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1 Pigment composition and photoprotection of Arctic sea ice algae during  
2 spring

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RPH: Galindo et al.: Photoprotection of bottom Arctic ice algae

20

21 ABSTRACT: From the beginning of spring to the melt period, ice algae in the bottom of Arctic  
22 sea ice experience a large irradiance range, varying from <0.1% up to 25 or 30% of the incoming  
23 visible radiation. The increase in spring is usually rapid, with a varying photoacclimative  
24 response by bottom ice algae to protect themselves against excess light, such as changes in  
25 cellular pigment composition. This study focused on the temporal variation in pigment  
26 composition of bottom ice algae under 2 contrasting snow depths (thin and thick) during spring.

27 Controlled experiments were also carried out to investigate the photoprotective capacity of ice  
28 algae to relatively high irradiances during a short-term period (<6 h). Bottom ice algae were able  
29 to photoacclimate rapidly and effectively to irradiance ranging from 10 to 100  $\mu\text{mol photons m}^{-2}$   
30  $\text{s}^{-1}$ . However, we observed contrasting responses in photoacclimation depending on the ice algal  
31 community composition and their light history. Our experimental results suggest that the  
32 xanthophyll cycle (diadinoxanthin to diatoxanthin conversion) and D1-protein recycling play an  
33 important role in stabilizing photoprotection in ice algae. In addition, bottom ice algae likely  
34 employed a ‘cellular light-exposure memory’ strategy in order to improve their photoacclimative  
35 response to changing light exposure. According to our data, this process could be maintained  
36 over at least 2 wk. Hence, ice algae may be more resilient to varying light conditions than  
37 previously thought, and may be well-adapted for the expected future light regime changes  
38 associated with variability in snow and sea ice cover.

39 KEY WORDS: Arctic · Snow melt · Ice algae · Pigments · Photoacclimation · Light memory

## 40 INTRODUCTION

41 The ice algal community resides mostly in the bottom 10 cm of sea ice (Smith et al. 1990,  
42 Riedel et al. 2008, Juhl et al. 2011) and is largely dominated by diatoms (Poulin et al. 2011), a  
43 very abundant and productive group of unicellular algae (Malviya et al. 2016). Diatoms are  
44 successfully adapted to polar conditions due to their unique low-light acclimation (Petrou et al.  
45 2016, Lacour et al. 2017). Ice algae represent the initial and most significant source of primary  
46 production during the winter–spring transition in Arctic waters. They contribute 5–20% of total  
47 marine primary production in Arctic seasonally ice-covered waters (e.g. Michel et al. 2006,  
48 Arrigo et al. 2010, Loose et al. 2011) and >50% in perennially ice-covered waters (Legendre et  
49 al. 1992, Gosselin et al. 1997). Primary production of ice algae is influenced by many  
50 environmental variables such as temperature (Arrigo & Sullivan 1992), salinity (Ryan et al.  
51 2004), and nutrient availability (Lizotte & Sullivan 1992, Lavoie et al. 2005), but mainly by  
52 irradiance in the range of photosynthetically active radiation ( $E_{\text{PAR}}$ ; 400 to 700 nm), which is  
53 principally regulated by the thickness of snow and ice cover (Mundy et al. 2005, Aumack & Juhl  
54 2015) in addition to the annual cycle and cloudiness.  $E_{\text{PAR}}$  reaching the bottom of first-year sea  
55 ice is often <1% of incident irradiance (Arrigo et al. 1993, Lazzara et al. 2007) at the beginning  
56 of spring, and thus the ice algal community is adapted to perform photosynthesis under very low

57 irradiance (e.g. Cota 1985, Johnsen & Hegseth 1991, Köhl et al. 2001). However, the rapid  
58 increase in light intensity and day length from winter to the spring melt period (Sakshaug &  
59 Slagstad 1991) results in a rapid increase in  $E_{PAR}$  of up to 25 or 30% of incident irradiance at the  
60 bottom ice (Perovich 2005, Campbell et al. 2014), exposing the ice algae to a large range of  
61  $E_{PAR}$ . Light conditions can also change rapidly on a daily basis, mainly due to opposite and/or  
62 cumulative effects of melting and storms (rain or snow) that modify the snow cover thickness  
63 and optical properties. Furthermore, the acceleration of global warming in the Arctic affects  
64 snow and sea ice cover. Snow cover declined by 40% between 1989 and 2009 (Screen &  
65 Simmonds 2012, Overland et al. 2014) and during some periods, precipitation has switched from  
66 snow to rain (Comiso & Hall 2014), while sea-ice extent has retreated by 45% in the last 3  
67 decades (Screen et al. 2011, Stroeve et al. 2012). All of these changes, accompanied by an earlier  
68 melt onset (Markus et al. 2009), are expected to increase the  $E_{PAR}$  levels transmitted through the  
69 sea-ice cover. This increase in transmitted  $E_{PAR}$  is foreseen to enhance ice algal biomass (Poulin  
70 et al. 2011) and production (Wassmann et al. 2011), but ice algae may also face light stress (Leu  
71 et al. 2016, Petrou et al. 2016) which may be of importance since they are adapted to very low  
72 light levels.

73         In order to sustain photosynthesis under changing light conditions, ice algae use some  
74 photobehavioral (i.e. vertical migration in pennate diatoms; Aumack et al. 2014) and  
75 photophysiological features described as photoprotection and photoacclimation. These  
76 photoprotective mechanisms allow algae to minimize oxidative photodamage generated by  
77 excess light exposure, and specifically to maintain photosystem II (PSII) photochemistry. They  
78 include changes in cellular photosynthetic and photoprotective pigment composition (Alou-Font  
79 et al. 2013), with an increase in antioxidant carotenes and xanthophylls depending on incident  
80 irradiance. On shorter time scales (i.e. <1 h) of light fluctuations, the most important  
81 photoprotective processes are the repair of damaged PSII (Petrou et al. 2010) and thermal  
82 dissipation of excess energy (Goss & Lepetit 2015). This process comprises a fast (seconds to  
83 minutes) enzymatic light-driven conversion of xanthophyll cycle (XC) pigments (Goss & Jakob  
84 2010). In diatoms, the XC consists of the de-epoxidation of diadinoxanthin (DD) to diatoxanthin  
85 (DT) (Brunet et al. 2011, Kuczynska et al. 2015). In polar conditions, the XC is very important  
86 for optimizing algal photosynthetic activity during the spring–summer transition when

87 transmitted irradiance at the ice–water interface increases (Kashino et al. 2002, Katayama &  
88 Taguchi 2013, Ha et al. 2016, Katayama et al. 2017).

89 As bottom ice algae strongly contribute to Arctic marine primary production during  
90 spring, several studies have described their photophysiological responses to a change in  $E_{PAR}$   
91 levels from winter to spring (e.g. Gosselin et al. 1985, Barlow et al. 1988, Kudoh et al. 1997,  
92 Manes & Gradinger 2009), through the spring season (e.g. Michel et al. 1988, Cota & Horne  
93 1989, Ban et al. 2006, Alou-Font et al. 2013) and from spring to summer (Rysgaard et al. 2001),  
94 with a special focus on the potential deleterious effects of ultraviolet radiation (UVR) (Enberg et  
95 al. 2015, Leu et al. 2016). A few works have also focused on the impact of change in snow cover  
96 on the photoacclimation of ice algae (Juhl & Krembs 2010, Lund-Hansen et al. 2014), but little is  
97 known about their capacity to acclimate to rapid light changes through pigment photoprotection  
98 (Kudoh et al. 2003, Katayama & Taguchi 2013, Petrou et al. 2016). Therefore, the main  
99 objectives of this study were to (1) determine the change in pigment composition including XC  
100 pigments related to the photoprotective response of the bottom ice algal community under 2  
101 dominant snow depths (thin and thick) from the beginning of spring to early summer, and (2)  
102 investigate the short-term photoacclimation response to an experimental light gradient of bottom  
103 ice algae acclimated to 2 snow cover sites.

## 104 MATERIALS AND METHODS

### 105 Study site, sample collection and experiments

106 The study was conducted on landfast first-year sea ice, located north of Davis Strait near  
107 Qikiqtarjuaq, Nunavut, Canada (67° 28' N, 63° 47' W; Fig. 1), as part of the Green-Edge project.  
108 Sea ice samples were collected for measurements of pigments every 2 d from 27 April to 6 July  
109 2015.

110 For the time series, ice sampling was performed at thick (>25 cm) and thin (15 to 20 cm  
111 less than thick snow) snow depths. Snow depth and ice thickness were measured on each ice  
112 sampling day with a ruler and an ice thickness gauge (Kovacs Enterprises), respectively.  
113 Transmittance of  $E_{PAR}$  at the ice–water interface was also measured on each sampling day (see  
114 details below). The bottom 3 cm sections were extracted from sea-ice cores using a 14 cm  
115 internal diameter ice corer (Mark V Coring System; Kovacs Enterprises). For pigment analysis,

116 at least 2 ice cores were extracted per snow site and pooled immediately in a dark isothermal  
117 container to avoid brine drainage losses. These ice core samples were melted in 0.2  $\mu\text{m}$  filtered  
118 seawater (FSW) (3 parts FSW to 1 part melted ice) to minimize osmotic stress on the microbial  
119 community during melting (Bates & Cota 1986, Garrison & Buck 1986). Ice–water interface  
120 samples for salinity and nutrient determination were collected through an auger hole with a  
121 battery-operated plastic submersible pump (Cyclone®) secured to the end of an articulated  
122 under-ice arm.

123 Three distinct types of experiments with ice algae were carried out on 11 occasions  
124 between 6 and 31 May 2015 (Table 1). For these experiments, the bottommost 1 cm of 3 sea-ice  
125 cores were quickly scraped (McMinn et al. 2005, 2010) and pooled in a dark isothermal  
126 container with 0.2  $\mu\text{m}$  FSW (ca. 38 parts FSW to 1 part melted ice) in order to reduce the time of  
127 melting, which can impact physiological processes. Indeed, too long of a dark period during the  
128 ice melting could result in DT to DD de-epoxidation (Goss & Jakob 2010). In our study, ice  
129 samples were melted in less than 30 min. The melted ice was gently mixed, and nutrients were  
130 sampled before the water was distributed into clear polycarbonate bottles under dim light  
131 conditions (i.e. diffusive light in a Polarhaven shelter with opaque walls and 2 end windows  
132 covered by 4 layers of black plastic sheeting).

133 During the first experiment (Table 1), three 500 ml polycarbonate bottles ( $E_{\text{PAR}}$   
134 transmittance of ca. 80%) containing ice melt water were placed in each experimental chamber.  
135 Each chamber was then exposed to one light intensity (10, 50, 100 or 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ )  
136 using cool white dimmable LEDs (9 W) and neutral density light filters (LEE Filters). During  
137 the experimental period, irradiance at the ice–water interface ranged from 0.3 to 8  $\mu\text{mol photons}$   
138  $\text{m}^{-2} \text{s}^{-1}$ , and therefore ice algae were acclimated to different light levels in their natural  
139 environment. The experimental chambers were continuously cooled with running seawater  
140 pumped from the ice–water interface using a small electric submersible pump (Lifegard Aquatics  
141 QuietOne Model 1200, 317 GPH). The ice algae were exposed to their respective treatments for  
142 3 h and then placed at the lowest light levels achievable in the field ( $<5 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ,  
143 incubators covered by 4 layers of black plastic sheeting) for a 2 h dark-recovery period. The  
144 same experiment was repeated on 7 occasions and the data from the same ice algae (from thin or  
145 thick snow) and the same period (before or during snowfall) were averaged. Subsampling for

146 pulse-amplitude modulation (PAM) fluorometry measurements (i.e. chlorophyll *a* [chl *a*]  
147 fluorescence) occurred at 0, 0.5, 1, 2, 3 and 5 h, while pigment composition was assessed at 0, 3  
148 and 5 h.

149 In the second experiment (Table 1), the relative importance of photoprotection and  
150 photorepair mechanisms were assessed using 2 inhibitors: dithiothreitol (DTT) and lincomycin.  
151 The xanthophyll inhibitor DTT prevents the de-epoxidation of DD into DT (Olaizola et al. 1994,  
152 Lavaud et al. 2002) whereas lincomycin prevents the transcription of chloroplast-encoded D1  
153 proteins (*psbA*) and therefore inhibits the repair of photodamaged PSII (Petrou et al. 2010).  
154 Duplicate 500 ml polycarbonate bottles containing melted ice water from a thin snow cover site  
155 were prepared (1) without inhibitor (i.e. control), (2) with DTT (final concentration 100  $\mu\text{mol l}^{-1}$ ;  
156 Olaizola et al. 1994) and (3) with lincomycin (final concentration 600  $\mu\text{mol l}^{-1}$ ; Kropuenske et  
157 al. 2009). Approximately 5 min after adding the chemical, the bottles were incubated for 6 h at  
158 the ice–water interface using a custom-built under-ice arm. Subsamples for PAM fluorescence  
159 and pigment analysis were collected every 2 h between 11:00 and 17:00 h (local time; UTC –  
160 05:00).

