

1 **Title:** Impacts of Changing Winters on Lake Ecosystems will Increase with Latitude

2 **Running head:** Larger Climate Impacts on High Latitude Lakes

3

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13

14 **Abstract:**

15 Climate warming is especially pronounced in winter and at high latitudes. Warming winters are leading  
16 to loss of lake ice and changing snow cover on seasonally freezing lakes. Past neglect of the ice cover  
17 period by lake scientists has resulted in critical data and theory gaps about the role of winter conditions  
18 in lake ecosystem function and the effects of changing winters on aquatic systems. Here we use simple  
19 models to show that the latitudinal interaction between ice cover duration and light flux seasonality has  
20 profound and underappreciated implications for lake ecosystems. Our models focus on light and  
21 temperature, two paramount drivers of ecosystem processes. We show that the amount of light arriving  
22 in lakes while they are ice covered increases non-linearly with latitude and that light climate of high  
23 latitude lakes is much more sensitive to changing winter conditions than that of lower latitude lakes. We  
24 also demonstrate that the synchronicity between light flux (a key controller of primary production) and  
25 temperature (which controls invertebrate production) decreases with latitude. Our results indicate that  
26 ice loss will lead to greater change to the productivity and nature of biotic interactions in higher latitude  
27 aquatic ecosystems and make several testable predictions for understanding the consequences of  
28 climate-induced changes across latitudinal gradients.

29

30 **Keywords:** Limnology, Climate Change, Winter Ecology, Ice, Arctic, Boreal

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32

### 33 **Introduction**

34 Climate warming in the northern hemisphere is especially pronounced and rapid during winter  
35 and at high latitudes (Overland et al. 2020; IPCC 2021). Warmer winters decrease lake ice cover duration  
36 and thickness, impact ice transparency, and modify winter precipitation patterns and the accumulation  
37 of snow on lake ice (Mudryk et al. 2020; Sharma et al. 2022; Weyhenmeyer et al. 2022). Determining  
38 how these changing winter conditions affect the ecology of seasonally frozen lakes —and how lakes will  
39 respond to future winter warming — is challenging due to historic neglect of the ice cover period by  
40 most aquatic scientists.

41 Growing recognition of this winter knowledge gap is motivating limnologists and other  
42 environmental researchers to pay closer attention to winter and how winter conditions shape terrestrial  
43 and aquatic ecosystems and set the stage for the following seasons (Hampton et al. 2016; Berge et al.  
44 2020; Hébert et al. 2021; Studd et al. 2021). Much of this new research is necessarily ecosystem- and  
45 site-specific and is only starting to produce synthetic frameworks for integrating winter into the full  
46 annual ecological cycle (e.g., Cavaliere et al. 2021; Jansen et al. 2021; Yang et al. 2021). The relative  
47 scarcity of winter data, regional focus of many winter studies, and gaps in theory make it difficult to  
48 detect patterns and test general hypotheses about winter ecology across broad spatial scales and to  
49 make predictions about the future of lake ecosystems.

50 Here we build on recent work in winter limnology to propose an explanatory framework for how  
51 winter conditions and processes integrate into the annual ecology of lakes across large latitudinal and  
52 climatic gradients. Our framework is focused on the interaction between latitudinal gradients in solar  
53 irradiance and latitudinal and regional patterns in ice and snow cover. We show that the interaction  
54 between these factors has important and not widely-recognized consequences for the light and  
55 temperature regimes of seasonally ice-covered lake. Light and temperature are paramount physical  
56 drivers of lake ecosystem function, directly affecting primary and secondary production and the fate of  
57 organic carbon. We demonstrate that the amount of light reaching the water column of lakes during the  
58 ice cover period increases non-linearly with latitude. We also show that high latitude lakes are more  
59 sensitive to climate-driven changes in their light climate than lower latitude lakes. Finally, we show that  
60 the synchronicity between light (a key controller of primary production) and temperature (which  
61 controls respiration and secondary production) decreases with latitude but becomes increasingly  
62 coupled with loss of ice.

63 Together, these results indicate that the ecological consequences of ice cover loss and other  
64 changes in winter conditions (e.g., changing ice clarity and snow conditions) will be greatest at high

65 latitudes, with the impacts of climate change increasing from temperate, to boreal, to arctic lakes. Many  
66 of the elements of our proposed framework are also highly relevant for high elevation lakes, which –  
67 even at lower latitudes– typically experience long periods of ice cover.

68

### 69 **Insolation and ice cover across latitudes**

70 From the equator to the poles, there is a 2.4-fold decrease in total, top-of-atmosphere, annual  
71 solar energy flux, from  $1.53 \times 10^5 \text{ W/m}^2$  at  $0^\circ$  to  $6.32 \times 10^4 \text{ W/m}^2$  at  $90^\circ\text{N/S}$ . The seasonality of solar flux  
72 also changes with latitude, becoming increasingly variable at higher latitudes. This culminates in periods  
73 of complete darkness in winter ('polar night') and continuous light in summer ('midnight sun') beyond  
74 the Arctic and Antarctic Circles ( $66.3^\circ\text{N/S}$ ). This global-scale variation in solar energy flux drives  
75 latitudinal temperature gradients, with generally longer and colder winters at higher latitudes. More  
76 severe winters lead to earlier ice-on, later ice-off, thicker ice, and longer ice cover duration on high  
77 latitude lakes (Fig. 1A, B).

78 Lakes are unevenly distributed across the Earth's surface (Downing et al. 2006). They peak in  
79 abundance between  $50$  and  $70^\circ\text{N}$ , regions with large seasonal variation in insolation and generally cold  
80 winters (Fig. 1B). It is well-known that most of the world's lakes freeze for at least part of the year (e.g.,  
81 Denfeld et al. 2018). What has not been as well-appreciated is that, on an annual basis, most lakes that  
82 freeze are frozen for longer than they are ice free. The median ice cover duration across the world's  
83 seasonally frozen lakes is estimated to be 218 days (Wang et al. 2022) and, on average, lakes above  
84  $\sim 55^\circ\text{N}$  are frozen for more than half of the year (Fig. 1B). At these high latitudes, lake ice persists late  
85 into the year and, moving poleward, increasingly overlaps with the summer period of peak light. High  
86 latitude lakes may therefore still be covered by ice during the 'midnight sun' period (Fig. 1C). At lower  
87 latitudes, many high elevation lakes also remain frozen for large parts of calendar spring and summer.

88 Crucially, the latitudinal interaction between lake ice cover duration and solar flux seasonality  
89 means that, at higher latitudes, a larger fraction of annual light reaches the Earth's surface when lakes  
90 are covered by ice (Fig. 1C, D). For example, at  $45^\circ\text{N}$ , approximately 28% of total annual solar radiation  
91 reaches the Earth's surface while lakes are ice covered. In contrast, at  $75^\circ\text{N}$ , approximately 56% of total  
92 annual solar radiation arrives while lakes are covered by ice (assuming median ice cover periods for both  
93 latitudes and discounting cloud cover; Fig. 1C, E). This variation in the timing of incoming solar energy in  
94 relation to ice cover phenology has important consequences for lake ecology and how lake ecosystems  
95 across latitudes respond to climate change.

