Does the Coralline Alga Leptophytum foecundum (Kjellman) Capture Paleoenvironmental Variability in the Arctic Ocean?

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Does the coralline alga *Leptophytum fœcundum* (Kjellman) capture paleoenvironmental variability in the Arctic Ocean?

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**Introduction**

The impact of the industrial revolution on climate is a key issue for the global community. To understand recent changes and model future projections of temperature, we need to quantify climate variability during the last several centuries prior to and since the industrial revolution. Because of its importance in modulating climate through changes in albedo, carbon-sink feedbacks, and the Atlantic meridional overturning circulation (AMOC), Arctic paleoenvironments are particularly important for understanding climate variability (ACIA, 2005; Kennett et al., 2003; Kerr, 2010). Approximately 70% of the Arctic Ocean is ice-covered throughout the year, but recent global warming since the mid-19th century has diminished the sea ice extent, changing carbon uptake by the Arctic Ocean (ACIA, 2005; Bauch et al., 2000). The increased freshwater flux from both glacial melt and the melting sea ice reduces surface salinity and increases the solubility of CO$_2$ (Arrigo et al., 2010). As the cold water from the Arctic Ocean contributes to the formation of the North Atlantic Deep Water (NADW), the current freshening of the Arctic Ocean may play a primary role in global climate through slowing the AMOC (Dickson et al., 2007; Jahn and Holland, 2013; Rennermalm et al., 2007). Thus, changes in carbon sink feedbacks and the strength of the AMOC linked to sea-ice melting in the Arctic could influence global climate evolution for the next decades through centuries (ACIA, 2005; Perovich et al., 2007).

Natural proxy archives that give indirect information on past climatic conditions extend environmental data in space and time. At high latitudes, most annual and decadal climate reconstructions are based on terrestrial proxies such as ice cores from glaciers, tree
rings, or varved lake sediments (Kaufman et al., 2009; Overpeck et al., 1997; Steffensen et al., 2008) that do not provide information about marine environmental conditions. The majority of annually to decadally resolved surface ocean climate reconstructions are almost exclusively based on hermatypic shallow-water corals (Grotzoli and Eakin, 2007), sclerosponges (Rosenheim et al., 2004), and bivalves (Schöne, 2013). However, hermatypic corals and sclerosponges are limited to tropical and subtropical seas, excluding the possibility of high-latitude climate reconstructions. Although bivalves provide the majority of extratropical near surface marine climate data (e.g., Wanamaker et al., 2011), they also have a limited biogeographical range (Dahlgren et al., 2000). Thus, little is known about the subannual to interannual evolution of the surface Arctic Ocean during the last several centuries, and reconstructions of past climatic variability in the high latitudes would benefit from additional high resolution environmental archives.

The crustose coralline algae *Clathromorphum* sp. and *Lithothamnion glaciale* are ideal biogenic marine climate archives of the mid- to high latitude environmental variability because of their incremental growth pattern, longevity, preservation potential, and incorporation of changes in their ambient environment into the geochemistry and sclerochronology of their skeleton (Chan et al., 2011; Halfar et al., 2013, 2008; Hetzinger et al., 2013; Kamenos et al., 2008, 2012; Williams et al., 2011). Seasonal decreases in temperature and light during winter periods reduce the calcification rate of the algae. The skeletal anatomy changes from narrow and elongate cells with dense walls to wider and shorter cells with thinner walls resulting in growth increment demarcations in the fall to early winter in its high Mg-calcite skeleton (Adey et al., 2001). Buried multiporate asexual conceptacles and stones (Athanasiadis and Adey, 2006) (Fig. 3). It is a crustose species with no major surface irregularity, except those created by overgrowing over an irregular substrate (Athanasiadis and Adey, 2006). Overgrowth of one plant by another is rare in this species (Adey et al., 2001). Buried multiporate asexual conceptacles ranging from 220 to 500 μm in diameter and 140 to 250 μm in height are very frequent (*L. facendum* var. *sandreae*) (Athanasiadis and Adey, 2006). Lateral growth rates based on specimens grown in laboratory experiments range from 1 to 9 μm day⁻¹ (= 365 to 3285 μm yr⁻¹), depending on ambient temperature and light (Adey, 1970).

