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LETTER

Stable isotopes reveal independent carbon pools across an Arctic hydro-climatic gradient: Implications for the fate of carbon in warmer and drier conditions

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Scientific Significance Statement

Arctic lakes in dry regions that have weak hydrological connectivity to their watersheds accumulate large amounts of carbon (C) as dissolved organic matter (DOM), exhibiting both autochthonous and allochthonous characteristics. The balance between these characteristics determines the CO_2 release from lakes. This study provides evidence that trends toward a warmer and drier Arctic obscures the relative balance of autochthonous and allochthonous DOM sources by increasing the importance of autochthonous macrophytes as sources of DOM in otherwise nutrient-poor lakes. In contrast, C stored in sediments of Arctic lakes mostly originates from autochthonous algal sources.

Abstract

Arctic lakes are poised for substantial changes to their carbon (C) cycles in the near future. Autochthonous processes in lakes which consume inorganic C and create biomass that can be sequestered in sediments are accompanied by allochthonous inputs of organic matter from the surrounding watershed. Both C sources can be mineralized and degassed as CO_2, but also become recalcitrant and accumulate in pelagic waters. Using stable carbon isotope (δ^{13}C) values and elemental ratios as geochemical proxies, we investigated diverse organic matter sources to lakes located across a hydro-climatic gradient in Southwest Greenland. Particulate organic matter (POM) and sediments were clearly of autochthonous algal origin, while dissolved organic matter (DOM) was a mix between autochthonous macrophytes and allochthonous watershed sources. Our results imply that a warmer and drier Arctic will lead to decoupled C pools: a water column dominated by increasingly autochthonous, macrophytic DOM, and sediments dominated by autochthonous algal POM.

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Understanding organic matter (OM) sources and cycling in lakes is important for ecosystem functioning as well as the degree of carbon (C) processing and its fate. Autochthony describes conditions under which in-lake formation of OM via primary production dominates. In contrast, allochthony describes conditions in which external inputs of nutrients and OM dominate. The relative balance within this "auto-allochthony" paradigm affects the fate and source-sink status of C in lakes (Wetzel 1992). Autochthonous lakes are net C sinks with the potential to sequester biologically-fixed C in lake sediments (Anderson et al. 2019). Allochthonous lakes mineralize and release large quantities of their OM input as CO_2 via photochemical and microbial degradation (Vähätalo and Wetzel 2008; Guillemette et al. 2016), but also may contribute to C burial in lakes via flocculation (Wachenfeldt and Tranvik 2008). In contrast to hydrologically connected systems in the boreal zone, sediment records from some arctic lakes suggest an increase in autochthonous C burial (Sobek et al. 2014; Anderson et al. 2019). The allochthony paradigm is essentially derived from studies of lake-watersheds that are hydrologically well connected, that is, boreal and wet, tundra environments (Kling et al. 1992). Climate change will, however, alter these connections and modulate the future fate of C in boreal to arctic regions.

Arctic lake ecosystems are poised to undergo rapid climatic change in the near future, both from changes in temperature and precipitation (Bring et al. 2016). The Arctic stores about 2 Pg of organic C in permafrost; this climate change will involve altered lateral transfers of OM from their watersheds (landscape) into lakes, leading to possible enhancement of terrestrial C processing in the water column and C storage in sediments (Schuur et al. 2015; Wauthy et al. 2018). Furthermore, as climate warms, an increase in vegetation development ("Arctic greening") occurs as biomes shift northward and expand locally, possibly also increasing the supply of this OM to lakes, strengthening lateral transfers across the terrestrial-aquatic interface (Elmendorf et al. 2012; McGowan et al. 2018; Tank et al. 2018). The source and reactivity of OM is important: terrestrial DOM supplies much of the energy to lake ecosystems (Pace et al. 2004). However, the production, mobilization, and transfer of this OM under warming conditions are unclear (Anderson and Stedmon 2007; Saros et al. 2015).

