INFLUENCES OF SALINITY ON THE PHYSIOLOGY AND DISTRIBUTION OF THE ARCTIC CORALLINE ALGAE, LITHOTHAMNION GLACIALE KJELLMAN (CORALLINALES, RHODOPHYTA)[1]

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ABSTRACT

In Greenland, free-living red coralline algae contribute to and dominate marine habitats along the coastline. *Lithothamnion glaciale* Kjellman, dominates coralline algae beds in many regions of the Arctic, but never in Godthåbsfjord, Greenland, where *Clathromorphum* sp. is dominant. To investigate environmental impacts on coralline algae distribution, calcification and primary productivity were measured *in situ* during summers of 2015 and 2016, and annual patterns of productivity in *L. glaciale* were monitored in lab-based mesocosm experiments where temperature and salinity were manipulated to mimic high glacial melt. The results of field and cold-room measurements indicate that both *L. glaciale* and *Clathromorphum* sp. had low calcification and photosynthetic rates during the Greenland summer (2015 and 2016), with maximum of 1.225 ± 0.17 or 0.002 ± 0.023 μmol $CaCO_3 \cdot g^{-1} \cdot h^{-1}$ and -0.007 ± 0.003 or -0.004 ± 0.001 mg $O_2 \cdot L^{-1} \cdot h^{-1}$ in each species respectively. Mesocosm experiments indicate *L. glaciale* is a seasonal responder; photosynthetic and calcification rates increase with annual light cycles. Further, metabolic processes in *L. glaciale* were negatively influenced by low salinity; positive growth rates only occurred in marine treatments where individuals accumulated an average of 1.85 ± 1.73 mg $\cdot d^{-1}$ of biomass through summer. These results indicate high freshwater input to the Godthåbsfjord region may drive the low abundance of *L. glaciale*, and could decrease species distribution as climate change increases fresh water input to the Arctic marine system via enhanced ice sheet runoff and glacier calving.

KEYWORDS: Arctic, *Clathromorphum* sp., ecophysiology, Greenland ice sheet, maerl, polar seaweeds, rhodolith, *L. glaciale*, salinity

ABBREVIATIONS: PAM, pulse amplitude modulated; DO, dissolved oxygen; GrIS, Greenland ice sheet; CCA, crustose coralline algae; E_c, compensating irradiance; DMSP, β-dimethylsulfoniopropionate; E_k, saturating irradiance; P_m, maximum photosynthesis; PAR, photosynthetically active radiation; Fv/Fm, maximum quantum efficiency; RLC, rapid light curve.

INTRODUCTION

Polar seaweeds are adapted to the extreme environmental and seasonal conditions of the Arctic and Antarctic oceans (Wiencke and Amsler 2012). They can tolerate temperatures close to freezing and many are shade-adapted, allowing them the ability to withstand periods of little to no light in the subtidal zone (Wiencke and Amsler 2012). There are many commonalities between polar communities, but they are constrained by the geographical history of each phytoregion. Antarctic species experience consistently low temperatures and high nutrient levels throughout the year in the Southern Ocean which isolates these marine communities from the Atlantic, Pacific, and Indian Ocean basins, making light the most influential factor in the algal environment (Gómez et al. 2009). Many Antarctic endemics are 'seasonal anticipators' (Wiencke et al. 2007), beginning growth in winter-spring in order to maximize growth in spring with the return of sunlight (Kain 1989). Arctic species ranges are broader, more influenced by recent ice ages (Provan et al. 2005), and temperature and nutrient concentrations in the Arctic marine environment fluctuate seasonally (Aguilara et al. 2002). Dominant North Pacific kelps are typical 'seasonal responders', using accumulated photosynthetic products from the summer for peak growth from autumn through winter when nutrients are available (Dunton and Dayton 1995). Out of the dominant habitat forming seaweeds, calcifying red algae (specifically coralline algae) have eluded focus in most high-latitude marine systems, likely because brown algal forests are significantly more productive and abundant (Freiwald and Henrich 1994).

Coralline algal habitats, composed of both crustose and free-living morphologies, are important from both an ecological (Foster 2001, Kamenos et al. 2004, Steller and Caceres-Martinez 2009, Teichert 2014) and biogeochemical perspective (Burrows et al. 2014). Coralline algae are slow growing, long lived species (up to 1200 years; Adey et al. 2015), and

can provide complex habitats that foster diverse faunal assemblages (Kamenos et al. 2004, Stellar and Caceres 2009, Teichert 2014). The free-living coralline species are often referred to as rhodoliths or maerl, the former developing on stones (nucleated), and the latter a finely branched morphology, continually regenerating when the thallus is fragmented (Irvine and Chamberlain 1994). These come in many shapes and sizes that can reflect the sedimentary characteristics of the habitat and influencing algae-associated fauna (Bosence 1979, Bosence 1983a). Thirteen coralline species commonly form habitats in the north Atlantic, from the Canary Islands to Svalbard (Hernandez-Kantun et al. 2017), and it is thought that temperature and light control the depth distribution of coralline algae habitats in the Arctic (growth decreases by ~4% $\cdot$ m^{-1} in *Lithothamnion glaciale* Kjellman; Freiwald and Heinrich 1994). Other factors that impact the persistence of coralline algae beds include sedimentation and burial through natural or anthropogenic disturbances (Wilson et al. 2004). Species respond to environmental factors individually and this is compounded by the habitat substrata and hydraulic energy for turning or biogenic movement (Bosence 1983b, Marrak 1999, James 2000).

Growth of maerl species in the north east Atlantic was measured monthly by Adey (1970) using capture and release methods. Almost all growth occurred during summer in a banding pattern of many small cells, but single large cells in winter, which may also be a product of calcification inhibition by orthophosphates in the environment (Freiwald 1998). Orthophosphates and nitrogenous compounds which are more abundant in winter are stored as proteinaceous inclusions in the coralline algal thallus (Giraud and Cabioch 1983, Pueschel 1992) to mediate the oligotrophic summers and support calcification during this growth period, rates of which can be twice that of winter growth in *Lithothamnion* spp. (Freiwald and Henrich 1994). In the summer, coralline algae store photosynthetically derived carbohydrates

as starches for use during the Polar Night (Adey 1973, Lüning 1990, Freiwald and Henrich 1994) and these substances can be translocated within the thallus through pit connections and cell fusions (Steneck 1986). The resulting annual bands in thallus material are analogous to tree rings in terrestrial habitats and can provide a historical record of marine climate through the Mg content and $^{18}\delta O$ of the coralline skeleton, which translate to temperature and salinity of the surrounding habitat over time (Kamenos et al. 2012, Adey et al. 2015). 'Rhodochronology' is particularly useful in reconstructing Arctic conditions as corals and trees used in paleoclimate studies at lower latitudes are scarce (Adey et al. 2015).

Calcification rates in the Arctic are low; calcification of *L. glaciale* were 17.9 mg · y^{-1} per branch at 7-m depth (895-1432 g $CaCO_3 \cdot y^{-1} \cdot m^{-2}$) and 4.2 mg · y^{-1} per branch at 18-m depth (420-630 g $CaCO_3 \cdot y^{-1} \cdot m^{-2}$) in Norway (Freiwald and Henrich 1994). In Svalbard, calcification rates were 113% higher in summer than winter and annual $CaCO_3$ production of *L. glaciale* was estimated to be 313.5 ± 78.4 g $CaCO_3 \cdot m^{-2} \cdot y^{-1}$ in individuals collected from 40 to 50-m depth (Cape Rubin, 80° 32' 19" N, 19° 50'40" E; Büdenbender et al. 2011). $CaCO_3$ production rates decrease with increasing latitude, polar night, and sea ice cover in Svalbard, accreting 100.9 g $CaCO_3 \cdot m^{-2} \cdot y^{-1}$ in Nordkappbukta (80° 30' 57" N 19° 40' 47"E) and 200.3 g $CaCO_3 \cdot m^{-2} \cdot y^{-1}$ in Floskjereet (78° 19' 43" N 14° 40' 18" E), which highlights the importance of light in productivity of these polar corallines (Teichert and Friewald 2013).