96

97 **Ice, snow, light, and temperature**

98 Ice and snow attenuate light, restricting the amount of solar energy that reaches the water  
99 column of ice-covered lakes and is subsequently available for photosynthesis and heating and mixing the  
100 water. Light attenuation by ice depends on ice clarity. Clear ('black') lake ice is much more transparent  
101 than cloudy ('white') lake ice. A 1-m layer of very clear black ice (with a light attenuation coefficient  
102  $K_d \approx 0.32 \text{ m}^{-1}$ , Belzile et al., 2001) transmits >70% of photosynthetically available radiation (PAR) reaching  
103 its surface, compared to less than 1% for the same thickness of white ice ( $K_d \approx 5 \text{ m}^{-1}$  or more). Snow  
104 attenuates light more efficiently than ice, and just 20 cm of snow can block 99% of PAR (Prowse &  
105 Stephenson 1986), with higher attenuation for new snow with low moisture content than for wet and/or  
106 metamorphosed snow (Perovich 2007). Thus the thickness and characteristics of ice, and even more so,  
107 snow, exert strong control on a lake's underwater light environment during winter (Cavaliere et al.  
108 2021). In regions where black ice predominates and there is little snowfall (or limited snow retention on  
109 the ice), under-ice light levels can be high (Prowse & Stephenson 1986; Welch et al. 1987; Imbeau et al.  
110 2021; Bramburger et al. 2023). This is also the case both during the late ice cover season when the snow  
111 has melted as well as in response to increasingly common mid- and late-winter rain-on-snow events  
112 (Hansen et al. 2014). On the other hand, in regions and periods characterized by thick snow and  
113 predominance of white ice, the under-ice environment can be very dark.

114 The large seasonality of solar flux at higher latitudes and overlap between the ice cover period and  
115 peak solar irradiance mean that ice and snow have increasingly important consequences for lake light  
116 regimes and total annual light budgets at higher latitudes. We illustrate these consequences using  
117 simple models where we use a combination of realistic ice and snow cover phenologies, light  
118 attenuation coefficients, and solar flux patterns to examine how the light environment of lakes changes  
119 across latitude and gradients in winter climate conditions (Fig. 2A, B). Briefly, we modeled the year-  
120 round light environment (i.e., the light flux reaching the top of the water column) of seasonally-frozen  
121 lakes at 45, 55, 65, and 75°N, using daily cloud-free irradiance data to determine the potential light flux  
122 to the lake. For ice cover periods, we included median, short (median minus 1 month), and long (median  
123 plus 1 month) ice cover durations, with median values based on the global lake ice phenology data from  
124 Wang et al. (2022). Short and long ice cover periods were included to explore how variation in ice cover  
125 duration, whether driven by anthropogenic factors (climate change-driven ice loss) or regional climate  
126 (altitude, continentality) interacts with light flux and impacts ecosystem processes. Seasonal ice and  
127 snow thickness and phenology were simulated based on literature data, published model results, and  
128 personal observations by the authors (e.g., Greenbank 1945; Schindler et al. 1974; Welch et al. 1987;

129 Dibike et al. 2012; Leppäranta 2015; Grosbois et al. 2017; Yang et al. 2020; Xie et al. 2023; Ghane and  
130 Boegman 2023). We used a range of realistic light attenuation coefficients for ice ( $K_d = 2-5$ ) and an  
131 intermediate attenuation coefficient for snow ( $K_d = 15$ ; Leppäranta et al. 2012) to estimate the potential  
132 amount of light reaching the water under the ice and snow. See supplementary information section for  
133 additional detail. This approach enabled us to evaluate total lake light budgets as well as the amount of  
134 light reaching the top of the water column during the open water and ice cover periods across the  
135 modeled scenarios.

136 Our models reveal several important and robust patterns. First, the total annual light flux reaching  
137 the water column of lakes across the full year decreases with increasing latitude and ice cover duration  
138 (Fig. 2A). Second, the total light flux reaching the water column during the ice cover period also tends to  
139 decrease with latitude, but has the potential to increase with ice cover duration in each latitude band,  
140 and is also very strongly influenced by ice transparency and snow cover conditions (Fig. 2B). In our  
141 simulations, ice thickness and clarity generally had less effect on the under-ice light environment than  
142 snow cover, and modeled under-ice levels were in good agreement with diverse empirical observations  
143 (e.g., Schindler et al., 1974; Welch et al. 1987; Belzile et al., 2001; Lei et al., 2011; Bramburger et al.,  
144 2023; Shchapov and Ozersky 2023). For example, 0.5 m of snow-free ice in our models transmitted  
145 between ~8 and 37% of the light reaching its surface, depending on the ice  $K_d$ . Just 5 cm of snow over  
146 white ice ( $K_d=5$ ), reduced under-ice light levels to <4% of surface light. Forty cm of snow over 0.5 m of  
147 ice, permitted less than 0.1% of incident light to reach the unfrozen water. Because of their large effect  
148 on light transmission, the degree to which snow and ice thickness and clarity influence total winter light  
149 flux also increases with increased duration of the ice cover period (Fig. 2B).

150 Third, the proportion of total annual light reaching the water column during the ice cover season  
151 increases with latitude and ice cover duration (Fig. 2C). In other words, lakes at high latitudes and with  
152 longer ice cover duration for a particular latitude band receive more of their total annual light budget  
153 when they are covered by ice. In our models, lakes at 75°N, received up to 40% of their total annual light  
154 budget during ice cover (median = 10.5 % across all simulation scenarios). In contrast, lakes at 45°N  
155 received no more than 17% of their total annual light budget during ice cover, with a median of 5.5%  
156 across all scenarios. Given the strong seasonality of cloud cover in the Arctic (high cloud cover in  
157 summer and early autumn and low cloud cover in late spring; Liu & Schweiger 2017), our approach may  
158 actually underestimate the amount of light reaching high latitude lakes during their ice-cover period.

159 Finally, the effects of natural and climate change-induced variation in ice cover duration are also  
160 magnified with latitude (Fig. 2D). Because a larger fraction of the annual light budget arrives during the

161 ice cover period at high latitudes, a one-month difference in ice cover duration has a larger effect on a  
162 lake's under-ice (and total annual) light environment at higher latitudes. This means that an equal  
163 duration of ice cover loss will have different impact on lakes across latitudes or lakes that experience  
164 different winter severity. In particular, high latitude lakes and lakes that have especially long ice cover  
165 periods (e.g., because of a strongly continental climate or high altitude), will experience much larger  
166 increases in their annual light budgets than lakes with shorter ice cover duration. For example, a loss of  
167 1 month of ice cover (15-day earlier ice-off in spring and 15-day later ice-on in fall) for a lake with  
168 median ice cover duration at 45°N (142 days) will lead to a 9 – 38% (median = 13%) increase in total  
169 annual light flux; an equivalent loss of ice cover for a lake that has an extra month of ice cover duration  
170 at 45°N will lead to an 17 – 80% (median = 20%) increase in total annual light. In contrast, similar losses  
171 of ice for a lake at 75°N, would result in an increase of 13 – 42% (median = 37 %) in annual light flux for a  
172 lake with a median (270 days) ice cover duration and of 20 –104% (median = 74%) for one that has an  
173 extra month of ice cover. The degree of increase in total light will be strongly related to snow depth and  
174 ice clarity, with the greatest increases for lakes that experience deep snow cover and thick white ice.