We compiled carbon stable isotope ($\delta^{13}C$) and molecular carbon to nitrogen ratio (C:N) values from terrestrial and aquatic environments covering a large limnological-climate-vegetation gradient in the Kangerlussuaq area of SW Greenland, an area with clearly defined regional climates (mean summer air temperature, m.s.t.; and mean annual precipitation, m.a.p., Table S1) that are representative of conditions found elsewhere across the Arctic (Mernild et al. 2015). We used these data to test the hypothesis that drier conditions in SW Greenland have influenced where allochthonous and autochthonous C sources are stored within these lakes. Our results highlight the need for the broadening (redefining) of the lake auto-allochthony paradigm in consideration of lake C cycling in a drier Arctic.

Materials and methods

$\delta^{13}C$ and C:N ratio data were compiled from a variety of lakes and their watersheds situated across SW Greenland, which have been sampled from 2001 through 2017 (Anderson et al. 2017; Table S1). The lakes have been grouped together along a hydro-climatic gradient of mean summer temperatures and precipitation in this study to determine differences in C pools: a Coastal lake group in a cool-wet climate (8°C, 410 mm); a Central lake group in a warm-dry climate (11°C, 183 mm); and an Ice margin lake group in a cool-dry climate (8°C, 269 mm) (Fig. S1 and Table S2) (Osburn et al. 2017). Stable oxygen ($\delta^{18}O$) isotope measurements on water from the lakes showed that the lower precipitation lake groups fall along an evaporative trend, which implies decreasing hydrological connectivity and longer residence times (Fig. S2; Leng and Anderson 2003).

POC samples (seston) were collected in 2011 and 2012 from a number of coastal lakes (Whiteford et al. 2016). Water samples were taken with a van Dorn sampler at 1-m water depth and filtered through baked 0.7 μm GFF filters (Whatman) and kept frozen until being freeze dried. Terrestrial plants and soils were air dried after collection. For the $\delta^{13}C$ analyses, plants were rinsed in 5% HCl to remove any calcite and freezer milled to a fine powder. The soils were treated in a similar fashion to the lake sediments (see below).

Stable carbon isotope values and C:N values on solids were measured in multiple laboratories from 2009 to 2014, however comparable methodologies for solid samples using elemental analysis (EA) coupled to isotope ratio mass spectrometers (IRMS) were conducted. Solid sediment samples measured via EA-IRMS were calibrated with acetanilide for concentrations and normalized against IAEA and NIST-traceable stable isotope standards for $\delta^{13}C$ values (Anderson et al. 2018*b*).

Soils and lake sediment samples were treated with 5% HCl to remove carbonate. The sediment was measured for %TOC and %TN concentrations (from which the C:N ratio was calculated) using a Carlo Erba 1500 elemental analyzer, calibrated through an internal acetanilide standard. Isotopic analyses were performed on the same instrument using an on-line VG Triple Trap and Optima dual-inlet IRMS. $\delta^{13}C$ values (‰) were calculated relative to the VPDB scale using a within-run laboratory standard (cellulose, Sigma Chemical prod. no. C-6413) calibrated against NBS 19 and NBS 22. Replicate analysis of sample material gave a precision of $\pm <0.1$‰ (1 SD). For lake particulate OM (POM), these values were measured on a Thermo 1112 Flash elemental analyzer coupled in continuous flow to a Thermo Delta V+ IRMS. The %OC and %TN values were calibrated an internal acetanilide standard, while $\delta^{13}C$ values were calculated relative to the VPDB scale using IAEA-C6, IAEA-C8, and IAEA-600 as within-run standards. Replicate analysis of standard material gave a precision of ± 0.3‰.

Isotope values were adjusted for the Suess effect, which is the increasingly depleted $\delta^{13}C$ value of atmospheric CO_2 (Verburg 2007).

