

# 1 Summer and winter MgCO<sub>3</sub> levels in the skeletons of Arctic bryozoans

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## 20 21 **Abstract**

22 In the Arctic, seasonal patterns in seawater biochemical conditions are shaped by physical,  
23 chemical, and biological processes related to the alternation of seasons, i.e. winter polar night  
24 and summer midnight sun. In summertime, CO<sub>2</sub> concentration is driven by photosynthetic  
25 activity of autotrophs which raises seawater pH and carbonate saturation state ( $\Omega$ ). In addition,  
26 restriction of photosynthetic activity to the euphotic zone and establishment of seasonal  
27 stratification often leads to depth gradients in pH and  $\Omega$ . In winter, however, severely reduced  
28 primary production along with respiration processes lead to higher CO<sub>2</sub> concentrations which  
29 consequently decrease seawater pH and  $\Omega$ .

30 Many calcifying invertebrates incorporate other minerals, in addition to calcium, into their  
31 skeletons, with potential consequences for stability of the mineral matrix and vulnerability to  
32 abrasion of predators. We tested whether changes in seawater chemistry due to light-driven  
33 activities of marine biota can influence the uptake of Mg into calcified skeletons of Arctic  
34 Bryozoa, a dominant faunal group in polar hard-bottom habitats. Our results indicate no clear

35 differences between summer and winter levels of skeletal  $\text{MgCO}_3$  in five bryozoan species  
36 despite differences in  $\Omega$  between these two seasons. Furthermore, we could not detect any  
37 depth-related differences in  $\text{MgCO}_3$  content in skeletons of selected bryozoans. These results  
38 may indicate that Arctic bryozoans are able to control  $\text{MgCO}_3$  skeletal concentrations  
39 biologically. Yet recorded spatial variability in  $\text{MgCO}_3$  content in skeletons from stations  
40 exhibiting different seawater parameters suggests that environmental factors can also, to some  
41 extent, shape the skeletal chemistry of Arctic bryozoans.

42

43 **Key words:** polar night, polar day, Mg-calcite, marine calcifier, light-driven changes, ocean  
44 acidification

45

## 46 **Introduction**

47 Magnesium is a common component of biogenic and abiogenic carbonates. In abiogenic  
48 minerals the concentration of Mg in carbonates is controlled by Mg/Ca ratios of the  
49 precipitation medium and the rate of crystal growth (e.g., Given and Wilkinson, 1985). The  
50 high Mg/Ca ratios of modern ocean water (Stanley and Hardie, 1998:  $\approx 5.2$ ) promote the  
51 precipitation of aragonite or calcite (the most common polymorphs of calcium carbonate) with  
52 high  $\text{MgCO}_3$  content (high-Mg calcite). For abiogenic marine carbonates, the precipitation of  
53 calcite *versus* aragonite is regulated solely by the crystal growth rate. In warm waters the crystal  
54 growth rate is faster, stimulating precipitation of high-Mg calcite and aragonite. On the other  
55 hand, in cool-water polar regions the growth rates is slower and therefore precipitation of low-  
56 Mg calcite is favoured (Given and Wilkinson, 1985). In biogenic mineralization, the synthesis  
57 of high-Mg calcite proceeds via an initial crystallization phase including an amorphous calcium  
58 carbonate (ACC) precursor and with assistance of organic macromolecules (Meldrum and  
59 Hyde, 2001; Long et al., 2014). Stanley and Hardie (1998), however, claim that marine  
60 organisms such as bryozoans, which are focus of this study, secrete carbonate skeletons in  
61 accordance with the ambient Mg/Ca seawater ratio and temperature pattern for abiogenic  
62 precipitation (Morse et al., 1997), i.e. skeletons are made of Mg-calcite in cool water areas and  
63 aragonite in tropical regions. Thus, we lack a consensus on mechanisms of Mg-calcite  
64 formation in many marine calcifiers.