To tolerate very low light habitats in the Arctic (~ 1 % of surface irradiance; Teichert et al. 2012, Teichert and Friewald 2013), coralline algae communities are probably shade-adapted like those in the Antarctic (Schwarz et al. 2005). Oxygen evolution of crustose corallines *Phymatolithon foecundum* (Kjellman) Düwel *et* Wegeberg and *Phymatolithon tenue* (Rosenvinge) Düwel *et* Wegeberg indicate average E_c between 0.7 - 1.8 µmol photons · m^{-2} ·

s^{-1} across seasons and depths in Young Sound, northeastern Greenland (Roberts et al. 2002). Average E_k for these species was between 7 - 17 µmol photons · m^{-2} · s^{-1} and P_m was 43-67 mmol O_2 · m^{-2} thallus · d^{-1} (250-400 g C · m^{-2} thallus · y^{-1}). The average dark respiration rate for these individuals was ~5 mmol O_2 · m^{-2} thallus · d^{-1} throughout the year, which translates to net production only during the months when irradiance can reach the benthos. These species have very low requirements for saturating irradiance but are not very productive. The low productivity of Arctic rhodoliths in Norway is discussed by Freiwald and Henrich (1994) who suggest this attribute is controlled by the season and sea ice conditions in a region. This has also been shown for CCA at Cape Evans in the Ross Sea, where PAM fluorometry alongside O_2 evolution corroborate an E_k of 2.9 - 3.2 µmol photons · m^{-2} · s^{-1} and an E_c of 0.10 µmol photons · m^{-2} · s^{-1} in benthic communities between 13-26 m depth, under sea ice (Schwarz et al. 2005). All data suggest that polar coralline algae have very high tolerance for environmental extremes as they persist through years of low productivity to great ages (Adey et al. 2015).

Coralline algae beds in the Arctic have been described as self-organizing communities that maintain low diversity but persist in wave-sheltered habitats (Freiwald 1993). These habitats have a patchwork distribution along the coastline of Greenland and can be composed of *Lithothamnion*, *Clathromorphum*, *Phymatolithon*, and *Leptophyllum* species, the deepest described at 77 m (Jørgensbye and Halfar 2017). Kelps also cover the coastlines of Greenland below the fucoid-dominated intertidal zone (Pedersen 2011), and coralline algae beds frequently punctuate these habitats. In this study we are specifically interested in the physiology of *L. glaciale* Kjellman, a monospecific branching-columnar maerl species (Bosence 1983a) whose range spans the north Atlantic (Hernandez-Kantun et al. 2017), is

ecologically important in the polar regions (Teichert 2014) and can be used as a paleoclimate record (Kamenos et al. 2012, Adey et al. 2015).

Dominant coralline algae species appear to vary across regions in Greenland, for instance *L. glaciale* forms large beds in Kangerlussuaq (Kamenos et al. 2012) and Disko Bay (Jørgensbye and Halfar 2017) but is not common in the large fjord system adjacent to Nuuk, Greenland. This region has three tidewater glacier outlets from the GrIS that make fjord-marine conditions turbid, cold, and hyposaline, the former perhaps having the greatest effect on maerl/rhodolith survival (Wilson et al. 2004). In Godthåbsfjord, Nuuk, the rhodolith *Clathromorphum* sp. (a sister species to *C. compactum*; Gabrielson pers. comm.) is dominant in areas where glacial silt and sediment are displaced by hydrodynamic forces, generally inlets between maritime islands at the mouth of Godthåbsfjord and Akia Peninsula (Schoenrock pers. comm.; Figure 1). *Clathromorphum* sp. here are mono-multispecific spheroidal-ellipsoidal laminar rhodoliths (Bosence 1983a). *L. glaciale* is intermittently present in *Clathromorphum* sp. beds and can be found in crustose or free-living morphologies in high sediment kelp forests of the Akia Peninsula (Schoenrock pers. comm.; Figure 1). Other rare species in the region include *Lithothamnion leave*, found in *Clathromorphum* sp. beds at the mouth of Købbefjord with *L. glaciale*, and *C. circumscriptum* (Gabrielson pers. comm.), which is found in high sediment kelp forests on the Akia Peninsula.

In this study we aim to identify how environmental factors (low temperature and salinity) that characterize the major fjord system outside of Nuuk, Greenland, affect the physiology of *L. glaciale.* We hypothesize that the freshwater input from the GrIS melt creates a hyposaline, cold habitat in this region that *L. glaciale* specifically cannot tolerate, but the abundant *Clathromorphum* sp. can. We compared physiological processes of calcification and

photosynthesis in *L. glaciale* and the dominant *Clathromorphum* sp. in the natural environment of Godthåbsfjord, Greenland to determine performance of each species. To compliment these data, a twelve-month lab-based mesocosm experiment manipulating temperature and salinity of sea water was used to measure productivity of *L. glaciale* throughout the year in conditions reflecting the fjord-marine environments outside Nuuk. In the future, cold, hyposaline systems are likely to become more common in Greenland due to increased ice sheet melt (Parizek and Alley 2004), and results from this study will not only describe environmental restrictions on the physiology of *L. glaciale* but may be used to describe present day and predict future distribution of this species.

METHODS

In August 2015 and 2016, coralline algae were collected from sites adjacent to the Akia peninsula, the seaward islands of Godthåbsfjord, and Købbefjord where the fjord meets the marine environment (Figure 1). Subtidal collection sites were chosen using Google Earth high resolution imagery and a drop camera (PVC frame with a GoPro HERO4) was used to verify coralline algae habitats were present in the selected locations. Specimens of each species were collected on SCUBA at each site (max collection depth 10 m) and brought to either a field camp or the Greenland Institute of Natural Resources (GINR), Nuuk, where calcification and photosynthesis were evaluated in natural conditions for both *Lithothamnion glaciale* (from Købbefjord and Akia Peninsula; Figure 1) and *Clathromorphum* sp. (from the seaward islands Site 124 and Dive 14; Figure 1). In 2015, collected specimens of *L. glaciale* were hand carried in 2-4 ºC seawater to the UK where long-term incubations of individuals from Akia peninsula were conducted in the Marine Mesocosm Facility at the University of Glasgow. Voucher specimens of both maerl species were sent to Dr. Paul Gabrielson at the

University of North Carolina to verify species identification because of the cryptic diversity in coralline algae.

To assess environmental parameters in the fjord and marine environments, profiles of the water column were measured at fjord and marine sites (n = 1 for each site) using a multi-parameter sonde in August, 2015 (YSI; Figure 1). Profiles were created by attaching the sonde to a 15-m line with 1-m increments, and slowly lowering the instrument to 10-m depth off the side of the marine vessel. The pH, DO, salinity, and temperature probe readings were allowed to stabilize before the sonde was slowly drawn up to the water's surface, measuring these parameters throughout the water column. Profile values from 10-m depth were then used to determine mesocosm conditions that reflect the low salinity and temperature conditions that result from high meltwater input (runoff and icebergs) from the GrIS during the summer. Salinity throughout the region ranged from 32.5 in the marine environment to 0 at the inner fjord, near tidewater glacier outputs (Table 1). In well mixed areas salinity could be 25.5 at 10 m (S24, Table 1). A value of 22 was used for the low salinity 'fjord' treatment while 33 was used for the 'marine' salinity. Temperature in the region ranged from 0 ºC to 11 ºC in summer, 2015 (Table 1) so low temperature ‘fjord’ treatments were set at 4 ºC and 'marine' treatments were 7 ºC. The four mesocosms reflected summer marine (control, 7 ºC and 33), low salinity (7 ºC and 22), low temperature (4 ºC and 33), and fjord conditions (4 ºC and 22) (Table 2). Sub-tidal light levels were measured in August 2015 adjacent to the Akia peninsula at 10-m depth using an Odyssey PAR logger (400-700 nm resolution) and ranged between 101- 196 µmol photons$\cdot$ $m^{-2} \cdot s^{-1}$ at midday. Total alkalinity (A_T) in the Nuuk area and beside the Akia Peninsula was 1845.54 µmol $\cdot$ kg^{-1} and 1651.59 µmol $\cdot$ kg^{-1} respectively during a flood tide, August 2016, which is low compared to the average for Greenland (2220-2260 µmol $\cdot$ kg $\cdot$ SW^{-1} units; Lee et al. 2006). Measurement of sea water alkalinity took place

at the University of Glasgow using 12-mL preserved samples following the A_T anomaly methodology described below.