The high-latitude crustose coralline alga *Leptophytum facendum* (Kjellman) may serve as a paleoenvironmental proxy to increase the number and spatial extent of records of environmental change in the Arctic Ocean. Thus, we measured growth rates and growth increment formation along with Mg/Ca, δ¹⁸O, and δ¹³C composition of the high-Mg calcitic skeleton in three specimens from the Beaufort Sea to evaluate the feasibility of extracting environmental signals from the skeleton of *L. facendum*. If this alga proves to yield a reliable record of Arctic Ocean parameters, future studies may use longer-lived specimens in order to reconstruct the climate evolution of the Arctic Ocean during the past centuries during which we have no instrumental data.

**Methods**

Three specimens of the coralline alga *Leptophytum facendum* (Kjellman) (BSA2, BSA3, and BSA7) were collected live from 5 m depth by SCUBA during a research cruise in the Beaufort Sea, close to Prudhoe Bay, off the Sagavanirktok River (Sag River) delta (70°20' N, 147°40' W) in July 2007 (Fig. 1). Sea surface temperatures (SSTs) derived from OBPG Aqua MODIS Ocean Color for the sampling site vary from −1.95 °C in the winter season (December through April/May) to 5 °C in July over the period of 2002–2008 (Acker and Leptoukh, 2007). On shore, the 289 km Sag River originates on the north slope of the Brooks Range in northern Alaska (Benke and Cushing, 2011) then flows across the Arctic Slope province before entering the Beaufort Sea in the Arctic Ocean (Fig. 1). It is principally fed by snowmelt with some groundwater and glacial influence (Benke and Cushing, 2011) and is frozen between September and May, thawing in late May to June. Surface temperatures for the Sag River have varied from 0 °C to 15 °C between 1990 and 2007 (temperatures provided by Mathew Schellekens [USGS]). Annual Sag River discharge and gage height vary from 28 to 69 m³ s⁻¹ and 5 to 7 m, respectively, on interannual time scales (Fig. 2, parts a and d) (data from http://waterdata.usgs.gov).

*Leptophytum facendum* (KJELLMAN)

*Leptophytum facendum* is an Arctic species that extends into the subarctic photic zone (Adey, 1970) and grows on pebbles and stones (Athanasiadis and Adey, 2006) (Fig. 3). It is a crustose species with no major surface irregularity, except those created by overgrowing over an irregular substrate (Athanasiadis and Adey, 2006). Overgrowth of one plant by another is rare in this species (Adey et al., 2001). Buried multiporate asexual conceptacles ranging from 220 to 500 μm in diameter and 140 to 250 μm in height are very frequent (*L. facendum* var. *sandreae*) (Athanasiadis and Adey, 2006). Lateral growth rates based on specimens grown in laboratory experiments range from 1 to 9 μm day⁻¹ (= 365 to 3285 μm yr⁻¹), depending on ambient temperature and light (Adey, 1970).

**FIGURE 1.** Study area in Beaufort Sea showing proximity to Prudhoe Bay and Sagavanirktok River, including the Sag River delta (inspired from Kline et al., 1998).
FIGURE 2. (a) Gage height with time; (b) gage height versus δ¹⁸O composition and (c) MgCO₃ content. (D) Discharge data for Sagavanirktok River (data from http://waterdata.usgs.gov) with time, (e) discharge data versus δ¹⁸O composition, and (f) MgCO₃ content.