161 In the third experiment (Table 1), duplicate 2 l polycarbonate bottles containing melted  
162 ice water from both snow covers were incubated in an opaque-walled incubator located on the  
163 snow, exposed to incident irradiance ( $E_{\text{PAR}} + \text{UVR}$ ) and continuously cooled with running  
164 seawater pumped from the ice–water interface using a small electric submersible pump  
165 (Pondmaster magnetic drive utility pump, Model 500 GPH). Subsamples were collected for  
166 PAM fluorescence and pigment analysis after 30 min and every hour thereafter for 3 h.

## 167 Irradiance measurement

168 During the study period, transmitted irradiance was measured every sampling day  
169 between 10:00 and 11:00 h (local time; UTC – 05:00) using a compact-optical profiling system  
170 (C-OPS; Biospherical Instruments). Incident and under-ice downward irradiances were recorded  
171 at 19 individual wavelengths (from 320 to 780 nm) by a cosine light sensor. The vertical profile  
172 of irradiance under the sea ice was measured by the IcePRO version of the instrument, which is  
173 specifically design to fit and sink through a 25 cm diameter ice auger hole.  $E_{\text{PAR}}$  was computed  
174 by constructing a piecewise cubic hermit interpolating polynomial (PCHIP) using downward

175 irradiance measured at all C-OPS wavelengths and then numerically integrating from 400 to 700  
176 nm to obtain final units of  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Mobley 1994). The transmitted irradiance at  
177 the ice–water interface was calculated as detailed in Belzile et al. (2000). The water column  
178 diffuse attenuation coefficient was determined from the linear portion of triplicate measurements  
179 of the natural logarithm of the transmitted irradiance versus depth. Due to the alteration of light  
180 profiles underneath the ice because of the auger hole and the snow added on it, the  $E_{\text{PAR}}$  plots  
181 were linear, on average, from 10 to 50 m. The  $r^2$  of the relationship between the natural  
182 logarithm of the transmitted irradiance versus depth was always  $>0.99$ .

183 To estimate incident irradiance and  $E_{\text{PAR}}$  at the ice–water interface over a day, we used  
184 incident downward shortwave (305 to 2800 nm) radiation, which was measured continuously (as  
185 1 min averages). The shortwave radiation measurements were made using the upward-looking  
186 cosine response pyranometer on a 4-sensor net radiometer (Kipp & Zonen; model CNR4) placed  
187 at an undisturbed site approximately 20 m west of the meteorological station at a height of 1 m  
188 above the snow. The instrument included a heater/ventilator unit (Kipp & Zonen; model CNF4)  
189 that cycled on for 5 min at the beginning of every hour to keep the instrument lenses free of  
190 snow and frost. We noticed that the heater/ventilator caused a transient increase in measured  
191 shortwave radiation under certain atmospheric conditions (light winds, clear skies). In these  
192 cases, we used a smoothing algorithm to remove minor data spikes. Incident downward  
193 shortwave radiation was converted to  $E_{\text{PAR}}$  (multiplied by 0.47) as described by Papaioannou et  
194 al. (1993). Then the  $E_{\text{PAR}}$  value in  $\text{W m}^{-2}$  was converted into  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  using a factor  
195 of 4.15 as described in Halverson & Pawlowicz (2013). As algae act as scalar collectors with a  
196 maximum interception of light incident from all directions due to the arrangement of their  
197 photosynthetic tissues, scalar irradiance is the preferred measurement (Kirk 2011). To calculate  
198 scalar irradiance at the ice–water interface, we first estimated downward irradiance at the ice–  
199 water interface by multiplying the incident downwelling  $E_{\text{PAR}}$  on the surface by the calculated  
200  $E_{\text{PAR}}$  transmittance (as detailed above). This subsequent downward irradiance was converted to  
201 downward scalar irradiance by dividing by an average cosine factor of 0.7 (Ehn & Mundy 2013).  
202 To simplify, we assumed that the upward scalar irradiance was negligible at the ice–water  
203 interface. Due to this assumption, we note that our scalar irradiance estimates are likely  
204 conservative. Although no direct measurements have been reported, the modeling study of



205 Pavlov et al. (2017) estimated scalar irradiance at the ice bottom to be ~1.8 times greater than  
206  $E_{PAR}$ , in comparison to our estimate that was scaled by a factor of 1.4.

## 207 **Salinity and nutrients**

208 Salinity of melted ice samples was measured with a hand-held conductivity meter  
209 (330i/SET; WTW) calibrated against a 15 N KCl solution at 20°C. Samples for nutrient  
210 determination at the ice–water interface and in the experiments were filtered through a pre-  
211 combusted (5 h at 450°C) Whatman GF/F glass-fiber filter (nominal porosity of 0.7  $\mu\text{m}$ ) inserted  
212 in a filter holder. The filtrate was collected into 20 ml polyethylene vials after thorough rinsing.  
213 Samples were poisoned with mercuric chloride (final concentration 10  $\mu\text{g ml}^{-1}$ ) according to  
214 Kirkwood (1992), and stored in the refrigerator until analysis. Nitrate plus nitrite (hereinafter  
215  $\text{NO}_x$ ), nitrite, phosphate and silicic acid were analyzed using a Bran Luebbe Seal autoanalyzer  
216 according to the method of Aminot & K erouel (2007). The analytical detection limits for  $\text{NO}_x$ ,  
217 phosphate and silicic acid were 0.05, 0.02 and 0.2  $\mu\text{mol l}^{-1}$ , respectively.

## 218 **Chl *a* variable fluorescence**

219 To study the photosynthetic responses of algae, PAM fluorometry was used. It is a widely  
220 used methodology that provides a rapid, non-invasive assessment of the photosynthetic apparatus  
221 of algal cells (Parkhill et al. 2001). It is also a useful tool to examine the ability of photosynthetic  
222 organisms to tolerate environmental stressors and the extent of damage caused by these stresses  
223 (Maxwell & Johnson 2000). Fluorescence measurements were made with a water-PAM cuvette  
224 version with blue LEDs (Walz) inside the **unheated field laboratory (Polarhaven shelter), which**  
225 **was set up at the sampling station.** All samples were placed in a small cooler containing 2 ice  
226 packs during their dark-acclimation for at least 30 min before the measurement of fluorescence.  
227 The samples were stirred during measurements.

228 Minimum ( $F_0$ ) and maximum fluorescence ( $F_m$ ) levels were assessed, and the maximum  
229 quantum yield of PSII photochemistry ( $F_v/F_m$ ) was calculated as follows:

$$230 \quad F_v/F_m = (F_m - F_0) / F_m \quad (1)$$

231  $F_m$  was obtained using a saturating pulse of ca. 3000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  for 0.8 s. When  
232 measured on a community,  $F_v/F_m$  changes must be interpreted with care (see, for example,

233 Parésys et al. 2005). Nevertheless, in our study, sea-ice algae communities were largely  
234 dominated by diatoms (see ‘Results’). Hence,  $F_v/F_m$  variations can be largely attributed to  
235 changes in the photosynthetic efficiency of diatoms.

236 Rapid light curves (RLCs) were also generated to determine the photosynthetic  
237 parameters under both snow covers as a function of snow conditions (before or during snow  
238 events). Dark-acclimated samples were exposed to successive increasing actinic light ranging  
239 from 0 to 139  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  for 30 s each. The actinic light was measured with a  
240 spherical micro quantum sensor US-SQS (Walz). The relative electron transport rate (rETR;  
241 dimensionless) values were calculated as follows:

$$242 \quad \text{rETR} = \phi_{\text{PSII}} \times E \quad (2)$$

243 where  $\phi_{\text{PSII}} = (F_m' - F') / F_m'$ , known as the operational PSII quantum yield and  $E$  is the  
244 irradiance applied.

245 Data from RLCs were fitted using the following equation (Eilers & Peeters 1988,  
246 Zonneveld 1998) using a Levenberg-Marquardt regression algorithm:

$$247 \quad \text{rETR} = E / (aE^2 + bE + c) \quad (3)$$

248 where  $E$  is irradiance, and  $a$ ,  $b$  and  $c$  are regression coefficients to fit the rETR versus  $E$  curve.  
249 RLC measurements allow us to describe the main photosynthetic properties of an algal sample,  
250 including the maximum (rETR<sub>max</sub>), the light use efficiency ( $\alpha$ ) represented by the initial slope of  
251 the curve ( $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ )<sup>-1</sup> and the light saturation coefficient ( $E_k$ ;  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ )  
252 (Ryan et al. 2009) using the following expressions:

$$253 \quad \alpha = 1 / c \quad (4)$$

$$254 \quad \text{rETR}_{\text{max}} = [b + 2(ac)^{0.5}]^{-1} \quad (5)$$

$$255 \quad E_k = \text{rETR}_{\text{max}} / \alpha \quad (6)$$

256 As for typical <sup>14</sup>C  $P$ - $E$  curves, these photosynthetic parameters were used to compare the  
257 photosynthetic performances and photoacclimation properties of algal communities.

## 258 **Pigments and CHEMTAX analysis**

259 The identification and concentration of algal pigments were determined by reverse-phase  
260 HPLC. Samples (50 to 200 ml, depending on the biomass) were filtered onto 25 mm Whatman  
261 GF/F filters using a vacuum pump (0.8 mm Hg), wrapped in aluminum foil and stored  
262 immediately at  $-80^{\circ}\text{C}$  until analysis. For the time series, the algal pigments of the bottom 3 cm  
263 of the ice were extracted at  $-20^{\circ}\text{C}$  in 3 ml 100% methanol, disrupted by 10 s of sonication  
264 (Bandelin Sonopuls HD2200) and filtered 1 h later through 25 mm Whatman GF/F filters. The  
265 pigments were separated and quantified as described in Ras et al. (2008), a method adapted from  
266 Van Heukelem & Thomas (2001). Pigments were analyzed using an Agilent Technologies 1200  
267 Series system with a narrow reversed-phase C8 Zorbax Eclipse XDB column ( $150 \times 3$  mm,  $3.5$   
268  $\mu\text{m}$  particle size) which was maintained at  $60^{\circ}\text{C}$ . A diode-array detector allowed measuring the  
269 absorption of most pigments at 450 nm, while chl *a* and its derivatives were detected at 667 nm.  
270 For the light experiments, the algal pigments were extracted as described in Alou-Font et al.  
271 (2013, 2016) and disrupted by 10 s of sonication (Heat Systems; model XL2010). The remaining  
272 pigment samples were analyzed using an Agilent Technologies 1200 Series but with a Symmetry  
273 C8 column ( $150 \times 4.6$  mm,  $3.5$   $\mu\text{m}$  particle size; Waters Corporation). Pigments were detected  
274 with a G1315P diode-array absorbance detector (400 to 700 nm) and chlorophylls were detected  
275 by fluorescence (excitation at 400 nm and emission at 650 nm; G1321A fluorescence detector).  
276 We used the HPLC separation method described in Zapata et al. (2000). For both methods,  
277 pigments were identified based on retention time and spectral properties of external pigment  
278 standards, even for degradation pigments (chlorophyllide *a*, pheophytin *a*, pheophorbide *a*) (DHI  
279 Lab Products) (Egeland et al. 2011). Limits of detection and quantification were estimated as in  
280 Bidigare et al. (2005) and pigments with concentrations below the limit of detection were not  
281 reported. In this study, total chl *a* (Tchl *a*) mentioned thereafter corresponds to the sum of chl *a*,  
282 chlorophyllide *a*, chl *a* allomer and epimer measured by HPLC. The ratios of photoprotective  
283 carotenoids (PPC; including DD, DT, violaxanthin, zeaxanthin and  $\beta,\beta$ -carotene) to  
284 photosynthetic carotenoids (PSC; including fucoxanthin, peridinin, 9'-cis-neoxanthin and  
285 alloxanthin) were also calculated. The de-epoxidation state (DES) index, an indicator of  
286 photoprotection (Barnett et al. 2015), was expressed as  $\text{DES} = \text{DT} / (\text{DD} + \text{DT})$  and calculated  
287 for the different experiments.