DOC stable C isotope ratios were measured on an OI Analytical 1030D TOC analyzer coupled in continuous flow to the Delta V+ IRMS (Osburn and St-Jean 2007). Prior to analysis samples were acidified with 85% H_3PO_4 to pH 2 and sparged for 10 min with ultra-high purity argon to remove inorganic carbon (as CO_2). DOC concentrations were calibrated each analytical day with prepared solutions of caffeine, and $\delta^{13}C$ values were calibrated VPDB scale with prepared solutions from IAEA-CH6 ($\delta^{13}C$ = −10.8‰) and IAEA-600 ($\delta^{13}C$ = −27.77‰). Error on DOC concentrations was < 3% and precision on $\delta^{13}C$-DOC values was ± 0.2‰ ($N = 23$). C:N values for DOM were estimated as from total N concentrations minus dissolved inorganic nitrogen (DIN) concentrations on samples collected in 2013 (methods detailed in Whiteford et al. 2016). Reproducibility on TN measurements was ± 0.1 mg L^{-1} and ± 0.01 mg L^{-1} on DIN.

We had an uneven number of samples for each pool within each lake group across the $\delta^{13}C$ and C:N data sets; furthermore, data for each lake group were not normally distributed. Therefore, we used a Monte Carlo approach to generate an equal number of samples constrained by the mean and standard deviation of each OM pool. We chose $N = 45$ to