175         Latitudinal patterns of solar flux and ice cover seasonality also have important consequences for  
176 lake temperatures and their response to future climate warming. At lower latitudes, ice-off generally  
177 occurs earlier in spring, when light levels are still increasing toward their annual maximum. At these  
178 latitudes, water temperature in most lakes increases rapidly after ice-off, stratification often sets in  
179 quickly, and the epilimnion continues to gain heat through the summer, reaching high temperatures by  
180 July (Fig. 3A). For example, in central Minnesota (USA, 45°N), ice-off typically occurs in late March,  
181 stratification sets in within 2 – 3 weeks, and peak summer temperatures reach 25°C or more (e.g.,  
182 Tansim et al. 2021). At high latitudes, ice cover persists longer (e.g., until mid-July on Victoria Island,  
183 Canada, 70°N; Imbeau et al. 2021), and overlaps more closely with the annual peak of solar flux than at  
184 lower latitudes (Fig. 3A). While radiative heating of the under-ice water does contribute to the heat  
185 budget of high latitude lakes and cause under-ice convective mixing, it rarely increases water  
186 temperatures above 4°C, and most of the heating does not occur until ice is off the lake. High latitude  
187 lakes that do stratify may do so sometime in June – July, reach peak temperatures of 12 – 15°C in  
188 August, then cool rapidly and freeze by September or October. In many parts of the Arctic, lakes above  
189 60°N never stratify, with peak summer temperatures of no more than 5 – 10°C (Schindler et al. 1974;  
190 Welch et al., 1987; Sorvari et al. 2000; MacIntyre et al. 2009; Saros et al. 2016).

191         These differences in the timing of water heating and solar flux lead to latitudinal variation in the  
192 synchronicity between the timing of peak light and peak temperatures. At lower latitudes, peak light and

193 peak temperatures are closely coupled. In central Minnesota, the period of peak irradiance occurs when  
194 lakes are stratified and the surface temperature is  $>20^{\circ}\text{C}$  (Fig. 3A). At high latitudes, the timing of peak  
195 light and temperature are decoupled. Irradiance peaks during late ice cover and shortly after ice-off  
196 when the lake is mixed and the water column is still cold. By the time lakes at  $70^{\circ}\text{N}$  reach maximum  
197 surface temperatures in August, light levels are already decreasing from their June peak. Thus, the  
198 portion of the annual light budget that arrives when water temperatures are low is greater at high  
199 latitudes. Light and temperature are the main physical controllers of many biological and  
200 biogeochemical processes, and the latitudinal variation in their synchronicity will have important  
201 consequences for lake ecosystems. This latitudinal pattern also once again highlights that high latitude  
202 lakes with long ice cover periods are more susceptible to ecological change due to ice loss than lower  
203 latitude lakes.

204

### 205 **Consequences for biology**

206 Light is the main physical driver of primary production in aquatic systems, with temperature  
207 becoming increasingly important under light-saturated conditions (Tilzer et al. 1986; Fahnenstiel &  
208 Scavia 1987; Sterner 2010, Edwards et al. 2016; Sherman et al. 2016). In contrast, invertebrate  
209 metabolism, activity, and production are strongly temperature-dependent, from the individual to the  
210 community level (Patalas 1975; Herzig et al. 1980; Plante and Downing 1987; Huntely and Lopez 1992;  
211 Hansen et al., 1997; Shuter and Ing 1997; Kelley and Jones 2023). Thus, seasonal variation in irradiance  
212 and temperature across latitudes should result in predictable latitudinal patterns in the timing and  
213 magnitude of primary and secondary production and the interaction between these processes. We  
214 explore how these processes play out across latitudes and snow and ice cover regimes with a simple  
215 conceptual model (see supplementary information section) of primary and secondary production and  
216 biomass dynamics for lakes at  $45^{\circ}\text{N}$  and  $75^{\circ}\text{N}$ , varying ice cover duration and snow conditions and using  
217 published and unpublished data to simulate annual temperature dynamics. In our models, primary  
218 production is driven primarily by light, with a secondary role for temperature ( $Q_{10} = 1.5$ ; Sherman et al.  
219 2016). Secondary production is primarily driven by temperature ( $Q_{10}=2.7$ ; Huntely and Lopez, 1992;  
220 Hansen et al., 1997). Primary producer biomass changes in response to production and due to grazing by  
221 invertebrates, with consumption proportional to consumer biomass. While this model relies on  
222 numerous simplifying assumptions, we believe it serves as a useful idealized representation of  
223 phytoplankton, periphyton, zooplankton, and littoral zoobenthos dynamics and highlights the main

224 consequences of the latitudinal variation in the seasonality of light and temperature, including due to  
225 variation in ice and snow regimes.

226         Latitudinal variation in total annual solar flux, solar flux seasonality, and ice cover duration –with  
227 lower and more seasonally variable solar flux and longer ice cover duration at high latitudes– suggest  
228 that total annual primary production of lakes should decrease with increasing latitude (as has been  
229 shown by, for example, Brylinsky and Mann 1973) and display greater seasonal variability. Longer ice  
230 cover and its greater overlap with the period of peak solar irradiance at high latitudes also means that a  
231 higher proportion of the total annual pelagic and benthic littoral primary production will occur under the  
232 ice and shortly after ice-off, when the water is still cold (Fig. 3). The greater overlap between peak  
233 irradiance and ice cover at higher latitudes also means that climate change-driven loss of late season ice  
234 cover will result in greater relative increases in total annual primary production in higher latitude lakes  
235 (Fig. 3). The degree to which snow cover conditions and ice clarity affect the timing and magnitude of  
236 under-ice primary production will also be generally greater at higher latitudes, meaning that changes in  
237 snowfall, its accumulation and retention, as well as ice transparency will have larger consequences for  
238 primary production at high latitudes (Fig. S3).

239         Integrated annual zooplankton and littoral zoobenthos production and biomass can also be  
240 expected to decrease with increasing latitude because of lower average annual temperatures and  
241 primary productivity (Fig. 3). The invertebrates of high latitude lakes experience long periods of low  
242 temperatures, darkness, and low plant food availability during late fall and most of winter. At 75°N, the  
243 open water period of most lakes is brief and peak temperatures rarely exceed 10°C. Thus, high latitude  
244 lakes will produce less invertebrate biomass across the year with lower peak summer production rates  
245 and biomasses compared to lower latitude lakes. The long period of unfavorable winter conditions in  
246 high latitude lakes should also result in lower invertebrate biomasses through the winter and less  
247 survival until spring (Kunkel, et al. 2016; Hébert et al. 2021).

248         The partly independent effects of light and temperature on primary and secondary production  
249 should result in an increasing mismatch between the timing of peak plant and invertebrate consumer  
250 growth with latitude. At lower latitudes, temperature and light increase approximately in tandem,  
251 peaking concurrently in mid-summer (Fig. 3A). At higher latitudes, there is a considerable lag between  
252 increasing light and maximum water temperatures, resulting in a peak solar flux when water  
253 temperatures are still around 4°C or lower (e.g., if lakes are still ice-covered). This increasing mismatch  
254 should have implications for plant-grazer interactions, the relative importance of top-down vs. bottom-  
255 up controls on primary producers, and the fate of primary production across latitudes.