288 The contribution of major algal groups to chl *a* was determined from marker pigment  
289 ratios using the CHEMical TAXonomy (CHEMTAX) program (Mackey et al. 1996, version 1.95

290 as used in Wright et al. 2009). According to Mackey et al. (1996), the accuracy of CHEMTAX  
291 calculations is optimized when calculations are done on smaller groups of samples, with stable  
292 pigment ratios. Thus, samples were separated into 4 data sets with similar environmental (snow  
293 depth) and biological (algal bloom phase) conditions. CHEMTAX was used separately on each  
294 data set, and the average was calculated for each condition. As the data sets were separated in the  
295 same way as those in Alou-Font et al. (2013), we used the same initial pigment ratio matrices  
296 defined therein. Therefore, to improve biomass estimation, 10 successive runs of CHEMTAX  
297 using the output from each run as the input for the next was used, as recommended by Latasa  
298 (2007) and used in recent studies (e.g. Eker-Develi et al. 2012, Liu et al. 2012, Wang et al.  
299 2015). The final ratio matrices are displayed in Table S1 in the Supplement at [www.int-  
300 res.com/articles/suppl/mXXXpXXX\\_supp.pdf](http://www.int-res.com/articles/suppl/mXXXpXXX_supp.pdf).

## 301 **Statistical analysis**

302 Normality of the data was determined using the Shapiro-Wilk test with a 0.05  
303 significance level. When the data were normally distributed, we used parametric tests. For the  
304 time series and the third experiment, paired *t*-tests were used to compare paired variables from  
305 the thin and thick snow cover sites. For non-parametric data, a Wilcoxon signed rank test was  
306 used instead. To determine differences among the 3 sampling periods, a 1-way ANOVA by ranks  
307 (Kruskal-Wallis test) was performed and completed by a multiple mean comparison test using  
308 rank sums (Dunn's test) adjusted with the Bonferroni method. In addition, Pearson's linear  
309 correlations (*r*) on parametric data were used to infer the relationship between 2 variables. For  
310 the first experiment, 1-way repeated ANOVA was performed followed by a post hoc Tukey's  
311 test to identify averages that were significantly different between treatments. A *t*-test was also  
312 conducted to determine the difference in algal responses (e.g. decline) depending on snow cover.  
313 The *t*-statistic, df and p-values are provided in brackets when reported. Statistical tests and  
314 graphics were produced with SigmaPlot v.12.3 (Systat Software) and R (R Development Core  
315 team 2009).

## 316 **RESULTS**

### 317 **Change in environmental conditions**

318 Because of temporal changes in snow cover depth resulting from major snow  
319 precipitation events on 16 and 20 May, we distinguish 3 sampling periods (i.e. before and during  
320 snow events, and snowmelt; Fig. 2). Snow depth remained relatively stable at both sites until 12  
321 May, and increased from ca. 10 to 30 cm and from ca. 25 to 51 cm on 20 May at thin and thick  
322 snow cover sites, respectively (Fig. 2a). Thereafter, snow depth slowly decreased at both sites  
323 until 9 June, when it decreased faster until reaching 0 cm on 20 June at the thin snow site and  
324 later at the thick snow site. Mean sea-ice thickness ranged from 132 to 96 cm during the  
325 sampling season (Fig. 2b) and was significantly thinner during the melting period (mean = 116  
326 cm) than during the 2 previous periods (mean = 124 cm) (Dunn's test,  $p < 0.05$ ).

327 Nutrient concentrations at the ice–water interface varied from 5.38 to 1.38  $\mu\text{mol l}^{-1}$  for  
328  $\text{NO}_x$  (Fig. 2c), from 0.22 to 0.04  $\mu\text{mol l}^{-1}$  for  $\text{NO}_2^-$ , from 7.4 to 5.5  $\mu\text{mol l}^{-1}$  for  $\text{Si}(\text{OH})_4$  and  
329 from 0.92 to 0.60  $\mu\text{mol l}^{-1}$  for  $\text{PO}_4^{3-}$ .  $\text{NO}_x$  concentrations oscillated between 4.21 and 5.38  $\mu\text{mol}$   
330  $\text{l}^{-1}$  from the beginning of the sampling period until 10 June and then started to decrease  
331 progressively down to 1.38  $\mu\text{mol l}^{-1}$  at the end of sampling (Fig. 2c). Mean concentrations of  
332  $\text{NO}_x$ ,  $\text{Si}(\text{OH})_4$  and  $\text{PO}_4^{3-}$  were significantly lower during the melting period (after 10 June) than  
333 during the 2 previous periods (Dunn's test,  $p < 0.05$ ).

334  $E_{\text{PAR}}$  transmittance through the ice and snow remained relatively constant at around  
335 0.06% of incident irradiance until 31 May and then increased progressively up to 4.6% on 6 July  
336 due to the complete snowmelt (Fig. 2d). Mean  $E_{\text{PAR}}$  transmittance was significantly higher after  
337 9 June than before this date (Dunn's test,  $p < 0.05$ ).

### 338 **Effect of snow events and snow cover depth on ice algal biomass, pigment** 339 **composition and photosynthetic properties**

340 During the first sampling period (i.e. before snow events), bottom ice Tchl *a*  
341 concentration, used as an index of ice algal biomass, was significantly higher under the thin  
342 snow (9.28  $\text{mg m}^{-2}$ ) than under the thick snow (5.14  $\text{mg m}^{-2}$ ) cover (paired *t*-test,  $t = 3.632$ ,  $\text{df} =$   
343 11,  $p < 0.01$ ) (Fig. 3a). During the following 2 periods (i.e. snow events and snowmelt), no  
344 significant difference in algal biomass was observed between the 2 snow cover conditions  
345 (paired *t*-test,  $t = 1.556$ ,  $\text{df} = 9$ ,  $p = 0.15$  during snow events and  $t = 0.566$ ,  $\text{df} = 4$ ,  $p = 0.60$   
346 during snowmelt). During the snow events period, bottom ice Tchl *a* concentration reached a

347 maximum value of 22 mg m<sup>-2</sup> on 27 May and 32 mg m<sup>-2</sup> on 2 June at the thick and thin snow  
348 sites, respectively. Thereafter, Tchl *a* concentrations decreased progressively to reach a  
349 minimum value of 0.18 mg m<sup>-2</sup> at the thick snow site during the snowmelt period. No samples  
350 were collected at the thin snow site after 24 June.

351 The concentrations of PSC and PPC followed the same trend as Tchl *a*. PSC variations  
352 were mainly influenced by fucoxanthin, while PPC were mostly governed by DD and β,β-  
353 carotene. The PPC:PSC ratio was relatively constant before and during snow events, with values  
354 around 0.1 wt:wt, followed by an increase up to 0.81 wt:wt during the snowmelt period (Fig. 3b).  
355 Before snow events, the PPC:PSC ratio was significantly higher under thin snow (0.12 wt:wt)  
356 than under thick snow (0.09 wt:wt) (paired *t*-test, *t* = 2.393, *df* = 11, *p* < 0.05). This ratio was  
357 positively correlated with *E*<sub>PAR</sub> transmittance at the ice–water interface under both thin (*r* =  
358 0.816, *p* < 0.001) and thick snow covers (*r* = 0.828, *p* < 0.001) and during the snowmelt period (*r*  
359 = 0.812, *p* < 0.001). Over the entire sampling period, the ratio of (DD+DT) to Tchl *a* followed  
360 the same trend as PPC:PSC (Fig. 3b,c). (DD+DT):Tchl *a* was stable around 0.03 wt:wt before  
361 and during snow events and increased to 0.28 wt:wt during the snowmelt period under both snow  
362 cover conditions. It was significantly higher under thin snow (0.04 wt:wt) than under thick snow  
363 (0.02 wt:wt) cover before snow events (paired *t*-test, *t* = 3.460, *df* = 11, *p* < 0.01) and was  
364 positively correlated with ice bottom *E*<sub>PAR</sub> transmittance during the snowmelt period (*r* = 0.667,  
365 *p* < 0.05).

366 The contributions of major algal groups to chl *a* were determined via CHEMTAX  
367 analysis, which showed that diatoms were always dominant under both snow covers during the  
368 entire sampling period (>82%; Fig. 4). Diatoms Type 2, containing fucoxanthin and chl *c*<sub>2</sub> and  
369 *c*<sub>3</sub>, were likely associated with pennate diatoms in Alou-Font et al. (2013), while diatoms Type 1  
370 were associated with centric diatoms. Some differences occurred depending on the snow cover  
371 and snow periods. Before snow events, diatoms Type 2 (i.e. pennate diatoms) totally dominated  
372 under the thin snow cover, while the algal community was more heterogeneous under thick snow  
373 with the presence of diatoms Type 1 (16%), cryptophytes (14%) and dinoflagellates (3%).  
374 Thereafter, during snow events, the algal community was more heterogeneous under both snow  
375 covers, but dinoflagellates (3%) and cryptophytes (2%) were relatively more abundant under thin  
376 snow cover. Finally, diatoms entirely dominated the algal community during the snowmelt

377 period (ca. 99%) with a dominance of diatoms Type 1 (i.e. centric diatoms), but diatoms Type 2  
378 (i.e. pennate diatoms) were 4 times more abundant under thick snow cover (20 vs. 5%). Hence,  
379 despite the dominance of diatoms in all samples, some differences in algal community  
380 (heterogeneous or diatom types) occurred depending on the environmental conditions.

381 Before the period of snow events, there was a clear difference in photosynthetic  
382 properties and photoacclimation in ice algae living under thin or thick snow cover (Table 2). As  
383 expected,  $\alpha$  was lower and  $rETR_{max}$  was higher under thin snow. As a result,  $E_k$  was twice as  
384 high (ca.  $45 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) under thin snow. During the snow event period, ice algae  
385 under the thin snow cover maintained  $rETR_{max}$  and increased  $\alpha$  resulting in a  $E_k$  decrease of half,  
386 reaching a value similar to that under the thick snow cover before the snow event period.  
387 Interestingly, ice algae under thick snow cover maintained  $\alpha$  (probably because it was already at  
388 its maximum), yet increased  $rETR_{max}$  to a similar level as ice algae under thin snow cover during  
389 snow events.

### 390 **Effect of a natural range of light exposure on the photophysiology of bottom** 391 **ice algae as a function of snow conditions**

392 Two types of experiments were performed to determine the short-term effect of enhanced  
393 irradiance on the photophysiological response of bottom ice algae (see Table 1). The aim of the  
394 first experiment was to assess the short-term effect of enhanced irradiance over a range typically  
395 observed at the ice–water interface (10 to  $200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; see Ryan et al. 2011, Alou-  
396 Font et al. 2013) on the photophysiological response of bottom ice algae acclimated to different  
397 light environments depending on the snow conditions (i.e. snow depth and snow events). Before  
398 snow events, the  $F_v/F_m$  ratio, a proxy for the maximum quantum yield for PSII photochemistry,  
399 was significantly lower after a 3 h light-exposure to the highest light treatment (i.e.  $200 \mu\text{mol}$   
400  $\text{photons m}^{-2} \text{s}^{-1}$ ) (1-way repeated ANOVAs completed by post hoc Tukey's tests,  $q = 4.644$  and  
401  $p < 0.05$  for thin snow, and  $q = 3.464$  and  $p < 0.05$  for thick snow cover) (Fig. 5a,b). The  
402 decrease in  $F_v/F_m$  was greater for thick snow ( $t$ -test,  $t = 24$ ,  $p < 0.05$ ). After 2 h of darkness,  
403  $F_v/F_m$  did not change. For the thin snow cover (Fig. 5a), the  $F_v/F_m$  response was different with an  
404 increase throughout the light exposure and recovery period, especially for the 10 and  $50 \mu\text{mol}$   
405  $\text{photons m}^{-2} \text{s}^{-1}$  treatments, and it reached final values higher than those at  $T_0$  (ca. 0.55). For

406 thick snow cover (Fig. 5b),  $F_v/F_m$  strongly decreased during the first 30 min of illumination in  
407 light treatments of 10, 50 and 100  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , followed by stabilization and a recovery  
408 to  $T_0$  values during dark recovery. During snow events (Fig. 5c,d), the  $F_v/F_m$  decrease for thin  
409 snow cover was significantly different from those before snow events ( $t$ -test,  $t = 3.702$ ,  $df = 7$ ,  $p$   
410  $< 0.01$ ) at 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ .  $F_v/F_m$  reached the same minima after 3 h of light exposure  
411 (ca. 0.30 to 0.35). For lower light intensity treatments,  $F_v/F_m$  was rather stable throughout the  
412 experiment, except for the 100  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  treatment for thick snow, which showed a  
413 stronger decrease and lower recovery than before snow events. Because  $F_v/F_m$  is also influenced  
414 by nutrient availability *in situ* (Lin et al. 2016) as well as in experimental conditions (Parkhill et  
415 al. 2001), we verified that nutrient concentrations were not limiting in our incubation bottles (see  
416 Table S2 in the Supplement). Furthermore, due to low primary production (maxima ranged from  
417 0.23 to 0.73  $\mu\text{mol C l}^{-1} \text{h}^{-1}$ ) at the beginning of the experiment (data not shown), dissolved  
418 inorganic carbon concentrations (ca.  $2105 \pm 9.12 \mu\text{mol kg}^{-1}$ ) were sufficient to provide enough  
419 carbon for the photosynthesis of ice algae. In addition to  $F_v/F_m$ , DES (an index of DD de-  
420 epoxidation in bottom ice algae) was assessed (Fig. 6). At  $T_0$ , DES varied between 0.05 and 0.09  
421 wt:wt and it increased significantly under the 2 highest light treatments (100 and 200  $\mu\text{mol}$   
422  $\text{photons m}^{-2} \text{s}^{-1}$ ) to a maximum level of 0.14 to 0.20 wt:wt. While it was strongly positively  
423 correlated with the increase of  $E_{\text{PAR}}$  at the ice–water interface ( $r = 0.85$ ,  $p < 0.001$ ), no significant  
424 difference was observed before or during snow events or between snow covers (thin or thick).  
425 After 2 h of dark-recovery, DES decreased back to its  $T_0$  values, independent of snow events and  
426 snow depth conditions.