The marine-fjord mesocosm experiment with *L. glaciale* began on 28 September, 2015 and ended on 8 September, 2016 (346 d). Each mesocosm was constructed using 200-L aquaria with a Teco TK15 recirculating chiller outfitted with a Vecton 120 nano UV sterilizer. Rio400 water pumps were used to maintain water flow within the aquaria and filter particulate material out of the water column. Light levels were consistently kept between 88-98 μmol photons · m^{-2} · s^{-1} (measured with Odyssey PAR logger) and daylight hours were adjusted to follow annual patterns for the Nuuk region (4-21 daylight hours). Mesocosm parameters were monitored throughout the year with an YSI DO and salinity probe (YSI Pro 2030, USA), VitalSine pH probe (Aquasonic, AU) (Table 2), and A_T was calculated periodically after January 2016 to ensure water chemistry remained stable (Table 2). Partial water changes were conducted once a month to ensure nutrient levels were consistent throughout the experiment (source Field Studies Council, Millport, Scotland), but sea water was never enriched. At the onset of the experiment large burrowing organisms, such as clams and sponges, were removed from each rhodolith with tweezers so that metabolic activity in the mesocosms would primarily be a product of the maerl itself. Biofilm communities were disturbed by lightly brushing the individual with a sterilized toothbrush once a month to mimic natural herbivory and prevent overgrowth on each individual.

Calcification

Daily calcification was measured using the A_T anomaly technique first described by Chisholm and Gattuso (1991). In all incubations individual maerl and rhodoliths were weighed (wet weight, WW), placed in 140-mL air tight containers with sea water, and kept in

ambient or mesocosm treatment conditions for 24-h. Incubations in natural conditions had a light: dark cycle representative for the time of year at Nuuk, Greenland, and were done directly after collection. In 2015, 'field' measurements with *L. glaciale* were collected in the intertidal next to a field camp in the Akia Peninsula (maximum natural light at 120 µmol photons · m^{-2} · s^{-1}, ~ 4 ºC). In 2016, 'cold room' measurements took place with both coralline algae species in the GINR cold room at 2 - 4 ºC with 98 µmol photons · m^{-2} · s^{-1} of down-welling light to reflect *in situ* conditions. For all treatments a control incubation was run without algae to account for fluctuation of A_T in the water column. Day (8 h) and night (16 h) incubations were conducted in each treatment to determine whether calcification rates were higher during light hours. The annual light cycle was disrupted to ensure all night incubations were conducted in complete darkness.

To measure A_T, sea water samples were taken prior to and directly after the incubations using two methods: 1) in Greenland field and cold room incubations 12-mL sea water samples were siphoned into Exetainer® (Labco, UK) vials and poisoned using $HgCl_2$ to stop biological activity (Dickson et al. 2007), and 2) at the University of Glasgow, 100-mL samples from mesocosm incubations were kept in a cool dark area and processed immediately to measure accurate A_T of sea water samples. Titrations were conducted following the methodology of Yao and Byrne (1998) using a 0.1 M HCl 0.6M NaCl titrant with an 848 Titrino plus potentiometric titrator (Mettler Toledo) and a sulfonephthalein indicator, Bromocresol green, with a DR5000 spectrometer (HACH, Canada). A_T was then calculated using the mass of titrant and pH of each sample calculated by absorbance at λ444 and λ616 (Breland and Byrne 1993). $A_{T\ start}$, $A_{T\ end}$, WW, incubation time (*t*, h), and volume of airtight incubation container (V, L) were used to calculate net calcification in µmol $CaCO_3$ · g $algae^{-1}$ · h^{-1} (eq 1, from Martin and Gattuso 2009).

$$G = (-(A_{T\,start} - A_{T\,end} - \Delta control) * V / (2*WW*t)) *1.025 \quad (1)$$

Calcification is expressed as a rate (G (µmol $CaCO_3 \cdot g^{-1} \cdot h^{-1}$)) for ease of comparison across treatments in natural conditions. In 2015, incubations were conducted in the field twice with *L. glaciale* from Akia Peninsula and then Købbefjord (n = 5 for both incubations). Calcification incubations in mesocosms took place in March, May, June, and September (n = 5 per treatment), and mesocosm day and night incubations took place in May and June (n = 5 per treatment) when light levels were increasing and we suspected individuals to have measurable productivity. In 2016, cold room incubations were repeated with *L. glaciale* from Akia Peninsula and Købbefjord (n = 9 from both locations), and *Clathromorphum* sp. from sites 124 and Dive 14 (n = 9 from both locations; Figure 1). We referred to individuals in field incubations as a 'holobiont' because infaunal organisms and biofilm organisms were also likely to be influencing our measurements of metabolic activity (Egan et al. 2012).

Primary production

PAM fluorometry was used to evaluate photosynthetic health of individuals *in situ* and across experimental treatments as this approach has previously been used successfully with polar coralline algae (Schwarz et al. 2003, Schwarz et al. 2005, Schoenrock et al. 2016). We used a DIVING-PAM fluorometer (Walz, Germany) and a 5-mm blue light diode to make measurements on the outer branches of individual maerl in Greenland (2015) and in mesocosm experiments. In the field (2015) Fv/Fm of *L. glaciale* was measured hourly from 0800 - 1800 to determine the dynamics of energy uptake in this species. A midday depression in Fv/Fm, but recovery period thereafter, shows dynamic photoinhibition is correlated with high PAR, which is typical for Arctic species (Hanelt and Nultsch 1995). In mesocosm

experiments PAM fluorometry measurements (RLCs) were taken between 1200 and 1400 during this midday depression. Fluorometry was used eight times throughout the incubation (n = 5 per treatment; December, January, March, April, May, June, July, and September) to evaluate the seasonality of photosynthetic characteristics across treatments and ensure the maerl were alive. From RLCs we use the effective yield (Y') at each irradiance level (PAR) to calculate relative electron transport rate (rETR; eq 2) at each irradiance and fit these values to Jassby and Platt's fit model (Jassby and Platt 1976). Using this model, parameters of the light curve including maximum electron rate between PSII and PSI ($rETR_{max}$), photosynthetic efficiency (α), and E_k were calculated as follows:

$$rETR = 0.5 * Y * PAR \quad (2)$$

Primary production was quantitatively measured as net O_2 production rate (mg $O_2 \cdot L^{-1} \cdot h^{-1} \cdot$ g $algae^{-1}$) during 24-h calcification incubations with *L. glaciale* (closed system) in both mesocosm experiments (n = 5 per treatment) and in the cold room incubations with both *L. glaciale* and *Clathromorphum* sp. 'holobionts', 2016 (n = 9). A YSI DO probe (YSI Pro 2030, USA) was used to measure % O_2 in seawater at ambient temperature prior (P_{start}) to the incubation and after incubation (P_{end}). A control container was always used to compensate for non-coralline respiration or productivity in the water column (R). Each % O_2 was converted to mg O_2 and production was calculated using WW, time (*t*, h), and volume (V, L; eq 3).

$$O_2 \text{ production} = ((P_{end}-P_{start}) + R) / t * V * WW \quad (3)$$

Measurements were calculated as a rate to compare across treatments when incubation times were slightly variable.

Growth

Growth of individuals was measured in mesocosm experiments using change in mass over time (n = 5 per treatment). Individuals were patted dry and weighed 12 April, 2016 (WW_{start}, mg) and again on 8 September, 2016 (WW_{end}, 153 d). This experimental period was chosen because it has been noted that maerl grow primarily during summer months when there is greater light availability (Adey 1970, Adey and Mckibben 1970). Growth (μ) was then calculated as a function of percent change in WW over time (*t*) in order to account for variation in growth due to size of the organism (eq 4).

$$\mu = ((WW_{end} - WW_{start}) / WW_{start}) / t \qquad (4)$$

Statistics

We considered 'field' incubations during August 2015 and 2016 to represent *in situ* calcification and primary productivity of these coralline algae species. A repeated measures MANOVA was used to determine impacts of the independent variables temperature and salinity on calcification and DO production of individuals in mesocosms over four time periods (SPSS v23, IBM). A repeated measures MANOVA was used to determine significant differences in day vs. night calcification rates at two time periods in mesocosm treatments (SPSS v23, IBM). PAM fluorometry measurements in mesocosms (E_k, $rETR_{max}$, and α) were compared across treatments over the eight sampling periods using a repeated measures MANOVA (SPSS v23, IBM). Growth was compared across treatments using a fixed-effect model, 2-way ANOVA (SPSS v23, IBM) and the Holm-Sidak pairwise multiple comparison posthoc test. All data met the assumptions of normality and equality of variance prior to running each test.