FIGURE 3. Anatomical characteristics of *L. fascundum* calcareous skeleton. (a) *L. fascundum* in life position growing on pebble (top view). (b) Cross section of *L. fascundum* (BSA2) perpendicular to growth direction showing growth direction, growth lines, and conceptacles.
SAMPLE PREPARATION AND ANALYSIS

After collection, a dozen of *L. fœcundum* specimens were air dried, separated from pebbles, and cut into 1-cm-thick slices perpendicular to the direction of growth using a circular diamond precision saw (Buehler IsoMet1000). Three specimens with the highest potential to record palaeoenvironmental data based on largest vertical height and best developed growth lines were selected for further visual and geochemical analyses. These samples were epoxied onto glass slides and machine polished to 1 μm with a Logitech CL50 using diamond-polishing suspensions with grit sizes of 9, 3, and 1 μm on a Buehler polishing disk. Polished sections were cleaned in an ultrasonic bath for 10 minutes with deionized water between each polishing step and dried overnight prior to sampling.

Digital images of the polished surface were produced using an Olympus reflected light microscope (VS-BX) attached to an automated mapping stage-imaging system equipped with geo.TS software (Olympus Soft Imaging Systems). This setup allows a two-dimensional mapping of the surfaces of the polished specimens using multiple images spliced together to generate one image. The resulting high resolution photomosaics enabled the identification of growth patterns over the entire sample and the subsequent selection of sampling locations (Fig. 4). The locations of conceptacles and annual growth increments were identified using the digital photomosaics.

Mg/Ca MEASUREMENTS

Mg/Ca values in specimens BSA3 and BSA7 were measured using a JEOL JXA 8900 RL electron microprobe at the University of Göttingen, Germany. For quantitative wavelength dispersive measurements, an acceleration voltage of 15 kV, a focused beam, and a beam current of 12 nA were used (see Hetzinger et al., 2009, for additional details). The electron beam was manually positioned on calcite within an individual algal cell. The sampling transects were preselected on the digital photomosaic images avoiding conceptacle cavities and recalcified portions of the skeleton (Fig. 4). Spot analyses were spaced 10 μm apart along a transect parallel to the direction of growth (Figs 4 and 5). Transects ranged in length from 890 μm (BSA3) to 1440 μm (BSA7). Counting statistics errors at the 99% confidence level varied between 0.035 and 0.087 t(°C) = 87.53 × Mg/Ca (mol/mol) – 5.46. (2)

DEVELOPMENT OF CHRONOLOGY

Chronologies were generated first by counting annual growth lines on the mapped and digitized image of the specimens. All samples were live collected; hence the top layer was assigned the year of collection, 2007, and calendar years were assigned to annual growth increments starting from 2007 and extending back in time. In addition, yearly growth-increment widths were calculated from annual Mg/Ca-element cycle widths that were obtained by electron microprobe for two specimens (BSA3 and BSA7). Age models were established on the basis of the seasonal cycle in algal Mg/Ca: high Mg values within the skeleton were assigned to July, which is on average the warmest month, and minimum values were tied to February, which is on average the coolest month at the study site (Benke and Cushing, 2011). The algal Mg/Ca time series were linearly interpolated between these anchor points using the AnalySeries software (Paillard et al., 1996) to obtain an equidistant proxy time series with a monthly resolution. Because of possible growth discontinuities prior to the year 2001 in BSA3 and 1997 in BSA7, only data after those years were interpreted. Linear regression tested for statistical correlation of the monthly resolved time-series between the two specimens, and with instrumental records of environmental conditions. The developed chronologies were refined and cross-checked for possible errors in the age model by comparing annual extreme values in the Mg/Ca ratio time series to mapped growth increment patterns for each individual year of algal growth.