256 Planktonic and benthic littoral grazers should exert weaker top-down pressure on spring and  
257 summer phytoplankton and periphyton in high latitude lakes, where under-ice and early spring plant  
258 growth occur at low temperatures that are less favorable to grazer activity. Weaker top-down effects on  
259 spring primary producers at high latitudes could also be exacerbated by less overwinter survival of  
260 zooplankton (Hébert et al. 2021) and littoral zoobenthos. This should result in higher annual primary  
261 producer to grazer biomass and production ratios at high latitudes as well as reduced utilization of  
262 primary production by consumers. High latitude lakes may therefore have more efficient export of  
263 ungrazed phytoplankton to the sediments for either burial or consumption by profundal benthic  
264 organisms, and higher relative standing stocks of littoral periphyton. Loss of ice will increase the  
265 synchronicity of light and temperatures at high latitudes, resulting in a possible reduction in primary  
266 producer to grazer production and biomass ratios and higher potential for top-down control of primary  
267 production (Fig. 3). In regions where climate change is leading to increased snow cover, deep snow (or  
268 opaque ice) can delay substantial primary production until later in spring, also increasing the  
269 synchronicity between primary and secondary production relative to lakes with little snow and clear ice  
270 (Fig. S3).

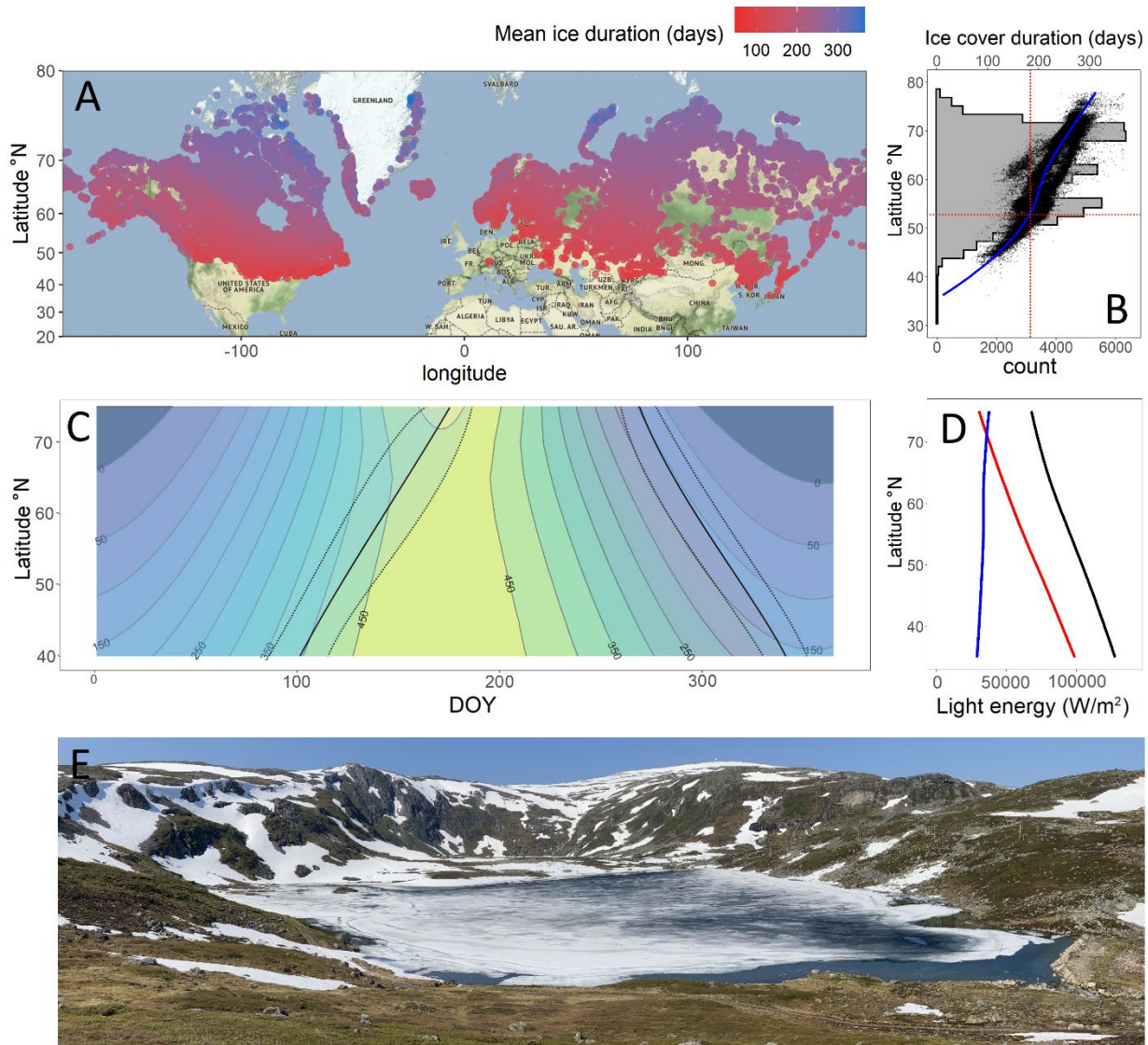
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## 272 **Caveats and conclusions**

273 Lakes vary widely in depth, elevation, concentrations of nutrients, optical properties regulated by  
274 dissolved and particulate matter, and species composition. To focus on the role of ice and snow cover in  
275 shaping lake ecosystems across latitudes, we chose to focus on how idealized phytoplankton-  
276 zooplankton and periphyton-littoral zoobenthos food chains may respond to expected changes in light  
277 and temperature, which are paramount drivers of lower food web processes in lakes. Our estimates of  
278 underwater light availability carry uncertainties related to seasonal and regional differences in cloud  
279 cover, snow phenology and characteristics, water clarity, and mixing regimes. Many factors and food  
280 web components (e.g., the microbial loop, fish) that were omitted here have important impacts on lake  
281 ecosystems, interact with ice and snow conditions and, like climate, vary across large geographical  
282 scales. As such, any small set of individual lakes from different latitudes may not conform to the  
283 patterns we discuss here. Nonetheless, our three key claims of: 1) an increased relative role of under-ice  
284 and cold water period primary production in high latitude lake ecosystems; 2) greater sensitivity of high  
285 latitude lakes to ongoing and predicted future changes in snow and ice conditions; and 3) the greater  
286 relative change in productivity and biotic interactions that high latitude lakes will experience with  
287 climate change driven reductions in lake ice cover, are based on first principles and suggest many