427 In a second, complementary experiment, we aimed to determine the respective  
428 importance of DD de-epoxidation and of the synthesis of PSII D1 (psbA) protein to support  
429 bottom ice algae in maintaining their photochemical performance when exposed to their natural  
430 light environment. For that purpose, bottom ice algae were collected under thin snow cover and  
431 incubated at the ice–water interface in the absence (control) and presence of the inhibitor of DD  
432 de-epoxidation (i.e. DTT), and of D1 protein synthesis (i.e. lincomycin) (Fig. 7). During the  
433 experiment, estimated ice bottom  $E_{\text{PAR}}$  transmittance progressively decreased from 105 to 53  
434  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  from 11:00 to 17:00 h local time (Fig. 7a), a range of irradiance  
435 encompassed by that of the first experiment. In all treatments,  $F_v/F_m$  decreased during the first 4



436 h (Fig. 7b; ca. -25 to -30%) until reaching similar values at mid-afternoon (15:00 h) and  
437 increased slightly thereafter concomitantly with the sharpest  $E_{PAR}$  decrease (from 75 to 53  $\mu\text{mol}$   
438 photons  $\text{m}^{-2} \text{s}^{-1}$ ). There was a greater  $F_v/F_m$  decline after 2 h light exposure in the presence of  
439 DTT and lincomycin (ca. -20 to -25%) in comparison with the control conditions (-5%). It is  
440 noteworthy that  $F_v/F_m$  response in control conditions after 2 h light exposure was similar to the  
441 response observed in our controlled experimental light treatment (Expt 1, thin snow cover, 100  
442  $\mu\text{mol}$  photons  $\text{m}^{-2} \text{s}^{-1}$ ; Fig. 5a). In control conditions, DES increased for the first 2 h from 0.063  
443 to 0.086 wt:wt and stabilized until 15:00 h, after which it decreased back to  $T_0$  values, while  $E_{PAR}$   
444 at the ice-water interface reached its lowest values (Fig. 7a). In DTT-treated samples, DES was  
445 stable around its  $T_0$  value. At  $T_0$ , DES in lincomycin-treated samples was significantly higher  
446 than in the control and DTT treatments, and did not change during the day, even when  $E_{PAR}$  at  
447 the ice-water interface decreased. At 17:00 h,  $F_v/F_m$  in DTT-treated samples was at 80% of the  
448 initial ratio, as for the control, while  $F_v/F_m$  in lincomycin-treated samples was only at 40% of the  
449 initial ratio. However, DES in lincomycin-treated samples was the highest by a factor of 2 in  
450 comparison with other treatments.

### 451 **Effect of high light exposure on the photophysiology of ice algae released from** 452 **bottom sea ice**

453 The aim of the third experiment (Table 1) was to assess the photoprotective capability of  
454 bottom ice algae when exposed to a sudden increase in irradiance, similar to what they would  
455 experience when carried into adjacent ice-free areas by surface currents after their release in the  
456 water column. Our hypothesis was that bottom ice algae from thin snow cover should be less  
457 light-sensitive than those from thick snow cover. To test this hypothesis, bottom ice algae were  
458 collected under thin and thick snow covers and exposed to incident irradiance (Fig. 8). During  
459 the experiment, incident  $E_{PAR}$  was constant at an average of  $1107 \pm 95 \mu\text{mol}$  photons  $\text{m}^{-2} \text{s}^{-1}$   
460 (Fig. 8a).

461  $F_v/F_m$  of bottom ice algae from thin and thick snow covers reached the same minimum  
462 value (ca. 0.05), illustrating a high level of photoinhibition (i.e. -75% in  $F_v/F_m$ ) when exposed to  
463 these over-saturating light intensities (10 times higher than the maximum average of bottom ice;  
464 see Fig. 8a) after a 3 h period. Nevertheless, the pattern of  $F_v/F_m$  variations was very different

465 between the 2 algal communities (Fig. 8b). For algae from thin snow cover,  $F_v/F_m$  decreased  
466 progressively during the first 2 h of light exposure, and sharply during the last hour of exposure.  
467 For thick snow cover,  $F_v/F_m$  showed a rapid drop close to 0 after the first 0.5 h, followed by a  
468 slight but significant recovery to its final value.

469 At the same time, ice algae underwent substantial changes in pigment content, with a  
470 Tchl *a* decrease (Fig. 8c) and DES increase (Fig. 8d); mean values were significantly different  
471 under thin and thick snow cover conditions (paired *t*-test,  $t = 12.394$ ,  $df = 5$ ,  $p < 0.001$  for Tchl *a*  
472 and Wilcoxon signed rank test,  $W = 21$ ,  $p < 0.05$  for DES). More specifically, under thin snow  
473 cover, Tchl *a* decreased by 20% (from 1228 to 987  $\mu\text{g chl } a \text{ l}^{-1}$ ) during the first 0.5 h of light  
474 exposure, followed by a slower but consistent decrease of 23% (from 987 to 759  $\mu\text{g chl } a \text{ l}^{-1}$ )  
475 during the rest of the experiment. Simultaneously, DES increased from a value of 0.09 to 0.19  
476 wt:wt during the first 0.5 h of light exposure and then stabilized around a value of 0.18 wt:wt at  
477 end of the experiment. Under thick snow cover, Tchl *a* followed a consistent decrease of 33%,  
478 from 146 to 98  $\mu\text{g l}^{-1}$  during the 3 h light exposure, while DES did not show significant changes,  
479 varying between 0.12 and 0.15 wt:wt.

## 480 DISCUSSION

### 481 **Effect of snow cover on the taxonomic composition and photosynthetic** 482 **properties of bottom ice algae**

483 According to previous studies at similar latitudes (ca. 70° N) (Renaud et al. 2007, Alou-  
484 Font et al. 2013), the ice algal bloom starts between the end of March and beginning of April. In  
485 2015, snow events around mid-May may have extended the ice algal bloom period by reducing  
486  $E_{\text{PAR}}$  penetration through the ice and thermally insulating the ice, which consequently delayed  
487 the melting process that usually terminates the bloom (e.g. Fortier et al. 2002, Mundy et al. 2005,  
488 Campbell et al. 2015). Thus, a positive relationship was observed between snow depth and Tchl  
489 *a* concentration ( $r = 0.693$ ,  $p < 0.001$ ), contrary to observations for early spring when light is  
490 limiting (Mundy et al. 2007, Alou-Font et al. 2013), but consistent with later bloom conditions  
491 (Campbell et al. 2015, Leu et al. 2015).

492 Under both snow covers (thin and thick), the bottom ice algal community was mainly  
493 composed of diatoms (Fig. 4), as confirmed by Imaging Flow CytoBot data (P. L. Grondin pers.  
494 comm.) and as also reported previously (Alou-Font et al. 2013). Whilst taxonomic studies in the  
495 Arctic have shown that pennate diatoms contribute to at least 68% of the abundance of total ice  
496 algae (von Quillfeldt et al. 2003, Poulin et al. 2011), we observed a change from a dominance of  
497 pennate diatoms (e.g. diatoms Type 2) before snow events to centric diatoms (e.g. diatoms Type  
498 1) during the snowmelt period. This diatom community change from the beginning to the end of  
499 spring has recently been observed in Dease Strait (Nunavut) during spring 2014 (Campbell et al.  
500 2017). The transition from pennate to centric diatoms could be associated with the increase in  
501 light conditions and changes in physico-chemical properties (e.g. lower brine salinity and limited  
502 nutrient availability) of sea ice through the spring season. Furthermore, before snow events (e.g.  
503 at the beginning of spring) the algal community under thick snow cover was more  
504 heterogeneous, with the presence of cryptophytes and dinoflagellates. This observation was  
505 already documented by Róžańska et al. (2009) in Franklin Bay, where diatoms were less  
506 abundant in sea ice under thick snow than under thin snow. They suggested that flagellates were  
507 more abundant due to their capacity to be mixotrophic instead of purely autotrophic (Sherr et al.  
508 2013, Unrein et al. 2014). Thus, the algal composition changed markedly depending on snow  
509 cover but also over the different sampling periods.

510 As the snow melting period progresses, ice algae grow and need to acclimate to higher  
511 light intensities. Before snow events, PPC:PSC and (DD+DT):Tchl *a* ratios were higher under  
512 thin than thick snow cover conditions (Fig. 3b,c) in accordance with higher light transmittance  
513 (Brunelle et al. 2012, Alou-Font et al. 2013). These findings were further corroborated by a  
514 lower  $\alpha$ , a higher  $rETR_{max}$  and a higher  $E_k$  under thin snow cover (details in Table 2), a typical  
515 high-light acclimation response (McMinn & Hegseth 2004, Manes & Gradinger 2009, Katayama  
516 & Taguchi 2013).

517 During the snowmelt period, bottom ice algae can be exposed for prolonged periods to  
518 relatively high light conditions. Thus, they need to be able to protect themselves through, e.g. the  
519 synthesis of carotenoids and other antioxidants. The lower bottom ice PPC:PSC ratio (up to 0.81)  
520 than previously reported in the Canadian Beaufort Sea (up to 1–3.5 wt:wt; Alou-Font et al. 2013)  
521 could be due to the dominance of centric diatoms at the end of spring instead of pennate diatoms.

522 However, the (DD+DT):Tchl *a* ratio (up to 0.28) was within the range of values reported in the  
523 Canadian Beaufort Sea (0.04 to 0.8 wt:wt; Alou-Font et al. 2013), in a high Arctic fjord of  
524 Svalbard (0.03 to 0.08 wt:wt; Leu et al. 2010) and in Antarctica (0.08 to 0.1 wt:wt; Petrou et al.  
525 2011, Arrigo 2014). The significant positive relationships between the PPC:PSC and  
526 (DD+DT):Tchl *a* ratios and  $E_{PAR}$  transmittance at the ice–water interface during the snowmelt  
527 period confirms the strong relationship between light transmittance and carotenoids synthesis. By  
528 rapid activation of the XC and a rapid decline in photochemical efficiency, bottom ice algae  
529 possess a high level of plasticity in their light-acclimation capabilities. Our observations and the  
530 previous work of Petrou et al. (2011) in Antarctica confirm that non-photochemical quenching  
531 (NPQ) via XC activation would be the preferred method of regulating energy flow to PSII and  
532 photoprotection. In addition, the dominance of centric diatoms at the end of spring (Campbell et  
533 al. 2017, our Fig. 4) seems to represent the ideal algal community to seed an under-ice bloom. In  
534 fact, centric diatoms, as observed with *Chaetoceros* sp. by Petrou & Ralph (2011), possess a high  
535 plasticity and are able to acclimate well to all environments, but perform best under pelagic  
536 conditions. Thus, in a future Arctic where sea ice will be thinner and consequently light  
537 intensities higher, the bottom ice algae could shift from pennate to centric diatoms, based on  
538 their differential photoacclimative ability.

### 539 **Ice algal photophysiological response: the ‘cellular light memory’ hypothesis**

540 When comparing the photophysiological response of ice algae as a function of snow  
541 depth before and during snow events, we observed that ice algae under thick snow cover were  
542 more light-sensitive, as indicated by the more rapid decrease of  $F_v/F_m$  under light exposure from  
543 10 to 200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Fig. 5). Before snow events, the algal community under thick  
544 snow cover was more heterogeneous with the presence of cryptophytes and dinoflagellates,  
545 which are more sensitive to greater light intensities than diatoms (Richardson et al. 1983, Demers  
546 et al. 1991). Differences in photoacclimative and photoprotective strategies have been reported  
547 between diatoms and other algal clades (Rajanaahally et al. 2015, Petrou et al. 2016, Lacour et al.  
548 2017) as well as among diatom strains (Lavaud & Goss 2014, Barnett et al. 2015, Petrou et al.  
549 2016). In addition, the lower DES before the experiment ( $T_0$ ) in this algal community confirmed  
550 that it was low-light acclimated before the experiment. Since our experiments were performed  
551 under constant temperature (ca.  $-1.2^\circ\text{C}$ ) and nutrient-sufficient conditions, the differences in

552  $F_v/F_m$  and DES between thin and thick snow cover depths could be attributed to the algal  
553 community composition and/or the light history of the cells. However, during snow events, the  
554 algal community was similar between snow covers, thus the difference in light sensitivity, such  
555 as the quicker response of DES and the **smaller** decrease of  $F_v/F_m$ , must be associated with the  
556 different light history. The algal community and the light history are then 2 essential factors  
557 which must be taken into account when looking at photoprotection and photoacclimation of  
558 bottom ice algae.