STABLE OXYGEN AND CARBON ISOTOPE ANALYSIS

Skeletal material for stable oxygen and carbon isotopes analyses was removed in specimens BSA2 and BSA7 by a high-precision, computer-driven New Wave Research Micromill attached to an x, y, and z stage using digitized milling path positions. Due to logistical constraints, we did not determine the isotopic composition of specimen BSA3. For specimens BSA2 and BSA7, sampling paths were defined using geo.TS software and transferred to the Micromill to mill 100 to 200 μg of calcite powder per sample resulting in a resolution of two to four samples per year. The sampling depth was 150 μm and sample path lengths averaged 1.30 cm for BSA2 and 1.15 cm for BSA7. Since skeletal material was bulk sampled to obtain sufficient material for analysis, conceptacles were not avoided. Material was removed from the outside edge of the specimen first, which represented the most recent growth followed by subsequent samples moving toward the oldest part of the sample. Using a razor blade, the milled powder was transferred into a glass vial used for the mass spectrometer. Sample amounts were 56 samples milled from BSA2 and 42 from BSA7.

Removal material was analyzed for δ18O and δ13C (‰ relative to Vienna Pee Dee Belemnite standard [VPDB]) using a Thermo-Finnigan MAT253 mass spectrometer connected to a gasbench and autosampler at the Geobiology Stable Isotope Lab.
oratory, University of Toronto. The international standard NBS-19 and two in-house standards (IAEA-CO-1 and IAEA-CO-2) were used for calibration of all samples. One standard deviation of the mean of duplicate measurements was ±0.08‰ for δ18O and ±0.16‰ for δ13C. Using the established chronology, a stable isotope time series was compiled for BSA2 and BSA7.

Since stable oxygen isotope fractionation during calcification is temperature dependent, the δ18O composition of calcium carbonates serves as a paleothermometer (Urey, 1947). Here, seawater temperatures were reconstructed using the temperature-oxygen isotope calibration established by Anderson and Arthur (1983) with modifications to account for the high Mg

FIGURE 4. Geo.TS images of (a and b) BSA2, (c) BSA7, and (e) BSA3 cross sections with selected transects for microprobe measurements for (d) BSA3 and (f) BSA7.
content (Jiménez-López et al., 2004) and vital effects (Halfar et al., 2008):

\[ T(\circ C) = 16 - 4.14 \times (\delta^{18}O_c - \delta^{18}O_{mS} + 3.5) + 0.13 \times \]
\[ (\delta^{18}O_c - \delta^{18}O_{mS} + 3.5)^2 + 0.17 \times \text{mol}\% \text{MgCO}_3. \quad (3) \]

A \( \delta^{18}O_{mS} \) value of –4.49‰ (Bedard et al., 1981; Schmidt et al., 1999) was used, which is consistent with end-member seawater values reported by Alkire and Trefry (2006) for seawater \( \delta^{18}O \) composition.

**Results**

**CHRONOLOGY**

The combination of a high number of large conceptacles and very low growth rates resulted in poorly delimited annual growth increments (Figs. 4 and 5). Despite this, image-based chronologies were established from 1997 to 2007 for BSA7, from 2000 to 2007 for BSA2, and 1998 to 2007 for BSA3. Average annual growth rates were 180 ± 26 μm yr\(^{-1}\) (max = 213 μm yr\(^{-1}\), min = 117 μm yr\(^{-1}\)) for BSA2, 243 ± 49 μm yr\(^{-1}\) (max = 330 μm yr\(^{-1}\), min = 160 μm yr\(^{-1}\)) for BSA7, and 190 ± 50 μm yr\(^{-1}\) (max = 243 μm yr\(^{-1}\), min = 109 μm yr\(^{-1}\)) for BSA3 (Table 1) (Fig. 6, part a).

Maxima in Mg/Ca were aligned with the center of each growth increment, and minima with growth increment lines in BSA3 and BSA7 resulting in ~15 samples year\(^{-1}\) for BSA3 and ~21 samples year\(^{-1}\) for BSA7 prior to interpolation. Using widths of the annual Mg/Ca cycle, annual growth rates averaged 215 ± 50 μm from 2001 to 2006 for BSA7 and 170 ± 47 μm from 2003 to 2006 for BSA3 (Table 1). The Mg/Ca-derived growth rates were comparable to the growth rates measured using the visual growth increments as a reference.