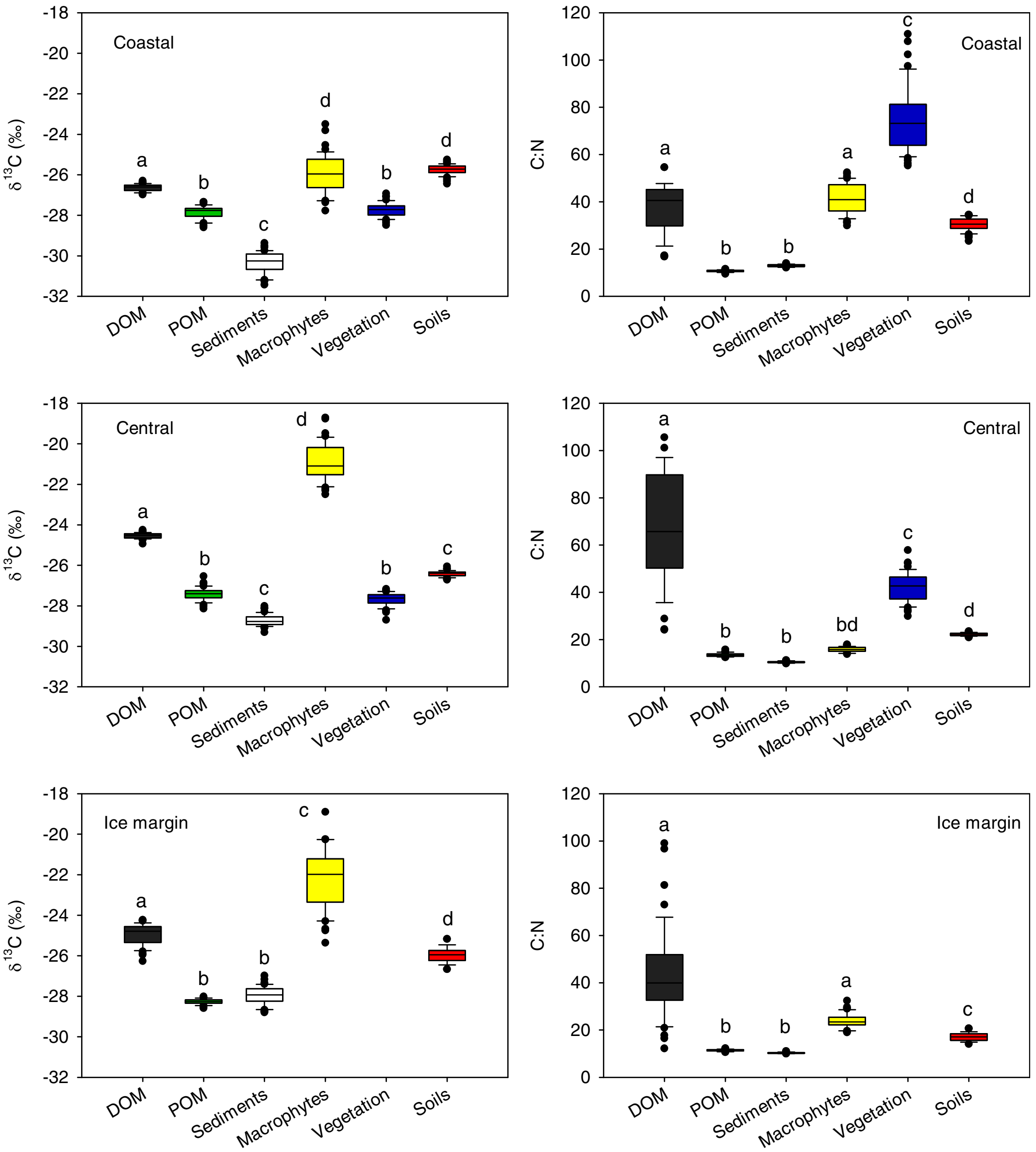

Fig. 1. Boxplots of $\delta^{13}C$ values (left panels) and C:N ratios (right panels). Boxes represent interquartile range, horizontal line within each box is the median, and bars represent the 95% range. Solid circles are outliers. Significant differences between sources are indicated as different letters above error bars ($p < 0.05$, Bonferroni post hoc test).

match the largest number of measurements we had for any one pool, which was macrophytes from the Central lake group (Table S2). By taking this approach, we could then confirm data were normally distributed then proceed with statistical tests of significance between groups, correlation, and regression. Linear mixing models based on stable isotope and elemental ratio values were used to determine contributions of vegetation, soil, and macrophyte sources to lake DOM and contributions of POM, soil, and vegetation sources to lake sediments (Table S2; Phillips et al. 2005). Two-way ANOVA (ANOVA) tests were used on δ^{13}C values and C:N ratios separately to determine significant differences in OM pools among the lakes grouped by precipitation regime. Monte Carlo resampling, statistical tests, and linear mixing models were conducted in Matlab v. 2018a (Mathworks).

Results

Dry conditions across the hydro-climatic gradient of SW Greenland (Fig. S2) created in the lakes a large and variable C pool of DOM derived from allochthonous terrestrial and autochthonous macrophyte sources, while autochthonous algal sources were overwhelmingly sequestered in lake sediments, irrespective of the hydro-climatic gradient (Fig. 1 and Table S2). δ^{13}C-DOM values of the higher precipitation Coastal lakes were depleted by about 2‰ relative to the lower precipitation Central and Ice margin lake groups; the latter two groups were not significantly different ($p > 0.05$) (Table S2 and Fig. 1; Osburn et al. 2017). Soils, terrestrial vegetation, POM, and lake sediments all had mean δ^{13}C values between −25‰ and −30‰, which were consistent with values reported on similar sources collected from and around ponds in the Kangerlussuaq area (Mariash et al. 2018). Macrophyte δ^{13}C values showed the widest variability (ranging from −33‰ to −9‰). Notably, sediment δ^{13}C values were most depleted, and overlapped with values for POM (Fig. 1). Mean δ^{13}C values of DOM were enriched by 1‰ to 3‰ relative to POM ($p = 0.002$; Table S2).

Values of C:N spanned the range typical for lacustrine OM sources (Lamb et al. 2006; Fig. 1 and Table S2). By and large, DOM was depleted in N relative to other C pools except terrestrial vegetation. The Central lake group, having the lowest precipitation, also had the highest mean C:N ratio (66) compared to the cool-dry Ice margin lake group (42) and the cool-wet coastal lake group (36). Mean C:N ratios for both soil and macrophyte sources exhibited an increase value with increasing precipitation (Spearman's rho = 0.52; $p < 0.001$ and Pearson's $r = 0.52$; $p < 0.001$, respectively; Fig. 2).