559 The differential photophysiological response as a function of snow depth was even more  
560 pronounced when ice algae were exposed to over-saturating light stress (ca. 1000  $\mu\text{mol photons}$   
561  $\text{m}^{-2} \text{s}^{-1}$  for 3 h) that mimicked their release from ice and exposure at the surface of open waters.  
562 Our experiment confirmed that bottom ice algae from thin snow cover were less light-sensitive  
563 than those from thick snow cover. Their light response was supported by their capacity to reduce  
564 excitation pressure on PSII ( $F_v/F_m$  relatively stable for 2 h) due to a higher DES and synthesis of  
565 DT (1.75 times higher than in ice algae from thin snow cover). A similar response was observed  
566 in ice algae from Antarctic pack ice (Petrou et al. 2011). Higher DT synthesis illustrates well the  
567 response of diatoms to higher average irradiance (Wilhelm et al. 2014) as reported from different  
568 algal communities which inhabit substrates and which are dominated by diatoms, i.e. ice algal  
569 communities (Arrigo et al. 2010, Petrou et al. 2011, Katayama & Taguchi 2013) as well as  
570 benthic diatoms that inhabit intertidal sediments (Laviale et al. 2015). Higher DT cellular content  
571 can originate from DD de-epoxidation and de novo synthesis when light conditions are harsher  
572 (Lavaud & Goss 2014). Increased DT (and DD) synthesis was recently shown to be directly  
573 dependent on the redox state of the plastoquinone (PQ) pool (Lepetit et al. 2013) and thus on the  
574 excitation pressure on the photosynthetic machinery, and it is likely related to the parallel  
575 synthesis of specific PSII light-harvesting antenna proteins (LHCx; see Wu et al. 2012, Lepetit et  
576 al. 2017). Higher DT content provides a stronger capacity to prevent/limit the harmful effects of  
577 excess light exposure on photosynthetic efficiency, namely PSII photodamage (Wu et al. 2012,  
578 Lepetit et al. 2013) and lipid peroxidation of thylakoid membranes (Lepetit et al. 2010). DT acts  
579 via 2 main processes: the dissipation of excess excitation energy in PSII antenna through NPQ  
580 (Lavaud & Goss 2014, Goss & Lepetit 2015) and the direct scavenging of reactive oxygen  
581 species (ROS) as proposed by Lepetit et al. (2010).

582 Surprisingly, ice algae under the same snow depth but during different time periods (ca.  
583 25 cm, i.e. thick snow before snow events and thin snow during snow events; Fig. 2a), did not  
584 show the same light response (Fig. 5b,c). For all light intensities, the  $F_v/F_m$  decrease was  
585 stronger for ice algae under thick snow before snow events, indicating a higher light sensitivity.  
586 The ice algae under thin snow during snow events showed a similar response to those under thin  
587 snow before snow events (Fig. 5a,c) even if they had spent 13 d under the new light conditions  
588 (i.e. less light availability because of thicker snow cover) when the experiment took place. This  
589 observation suggests that ice algae from thin snow kept their acclimation status similar to that  
590 before the snow events, even if they were exposed to lower irradiance (due to snow events) for  
591 several days. A similar process, so-called ‘cellular light memory’, has been reported in higher  
592 plants and it can persist for several days (Szechyńska-Hebda et al. 2010, Karpinski &  
593 Szechyńska-Hebda 2012). The cellular memory of excess light exposure is based on a complex  
594 network in plant tissues which starts in the plastids of leaves, and which orchestrates a  
595 physiological response to improve photoacclimation under changing light conditions. It is  
596 associated with photoelectrochemical retrograde signaling due in part to changes in PSII redox  
597 state, and with photoprotective processes such as the XC-related NPQ. Although diatoms are  
598 unicellular organisms, they possess a photoelectrophysiological activity across thylakoid  
599 membranes (Bailleul et al. 2015), a redox-based plastid-to-nucleus retrograde signaling pathway  
600 (Lepetit et al. 2013) and a strong NPQ tightly associated with the XC (Lavaud & Goss 2014).  
601 Based on similar features for photochemistry and light dissipation between higher plants and  
602 diatoms, we surmise that diatoms also possess this process of cellular light memory.

### 603 **Photoprotective mechanisms in low-light acclimated algae**

604 Our study confirms that ice algae were adapted to very low light intensities, but could  
605 maintain photosynthesis over a range of irradiances corresponding to those measured at the ice–  
606 water interface (up to ca.  $100 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ; Fig. 7a). Indeed, fast (within 30 min light  
607 exposure) and major changes in PSII photochemistry (decrease in  $F_v/F_m$ ) and DD de-epoxidation  
608 (increased DES) were observed for irradiance of  $100 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ . Below this light  
609 intensity, the non-significant changes in  $F_v/F_m$  and DES indicate that bottom ice algae were  
610 acclimated to an irradiance ranging between 50 and  $100 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  and probably  
611 closer to  $50 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  according to our experiments. This observation agrees with the

612 results of Juhl & Krembs (2010), who showed that *Nitzschia frigida* (the most abundant bottom  
613 ice pennate diatom in the Arctic) could acclimate up to 110  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  in laboratory  
614 conditions. Also similar to our data, Cota & Horne (1989) reported that the optimal  
615 photosynthetic irradiance range for ice algae was from 16 to 100  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ . When  
616 exposed to 200  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ , and despite the significant increase of DES index, ice  
617 algae underwent an important drop down of their photochemistry as indicated by the very low  
618  $F_v/F_m$  (ca. 0.3) and its only partial recovery, which well illustrates PSII photoinactivation and/or  
619 photodamage (Petrou et al. 2010). This light-response has already been reported for ice algae in  
620 Antarctica (Petrou et al. 2010, 2011). In contrast, studies in Greenland and Antarctica found that  
621 highly shade-adapted ice diatoms showed a photoinhibitory response at irradiances as low as 25  
622 to 50  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  (e.g. Rysgaard et al. 2001, McMinn et al. 2007, Mangoni et al. 2009,  
623 Ryan et al. 2011). Nutrient availability (Cota & Horne 1989) could well explain this discrepancy  
624 with our data as well as differential photoadaptation abilities among diatom species and  
625 communities between our data and others (Laviale et al. 2015, Petrou et al. 2016). Thus,  
626 environmental (e.g. nutrient concentrations and light conditions depending on snow depth) and  
627 biological (e.g. algal community composition) conditions influence the photo-response of ice  
628 algae, which can acclimate to a range of irradiances from 25 up to 100  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$   
629 according to the literature and this study. It is noteworthy that ice algae could be more light  
630 resistant when aggregated (a behavioral feature we could not assess with the design of our  
631 experiments). In fact, aggregation of ice algae during spring and generated self-shading are 2  
632 processes often mentioned in Arctic studies (Glud et al. 2002, Assmy et al. 2013, Fernández-  
633 Méndez et al. 2014), and it could expand their range of light resistance beyond 100  $\mu\text{mol}$   
634  $\text{photons m}^{-2} \text{ s}^{-1}$ .

635 In order to better understand the photophysiological response of ice algae, we compared  
636 the effects of presence and absence of an inhibitor of de-epoxidation of DD into DT (i.e. DTT)  
637 and of PSII photodamage repair (i.e. lincomycin). This single experiment with duplicate samples  
638 gives us an idea of the relative importance of DT and PSII D1 protein synthesis in  
639 photoprotection and in the maintenance of photosynthesis under an irradiance range (ca. 50 to  
640 100  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) that ice algae experience at the ice–water interface (Fig. 7a).  
641 Although this type of experiment has been previously conducted (DTT: Kudoh et al. 2003,

642 Griffith et al. 2009; lincomycin: Petrou et al. 2010), this was the first time that such a combined  
643 protocol was applied on an Arctic ice algal community. As during our controlled experiments,  
644 bottom ice algae were able to maintain their photosynthetic capacity (mostly high and stable  
645  $F_v/F_m$ ) under these light conditions. Differential light-response between control conditions and  
646 inhibitor treatments indicate that PSII photochemical functionality was supported by both DT  
647 and D1-psbA protein synthesis with an apparently stronger photoprotective capacity by DT  
648 synthesized from DD de-epoxidation (i.e.  $F_v/F_m$  decrease was significantly higher when DTT  
649 was added as compared to lincomycin). This is in agreement with previous reports on Antarctic  
650 bottom ice algae, showing that they are well adapted to their changing *in situ* light environment  
651 as indicated by no/low PSII photodamage due to DT and D1-psbA protein synthesis (Petrou et al.  
652 2010, 2011). However, when ice algae were exposed to an over-saturating light stress (ca. 1000  
653  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ), their photochemical capacity was nearly abolished after 3 h, although  
654 efficient DT-driven photoprotection occurred during the first 2 h. This response could be  
655 associated with high  $E_{\text{PAR}}$  but also with the presence of UVR in this experiment, while it was  
656 absent in the others. Some studies showed that pennate diatoms were relatively tolerant of UVR  
657 (Zacher et al. 2007, Wulff et al. 2008), while a recent study on ice algal communities in the  
658 Baltic Sea observed that UVR was one of the controlling factors (Enberg et al. 2015). In  
659 addition, studies on Antarctic algal cultures exposed to UVR observed an increase in mortality  
660 (McMinn et al. 1999), a reduction in photosynthesis (Schoeld et al. 1995, Villafañe et al. 2004)  
661 and a decline in productivity (Marcoval et al. 2007). Such light conditions can occur when ice  
662 algae released from sea ice are exported towards the surface of open waters along a receding ice  
663 edge. Our observation strongly points to the inability of ice algae to manage with a high rate of  
664 PSII photodamage generating photoinhibition. However, as mentioned above, they can also  
665 protect themselves via self-shading by forming aggregates when released into the water column  
666 (Glud et al. 2002, Assmy et al. 2013, Fernández-Méndez et al. 2014). This process enhances the  
667 sinking rate of sea ice algae, especially of diatoms (Raven & Waite 2004, Aumack & Juhl 2015),  
668 and their export to deeper water layers where they can feed both pelagic and benthic food webs  
669 (Kohlbach et al. 2016).

670

## CONCLUSIONS



671 In this study, bottom ice algae were dominated by diatoms and were well adapted to daily  
672 and weekly changes in their light environment during Arctic spring. This is in agreement with  
673 previous studies in Antarctica (e.g. McMinn et al. 2007, Mangoni et al. 2009, Petrou et al. 2011,  
674 Rajanahally et al. 2015). Their rapid response to excess light exposure is supported by central  
675 photoprotective processes such as XC and the repair of photodamaged D1 protein in PSII. We  
676 found that the photoprotective ability of bottom ice algae depends on their light history,  
677 controlled by the overlying snow depth through its influence on light transmittance to the bottom  
678 ice environment. We propose that, in order to acclimate to their permanently changing light  
679 environment driven by snow events and winds, bottom ice algae perform ‘cellular light memory’  
680 similar to higher plants (Szechyńska-Hebda et al. 2010). According to our data, cellular light  
681 memory can prolong over at least 2 wk, enabling ice algae to improve their photoacclimative  
682 response to changing light conditions over different periods (days vs. weeks).

683 In a context of global warming in the Arctic, it has been predicted that the snow cover  
684 will potentially undergo rapid changes during future Arctic spring due to the combined effects of  
685 an increase in snow events (Singarayer et al. 2006, AMAP 2011) yet a decrease in snow depth  
686 (Webster et al. 2014) and duration (Callaghan et al. 2011, Derksen & Brown 2012, Overland et  
687 al. 2014). This will directly and strongly affect the light availability for bottom ice algae. The  
688 high plasticity of ice algae to acclimate to relatively large variations in irradiance over very  
689 different time scales suggests that ice algae may be more resilient to future changes than  
690 previously anticipated. However, ice algae will likely face more frequent light stress due to  
691 disturbed sea ice dynamics and especially an earlier melt (Leu et al. 2016). As shown in our  
692 study, bottom ice algae can only sustain reversible photoinhibition under high-light conditions  
693 for a limited period (less than 3 h), greatly reducing their productivity and survival potential once  
694 released into the water column at the ice edge (Yamamoto et al. 2014). In this context, the timing  
695 between snowmelt, the release of ice algae and their stage of development will certainly affect  
696 their photoacclimative and photoprotective responses. Thus, it would be of interest to achieve  
697 similar light-response experiments on bottom ice algae during the decline of their spring bloom  
698 and the beginning of their release from sea ice.