**Mg CONTENT**

The average MgCO\(_3\) content did not significantly differ between the specimens BSA3 and BSA7 (\( p = 0.36, n = 57; \) Table 1). Using monthly interpolated values, the MgCO\(_3\) content did not significantly correlate between the two specimens (\( p = 0.82, r^2 = 0.03, n = 57; \) Fig. 6, part b).

Using Equation 1, reconstructed temperatures averaged –0.05 ± 2.0 °C (min = –3.9 °C, max = 3.9 °C) for BSA3 (period: 2001–2006) and –0.3 ± 1.9 °C (min = –4.5 °C, max = 4.5 °C) for BSA7 (period: 2000–2006; Fig. 7, parts b and c). Using Equation 2, reconstructed temperatures averaged 2.3 ± 2.1 °C (min = –1.7 °C, max = 6.6 °C) and 2.1 ± 2.0 °C (min = –2.4 °C, max = 7.2 °C) for BSA3 and BSA7, respectively, for the same periods as above (Fig. 7, parts b and c). Using annually averaged values, neither temperature reconstruction significantly correlated with satellite-derived SST (\( p = 0.37, r^2 = 0.12, n = 57 \) and \( p = 0.55, r^2 = 0.07, n = 72 \) for BSA3 and BSA7, respectively).

**STABLE OXYGEN ISOTOPE VALUES**

The \( \delta^{18}O_{alg} \) values did not significantly differ between the specimens BSA2 and BSA7 (\( p = 0.30, n = 7; \) Table 1). Using annually averaged values, the \( \delta^{18}O_{alg} \) values significantly correlated between the two specimens from 2000 to 2006 (\( p = 0.045, r^2 = 0.59, n = 7; \) Fig. 6, part c). Neither of the annually averaged \( \delta^{18}O_{alg} \) records significantly correlated with growth rates or Sag River discharge or streamflow. The \( \delta^{18}O_{alg} \) record for growth specimen BSA7 significantly correlated with gage height from 1997 to 2006 (\( p = 0.03, r^2 = 0.46, n = 10; \) Fig. 2, part b).

Using Equation 3, the oxygen isotopic composition of L. foveiculum yielded average seawater temperatures of –0.22 ± 0.99 °C and –0.03 ± 1.12 °C for specimens BSA2 and BSA7, respectively (Fig. 7, parts d and e). Neither temperature reconstruction significantly correlated with satellite-derived SST (\( p = 0.74, r^2 = 0.16, n = 7 \) and \( p = 0.76, r^2 = 0.11, n = 10 \) for BSA2 and BSA7, respectively).

**STABLE CARBON ISOTOPE VALUES**

The average (±stdev) \( \delta^{13}C_{alg} \) values significantly differed between the specimens BSA2 and BSA7 (–1.93% ± 0.18‰ and –1.59% ± 0.31‰, respectively) for the common period 2000–2006 (\( p = 0.0009, n = 14; \) Fig. 6, part d). Using annually averaged values, the \( \delta^{13}C_{alg} \) values did not significantly correlate between the two specimens, or with Sag River discharge or gage height. The annually averaged \( \delta^{13}C_{alg} \) values significantly correlated with annual growth rates in specimens BSA2 (\( p = 0.014, r^2 = 0.86, n = 7 \)) but not BSA7.