Two-way ANOVA results revealed OM characteristics in the lakes were influenced by sources and precipitation regime (Tables S3 and S4). There was a statistically significant difference in δ^{13}C value based on source of OM: $F_{5,296} = 20.13$, $p < 0.0001$, as well as on lake group, which varied by precipitation: $F_{2,296} = 3.88$, $p = 0.022$ (Table S3). C:N ratios exhibited similar distinctions (Table S4). Each source of OM was significantly different with respect to mean C:N ratios of the lake groups across the hydro-climatic gradient. For both two-way ANOVA tests, interaction between the OM source and lake group also was significant (Tables S3 and S4). Thus, the differences in OM quality in the lakes depended both on the sources of OM to them and the regional climatic patterns where they are located.

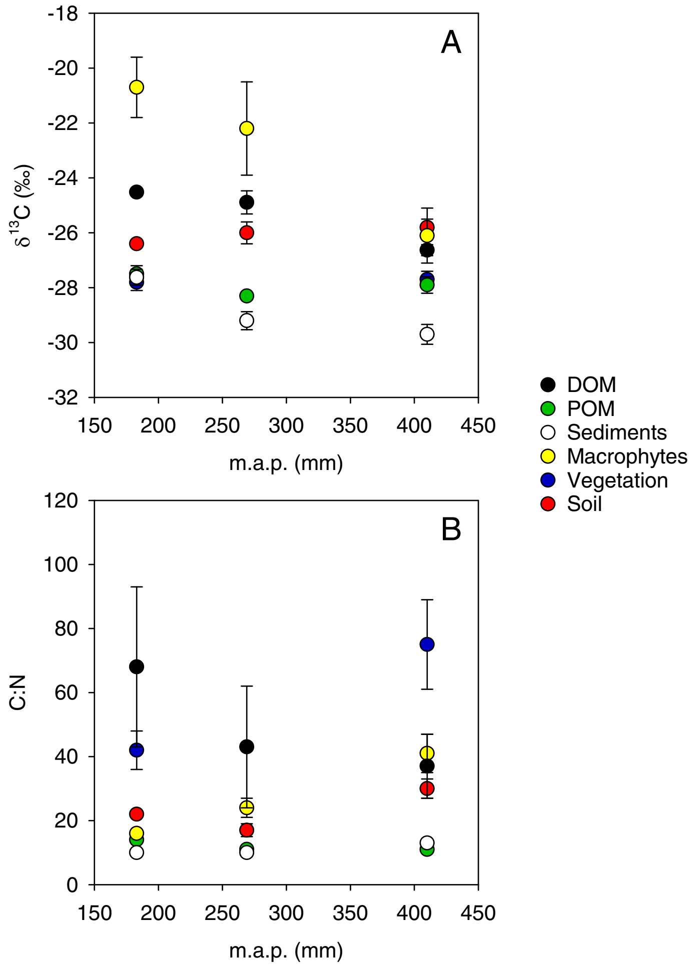

Fig. 2. Plots of mean δ^{13}C ratios (top) and mean C:N ratios (bottom) against the mean annual precipitation for the three lake regions in SW Greenland. Error bars denote standard deviation over range of values.

Dissolved inorganic carbon (DIC) δ^{13}C values were available for the lakes near Kellyville from 2001 and 2009 only. These values provide context for interpreting δ^{13}C values from primary production. The mean δ^{13}C-DIC was −1.6‰, while the minimum was −8.7‰ and the maximum was +3.4‰. DIC concentrations were recalculated from water chemistry data (Whiteford et al. 2016).

Linear mixing models revealed distinct sources of OM to DOM and to sediments, respectively (Table 1). In order to estimate the relative importance of these C sources in DOM and

Table 1. Results from mixing model of organic matter sources to DOM and sediments in SW Greenland lakes, by group. Sources for DOM were vegetation, soil, and macrophytes. Sources for sediments were vegetation, soil, and POM.