RESULTS

Calcification

Calcification rates in natural conditions were low, indicating daily summer calcification values ranging from net dissolution to max 1.225 µmol $CaCO_3 \cdot g^{-1} \cdot h^{-1}$ in *L. glaciale* and *Clathromorphum* sp. (Table 3). In 2015, *L. glaciale* calcification rates were 10-fold lower than in 2016, which may be because cold room incubations occurred 10 - 20 days later in the month that year (natural cycle seen in marine treatments of the mesocosm). Twenty four hour calcification rates of *L. glaciale* in mesocosm treatments from March - September showed that calcification changed throughout the summer, and rates were significantly reduced in low salinity and temperature treatments (repeated measures MANOVA, $F_{3, 16} = 5.185, 4.013$, $p = 0.013, 0.03$ respectively; Figure 2a). *L. glaciale* in marine treatments (7 °C and 33) increased calcification rates through summer, but rates declined with the onset of autumn (Figure 2a). Calcification rates of *L. glaciale* in other treatments fluctuated over time; individuals in fjord (4 °C and 22) and low temperature (4 °C and 33) treatments had reduced calcification rates and did not display the seasonal pattern observed in individuals exposed to marine treatments (Figure 2a). Calcification rates of *L. glaciale* in low salinity (7 °C and 22) treatments were highly erratic with large variation between individuals (Figure 2a). Night calcification rates were frequently greater than daytime calcification rates in *L. glaciale* from all but marine treatments (repeated measures MANOVA, $F_{3, 16} = 9.88$, $p = 0.006$). Individuals exposed to low temperature and fjord treatments had negative to low calcification rates during the day which significantly increased over the May and June night measurements (repeated measures MANOVA, $F_{3, 16} = 22.793$, $p < 0.001$; Figure 3), while individuals in low salinity treatments had erratic calcification patterns with the highest calcification rate on average at night in May and the lowest rate during the day in June (Figure 3).

Primary production

In individuals from all treatments values of α changed significantly over the year, generally increasing from November to January and decreasing from June to September (time, repeated measures MANOVA, $F_{7, 10} = 46.952$, $p = 0.000$; Figure 4a). Individuals in low salinity treatments had variable α values during November and January and lower values of α in March to June (repeated measures MANOVA, $F_{7, 10} = 3.288$, $p = 0.044$; Figure 4a). Individuals in low temperature treatments significantly increased α in January, but lower values, comparable to marine treatments, were measured the rest of the year (repeated measures MANOVA, $F_{7, 10} = 3.686$, $p = 0.032$). The combination of low temperature and salinity in fjord treatments reduced the effect of hyposaline conditions on *L. glaciale*, and α values were consistently lower in fjord than marine treatments (repeated measures MANOVA, $F_{7, 10} = 3.715$, $p = 0.031$; Figure 4a). Average $rETR_{max}$ in *L. glaciale* from each treatment changed significantly over time (repeated measures MANOVA, $F_{7, 10} = 21.962$, $p < 0.000$; Figure 4b), and was significantly reduced in individuals exposed to low salinity (including fjord treatments) at many time periods beginning in March (repeated measures MANOVA, $F_{7, 10} = 4.594$, $p = 0.015$; Figure 4b). In marine treatments, E_k fluctuated significantly over time, decreasing from November to June and gradually increasing June to September (repeated measures MANOVA, $F_{7, 10} = 13.98$, $p = 0.000$; Figure 4c). *L. glaciale* in low salinity, low temperature, and fjord treatments generally had lower E_k values than individuals in marine treatments (repeated measures MANOVA, $F_{7, 10} = 3.653$ and 13.039, $p = 0.036$ and 0.000 respectively), but individuals exposed to fjord treatments in January and low salinity treatments in March had unusually high average E_k (Figure 4c).

Average values of net respiration were observed in 24-h incubations with holobiont *L. glaciale* and *Clathromorphum* sp. in the cold room incubations (Table 3). In mesocosms

treatments, O_2 production significantly decreased in individuals exposed to low salinity, and fluctuated from May to September (repeated measures MANOVA, $F_{3, 16} = 3.642$ and 3.76, p = 0.039 and 0.036 respectively; Figure 2b). Individuals in marine treatments increased O_2 production over the summer months and then decreased production levels to net respiration by September (Figure 2b). Productivity of individuals in low salinity treatments continually indicated net respiration, and decreased O_2 production by September (Figure 2b). Maerl in low temperature treatments had O_2 production levels greater than marine treatments, which increased through summer, decreasing in September maintaining net production (Figure 2b). Individuals exposed to fjord treatments had high O_2 production rates in May, but production decreased through the summer to net respiration (Figure 2b).

Growth

Net growth only occurred in marine conditions, where average growth rates of *L. glaciale* were 1.85 ± 1.73 mg · d^{-1}. There was a significant interaction between the two fixed factors indicating temperature effects were impacted by salinity (2-way ANOVA, $F_{3, 16} = 5.246$, p = 0.033), but there was no significant effect of temperature or salinity alone (2-way ANOVA, $F_{3, 16} = 2.754$ and 0.525, p = 0.113 and 0.477 respectively). Individuals kept at 4 °C had a lower growth rate than individuals in fjord treatments (Holm-Sidak posthoc test, t = 0.446 and t = 2.132, p = 0.011 and p = 0.046 respectively). In low temperature treatments, average growth rates of individuals were the lowest at -16.56 ± 8.18 mg · d^{-1}, followed by average growth rates of -5.447 ± 1.68 mg · d^{-1} in individuals exposed to low salinity treatments, and average growth rates of -2.51 ± 3.76 mg · d^{-1} in individuals exposed to fjord treatments. Extrapolating average growth rates of individuals in marine treatments, *L. glaciale* has the potential to increase its biomass by 43.8 to 1310 mg · y^{-1} in marine conditions.

DISCUSSION

This study describes the environmental factors that affect the physiology of *L. glaciale* and provides the first record of photosynthesis and calcification for both *L. glaciale* and *Clathromorphum* sp. in natural conditions for southwestern Greenland. Annual patterns of primary production and calcification in *L. glaciale* indicate that the species can tolerate low temperatures, and may even become more productive under these circumstances. By contrast, individuals subject to low salinity are not productive (net respiration in incubations) and have low calcification rates. This study also highlights the low *in situ* calcification and O_2 production rates in both *L. glaciale* and *Clathromorphum* sp. and the occurrence of greater calcification rates during night rather than day. This information on the ecophysiology of both *Clathromorphum* sp. and *L. glaciale* makes a valuable contribution to understanding biogeography of species around Greenland, paleoclimate reconstructions, and community ecology. Further, quantifying the physiological response of *L. glaciale* to high melt conditions is important for predicting future range restrictions that may be expected with increased precipitation, glacial surface melt and calving in Greenland's climate systems (Bintanja and Andry 2017).