**Discussion**

**DEVELOPMENT OF CHRONOLOGY**

The large conceptacles (140–250 μm diameter) relative to very low growth rates (180 to 240 μm yr\(^{-1}\)) obscured the annual growth bands in some instances. In addition, not all growth increments identified in the digital images of each specimen were continuous laterally, and growth interruptions distorted the chronology because their duration was unknown (Fig. 5). Thus, chronologies prior to growth discontinuities in each specimen were not assigned (Table 1). Despite this, measured growth rates in the specimens were similar to thickness growth rates obtained for Arctic to Subarctic species of the climate archive Clathromorphum compactum (Adley et al., 2013). Cross dating of both algae using the same method as for tree rings (i.e., to correlate years with the same thickness of growth increments) was not possible because a variety of specimen-specific biotic factors alters growth, including shading of a specimen for an extended period, differential grazing, and/or other unknown factors. The chronology deduced from the width of annual Mg/Ca cycles was established with difficulty because of noise in the elemental signal (Fig. 6, part b), likely resulting from the small-scale variability in annual growth banding and the sometimes low seasonal variability in seawater surface temperatures (Fig. 7, part a). Despite this, growth rates determined from the annual cycle in Mg content were consistent with those determined from the visually measured growth increment widths. The difficulty in determining the growth increments and short lifespans in the specimens collected, along with restricted development of the perithallium (Adley et al., 2001), indicates that long-lived specimens of this species with clear chronologies may be difficult to find. Newer collections of this species from the Labrador Sea Coast, unaffected by freshwater influx, appear more regular and may provide better climate archive data (Adley, specimens in herbarium US).

**Mg/Ca–DERIVED SEA SURFACE TEMPERATURES**

SSTs reconstructed using the L. glaciale–derived transfer function yielded similar average temperatures to the satellite SST data (±0.7 °C difference, Fig. 7, parts a and b); however, the winter minima far exceeded satellite values (e.g., –3.9 °C\(_{alg}\) and –4.5 °C\(_{alg}\) vs. –1.8 °C\(_{satellite}\)). SSTs reconstructed using the C. nereostratum–derived transfer function yielded average reconstructed SSTs exceeding the
satellite SST data (2.8–3.0 °C difference) due to overestimation of the summer maxima (e.g., 6.6 °C_	ext{sea} and 7.2 °C_	ext{sea} vs. 2.8 °C_	ext{satellite}) (Fig. 7, parts a and b). Thus, the transfer functions developed for other coralline algal species cannot be applied successfully to *L. fœcundum*, potentially due to taxa-specific vital effects or because of site-specific environmental variability. Such differences between

FIGURE 5. Chronologies for (a) BSA2, (b) BSA7, and (c) BSA3. Blue lines delimit annual growth increments. Calendar years were assigned to annual growth increments starting from the year of collection and extending back in time. Red lines underline a growth interruption across an entire year, and orange circles point to discontinuities where a section of growth is missing within a single year.
SST and bottom temperature necessitate in situ calibrations for coralline algae or just a species-specific calibration. In addition, it is apparent from parallel studies of the high latitude climate archive C. compactum that growth can cease for a number of months in mid-winter, during the later phases of Arctic winter darkness, further complicating coralline archives from different latitudes.

Salinity affects the incorporation of Mg into the skeleton of the alga C. nereostratum (Chan et al., 2011), hence a freshwater influence from the Sag River may alter the incorporation of Mg in the skeleton to changes in temperature. Recent studies of high-Mg calcite in echinoderm skeletons and foraminiferal tests field-collected or cultured in different salinities have demonstrated a clear negative effect of salinity on Mg/Ca ratios (Ferguson et al., 2008; Kısakürek et al., 2008). This effect might explain the cold temperatures calculated in this study using the L. glaciale–derived transfer function, as the salinity in Beaufort Sea is very low (between 15‰ and 30‰) and the Sag River contributes significant amounts of freshwater to the collection site. More experiments that monitor temperature and salinity would therefore be necessary to establish a new calibration linking Mg/Ca (mol%) and temperature in waters with low salinity. Regardless, our data indicate that without further exploration, L. fœcundum may integrate the ambient Mg content in skeletal Mg/Ca ratios without further calibration due to the high Mg/Ca ratio in its skeleton.