65 It is well documented that most marine invertebrates can actively regulate the level of  
66  $\text{MgCO}_3$  in their skeletons (e.g., Ebert, 2007; Long et al., 2014; Iglukowska et al., 2018a, 2018b).  
67 During precipitation of low-Mg calcite, the organism removes Mg ions from the calcifying  
68 fluid, but during intermediate- and high-Mg calcite secretion, the mechanism regulating Mg-

69 ion concentration is not fully understood (Morrison and Brand, 1986). Mg present in  
70 invertebrate skeletons influences their chemical and mechanical properties (Ma et al., 2008;  
71 Kunitake et al., 2012). The addition of Mg ions into calcareous skeleton may enhance its  
72 density, strength and elasticity, but may also decrease the thermodynamic stability of skeletal  
73 calcite (e.g., Morse et al., 2006, 2007). Ries et al. (2009) showed that the highest net dissolution  
74 under the high CO<sub>2</sub> treatment was in species producing high-Mg calcite. Since the solubility of  
75 skeletal carbonate increases with increasing content of MgCO<sub>3</sub> (e.g., Morse et al., 2006;  
76 Andersson et al., 2009), understanding factors controlling level of Mg in biogenic carbonates  
77 in the light of currently rapidly changing pH in marine systems is an important issue.

78 Ocean acidification (OA) and its associated decrease in carbonate saturation state ( $\Omega$ )  
79 have raised serious concerns about possible consequences for precipitation of calcareous  
80 skeletons and the biology of marine calcifiers. Biogenically calcifying organisms use Ca<sup>2+</sup>  
81 and HCO<sub>3</sub><sup>-</sup> to precipitate their calcareous skeleton (e.g., Moya et al., 2008; Jury et al., 2010)  
82 and H<sup>+</sup> is a by-product of this process (e.g., Bach, 2015; Cyronak et al., 2016). Because high  
83 H<sup>+</sup> concentration creates low pH of calcifying fluid, which is not favourable for  
84 biomineralization, organisms must actively or passively remove H<sup>+</sup> to the ambient environment  
85 (e.g., Allemand et al., 2011). There is a positive relationship between pH and  $\Omega$ , and thus,  
86 numerous studies show low  $\Omega$  is unfavourable for calcification processes. Thus, OA is  
87 suggested to hinder biomineralization processes and accelerate dissolution of skeletal  
88 carbonate, with potential impacts on growth rates, competitive abilities, and survival of  
89 calcifying organisms (e.g., Andersson et al., 2008; Feely et al., 2009; Mollica et al., 2018).

90 Decrease in  $\Omega$  seems to be particularly pronounced in high latitudes as CO<sub>2</sub> has higher  
91 solubility in cold water, leading to higher uptake from atmosphere than in warmer waters (e.g.,  
92 Andersson et al., 2008). Therefore, carbonate (CaCO<sub>3</sub>) sediments and skeletons at high latitudes  
93 are at higher risk of being exposed to undersaturated conditions, a problem even more  
94 pronounced for carbonates containing high-Mg calcite (e.g., Andersson et al., 2008).

95 During the polar summer, the sun stays above the horizon all season (hereafter referred  
96 to as polar day). This results in a continuous primary production with distinct peaks in  
97 phytoplankton blooms due to variable light intensity and nutrient content (e.g., Piwosz et al.,  
98 2009; Shadwick et al., 2011). Biological CO<sub>2</sub> uptake due to the intensive photosynthesis during  
99 spring-summer leads to an increase in seawater pH and  $\Omega$  (e.g., Fransson et al., 2016). The  
100 elevated productivity is observed primarily in the upper layer of the water column (euphotic  
101 zone), which creates clear gradients in oxygen production with depth (e.g., Fransson et al.,  
102 2016). Moreover, in Arctic fjords, the spring melt of sea ice contributes to surface-water

103 stratification. As primary production in the Arctic is limited to <40 m depth (Hill and Cota,  
104 2005), we should observe different O<sub>2</sub>-CO<sub>2</sub> proportion below that zone, which may affect the  
105 seawater pH. At greater depths, organic-matter degradation releases CO<sub>2</sub> which consequently  
106 leads to pH decrease that influences  $\Omega$  (e.g., Andersson et al., 2008; Chierici et al., 2011). Thus,  
107 during polar day in the Arctic we can observe stratification between shallow water masses  
108 characterized by high  $\Omega$  (Fransson et al., 2016:  $\Omega = 3.50-3.75$  for July 2014 in Kongsfjorden,  
109 Svalbard at the surface), and deep-sea areas showing lower levels of  $\Omega$  (Fransson et al., 2016:  
110  $\Omega = 2.50-2.60$  for July 2014 in Kongsfjorden at 250-300 m depth).