Glacial melt is accompanied by low salinity and temperatures, which can restrict metabolic processes in algae including the corallines (Hurd et al. 2014). Coralline algae are rare near the GrIS and only found in crustose morphologies (Schoenrock pers. comm.), most likely because fjord conditions are sub-optimal for coralline algae. Aside from cold, hyposaline conditions free-living coralline algae cannot withstand heavy sediment loads, or smothering, which can be a product of sedimentation from high subglacial meltwater discharges or anthropogenic inputs including sewage and tidal disruption (Wilson et al. 2004). Low abundance of this species in Godthåbsfjord, near the marine environment, is likely due to the

pulses of low salinity glacial melt water entering the fjord system during the summer to autumn months. Evidence for this is the low O_2 production and calcification rates measured, the less efficient α values (but erratic trends across the year, Figs. 2, a-b, and 4a), and negative growth over the year in individuals exposed to low salinity mesocosm treatments. The salinity tolerance of other polar seaweeds, such as eulittoral Chlorophyta in Antarctica, is due to regulation of cellular osmolytes, which range from inorganic-organic compounds (including potassium ions, carbohydrates, and DMSP), which allow these species to tolerate a range of 7-102 psu (Jacob et al. 1991, Karsten et al. 1992). DMSP is a known cryoprotectant that increases concentration with lower temperatures (Karsten et al. 1996) and is commonly found in coralline algae (Malin and Erst 1997)**.** Regulation of DMSP and other osmolytes was not investigated in this study, but DMSP in *L. glaciale* has been investigated before by Burdett et al. (2015) in a 21-day study that indicated DMSP concentrations were not influenced by salinity in a Scottish habitat and may not function as an osmolyte in this species. Future study on the role of DMSP in temperature tolerance of polar *L. glaciale* ecotypes could be pertinent because of the negative physiological effects on *L. glaciale* in low salinity conditions.

Temperature and light are commonly the primary factors controlling distribution of other coralline algae communities in the North Atlantic (Adey and Adey 1973). *L. glaciale* persists in low temperature and low light habitats, for instance beds dominated by *L. glaciale* are prominent in low light conditions from Greenland to Svalbard (Teichert et al. 2012), and primary production (measured through O_2 production) was positive at low temperatures in this study. A pilot study investigated linear extension of *L. glaciale* from Svalbard at low light and found greatest growth in individuals at 4 °C (L. Hofmann, pers. comm.). In contrast, the lowest growth rates in this study were seen in individuals exposed to low temperature,

then low salinity, and then fjord conditions, suggesting temperature restricted growth rate but salinity ameliorated negative effects. Individuals in low temperature treatments had positive O_2 production (sometimes greater than 'marine' individuals) and calcifying rates (Figure 2a-b) indicating that energy produced was not necessarily going into growth. The energy created through increased productivity (noted by increase in O_2 production) may go into other metabolic processes that draw away from investment in biomass such as reproduction (Edyvean and Ford 1987, De Wreede and Klinger 1988). We noted the appearance of conceptacles and spore settlement in each treatment but did not quantify reproductive effort to compare investment. Sloughing occurred around reproductive structures on branches, which was not previously recorded for *L. glaciale* (Freiwald and Henrich 1994). Overall *L. glaciale* has broad temperature tolerance because it dominates marine habitats (Loch Sween, Scotland; Kamenos et al. 2004, Donohue 2015) in temperate waters where higher average temperatures prevail.

Calcification and O_2 production in *L. glaciale* occur independently in the day vs. night incubations, demonstrating that dark calcification is an important process, and contributes to a significant portion of net calcification in some individuals over a 24-h period (Figure 2a, Figure 3). Of all incubations, the highest calcification rates of *L. glaciale* were in dark, low salinity treatments during June (Figure 3), which was a higher rate than measured in 24-h incubations and may indicate a compensatory action after stress during light hours, as net dissolution or weight loss was measured in the growth of individuals in this treatment. Yet, dark calcification is not uncommon in coralline algae; it contributes to net calcification in temperate intertidal corallines around the world (McCoy et al. 2016, Williamson et al. 2017). Our results suggest that calcification is not reliant on photosynthesis in this cold-water species, contradicting the broad assumption that they are strongly linked in calcifying

autotrophs (Borowitzka 1981). For dark calcification to occur carbonate, a precursor for precipitation of $CaCO_3$ extracellularly, may be in abundance in the environment (Borowitzka 1981), as noted in a study with rockpool species in the UK (Williamson et al. 2017). Further, Hofmann et al. (2016) found evidence for a Ca^{2+}/H^{+} pump in a tropical *Porolithon* sp. which drove light-mediated, but photosynthesis independent, net uptake of Ca^{2+} throughout the day. Calcification mechanisms in corallines have been investigated using targeted microsensors to define the characteristics of the algae microenvironment (Hofmann et al. 2016) and similar methodology should be used to measure this in polar species to provide insight into species adaptation to extreme polar environments.

The calcification and O_2 production of both coralline algae species as a 'holobiont' (without removal of embedded organisms or biofilms) was very low, signifying coralline habitats are not productive systems. Results indicate that calcification in these species may result in maximum accretion of 0.73 g $CaCO_3$ g $maerl^{-1} \cdot y^{-1}$ in *Clathromorphum* sp. and a maximum accretion of 447.13 g $CaCO_3$ g $maerl^{-1} \cdot y^{-1}$ in *L. glaciale*. In the mesocosm study, calcification and growth rates of *L. glaciale* in the marine treatments and in natural conditions were like previous measurements in the Arctic (Freiwald and Henrich 1994, Büdenbender et al. 2011, Teichert and Friewald 2013), but lower than those recorded at 4 °C in Scotland (Donohue 2015). The growth rate projected for individuals here, especially *L. glaciale*, cannot be extrapolated to m^{-2} as most studies do because there are no records for density of individuals. This is the first record of net dissolution of algal individuals in natural conditions (mostly *Clathromorphum* sp.), which is novel because this is only projected to occur when aragonite saturation levels are between 0.9-1.1 (specifically in *L. glaciale*; Büdenbender et al. 2011). These saturation levels are anticipated to be reached during 2030-2050 for the high Arctic (IPCC 2013), so it is more likely that other calcifying organisms or the microbial

community (Lewis et al. 1985, Freiwald 1995) of the holobiont are adding or detracting from the calcification rate calculations. When we compare mesocosm incubations to measurements in natural conditions, *L. glaciale* in marine treatments (without the associated invertebrates, i.e. clams and sponges) grew at rates of 1.31 g to 43.8 mg individual^{-1} · y^{-1}, a lower estimate than natural measurements which may be due to handling individuals in an artificial environment. Recently, isotope analyses showed that marine detritus (kelp specifically) is an important nutrient resource in maerl bed habitats (Gabara 2014), perhaps even specifically to the maerl. Sediment and particulate organic matter (SPOM) is also important in maerl bed food webs (Grall et al. 2006), indicating that growing maerl in mesocosms probably deprived them of natural resources. Care should therefore be taken when comparing mesocosm results to outcomes from the studies in natural conditions.

Biofilms can play a major role in the ecosystem function of coralline algae. Freiwald (1993) proposed that biofilm bacterial species were recruiting herbivore larvae to maerl beds to prohibit kelp settlement in this habitat. Bacterial cues are shown to elicit settlement of invertebrates in sub-tropical maerl beds in the Gulf of California (Steller and Caceres-Martinez 2009). Cues for abalone larvae have been identified from both corallines and their biofilm communities on temperate reefs (Daume et al. 1999) and tropical reefs with coral larvae (Heyward and Negri 1999). Similarly, allelopathic compounds have been found in corallines and their biofilm communities, preventing the settlement and growth of other algal species in temperate and tropical systems (Suzuki et al. 1998, Kim et al. 2004, Gomez-Lemos and Diaz-Pullido 2017). Interactions of this sort in polar habitats are not known, but organisms in the biofilm, or diffusion boundary layer, certainly contribute to the algal microenvironment (Hurd 2000). Microbial communities could contribute to cell wall sloughing and breakdown and have been linked to decomposition processes (bacterial

oxidation) of the epiphytic communities on algae (Lewis et al. 1985, Freiwald 1995), contributing to net respiration of the maerl holobiont. Because mesocosm treatments were not axenic, the effect biofilms may have had on *L. glaciale* could not be determined. Environmental factors can determine the community composition of biofilms (Lachnit et al. 2009), which may alter metabolic activity of the holobiont depending on the function of the bacteria.