		Fraction of source (mean±SD)		
Lake group	**DOM**	**Vegetation**	**Soil**	**Macrophytes**
Coastal		0.43±0.10	0.42±0.21	0.15±0.23
Central		0.52±0.09	0.03±0.10	0.45±0.03
Ice margin		0.45±0.17	0.09±0.21	0.46±0.11
	Sediment	**Vegetation**	**Soil**	**POM**
Coastal		0.21±0.04	0	0.88±0.04
Central		0	0	1.0±0.1
Ice margin		0	0.14±0.13	0.86±0.14

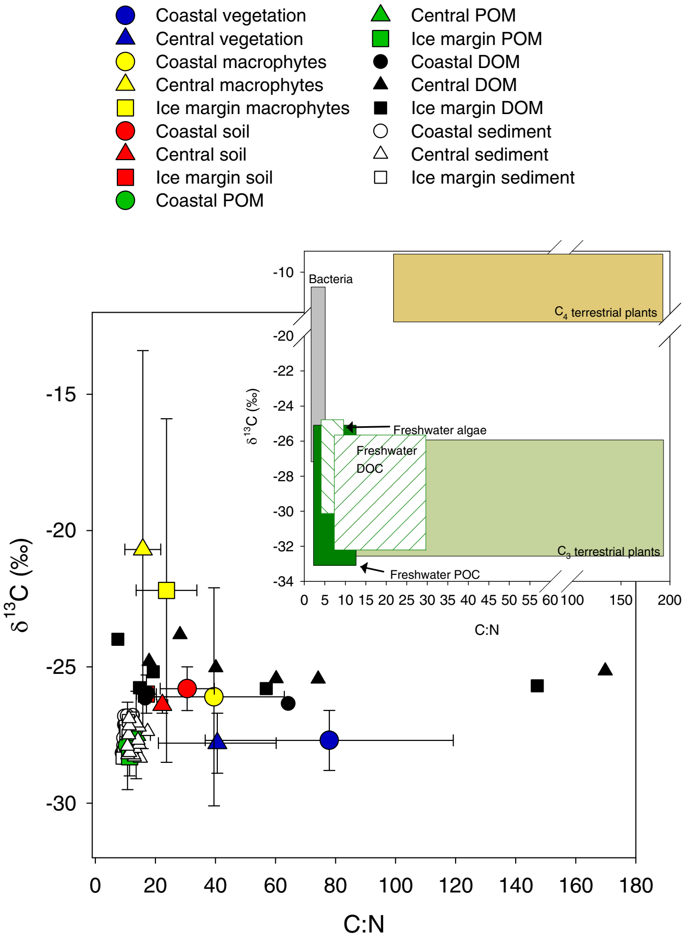

Fig. 3. Biplot of C:N ratios and $\delta^{13}C$ values for organic matter pools in SW Greenland lakes. Single markers are means and error bars represent standard deviations. Individual lake data are shown for DOM and sediments. POM values are mostly obscured by the range of sediment observations. Inset figure shows regions of organic matter sources and is redrawn from Lamb et al. (2006).

in sediments, a mixing model was developed based on mean $\delta^{13}C$ values and the inverse of C:N ratios (C:N^{-1} or N:C ratios), which more accurately trace the contribution of terrigenous C than do C:N ratios (Perdue and Koprivnjak 2007; Table S5 and Supporting Information). Results showed that terrestrial vegetation comprised about 40% of the Coastal lake DOM and about 50% of the Central and Ice margin lake DOM. Soil-derived C comprised 42% of the Coastal DOM pool and 9% in Ice margin lake DOM. Soil inputs were practically absent in the Central lakes. Macrophytes as a source of DOM was greatest for the Central lake group (45%) and the Ice margin (39%) lake group, and decreased for the Coastal (12%) lake group. The mixing model revealed that POM was the overwhelming source of OM to the sediments of the Coastal and Ice margin lake groups (> 80% for each) and the only source to the Central lake group sediments.

Discussion

Hydrological connectivity and lake OM characteristics

Lakes in SW Greenland exhibited consistently distinct characteristics, which reflected different sources of C stored in the water columns and sediments of these lakes (Fig. 3). This distinction became more apparent across the hydro-climatic gradient as the degree of hydrological connectivity decreased from the relatively higher precipitation Coastal lake region to the lower precipitation Central lake region, in which water isotopes indicated substantial evaporation (Fig. S2; Leng and Anderson 2003). The Coastal lakes were more similar to terrestrial-OC dominated boreal lakes, yet the similarity declined as hydrological connectivity decreased and the Central and Ice margin lakes became dominated more by autochthonous sources. The decrease in hydrological connectivity evidenced by increasingly evaporative conditions (Fig. S2) resulted in DOM becoming more influenced by macrophytes than by soils or terrestrial vegetation (Table 1). However, the sediments were consistently sourced from a variable mix of benthic and planktonic algal OM across all lake groups. These results confirmed our hypothesis and imply that drier conditions reduced the terrestrial C subsidy to these lakes.