111 On the other hand, during polar night, there is no sunlight and the primary production is  
112 significantly reduced or not taking place (e.g., Smetacek and Nicol, 2005; Berge et al., 2015;  
113 Johnsen et al., 2020). Thus, for the months of polar night, the system is in a heterotrophic state,  
114 dominated by oxygen consumption and CO<sub>2</sub> production processes, which consequently causes  
115 the decrease in seawater pH and  $\Omega$  (e.g., Chierici et al., 2011). This, combined with the water  
116 column being well mixed during polar night, leads to CO<sub>2</sub> levels being rather homogenous with  
117 depth. This seasonality in pH and  $\Omega$  creates a suitable model system to study influence of these  
118 variables on skeletal structure and concentration of magnesium. We predict that greater  
119 fluctuations in CO<sub>2</sub> and O<sub>2</sub>, and thus in  $\Omega$ , over a seasonal scale will lead to greater variability  
120 in Mg skeletal content in organisms from the shallow, euphotic zone.

121 This study uses bryozoans as model organisms to investigate whether Mg level in the  
122 calcitic skeleton is controlled by currently occurring pH and  $\Omega$  variability in an Arctic system.  
123 Bryozoans are colonial, suspension feeders occurring worldwide at broad depth ranges from  
124 abyssal to intertidal zone. Because of their high abundance and diversity (>300 species: Kluge,  
125 1975), bryozoans are considered important components of the Arctic ecosystem and significant  
126 carbonate producers in this area. The Arctic bryozoan colonies often consist of thousands of  
127 units (zooids) in most cases composed of calcite with variable amount of MgCO<sub>3</sub> (Kuklinski  
128 and Taylor, 2009). Environmental parameters including temperature and seawater chemistry  
129 are believed to control the uptake of Mg into bryozoan skeletons, although it is still not fully  
130 understood to what degree (Kuklinski and Taylor, 2009). In Arctic Bryozoa, the skeletal  
131 concentration of Mg can range from 0 to 8.8 mol% (Kuklinski and Taylor, 2009), and high  
132 variability can be observed even within a single taxon (e.g., Piwoni-Piórewicz et al., 2020). As  
133 the bryozoan colony has continuous growth, each zooid is a potential archive of ambient  
134 environmental conditions when the zooid skeleton was deposited. If skeletal chemical  
135 composition (Mg content) in marine bryozoans is controlled by differences in environmental  
136 parameters related to polar night and day, this should be reflected in their skeletons by different

137 concentrations of magnesium. If no differences are exhibited in skeletal magnesium level, in  
138 spite of carbonate and pH differences in the water, we assume organisms can control their  
139 skeletal composition biologically or that difference in water-mass chemical parameters of  
140 winter and summer periods are not large enough to drive those changes. Therefore, the current  
141 study aims to test the following hypotheses: (1) there is a seasonal variation in Mg content,  
142 which may indicate environmental control of skeletal parameters, and (2) there is a spatial  
143 variation in Mg content in skeletons with depth, and the pattern varies seasonally.

144

## 145 **Material and methods**

### 146 **Study area**

147 The investigation was conducted in a high Arctic location – Kongsfjorden and its close  
148 vicinity. The area is situated on the northwest coast of Spitsbergen (Svalbard Archipelago)  
149 between 78°50' and 79°04'N, and 11°10' and 12°30'E (Fig. 1). The fjord itself is 26 km long  
150 and on average 8 km wide. The maximum depth of the fjord is 428 m with mean depth ≈140  
151 m.

152 The hydrological conditions of the area are shaped by interactions of two main water  
153 masses: Arctic-type waters and water masses of Atlantic origin. The shelf waters of  
154 Kongsfjorden are influenced by relatively cold and fresh Arctic water masses, that originate  
155 from the east coast of Spitsbergen, rounding the Sørkapp (southern tip of Spitsbergen) and then  
156 flowing northward along the shelf of the west Spitsbergen coast. Furthermore, along the shelf,  
157 surface water conditions are influenced by glacial melt and river water discharge which may  
158 contribute to a decrease in salinity as low as 28 close to the glaciers (Cottier et al., 2005).  
159 Warmer and more saline Atlantic waters originating from the West Spitsbergen Current  
160 transport a great amount of heat and salt northward and thus keep the shelf waters of the fjord  
161 ice-free. The dynamic of the sea-air CO<sub>2</sub> flux in the Arctic Ocean is complex although both  
162 Atlantic and Arctic water masses serve as a CO<sub>2</sub> sink when calculated on an annual basis (Bates  
163 and Mathis, 2009; Schuster et al., 2012).