PAM fluorometry was helpful in assessing the characteristics of the photosynthetic apparatus throughout the year, which can inform how this species responds to the annual light cycle in southwestern Greenland. When we combine PAM measurements with daily O_2 and calcification incubations, primarily in marine treatments, trends indicate that *L. glaciale* is a seasonal responder increasing its productivity with increased light hours in its environment. In all treatments, peak $rETR_{max}$ occurred in late winter-early spring, and decreased through summer. E_k decreases over time (from the beginning to end of the experiment) but peaks again in summer, responding to longer day lengths. Individuals have efficient levels of α in winter-spring, but become inefficient at the end of summer. This seasonal increase in productivity in the spring supports pulses of annual growth that have repeatedly been used in paleoclimate reconstructions (Kamenos et al. 2012), though high pCO_2 can obscure the use of Mg/Ca as a temperature proxy in the carbonate skeleton of *L. glaciale* (Raggazola et al. 2016). Investigation into the diurnal patterns of calcification in these organisms and carbonate chemistry of their environments is warranted, especially on an annual scale, to determine how these organisms persist within and dominate Arctic marine habitats despite low productivity and calcification.

We were particularly interested in the physiological performance of both coralline algae species in their natural environment to determine whether the dominance of *Clathromorphum* sp. in coralline algae beds was due to superior photosynthetic effort and calcification in the environmental conditions of Godthåbsfjord. Measurements of holobionts show that *L. glaciale* was more productive and had a higher calcification rate than *Clathromorphum* sp., leaving us with many questions about the ecophysiology of *Clathromorphum* sp. and ecological interactions such as grazing and competition. Competition could begin with settlement and growth of free-living coralline algae; species differentially colonize the variable size classes of sediment that form the core of a rhodolith (pebbles, stones, etc.), and the inner species of the rhodolith or maerl may also be different from the exterior species (Bosence 1983b). Along with the negative influence of low salinity, it is possible that *L. glaciale* requires a specific composition of sediment to promote spore settlement and bed formation. Importantly, little is known about competitive interactions between free-living coralline algae, though crustose corallines exhibit herbivore mediated competition for space in the intertidal zone (Steneck et al. 1991) and natural succession occurs in coralline communities (Steneck 1986, Matsuda 1989). In Svalbard individual *L. glaciale* can house up to 59 species of invertebrates (Teichert et al. 2012), and hollow rhodoliths are especially important, dominated by crustaceans, echinoderms, and mollusks like the Arctic clam (Teichert 2014). In Nova Scotia, *L. glaciale* beds house a diverse array of species that are dominated by brittle stars and chitons (Gagnon et al. 2012), which are also the key dominant taxa found in Norway (Freiwald and Henrich 1994). *Clathromorphum* sp. dominance could be facilitated by similar faunal assemblages, as herbivores like the common urchin are 10 times more abundant in coralline algae habitats than kelp forests in the Godthåbsfjord region (Schoenrock pers. comm.). Further research should be done to assign liability to grazers in these habitats.

Climate change followed by an increase in fishing pressure and commercial traffic throughout the Arctic is a threat to polar communities. An air temperature increase of 6 to 8 °C is predicted by 2100 for west Greenland (Rysgaard et al. 2003) and freshwater input has been increasing from the glaciers that flow into Godthåbsfjord (Juul-Pedersen et al. 2009, Van As et al. 2014). Increased runoff and decreased water transparency is a threat for *L. glaciale* in Svalbard where beds structure communities at 30-50 m depth (Teichert and Friewald 2013), and ocean acidification reduces productivity of *L. glaciale* from this region (Büdenbender et al. 2011) as well as the growth and structural integrity of the skeleton (Ragazzola et al. 2012, 2013). In Greenland, coralline algae are likely to be exposed to high melt from the GrIS, and increased runoff which will both decrease the temperature and salinity of their habitats (Bintanja and Andry 2017). Increased ice sheet melt could result in conditions where organisms reach the limit of their thermal tolerance, where low survival temperature (LST) and low salinity would create difficult conditions for physiological processes. In this study low salinity has a negative influence on *L. glaciale* physiological performance, which may explain its low abundance in Godthåbsfjord and potentially restrict larger populations around Greenland and the Artic in predicted climate future (Brodie et al. 2014). High levels of fishing traffic could cause greater disturbance to benthic communities (Barbera et al. 2003), though trawling currently occurs outside of rhodolith depths (Jørgensbye and Halfar 2017). Future work should investigate the microscale mechanisms of calcification in these species, and determine where the substrates and energy for this process are derived from. Further effort should be made to investigate *Clathromorphum* sp. from this region to see if annual growth and productivity occur at competitive rates with those of *L. glaciale* in hyposaline and colder environments. Studying the biodiversity of these habitats

could add further insight into how faunal assemblages and species may be preventing *L. glaciale* from establishing itself in marine habitats immediately around Nuuk.

Data is available through the University of Glasgow data repository, accessible via the UofG library system: http://dx.doi.org/10.5525/gla.researchdata.645

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FIGURES

Figure 1. Map of the fjord system from the Kangiata Nuňata Sermia glacier to the seaward islands outside of Nuuk (star). Small dots indicate SONDE sampling sites (Table 1) and large dots indicate coralline algae collections sites (note Købbefjord is a SONDE and maerl collection site, Table 1). Inset is an orientation to the Nuuk region within Greenland.

Figure 2. Average a) calcification and b) O_2 production rates of *Lithothamnion glaciale* in mesocosm treatments at four sample periods from May-September (n = 5, mean ± SE).

Figure 3. Day vs. Night calcification rates of *Lithothamnion glaciale* in mesocosm treatments during both May and June (n = 5, mean ± SE).

Figure 4. PAM fluorometry measurements a) photosynthetic efficiency (α), b) $rETR_{max}$, and c) E_k of *Lithothamnion glaciale* in mesocosm treatments represented by group average (n = 5, mean ± SE).

TABLES

Table 1. Values for temperature, salinity, dissolved oxygen (DO) and pH from multiple sites (n = 1 per site) throughout the fjord system from Kangiata Nuňata Sermia to seaward islands of Godthåbsfjord taken in August, 2015. All measurements were taken at a depth of ~0.5-11-m using a multi-parameter sonde (YSI) outfitted with temperature, salinity, DO, and pH probes.

Site	**Depth (m)**	**Salinity**	**Temperature (°C)**	**DO (O_2 mg · L^{-1})**	**pH**
Marine					
Købbefjord	0.28	28.08	6.404	11.95	8.09
S76	6.251	31.87	4.508	10.84	7.95
S59	4.747	29	7.279	10.77	8.22
Avg		29.65	6.06	11.19	8.09
Kangersunneq-Godthåbsfjord					
S9	5.335	28.05	2.96	11.94	8.18
S20	6.496	27.61	5.48	13.02	8.29
S30	10.198	30.31	-0.01	13.22	8.13
S32	9.337	30.54	0.03	8.92	8.09
S33	9.257	29.39	0.30	9.07	8.08
S24	5.84	25.62	11.54	9.50	8.13
S16	5.114	29.84	3.70	12.47	8.17
S31	11.157	30.60	0.08	8.35	8.50
S64	9.695	29.77	5.35	9.77	8.13
Avg		30.07	3.04	10.20	8.27
Ameralik					
S66	9.47	32.55	5.20	10.73	8.21
S69	9.716	32.43	5.13	11.29	8.18
S70	10.433	32.44	4.42	11.46	8.15
Avg		32.47	4.91	11.16	8.18

Table 2. Dissolved oxygen (DO), temperature, salinity, pH and A_T (mean ± SE) of each mesocosm treatment throughout the 346-d experimental period. All DO, temperature, salinity and pH values were recorded five days a week in each treatment (n = 213 per treatment) and A_T was measured monthly (n = 10 per treatment).

	DO (mg O_2 · L^{-1})	Temperature (°C)	Salinity	pH	A_T (µmol · kg^{-1} SW)
Marine	107.13 ± 0.52	7.02 ± 0.04	32.0 ± 0.08	8.1 ± 0.02	2168.92 ± 25.41
Low salinity	106.75 ± 0.51	7.19 ± 0.04	22.48 ± 0.04	8.08 ± 0.02	1679.35 ± 44.82
Low temperature	112.34 ± 0.59	3.86 ± 0.05	31.58 ± 0.11	8.19 ± 0.02	2155.45 ± 37.84
Fjord	111.08 ± 0.65	4.32 ± 0.05	21.83 ± 0.03	8.04 ± 0.02	1690.08 ± 29.63

Table 3. Calcification rates of *Lithothamnion glaciale* and *Clathromorphum* sp. in natural conditions. In 2015 these rates were measured through incubations in field camps at ~4 ˚C under ambient light levels (n = 5, mean ± SE). In 2016 they were measured in incubations in a cold room with constant temperature of 2 - 4 °C, and ambient day: night light cycles (n = 9, mean ± SE).