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1124 Table 1. Details of the 3 different experiments conducted during this study. DES: de-epoxidation state; PSII: photosystem II; DTT:  
 1125 dithiothreitol

Expt	Snow cover	Objective	Period	Light source	Light exposure	Recovery period	Inhibitor treatment
1	Thin and thick	To assess the short-term effect of irradiance range observed at the ice–water interface on the photophysiological response of bottom ice algae	Before and during snow events	Cool white LEDs: 10, 50, 100, 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$	3 h	Yes: 2 h, $<5 \mu\text{mol m}^{-2} \text{s}^{-1}$	No
2	Thin	To determine the respective importance of DES and of the synthesis of PSII D1 protein to support bottom ice algae in maintaining their photochemical performance when exposed to their natural light environment	During snow events	<i>In situ</i> irradiance at ice–water interface: from 105 to 53 $\mu\text{mol m}^{-2} \text{s}^{-1}$	6 h	No	Yes: DTT and lincomycin
3	Thin and thick	To assess the photoprotective capability of bottom ice algae when they are exposed to a sudden increase of irradiance	Before snow events	<i>In situ</i> irradiance at water surface	3 h	No	No

1126 Table 2. Photosynthetic properties in bottom ice algae acclimated to thin or thick snow cover  
 1127 before and during the snow events. Values are means ( $\pm$ SD) calculated from n samples of the light-  
 1128 use efficiency for low irradiances ( $\alpha$ ), the relative maximum electron transport rate ( $rETR_{max}$ ) and  
 1129 the light saturation coefficient ( $E_k$ )

Photosynthetic parameter	Before snow events		During snow events	
	Thin snow	Thick snow	Thin snow	Thick snow
$\alpha$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) <sup>-1</sup>	0.21 $\pm$ 0.04 (n = 7)	0.25 $\pm$ 0.11 (n = 6)	0.27 $\pm$ 0.05 (n = 16)	0.28 $\pm$ 0.09 (n = 22)
$rETR_{max}$ (no units)	7.84 $\pm$ 1.61 (n = 7)	3.46 $\pm$ 0.75 (n = 7)	7.27 $\pm$ 6.08 (n = 18)	7.30 $\pm$ 4.63 (n = 22)
$E_k$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	45.8 $\pm$ 8.5 (n = 6)	22.2 $\pm$ 11.2 (n = 5)	26.5 $\pm$ 15.9 (n = 17)	29.9 $\pm$ 13.1 (n = 21)

1130

1131 Fig. 1. Ice camp location (black dot) near Broughton Island (67° 28' N, 63° 47' W). The hamlet of  
 1132 Qikiqtarjuaq is also indicated

1133

1134 Fig. 2. Time series of (a) thin and thick site-averaged snow depth, (b) site-averaged sea ice  
 1135 thickness, (c) nitrate plus nitrite ( $NO_x$ ) concentration and (d) photosynthetically active radiation  
 1136 ( $E_{PAR}$ ) transmittance at the ice-water interface during the 3 sampling periods (before and during  
 1137 snow events, and snowmelt). Average was calculated on 9 to 11 values for (a) and (b), and on 2 to  
 1138 8 values for (d); bars are  $\pm$ SD

1139

1140 Fig. 3. Time series of (a) total chlorophyll *a* (Tchl *a*) concentration, (b) the ratio of photoprotective  
 1141 (PPC) to photosynthetic carotenoids (PSC) and (c) the ratio of the sum of diadinoxanthin and  
 1142 diatoxanthin (DD+DT) to Tchl *a* under thin and thick snow cover sites during the 3 sampling  
 1143 periods (before and during snow events, and snowmelt). No sampling at thin snow site was  
 1144 performed after 24 June

1145

1146 Fig. 4. Site-averaged relative contribution of major algal groups to chl *a* concentrations  
 1147 (CHEMTAX analysis) under (a) thin and (b) thick snow covers during the 3 sampling periods  
 1148 (before and during snow events and snowmelt). Average was calculated for each snow cover from

1149 8 and 12 samples before and during snow events, respectively. During snowmelt, the average was  
1150 calculated from 5 samples for thin snow and 9 samples for thick snow

1151

1152 Fig. 5. Maximum quantum yield of PSII photochemistry ( $F_v/F_m$ ) of bottom ice algae exposed to 10,  
1153 50, 100 and 200  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ . Bottom ice algae were collected under (a,c) thin and (b,d)  
1154 thick snow cover sites (a,b) before and (c,d) during snow events. Samples were exposed to the  
1155 different light conditions for 3 h, followed by 2 h of recovery at low light ( $<5 \mu\text{mol photons m}^{-2}$   
1156  $\text{s}^{-1}$ ). Values are mean  $\pm$  SD of experiments performed on (a) 14 May ( $n = 3$ ), (b) 6 and 12 May ( $n =$   
1157 6), (c) 25 and 29 May ( $n = 6$ ) and (d) 27 and 31 May ( $n = 6$ )

1158

1159 Fig. 6. De-epoxidation state index ( $\text{DES} = \text{DT} / [\text{DD} + \text{DT}]$ , where DT is diatoxanthin and DD is  
1160 diadinoxanthin) for bottom ice algae exposed to 10, 50, 100 and 200  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ . Bottom  
1161 sea ice algae were collected under (a,c) thin and (b,d) thick snow cover sites (a,b) before and (c,d)  
1162 during snow events, respectively. Samples were exposed to different light conditions for 3 h,  
1163 followed by 2 h of recovery at low light ( $<5 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ). Values are averages  $\pm$  SD of  
1164 experiments performed on (a) 14 May ( $n = 3$ ), (b) 6 and 12 May ( $n = 6$ ), (c) 25 and 29 May ( $n = 6$ )  
1165 and (d) 27 and 31 May ( $n = 6$ ). Asterisks indicate a significant difference with  $T_0$  of the respective  
1166 light treatment: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$

1167

1168 Fig. 7. Variation in (a) estimated photosynthetic active radiation ( $E_{\text{PAR}}$ ) at the ice–water interface,  
1169 (b)  $F_v/F_m$  and (c) DES(see Fig. 6) of bottom ice algae in the presence or absence of the inhibitor of  
1170 DD de-epoxidation (DTT) and of D1 protein synthesis (lincomycin). Duplicate samples of bottom  
1171 ice algae were collected under thin snow cover site and exposed to *in situ* irradiance at the ice–  
1172 water interface from 11:00 to 17:00 h (local time, UTC – 05:00) on 21 May

1173

1174 Fig. 8. Variations in (a) incident PAR, (b)  $F_v/F_m$ , (c) total chlorophyll *a* (Tchl *a*) and (d) de-  
1175 epoxidation state index ( $\text{DES} = \text{DT} / [\text{DD} + \text{DT}]$ , where DT is diatoxanthin and DD is  
1176 diadinoxanthin) for bottom ice algae exposed to incident irradiance from 12:15 to 15:15 h (local  
1177 time, UTC – 05:00) on 3 May 2015.  $E_{\text{PAR}}$  data were not recorded between 14:44 and 15:27 h.  
1178 Bottom ice algae were collected under thin and thick snow cover sites. In (b–d), values are mean  
1179 ( $\pm$ SD) calculated from duplicate samples. DES is missing for the thick snow cover site at 15:15 h

Table 1.

Experiment	Snow cover	Objective	Period	Light source	Light exposure	Recovery period	Inhibitor treatment
1	Thin and thick	To assess the short-term effect of irradiance range observed at the ice-water interface on the photophysiological response of bottom ice algae	Before and during snow events	Cool white light-emitting diodes: 10, 50, 100, 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$	3 h	Yes, 2 h, $< 5 \mu\text{mol m}^{-2} \text{s}^{-1}$	No
2	Thin	To determine the respective importance of DES and of the synthesis of PSII D1 protein to support bottom ice algae in maintaining their photochemical performance when exposed to their natural light environment	During snow events	<i>In situ</i> irradiance at ice-water interface: from 105 to 53 $\mu\text{mol m}^{-2} \text{s}^{-1}$	6 h	No	Yes: DTT and lincomycin
3	Thin and thick	To assess the photoprotective capability of bottom ice algae when they are exposed to a sudden increase of irradiance	Before snow events	<i>In situ</i> irradiance at water surface	3 h	No	No

Table 2.

Photosynthetic parameter	Before snow events		During snow events	
	Thin snow	Thick snow	Thin snow	Thick snow
$\alpha$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) <sup>-1</sup>	0.21 ± 0.04 (n = 7)	0.25 ± 0.11 (n = 6)	0.27 ± 0.05 (n = 16)	0.28 ± 0.09 (n = 22)
rETR <sub>max</sub> (no unit)	7.84 ± 1.61 (n = 7)	3.46 ± 0.75 (n = 7)	7.27 ± 6.08 (n = 18)	7.30 ± 4.63 (n = 22)
E <sub>k</sub> ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	45.8 ± 8.5 (n = 6)	22.2 ± 11.2 (n = 5)	26.5 ± 15.9 (n = 17)	29.9 ± 13.1 (n = 21)

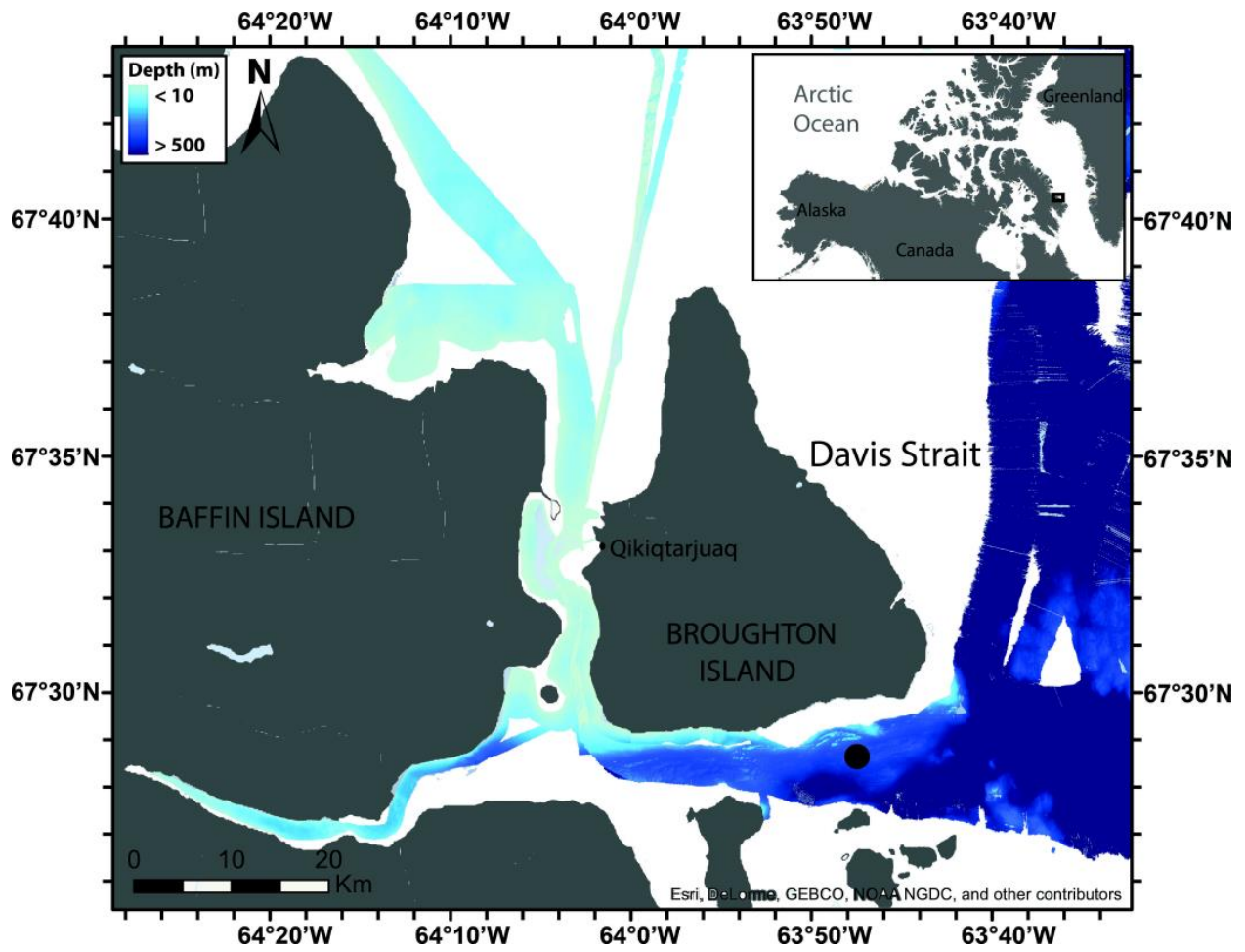


Figure 1.