Accumulation of terrestrial and autochthonous DOM in the water column

Soil-derived DOM sources became less important to SW Greenland lakes under drier conditions (Table 1). Lack of soil development in the watersheds of these lakes (south facing slopes are often devoid of vegetation and soils due to moisture stress) was consistent with the relatively low estimates for soil-derived DOM influencing the lakes, though as pointed out by Osburn et al. (2017), seasonal variability can be quite marked. For example, fresh inputs of soil-derived DOM following active layer melt in the spring may give way to larger inputs from macrophytes during the summer (Syväranta et al. 2006). Despite these spring pulses, the fraction of soil-derived DOM decreased significantly with decreasing precipitation (Spearman's rho = 0.68; $p < 0.001$), reflecting the general decrease in hydrological connectivity and increase in evapoconcentration (Fig. S2). Overall, the lack of soil-derived DOM in the Central and Ice margin lake groups could result from its rapid photochemical and/or microbial degradation after active layer thaw (Osburn et al. 2017).

Across the region of SW Greenland, conditions favorable to plant growth led to greater relative contributions from autochthonous DOM sources. These lakes have deep euphotic zones that reach to > 80% of their maximum depth (Whiteford et al. 2016). Low mass-specific DOM absorbance and low particulates in the Central and Ice margin lakes near Kangerlussuaq results in a larger euphotic zone depth than in most boreal lakes (Whiteford et al. 2016; Osburn et al. 2017), although transparency is changing (Saros et al. 2016). Primary production in Arctic lakes tends to be dominated by the benthos including periphyton, macrophytes, and their associated epiphytic communities (Vadeboncoeur et al. 2003). Deep euphotic zones support extensive and diverse macroalgal and macrophyte beds in these lakes (*Chara*, *Potamogeton spp* and aquatic mosses such as *Depranocladus spp*.). Macrophyte exudation and senescence can thus account for a large proportion of DOM in shallow lakes with substantial littoral zones and high light transparency, particularly where allochthonous inputs are low (Wetzel 1992). This was very clear from the results of our mixing models that showed large contributions (ca. 45%) of autochthonous macrophytes to DOM in the Central and Ice margin lakes (Table 1).

Stable isotope and C:N results from this study support evidence from DOM's optical properties that indicated macrophytic sources dominated the water column DOM in southwest Greenland lakes (Osburn et al. 2017). Stable hydrogen (δD) and δ^{13}C values of DOM from a series of ponds near Kangerlussuaq likewise showed the importance of macrophytes to water column DOM (Mariash et al. 2018). Results also are comparable to lakes of the Mackenzie River delta, in which littoral primary production was distinct from pelagic primary production in contributing to lake OM cycles, especially in shallower systems (Tank et al. 2011; Mendonça et al. 2013). The Mackenzie Delta lakes have considerable DOM inventories but exhibit a stronger connection to macrophytic DOM sources as hydrological connectivity declines (Tank et al. 2011). Therefore, a shift in lake DOM source from soils to macrophytes is thus quite reasonable to occur under drier conditions in the Arctic, exemplified by the evaporative conditions of the Central lake group (Fig. S2).

Accumulation of autochthonous OM in sediments

Sediment OM was dominated by autochthonous processes despite the hydro-climatic gradient (Table 1). In fact, a terrestrial C signature was absent in the sediments of the lakes as evidenced by the general lack of visible terrestrial macrofossils (Anderson et al. 2009). As in many oligotrophic lakes globally, the SW Greenland lakes had POM concentrations that were generally much lower than DOM concentrations (Tranvik et al. 2009; Whiteford et al. 2016). Consequently, organic C burial rates are low (Sobek et al. 2014; Anderson et al. 2019). Therefore, we argue that despite the hydro-climatic gradient, low carbon accumulation rates in sediments reflect a decoupling from landscape influence with C burial being strongly controlled by autochthonous planktonic processes.