Species	Year	Collection site	G (µmol $CaCO_3 \cdot g^{-1} \cdot h^{-1}$)	O_2 (mg $O_2 \cdot L^{-1} \cdot h^{-1}$)
L. glaciale	2015	Akia Peninsula	0.037 ± 0.182	----
L. glaciale	2015	Købbefjord	-0.194 ± 0.172	----
L. glaciale	2016	Akia Peninsula	1.107 ± 0.223	-0.023 ± 0.003
L. glaciale	2016	Købbefjord	1.225 ± 0.17	-0.007 ± 0.003
C. compactum	2016	Dive 14	-0.006 ± 0.009	-0.011 ± 0.001
C. compactum	2016	Site 124	0.002 ± 0.023	-0.004 ± 0.001

Figure 1:

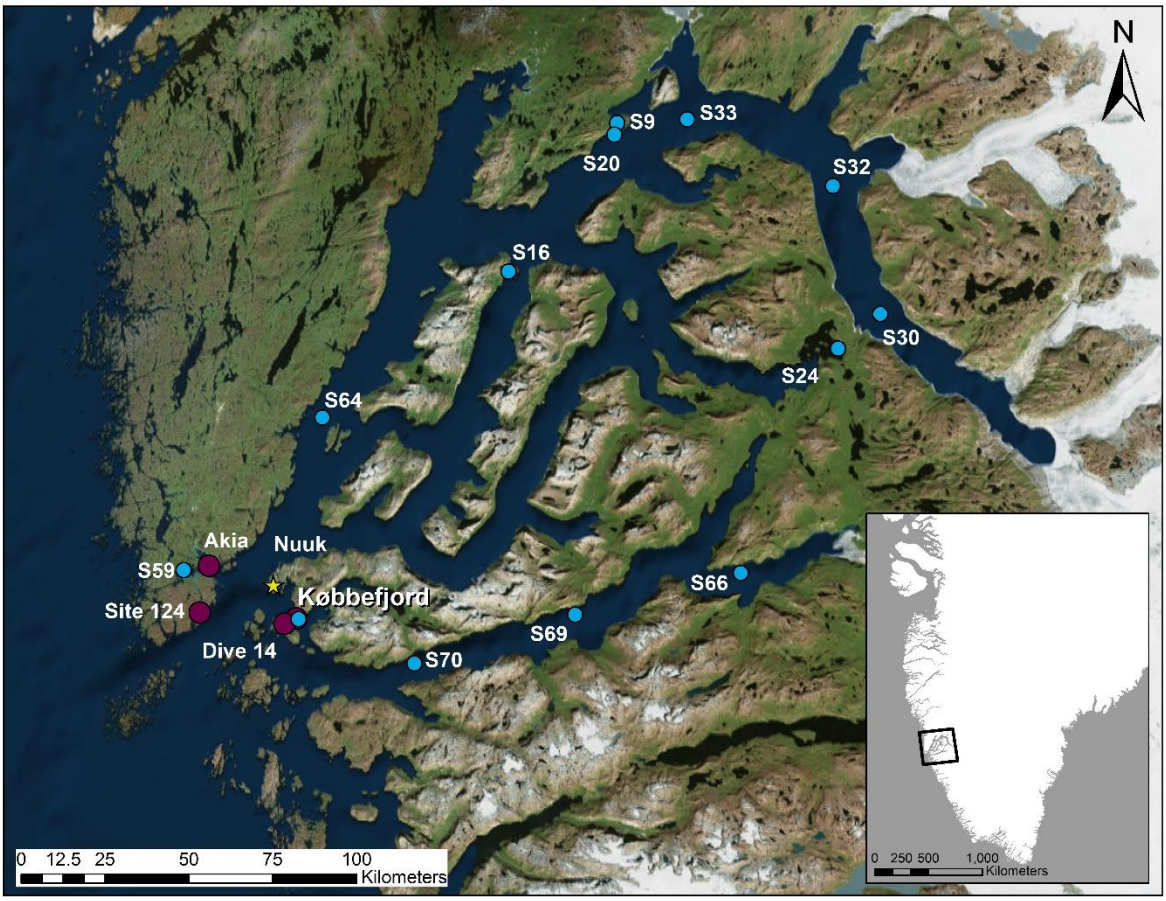

N
S9
S33
S20
S32
S16
S30
S24
S64
Akia
Nuuk
S59
Site 124
Købbefjord
Dive 14
S66
S69
S70
0 12.5 25 50 75 100
Kilometers
0 250 500 1,000
Kilometers

Figure 2

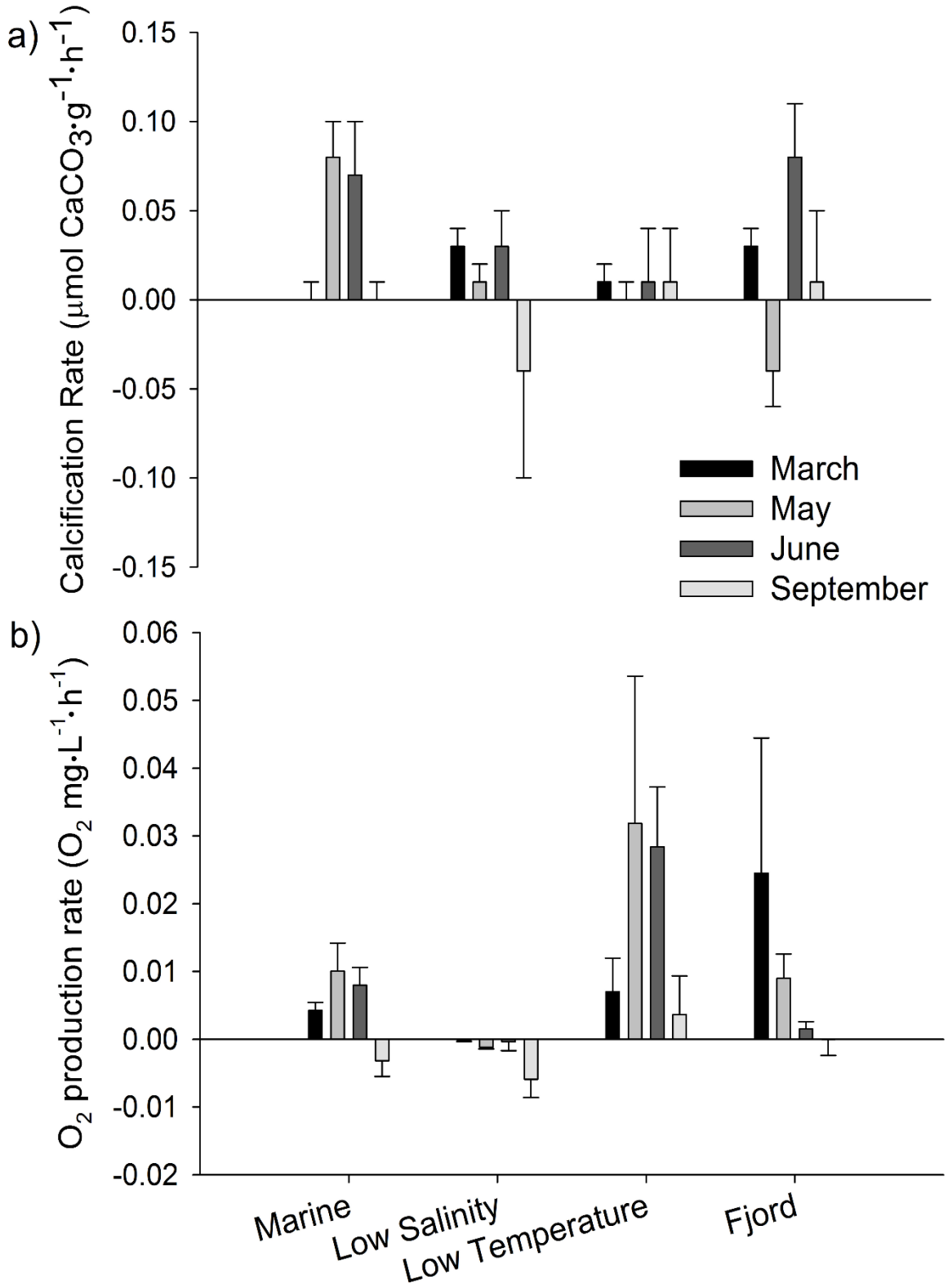

a)
Calcification Rate (µmol CaCO3·g-1·h-1)
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
March
May
June
September
b)
O2 production rate (O2 mg·L-1·h-1)
0.06
0.05
0.04
0.03
0.02
0.01
0.00
-0.01
-0.02
Marine
Low Salinity
Low Temperature
Fjord