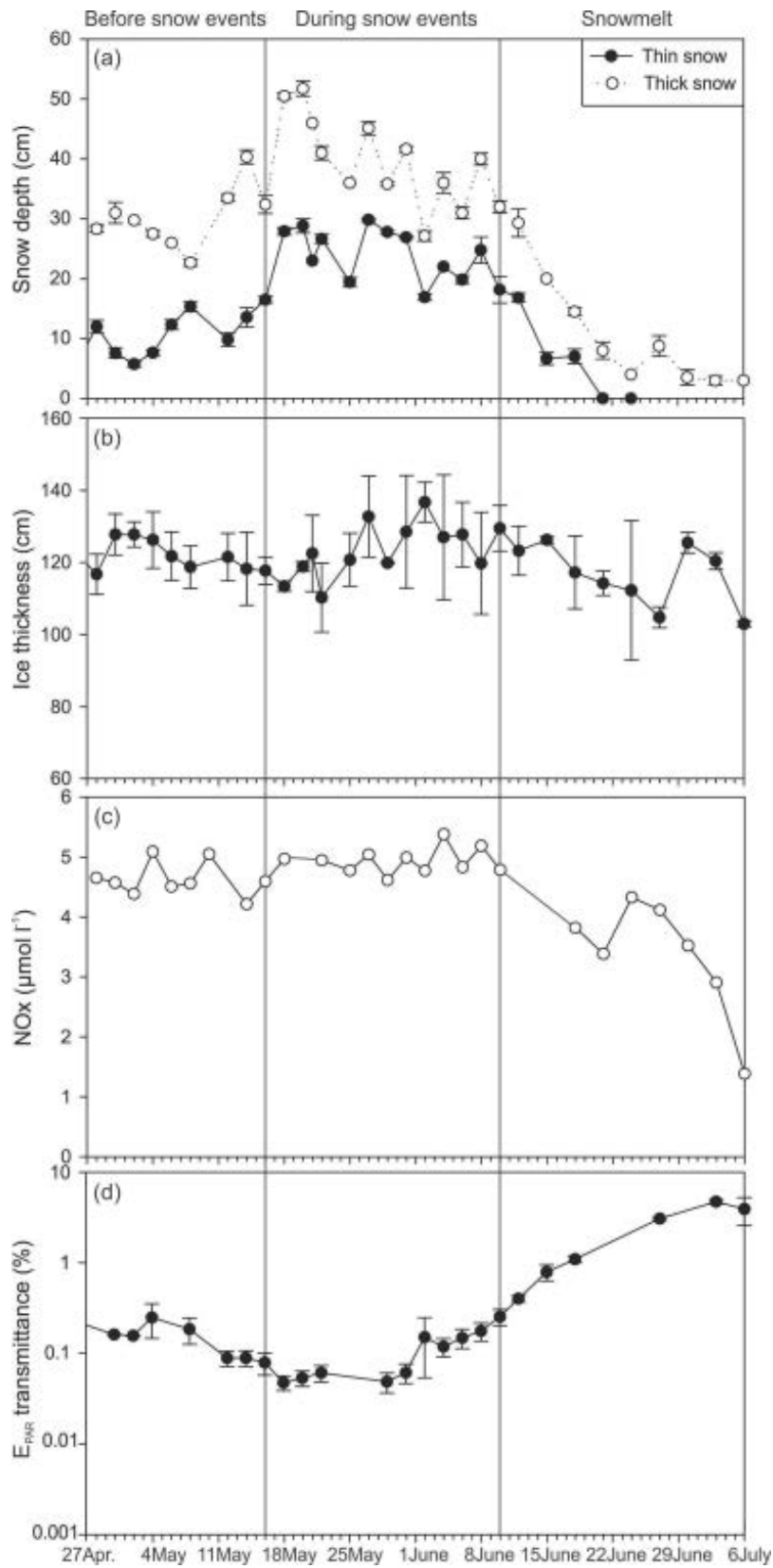


Figure 2.

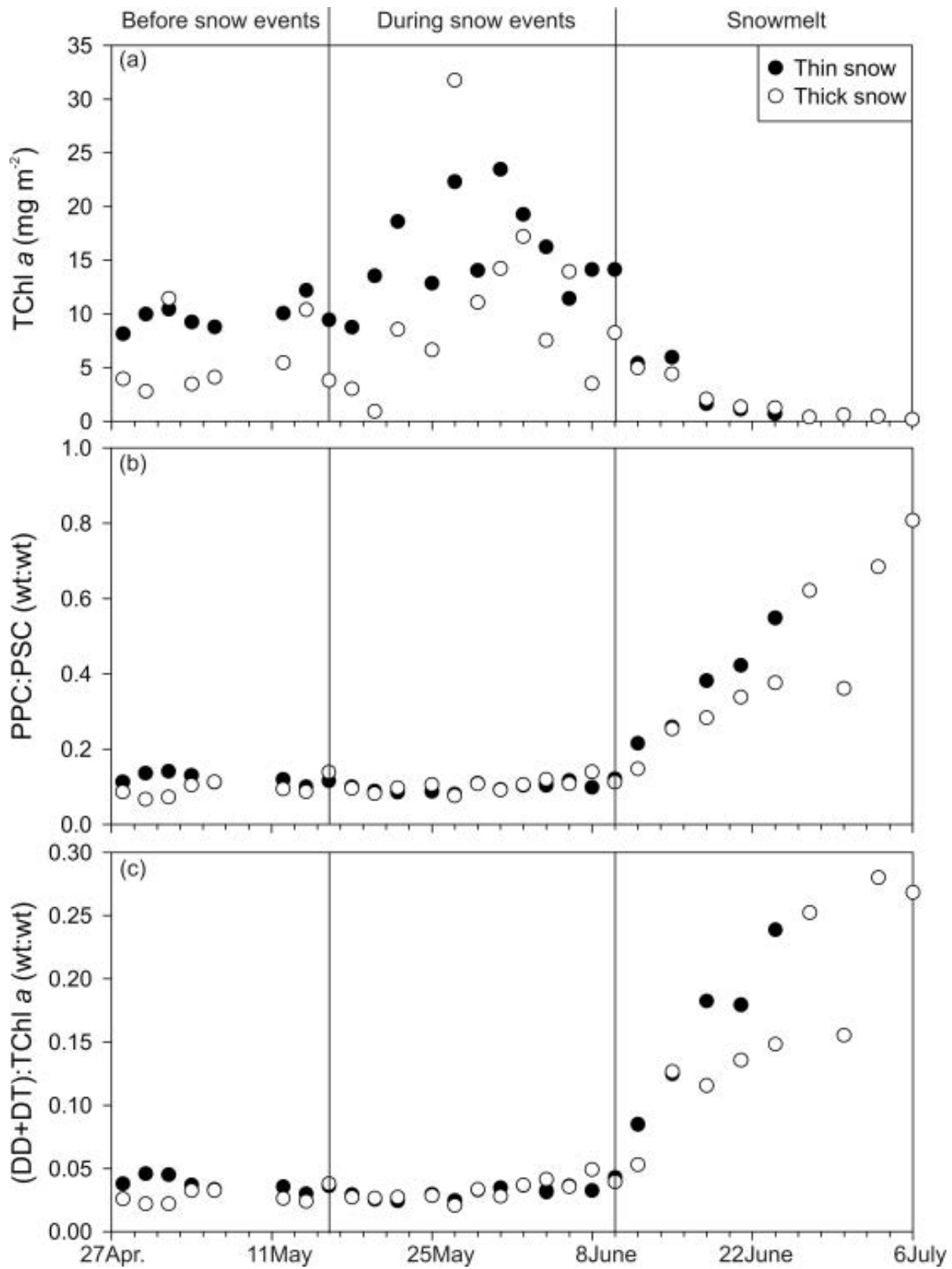


Figure 3.

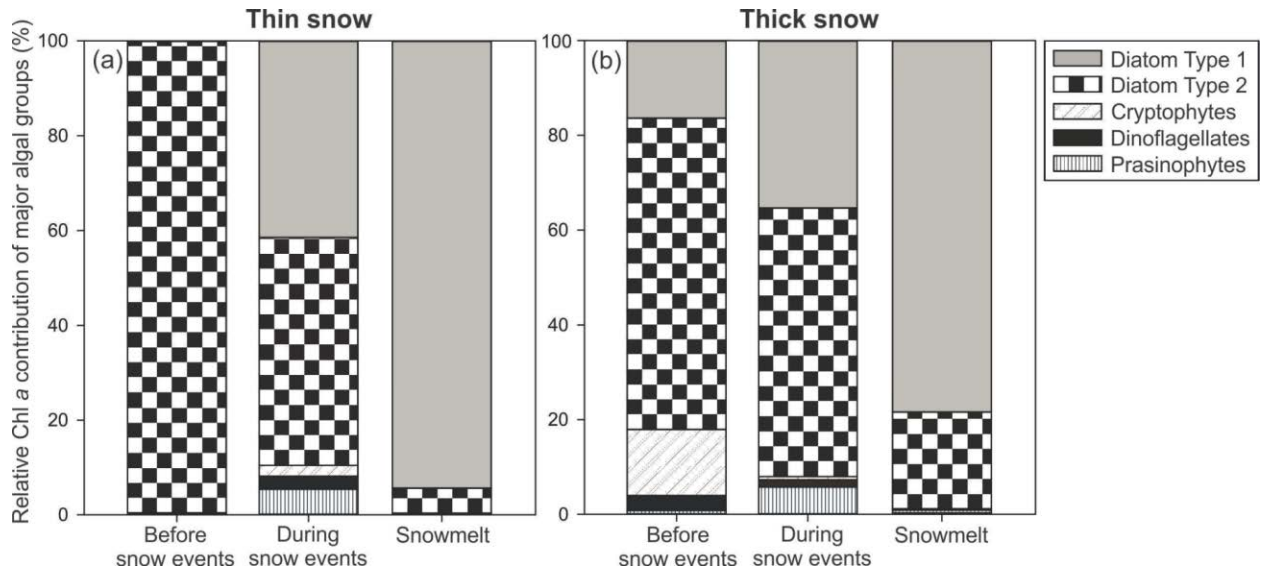


Figure 4.