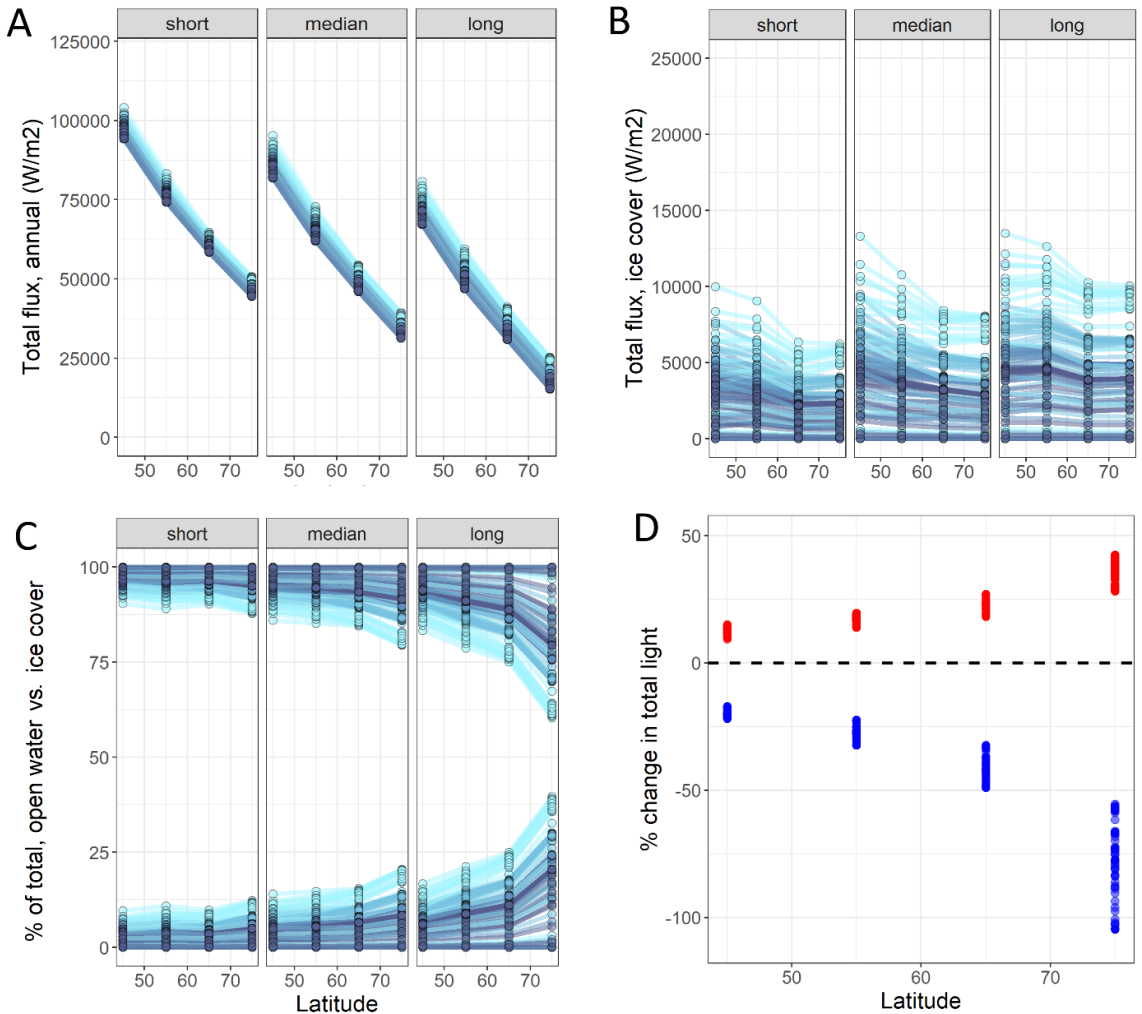
288 testable predictions about the full year seasonality of lakes across broad latitude gradients, including the  
 289 role of winter and ice cover in shaping lake ecosystems.

290 **Figures:**

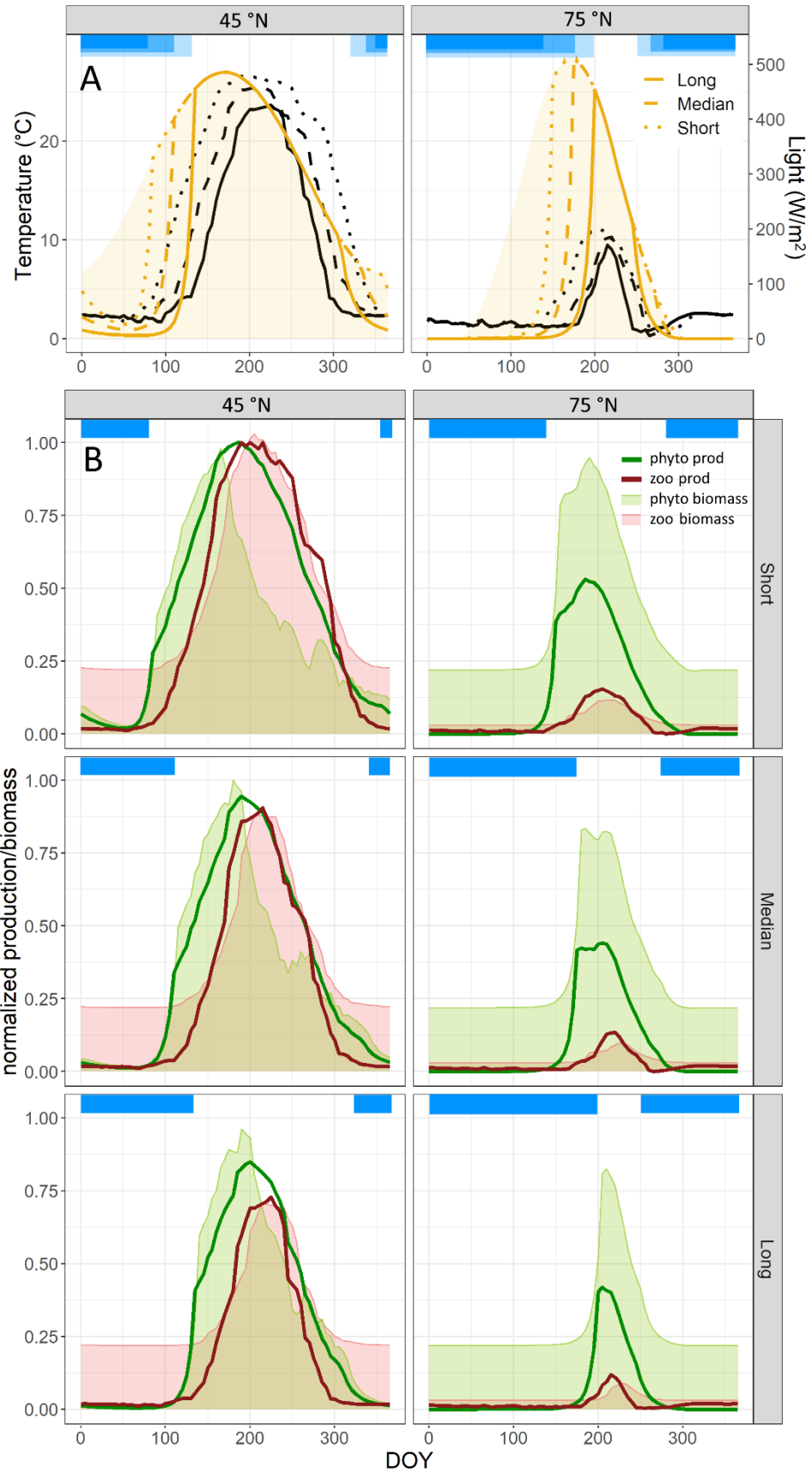


291  
 292 *Fig 1: A) ice cover duration across 67,291 lakes from Wang et al. (2022); B) frequency distribution of seasonally-*  
 293 *freezing lakes (gray histogram), with median ice cover duration across latitudes (blue line) in the northern*  
 294 *hemisphere; and red dashed lines showing approximate latitude where median ice cover duration = 183 days*  
 295 *(based on results from Wang et al. 2022); C) contour plot showing annual pattern of solar flux (W/m<sup>2</sup>/day) between*  
 296 *30°N and 80°N with average (solid black line) and ±1SD (dotted black line) timing of ice-on and ice-off across the*  
 297 *67,291 lakes shown in panel A; D) change in total potential (not accounting for clouds) solar irradiance arriving at*  
 298 *the Earth's surface (black line) across latitudes in relation to amount of light arriving during the typical ice cover*

299 period (blue line) and open water periods (red line) for lakes with median ice cover duration across latitudes; E)  
 300 Lake Mellomvatnet, (69.71°N, 18.82°E; 396 m A.S.L) on June 27, 2022, one week after the summer solstice.  
 301



302  
 303 Fig 2: Light environment in lakes as a function of latitude and ice and snow conditions. A) total light flux reaching  
 304 the water column of lakes across latitudes (45°N to 75°N) under short, median, and long ice cover duration  
 305 scenarios for each latitude band. Points and lines represent variation due to snow cover conditions (duration &  
 306 thickness) and variation in light attenuation by ice ( $K_d$  ranging from 1 to 5, represented by light to dark blue color).  
 307 B) same as in A, but showing total flux reaching the water column during the ice cover period. C) the relative  
 308 portion of total annual light flux reaching the water column during the open water period (lines and points along  
 309 top portion of panel) vs. during the ice cover period (bottom portion of panel); interpretation of points and lines as  
 310 in panels A and B. D) percent change in the total annual light level arriving into a lake among median (black dashed  
 311 line), short (red points), and long (blue points) ice cover duration scenarios across latitudes.