CARBON ISOTOPE VALUES

SSTs reconstructed from the algal-δ18O composition generated average seawater temperatures that were consistent with the satellite SST data (Fig. 7, parts a and d). Thus, seawater temperature is a primary control driving the δ18O composition of L. fœcundum at this location. However, the algal-derived SSTs do not significantly correlate with the satellite SSTs at interannual timescales, nor do they vary seasonally as is evident in the satellite data. Thus, other factors in addition to seawater temperature drive the temporal variability in skeletal oxygen isotopic composition. Given that the oxygen isotopic record does not vary consistently subannually, seasonal freezing and melting of sea ice with isotopically light δ18O likely does not influence the oxygen composition of the algal skeleton. Indeed, even if seawater becomes enriched in 18O as it freezes, the isotopic fractionation observed in sea ice is typically small (Cooper et al., 2005). Instead, runoff from Sag River likely influences the isotopic composition off the delta, along with other factors. As the source of Sag River is located in the high altitudes of the Brooks Range in Alaska with a continental climate, the runoff is strongly depleted in 18O (Cooper et al., 2005). In addition, Sag River temperatures are significantly warmer than the Beaufort Sea (Fig. 7, part a). As such, enhanced Sag River runoff would be expected to drive negative deviations in the algal δ18O composition, which is not supported by the data here. Thus, while the δ18O values of the two specimens significantly correlate with each other, supporting a common environmental driver of algal δ18O composition and suggesting that specimen-specific variables such as diagenesis of the conceptacles is not a concern, seawater temperature and salinity, and fresh water from the Sag River likely combine to influence the oxygen isotopic composition. In addition, L. fœcundum may integrate the ambient water δ18O signal over several years, further compounding the drivers of the alga’s oxygen isotopic composition.

TABLE 1

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Growth rates: 183 ± 30 µm yr⁻¹ (2000–2006)</th>
<th>MgCO₃ (Mol%) measurements</th>
<th>δ¹³C and δ¹⁸O measurements</th>
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OXYGEN ISOTOPE VALUES

Intrinsic characteristics of each specimen may control the δ¹³C values. Generally, more negative δ¹³C values are associated with faster rates of skeleton formation in other calcium carbonate marine organisms (Butler et al., 2011; Swart et al., 2010). In fact, the δ¹³C may reflect kinetic isotopic disequilibrium at high growth rates. During the years of relatively low growth rates, a relative increase in the proportion of metabolic carbon available for skeleton construction may deplete the skeletal δ¹³C (Butler et al., 2011; Lorrain et al., 2004). Thus, an increase in extension rate is coupled with a decrease in δ¹³C and vice versa. However, growth rates positively correlate with δ¹³C in specimen BSA2, while no clear pattern is present in specimen BSA7 (Fig. 6, part d). Therefore, the source of variability in the skeletal δ¹³C values may not in fact be intrinsic to the coralline alga. Exploration of external factors driving δ¹³C changes in the ambient dissolved inorganic carbon (DIC) that is the source of carbon to the alga, may thus be useful.

Anthropogenic burning of isotopically light fossil fuels is decreasing the isotopic composition of the carbon in the atmosphere and the oceans. This century-scale trend toward lighter carbon isotopes—the δ¹³C-Suess effect (Nozaki et al., 1978; Suess, 1953)—is recorded in calcareous skeletons of long-lived marine organisms (Swart et al., 2010). A decline in δ¹³C of ~0.9‰ per decade for the 1990s was measured in coralline algae in the northern North Pacific Ocean/Bering Sea (Williams et al., 2011), and ~0.9‰ from 1850 to 1987 in the Arctic Ocean in the polar planktic foraminifer Neogloboquadrina pachyderma (Bauch et al., 2000). These rates are high relative to values measured in other areas of the world oceans in low latitudes and may represent changes in ventilation of the surface waters (Bauch et al., 2000; Williams et al., 2011). Here, the clear absence of a decreasing trend for δ¹³C in BSA2 and BSA7 implies that anthropogenic carbon is either not being taken up by the ocean locally or the decreasing isotopic composition of the DIC is being offset by other processes. The Beaufort Sea is partly sea-ice covered all year round (Pabi et al.,...
which could decrease the exchange between atmosphere and ocean and can explain the absence of an oceanic Suess effect in the Beaufort Sea. Alternatively, a potential increase in primary productivity in the Beaufort Sea (Pickart et al., 2013; Tremblay et al., 2011) may be offsetting the decline in skeletal $\delta^{13}C_{\text{cal}}$.