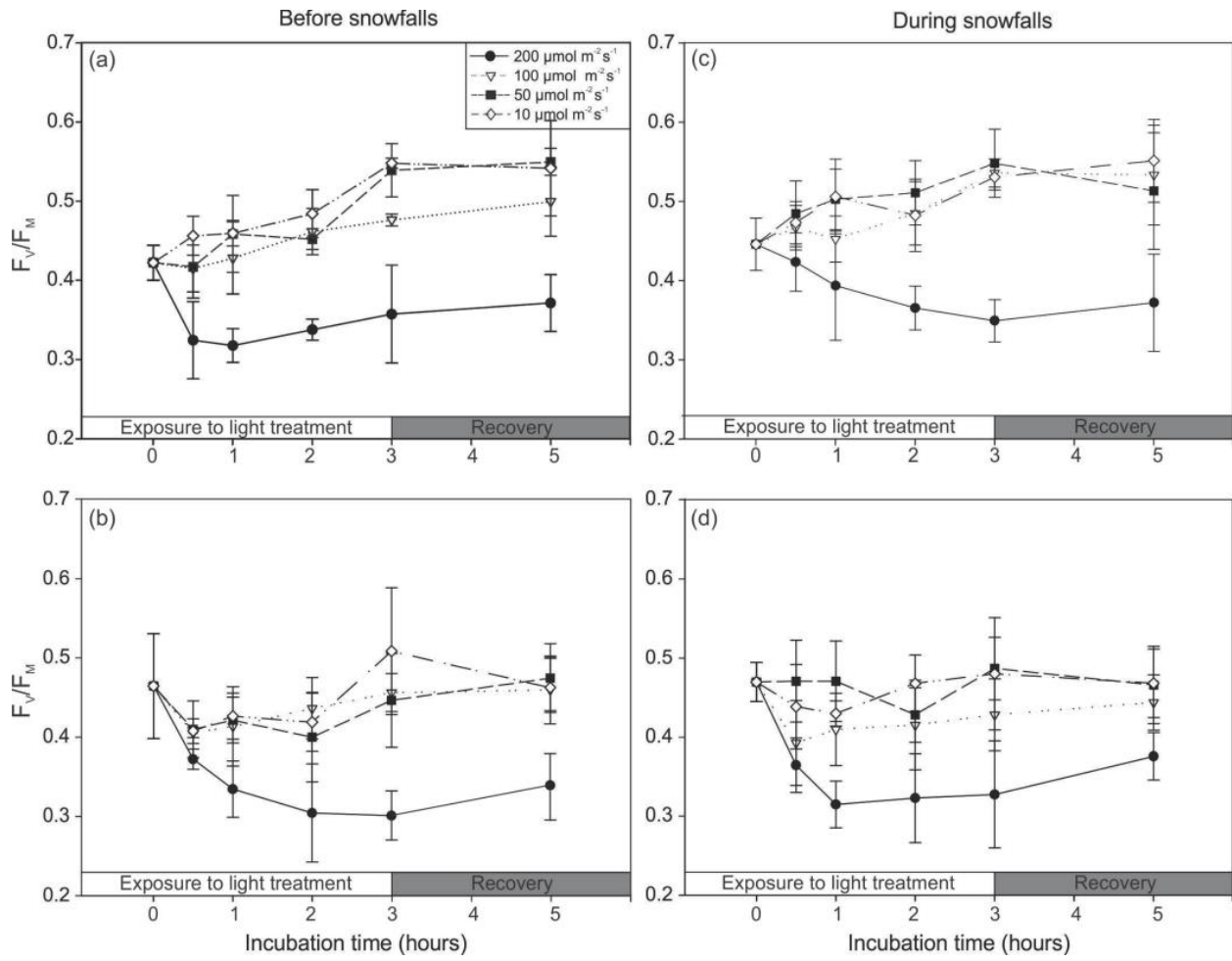


Figure 5

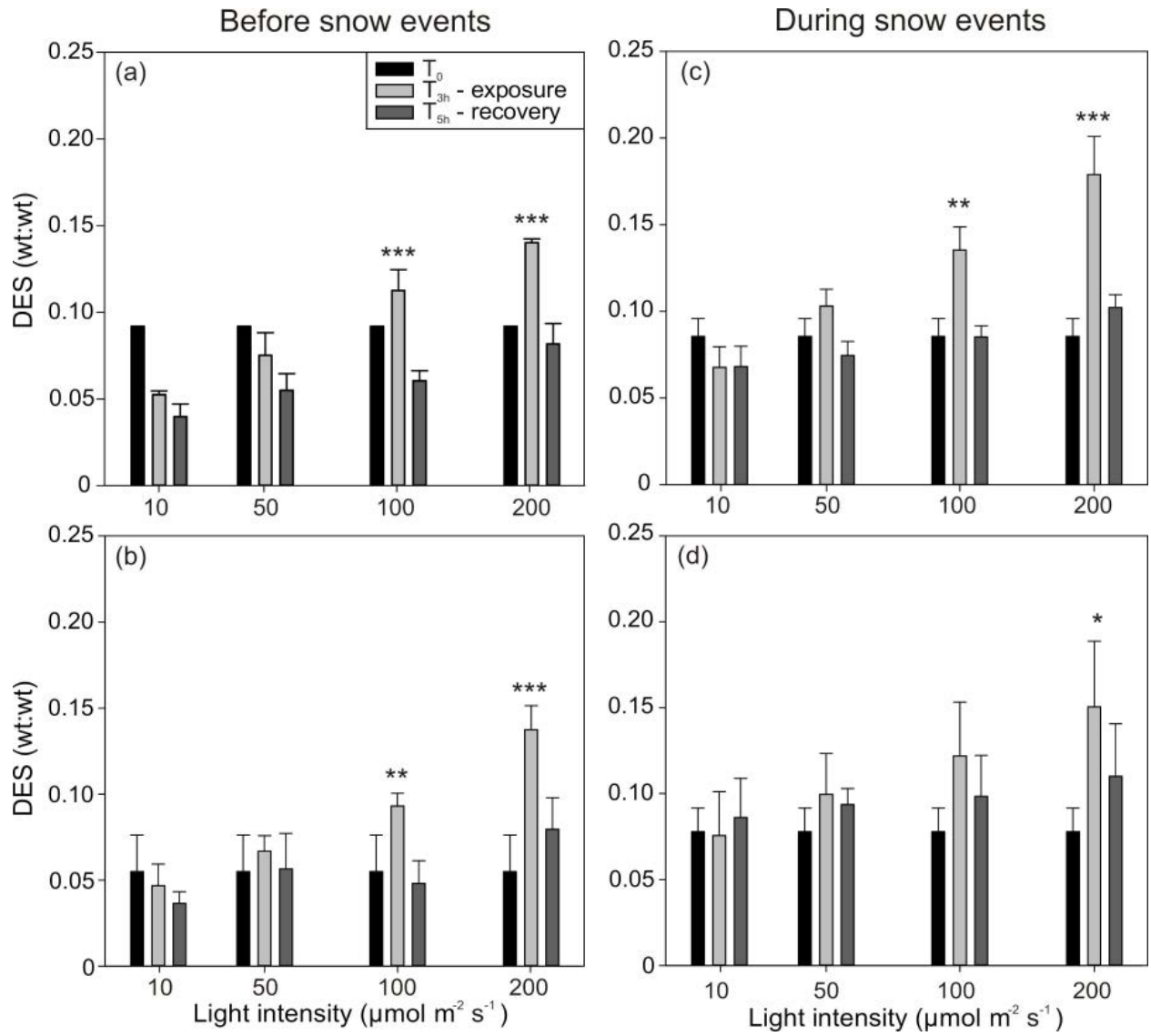


Figure 6.

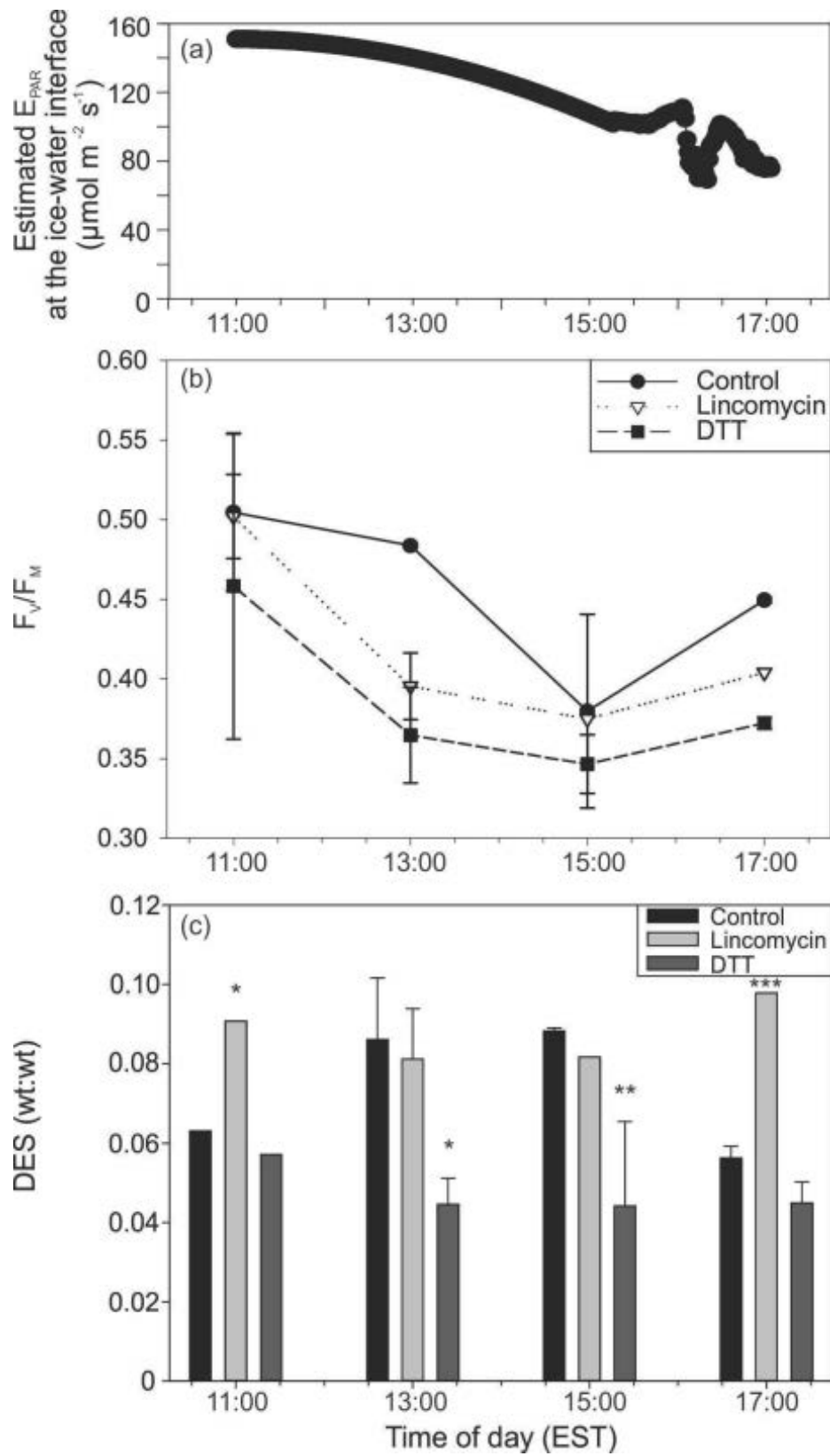


Figure 7.

3 May 2015

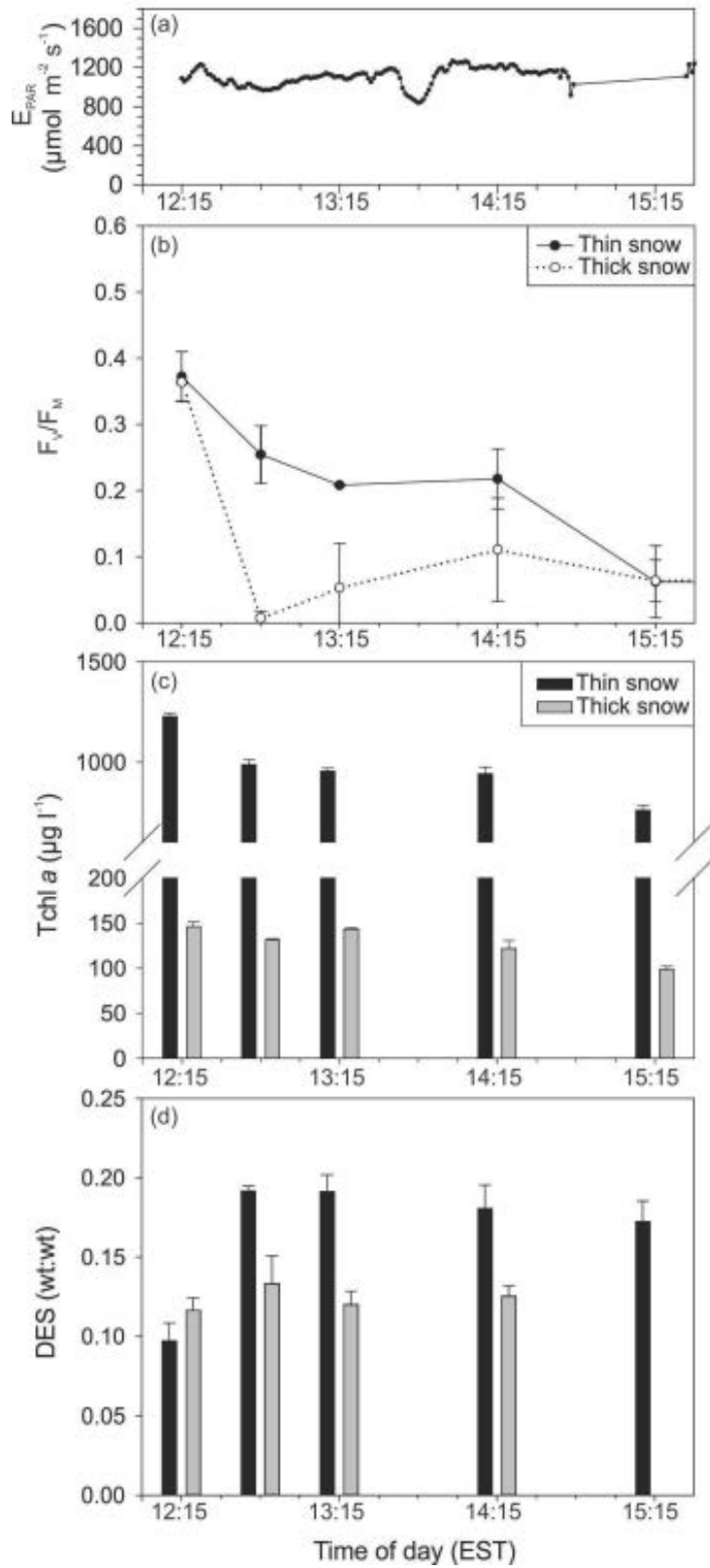


Figure 8