313 *Fig 3: Seasonality and predicted effects of variation in ice cover duration on physical conditions (light,*  
314 *temperature) and plankton and littoral benthic productivity/biomass at 45°N and 75°N. A) Seasonality of solar flux*  
315 *(light yellow background) and effect of attenuation by ice and snow (ice  $K_d=3$ , snow duration at 80% of ice cover*  
316 *duration, 5 cm max thickness) on the under-ice light environment (yellow lines), along with surface water*  
317 *temperature (black lines), with line type (solid, dashed, dotted) corresponding to different ice cover duration*  
318 *scenarios (short, medium, long). B) Normalized modelled primary (phytoplankton and phyto-benthos) and secondary*  
319 *(zooplankton and littoral zoobenthos) production and biomass across ice cover duration scenarios. Light blue blocks*  
320 *show ice cover duration for the three ice cover duration scenarios.*

321

#### 322 **Data availability**

323 No original data were used in this manuscript. All sources of published data are referenced.

324

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329

#### 330 **Author contributions:**

331 TO and AP conceived the manuscript and TO, AP, MR, and EL developed the ideas. TO led writing  
332 of the text, with input from AP, MR, and EL. TO performed all modelling and data visualization with input  
333 from AP, MR, and EL.

334

#### 335 **Competing interest declaration:**

336 The authors declare no competing interests.

337

#### 338 **Supplementary information:**

339 This file contains additional information on modelling ice and snow cover conditions, light  
340 penetrations through snow and ice, and primary and secondary production, as well as figures S1-3. Fig.  
341 S1 illustrates the ice and snow cover duration and thickness scenarios used to model the underice light  
342 flux. Fig. S2 shows the effect of different snow and ice cover duration and thickness scenarios, along  
343 with effects of varying the ice light attenuation coefficient on the underice light environment across

344 modelled scenarios in relation to potential available solar flux. Fig. S3 illustrates the effect of extreme  
345 snow conditions on light, temperature and biotic processes.

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## 528 **Supplementary information section**

### 529 ***Model details:***

530 Ice and snow cover scenarios: to assess the effect of snow and ice cover on the light climate of lakes  
531 across latitudes, we constructed ice and snow cover scenarios for lakes in 10° latitude intervals (45, 55,  
532 65, 75 °N). Ice cover duration, ice-on, and ice-off dates were determined based on values in the Global  
533 Annual Lake Ice Phenological Dataset 1861-2099 (Wang et al. 2022). The dataset contains satellite-  
534 derived ice phenology data for the years 2001-2020 for 74,245 global lakes. We trimmed the dataset by  
535 excluding lakes that did not freeze every year during the 20 years of the observation period, lakes that  
536 were < 30 °N, and lakes at elevation >1,000 m above sea level (ASL), leaving us with a set of 67,291  
537 observations. We averaged ice-on, ice-off and ice-cover duration data for the available 20 years for each  
538 of the lakes. Few low-elevation lakes below ~40 °N regularly froze, so further analyses were restricted to  
539 the 45-75 °N latitude interval.

540 Ice thickness evolution for each latitude (e.g., 45 °N) was modelled based on the median ice-on and ice-  
541 off dates for lakes in the corresponding 10 ° latitude band (e.g., 40-50 °N), a wide range of literature  
542 data on empirical and modelled ice evolution in diverse lakes (Greenbank 1945; Schindler et al. 1974;  
543 Welch et al. 1987; Dibike et al. 2012; Leppäranta 2015; Grosbois et al. 2017; Yang et al. 2020; Clark et al.  
544 2022; Xie et al. 2023; Ghane and Boegman 2023; Shchapov and Ozersky 2023), and the author's  
545 personal observations. Ice growth in fall/winter and its destruction in the spring were modelled as a 4th-  
546 order polynomials (Fig. S1), with maximum thickness increasing from 0.7 to 1.5 m from 45 to 75 °N. In  
547 addition to these 'median' scenarios, we created ice cover models for a hypothetical 'long' ice cover  
548 season for each latitude (e.g., for a high elevation location or a location with a cold continental climate),  
549 and 'short' ice cover season scenarios, as might be expected under continuing climate change or a  
550 relatively warm maritime climate. The 'long' and 'short' scenarios have 1-month longer and 1-month  
551 shorted ice cover scenarios compared to the median scenarios, with lakes in the 'long' scenarios having  
552 a 15-day earlier ice-on and 15-day later ice-off than the 'median' lakes. Similarly, the 'short' scenario  
553 lakes have 15-day later ice-on and 15-day earlier ice-off than 'median' lakes. These 'long' and 'short' ice  
554 cover scenarios allowed us to assess how lakes with different ice cover duration and at different  
555 latitudes compare and respond to climate-driven ice loss. The maximum ice thickness for each latitude  
556 bands was increased or decreased by 20 cm for the 'long' and 'short' scenarios, respectively to  
557 represent the decreased ice thickness that typically corresponds to shorter ice cover duration.  
558 Snowfall amounts and the accumulation of snow on lakes are highly variable on global and regional  
559 scales (Kunkel et al. 2016; Pulliainen et al. 2020; Dou et al. 2021). We modelled several snow cover

560 scenarios for all of the above-described ice cover scenarios. Three basic scenarios were examined: 60%,  
561 80%, and 100% scenarios corresponded to snow cover over the ice for 60%, 80%, and 100% of the ice  
562 cover season, centered on the middle of the ice cover period. Thus, for 60% scenarios, the first and last  
563 20% of the ice cover period were snow free, and so on. The near absence of snow over the ice at the  
564 start and end of the ice cover season is typical of many locations. For each snow-cover duration scenario  
565 we also varied maximum snow thickness in 5 cm increments, from 0 cm to 80 cm. Snow accumulation  
566 and melting was modelled 3rd order polynomial equations (Fig. S1). Thus, our snow cover scenarios  
567 capture diverse conditions between the two extremes of completely snow-free ice (e.g., lakes in cold  
568 desert regions) and ice that is covered by a thick blanket of snow for the entire period of ice cover (e.g.,  
569 high elevation lakes).