Figure 3

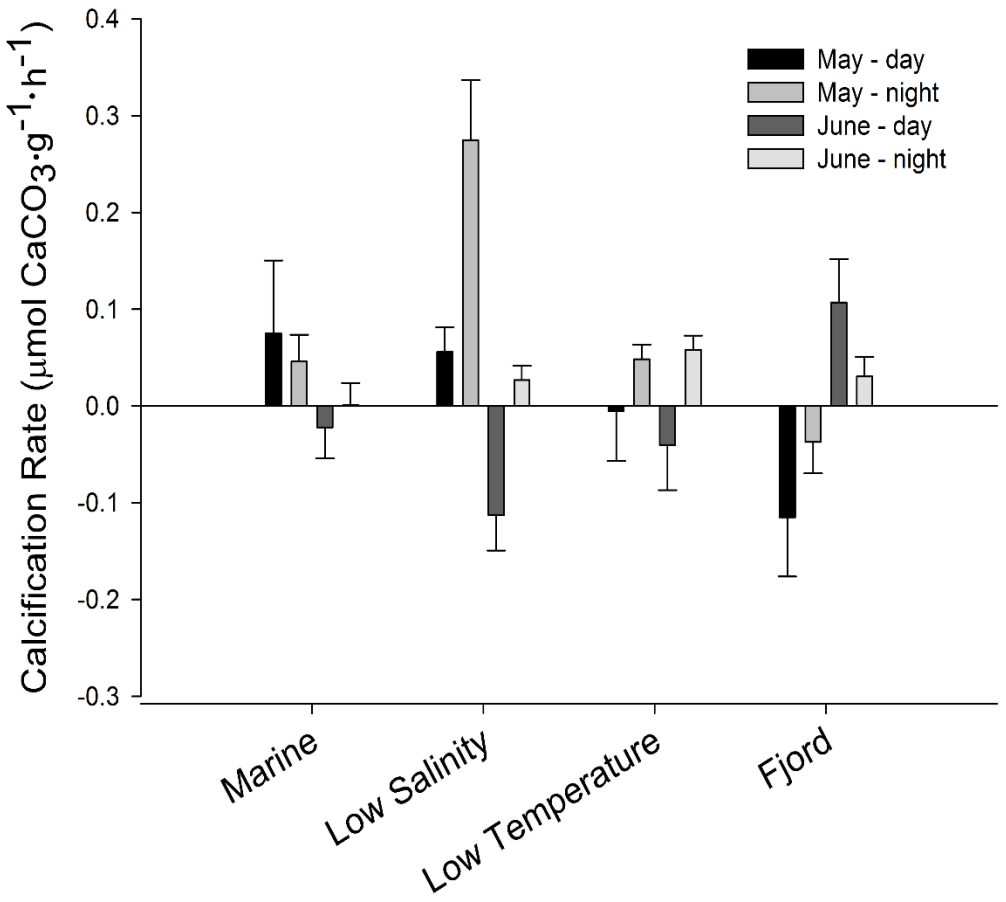
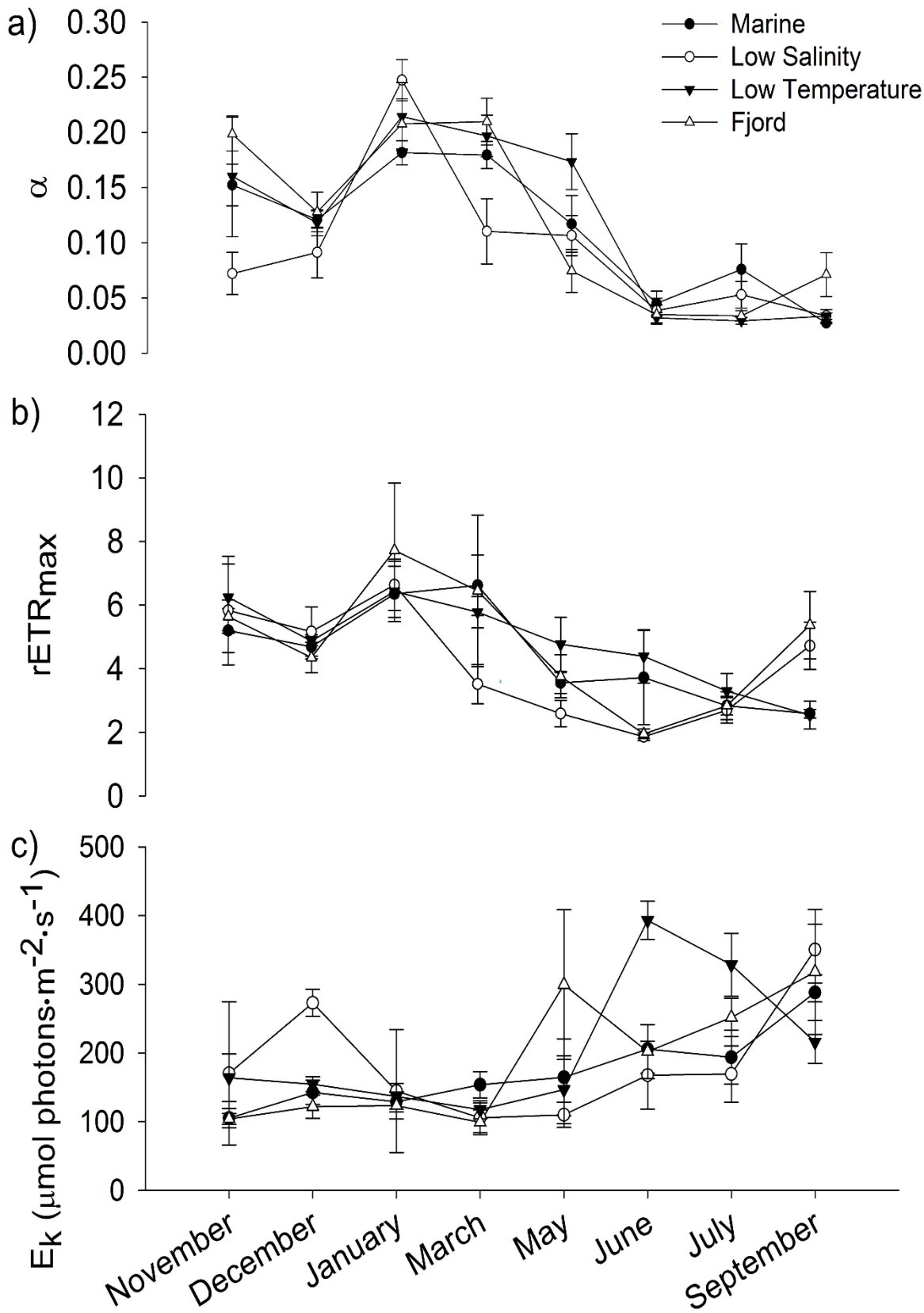

Calcification Rate (µmol CaCO3·g-1·h-1)
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
May - day
May - night
June - day
June - night
Marine
Low Salinity
Low Temperature
Fjord

Figure 4


a)
0.30
0.25
0.20
0.15
0.10
0.05
0.00
α
Marine
Low Salinity
Low Temperature
Fjord
b)
12
10
8
6
4
2
0
rETRmax
c)
500
400
300
200
100
0
Ek (µmol photons·m-2·s-1)
November
December
January
March
May
June
July
September