The absence of decreasing $\delta^{13}C$ values in $L. fœcundum$ also indicates that there has been no release of methane hydrates associated with decreasing subsea permafrost recorded by the $\delta^{13}C_{\text{ice}}$ composition (Rachold et al., 2007). The large amount of ancient organic matter contained in permafrost might be involved in current biogeochemical cycling due to thawing of the upper permafrost and restoration of the activity of viable methanogens preserved inside the permafrost (see Shakhova and Semiletov, 2007, and reference therein). However, the isotopic signatures of organic matter incorporating methane-derived carbon range from $-60\%_o$ to $-65\%_o$ (Dickens et al., 1995; Kvenvolden, 1993) relative to that of other oceanic and atmospheric carbon reservoirs with a $\delta^{13}C = 0\% \pm 7\%$ (Paull et al., 2002). Thus, if gas hydrate dissociation is observed on the East Siberian Arctic shelf (Heimann, 2010; Shakhova et al., 2010), no isotopic trace of such a phenomenon is recorded in the corallines of the Beaufort Sea Arctic shelf.

Finally, riverine influx from the Sag River can influence the surface water $\delta^{13}C_{\text{DIC}}$ and might be recorded by the $\delta^{13}C_{\text{ice}}$. As river
waters tend to have a more negative carbon isotope signature than
the ocean (Degens et al., 1991), we expect an anticorrelation with
gage height or discharge in the δ13C recorded. However, no cor-
relation between the variations of the river’s regime and δ13Cwas noticed. The most likely explanation is that the proximity of
the Sag River delta and sediment input in the study area disturb
the record of the Beaufort Sea isotopic composition, although no
clear external cause for the observed carbon isotopic record can be
identified here.

Conclusion and Prospects

Leptophytum fœcundum forms a banded skeleton with large
conceptacles relative to annual growth rates in the high Arctic,
making image-based chronologies difficult to establish. In addition,
potential growth discontinuities present in the skeleton limited
the duration of paleoenvironmental records that could be extracted
from the skeleton. A secondary method of dating, such as radio-
metric dating, is needed to verify algal age prior to the potential
growth discontinuities but is difficult to do considering the young
ages of the specimens. This, combined with the restricted develop-
ment of the perithallium (Adey et al., 2001), limits the duration of
records that are feasible to extract from L. fœcundum.

The absence of significant correlation between L. fœcundum
skeletal geochemistry and environmental records further indicate
the difficulties in generating paleoenvironmental records from the
algae at this location. Average Mg content was similar between the
two samples but varied differently over time. In addition, Mg con-
tent–derived reconstructed seawater temperatures using transfer
functions developed for other taxa of coralline algae yielded tem-
peratures that were inconsistent with satellite data. The location of
the two specimens close to the discharge of the Sag River suggests
a salinity influence in addition to temperature on the Mg content
in L. fœcundum. Alternatively the algal-Mg to SST transfer functions
developed for other taxa are not applicable to L. fœcundum or the
satellite data do not accurately capture bottom temperatures that
bath the coralline algae. Significant correlation of the δ18O be-
tween the two specimens supports an external environmental driver
of algal skeletal δ18O. This driver is likely a complex combination
of Beaufort Sea seawater δ18O composition and temperature com-
bined with Sag River freshwater δ18O composition and tempera-
ture during high flow periods. Average δ13C composition differed
between the two specimens and over time. Documented changes
in the source carbon to the region (e.g., δ13C-Suess effect) would
cause a decline in skeletal δ13C values not present in the skeleton.
As a result of this study, specimens of L. fœcundum do not appear
to provide a reliable new paleoenvironmental proxy for the Arctic Ocean, although studies of L. joecundum specimens removed from a freshwater influence might prove more useful.

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References Cited

FIGURE A1. Microprobe analysis and algal chronology. Red and green lines indicate position of measurement transects.