570 Underice light climate: We used our snow and ice cover scenarios to model the potential light climate  
571 under ice and snow cover for lakes across latitudes and with varying ice cover and snow cover regimes.  
572 We obtained daily cloud-free solar flux data (as W/m<sup>2</sup>) for 45, 55, 65, and 75 °N from NASA's ModelE  
573 AR5 Insolation at Specified Location website (NASA 2023). Daily solar flux data were combined with daily  
574 modelled ice and snow thickness and with realistic ice and snow light attenuation coefficients (kd) to  
575 determine the amount of solar energy potentially penetrating the snow and ice cover and entering the  
576 unfrozen water (Fig. S2). We varied ice kd values from 2 to 5 in increments of 1 to include the natural  
577 variation in ice clarity on our estimates of light climate; snow kd was set at 15 (Prowse & Stephenson  
578 1986; Belzile et al., 2001; Leppäranta et al. 2012; Bramburger et al. 2023; Shchapov and Ozersky 2023).  
579 The combination of solar flux data with modelled ice and snow phenology allowed us to determine how  
580 much solar radiation arrived into lakes during the open-water and the ice-cover period across diverse ice  
581 and snow cover scenarios and to assess how variation in snow cover and ice duration affects the light  
582 budget of lakes across latitudes.

583 Primary and secondary production and biomass: to illustrate the ecological consequences of latitudinal  
584 variation in light and thermal regimes we used simple models to approximate how primary producer  
585 (phytoplankton and periphyton) and consumer (zooplankton and littoral zoobenthos) production and  
586 biomass responds to seasonal variation in light and temperature conditions for a lakes at 45 °N and at 75  
587 °N, experiencing 'median', 'short', and 'long' ice cover. Our models are not meant to be fully realistic,  
588 but rather to capture how the relatively independent effects of light and temperature affect primary and  
589 secondary production and their synchronicity. Primary production was estimated mainly as a linear  
590 function of light with a secondary effect of temperature, using a Q10 value 1.5 (Sherman et al. 2016).  
591 Secondary production was modelled solely as a function of temperature, using a Q10 value 2.7 (Huntley

592 and Lopez 1992). Consumer biomass is simply a function of production and mortality, the latter  
593 parametrized to ensure that values return to baseline at the end of the year. Primary producer biomass  
594 is a function of production and loss, which is proportional to consumer biomass and also parametrized  
595 so it returns to baseline values at the end of the year. We emphasize that we do not claim that our very  
596 simple model is a realistic and complete representation of producer-consumer interactions and  
597 dynamics. Rather, it serves as an idealized heuristic representation of plant and animal dynamics (e.g.,  
598 Sommer et al. 2012), which are differentially affected by light and temperature.

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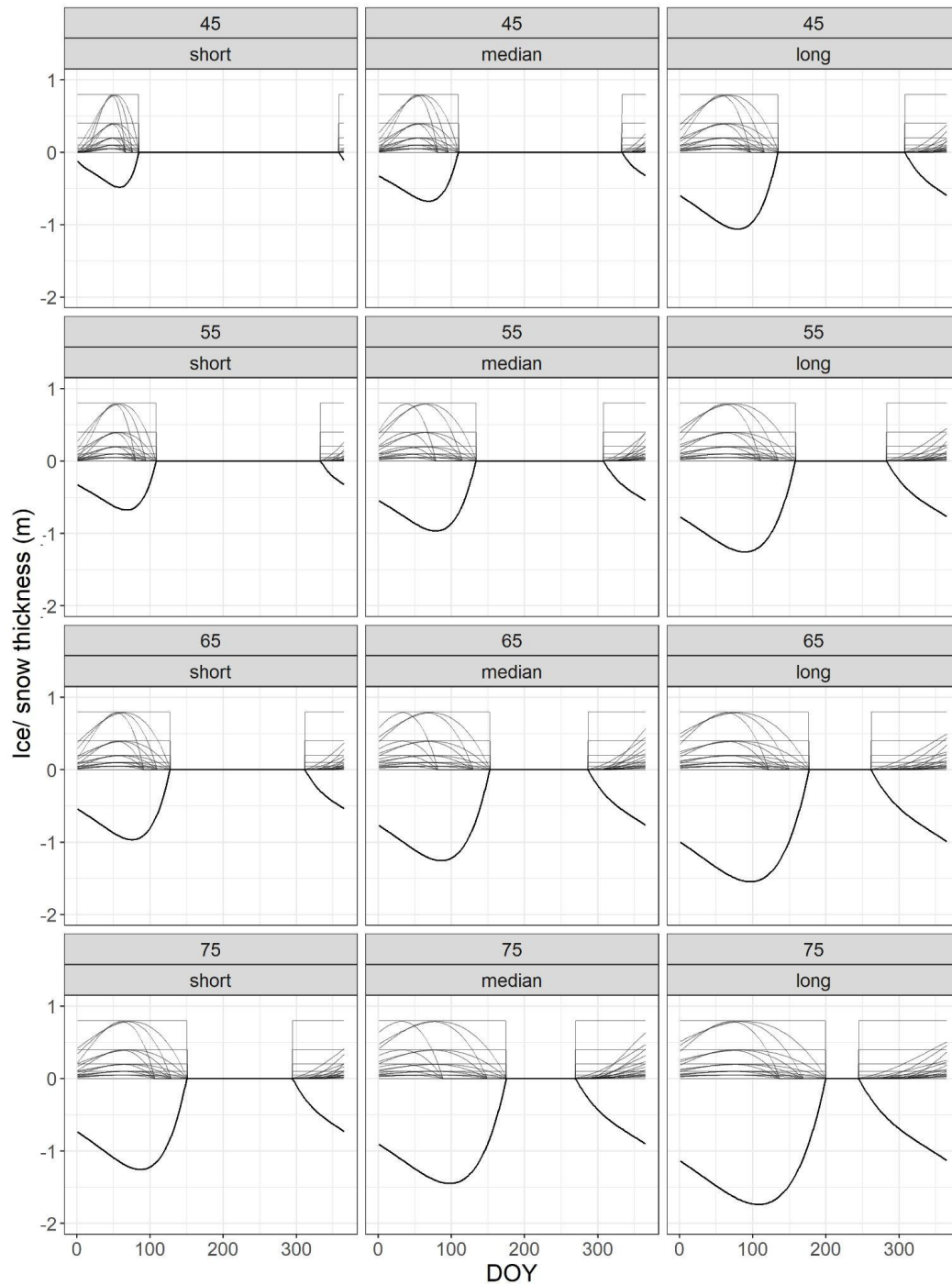
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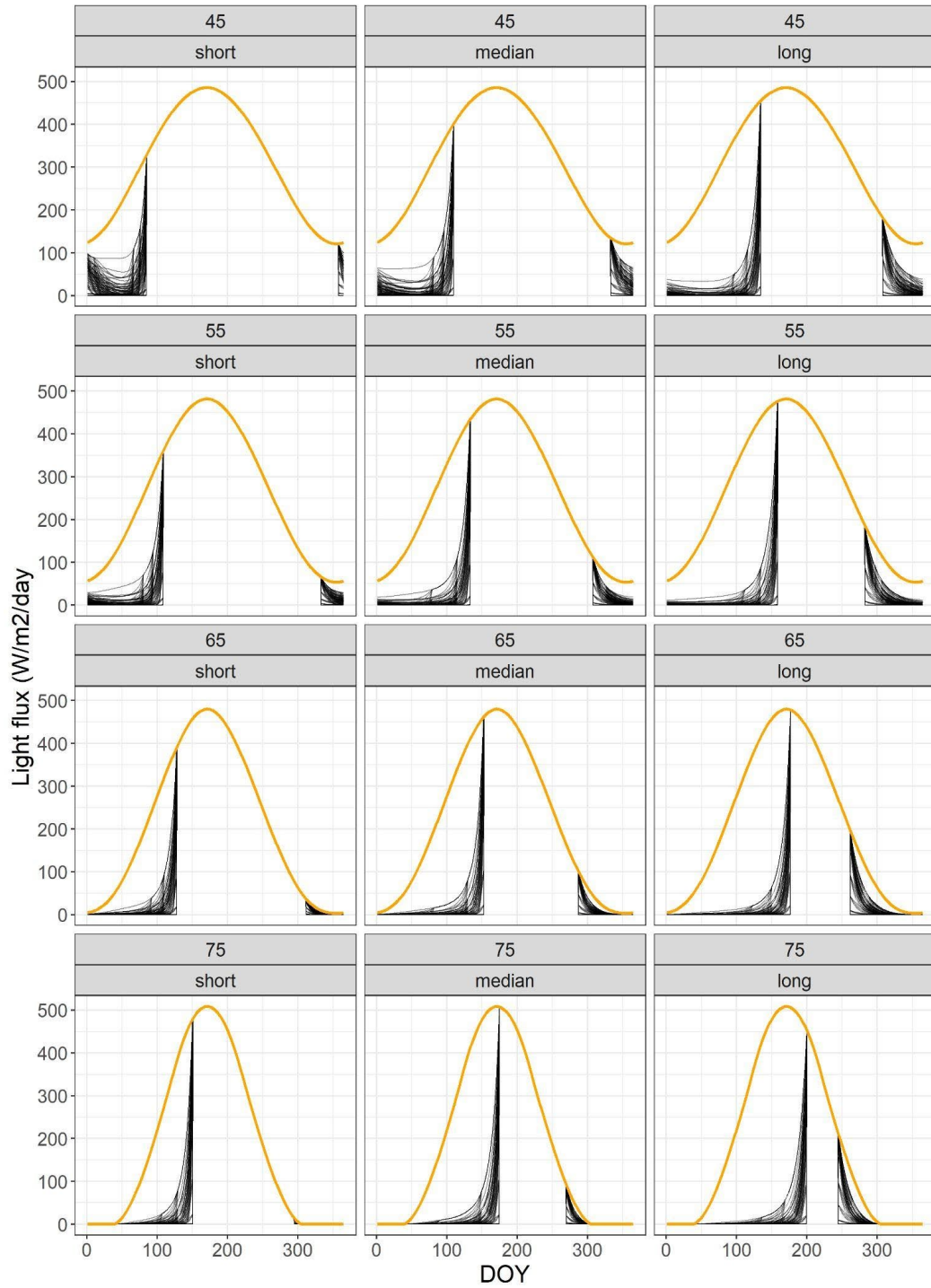
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688 **Supplementary figures:**