The geochemical proxies measured in this study support this argument (Fig. 3). C:N values in sediment cores were ca. 10 at surface and increased with depth, while δ^{13}C values ranged from −30‰ to −28‰ with the more negative values in surface sediments. The ranges for each proxy encompass freshwater POC as influenced by freshwater algae (inset to Fig. 3; Lamb et al. 2006). Diagenesis possibly exerted a weak influence on the sedimentary OM as was indicated for several of these lakes previously (Sobek et al. 2014). This would explain the mean C:N ratios for each lake group that were slightly greater than Redfield ratio for plankton (i.e., > 7) especially if N was removed. Two-way ANOVA results clearly showed no link between DOM and sediments characteristics that would suggest substantial release of pore water DOM into the water column, from whence our observations were obtained, that would imply substantial diagenesis (Tables S3 and S4). This further underscores the disconnect between C cycles in the water column of the lakes and C cycles in their sediments.

Sediment δ^{13}C and C:N values implied that DOM in the Kangerlussuaq lakes is not readily flocculated by the physicochemical processes that dominate C accumulation in boreal lake sediments (Wachenfeldt and Tranvik 2008; Guillemette et al. 2017). Notably, even sediments from lakes at the Greenland coast exhibited mostly autochthonous algal characteristics (Table 1; Olsen et al. 2013; Anderson et al. 2018*a*). This contrast between sediment C characteristics of boreal lakes vs. the Kangerlussuaq lakes further emphasizes that the breakdown of the terrestrial-aquatic linkage will weaken as the Arctic becomes drier. Despite this disconnect, increases in reactive nitrogen from the atmosphere may enable the nutrient-limited SW Greenland lakes to continue to sequester CO_2 in their sediments from autochthonous aquatic primary production (Anderson et al. 2019).

Implications for lake C cycling in a drier Arctic

As the Arctic warms, regions are predicted to become greener via shrubification, leading to enhanced terrestrial vegetation in catchments and possibly increasing relative amounts of vegetation and soil inputs to Arctic lakes (Phoenix and Bjerke 2016; Anderson et al. 2017). Many Arctic lakes that have large DOM inventories, e.g., the well-studied Alaskan lakes near Toolik, accumulate this C via strong hydrological connectivity to their watersheds originating from seasonal inputs from active layer thawing, a process that will be enhanced by permafrost melt (Judd and Kling 2002). However, altered hydrological pathways, either reduced due to drought or enhanced by permafrost melt will result in changes to C cycling and terrestrial-aquatic linkages, such as the "active-pipe" model (Cole et al. 2007; Schuur et al. 2015).

Much of the Arctic also is predicted to become drier, likely transitioning large regions from cool-wet tundra conditions similar to the Coastal lake group, to warm-dry steppe conditions similar to our Central lake group (Hu et al. 2010). Current estimates place environments such as those observed in the dry Central lake region at roughly 25% lake area within the northern circumpolar permafrost landscape (Bogard et al. 2019). Our results suggest that under these climatic changes, lakes will diverge from landscape influence and store more autochthonous macrophyte-derived C as potentially recalcitrant DOM in the water column, and store autochthonous algal-derived C in sediments, even under low C accumulation rates.

The auto-/allochthonous balance of lakes is largely derived from studies of boreal lakes and eutrophic lakes. However, our study revealed that drier conditions will shift C sources from allochthonous subsidies to autochthonous processes. Further, our results suggest the need for a broadening the context of changing lake-landscape interactions in response to global warming and land cover changes. Given the importance of the Arctic for future global C dynamics (Schuur et al. 2015; Anderson et al. 2017), the interaction and transfer of terrestrial C between land and water need to incorporate the impact of reduced runoff and drier conditions, which may modulate the sources of C delivered to them.

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