for differences in sampling strategy in June–July 2011 when considering seasonal variability in coastal lakes. However, no significant differences in phytoplankton community composition were reported at the coast, and no significant regional differences were recorded across the three locations in June–July 2011.

## Variation in Phytoplankton Community Composition

Photosynthetic pigment assemblages were comparable in all locations, indicating similarities in phytoplankton community composition and succession across the region. Although variation in the timing of ice melt has been shown to influence phytoplankton community structure and seasonal succession patterns (Weyhenmeyer et al., 2013) as a result of group-specific differences in nutrient acquisition strategies and growth rates, this is not a uniform lake response. Adrian et al. (1999) and De Senerpont Domis et al. (2007) also reported no effect of ice duration on the seasonal succession pattern of lake phytoplankton. The under-ice phytoplankton community principally comprised dinoflagellates (peridinin), siliceous algae (fucoxanthin), cryptophytes (alloxanthin), chlorophytes, and cyanobacteria (lutein-zeaxanthin and Chl *b*). In many high latitude lakes, the algal community under ice is dominated by small cyanobacteria and chlorophytes that contribute to the picophytoplankton community (0.2–2 µm) (Hobbie and Laybourn-Parry, 2008). This group of phytoplankton are highly efficient at light interception and nutrient uptake (Peltomaa and Ojala, 2012), although despite their numerical importance, their small size probably contributes lower biomass than other algal groups. Flagellated chlorophytes can gain a competitive advantage under conditions of low light and turbulence by actively migrating through the water column to maximize both light and nutrient interception (Veillette et al., 2010). Siliceous algae and dinoflagellates are strong competitors for nutrients (especially P) in low water temperatures and commonly dominate algal communities under ice

cover (Killi et al., 2009;Vehmaa and Salonen, 2009). Many chrysophytes and cryptophytes are phagotrophic, heterotrophic, or facultatively mixotrophic (Laybourn-Parry and Marshall, 2003), allowing them to acquire nutrients, including carbon from dissolved organic matter (DOM) uptake, reducing energy demands of photosynthesis under conditions of low light and bioavailable nutrient supply (Laybourn-Parry et al., 2005; Laybourn-Parry, 2009).

Increased phytoplankton production following ice melt was associated with increased light availability, warmer surface water temperatures, and a concomitant decrease in inorganic N availability, used by phytoplankton to support growth (Forsström et al., 2005;Vehmaa and Salonen, 2009). Following ice melt, fucoxanthin and lutein–zeaxanthin accounted for the majority of measured pigment concentration (more siliceous algae, dinoflagellates, and chlorophytes), consistent with observations post ice-melt in previous surveys across SW Greenland (Brutemark et al., 2006) and other lake ecosystems (Villar-Argaiz et al., 2001; Blank et al., 2009). Heavy silicified algae are maintained in the euphotic zone during spring mixing (Sommer, 1989), while motile chlorophytes retain a competitive advantage by actively moving into areas of optimal light and nutrient supply. Peridinin decreased by up to 80% in all lakes following ice melt, evidencing a marked decline in dinoflagellates which might be encysting at this time (Rengefors and Meyer, 1998).

All lakes in late summer were dominated by chlorophytes (lutein-zeaxanthin and Chl $b$), siliceous algae, dinoflagellates (fucoxanthin), and cyanobacteria (canthaxanthin). Lower lutein-zeaxanthin in lakes at the ice sheet margin suggests reduced abundance of chlorophytes and cyanophytes and may reflect low nutrient availability, most likely due to rapid depletion of bioavailable nutrient forms following ice melt and scarce, periodic replacement inputs throughout the open water season from wet and dry sources.The large proportion of canthaxanthin (cyanobacteria) in all lakes in July–August 2010 is typical of the seasonal phytoplankton succession pattern in mid- to late summer in high latitude lakes as nutrient depletion is enhanced, as many species in this group can undertake $N_2$-fixation (McKnight et al., 1990).

In July–August 2010, dissolved oxygen profiles through the water column revealed that algal pro-

duction was not restricted (or necessary maximal) in the surface waters. Lakes at the ice sheet margin showed a peak in dissolved oxygen around the metalimnion. A deep water algal bloom is a characteristic feature of many transparent, oligotrophic high latitude lakes (Lizotte, 2008) where algae that have sedimented out of the mixed zone still remain within the euphotic zone and have a source of nutrients associated with recycling in the metalimnion. Oxygen profiles at the coast during summer suggested high benthic standing stocks, in agreement with many oligotrophic polar lakes where high benthic production can dominate total algal production (Vadeboncoeur et al., 2003; Rautio et al., 2011). Further investigation at multiple sampling depths is required to gain a more complete understanding of biological, chemical, and physical properties and their interactions in study lakes, both regionally and seasonally.

## CONCLUSION

From the current study, it is evident that controls over phytoplankton production can differ markedly across a small geographic area. This has large implications when interpreting aquatic ecological change from paleo-records, which are often taken from a single site in remote lakes across the Arctic. Given the high degree of variation in local controls over phytoplankton production, consideration of site-specific, local-scale impacts on aquatic ecology must be taken into account where interpretations are up-scaled to broad conclusions on regional or pan-Arctic levels.

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