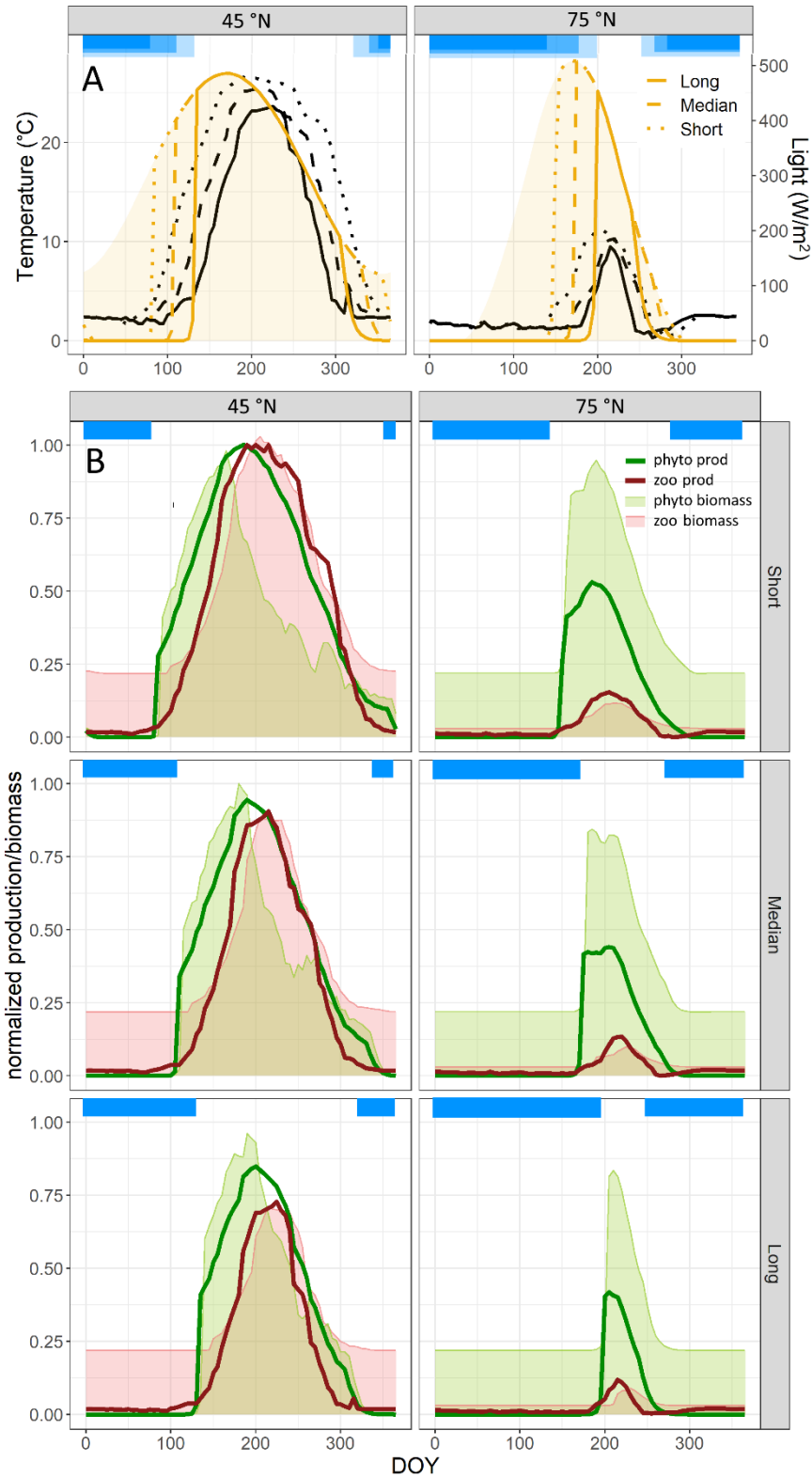


689 **Fig S1:** Modelled ice (negative values) and snow (positive values) thickness scenarios across latitudes  
690 and ice cover duration ranges. These ice and snow scenarios, along with realistic snow and ice light  
691 attenuation values, were used to model under-ice light regimes (Fig. S2).



692

693 **Fig S2:** Modelled light flux scenarios. Yellow lines represent maximum (cloud-free) potential daily light  
 694 flux, not accounting for attenuation by snow and ice. Thin black lines represent underice light, after  
 695 accounting for attenuation by light and snow under different ice and snow duration and thickness  
 696 scenarios and attenuation coefficients.



697

698 **Fig S3:** same as main text Figure 3, but for long (snow cover duration= 100% of ice cover duration) and

699 thick (80 cm) snow cover.