164 In the inner part of Kongsfjorden three tidal glaciers are present (Kongsbreen,  
165 Kronebreen and Kongsvegen; shaded ovals in Fig. 1). At the glacier front, seawater conditions  
166 are shaped by melt-water discharge contributing to the subsequent stratification of surface  
167 waters during summer (Svendsen et al., 2002; Halbach et al., 2019). The upper layer in summer  
168 is affected by freshening, warming and higher CO<sub>2</sub> consumption by autotrophs, whereas bottom  
169 layers are dominated by more saline and colder waters, which are rich in CO<sub>2</sub> due to  
170 heterotrophic activity of biota (Fransson et al., 2016).

171 The timing and dynamics of primary production in Kongsfjorden are variable (Hegseth  
172 and Tverberg, 2013), but the spring bloom usually starts between April and May when the  
173 highest chlorophyll *a* concentrations are observed in the inner parts of the fjord (Hodal et al.,  
174 2012; Hegseth and Tverberg, 2013), although suspended sediments at the glacier front cause  
175 local light limitation and reduced primary production in July (Lydersen et al., 2014; Halbach et  
176 al., 2019). Biochemical processes such as sea-ice melt and primary production influence the  
177 seawater pH and  $\Omega$ . The addition of melting fresh water, which is characterized by naturally  
178 low alkalinity and total inorganic carbon, decreases  $\Omega$  as a result of seawater dilution (Chierici  
179 and Fransson, 2009). In contrast, biological consumption of CO<sub>2</sub> by autotrophs increases the  
180 seawater  $\Omega$  (Fransson et al., 2016). In winter 2014, the seawater pH varied from 8.11 in the  
181 middle part to 8.13 in the inner part of Kongsfjorden, whereas calcite saturation states ( $\Omega_c$ ) were  
182 2.73 and 2.61, respectively (Fransson et al., 2016). Due to biological CO<sub>2</sub> uptake, summer  
183 values in 2014 for pH were 8.28 and 8.26, and for  $\Omega_c$  were 4.00 and 3.68 in the middle and  
184 inner parts of Kongsfjorden, respectively (Iglikowska et al., 2017a).

185

## 186 **Species**

187 For the purpose of this study, five encrusting cheilostome bryozoan species were  
188 selected since they are abundant and widely distributed inhabitants of Arctic seas, including the  
189 study area. These are *Hincksipora spinulifera* (Hincks, 1889) (Fig. 2A and B); *Microporella*  
190 *klugei* Kuklinski & Taylor, 2008 (Fig. 2C and D); *Myriozoella plana* Dawson, 1859;  
191 *Stomacrustula pachystega* (Kluge, 1929) (Fig. 2G and H); *Smittina bella* (Busk, 1860) (Fig. 2I  
192 and J). In the study area these species appear across the investigated depth range (Kuklinski,  
193 2002; Kuklinski et al., 2005). The species mostly occur on rocks, yet they also grow on living  
194 and dead mollusc shells (Kluge, 1975; Kuklinski and Barnes, 2005).

195

## 196 **Sampling, mineralogical analysis and environmental data**

197 Samples of the five targeted bryozoan species were collected in Kongsfjorden using a  
198 bottom dredge during a winter cruise of RV *Helmer Hanssen* and a summer cruise of RV  
199 *Oceania*. Sampling was carried out in January 2014, August 2014 and January 2015 (Table 1,  
200 Fig. 1).

201 On-board the vessel, samples were sorted and then transported dry to the laboratory of  
202 Institute of Oceanology in Poland. In the laboratory, bryozoan colonies were identified to  
203 species level using a stereomicroscope. To confirm taxonomic identification selected species  
204 were bleached in 20% sodium hypochlorite (NaClO) for 24h to remove organic material and

205 then examined using a scanning electron microscope (LEO 1455VP low-vacuum SEM in  
206 Natural History Museum, London, UK) at magnifications ranging from 70× to 200×. All  
207 studied specimens were dissected off rocks and shells using a scalpel, and care was taken to  
208 separate the bryozoan from the substrate and epibionts. Nevertheless, in some calcitic bryozoan  
209 species, aragonite contamination was detected, likely originating from aragonitic material of  
210 mollusc shell substrate. Only 5 mm of the colony edge of each individual was taken for  
211 mineralogical analysis in order to ensure that only the most recent growth was sampled. The  
212 relative amount of the colony used for analysis was estimated on the basis of our long-term  
213 observations on growth rates of Arctic bryozoans (unpublished data) and data by Smith (2007)  
214 on the growth rates of Antarctic bryozoan species.

215 For MgCO<sub>3</sub> measurements X-Ray Diffraction (XRD) was used. XRD methodology was  
216 selected as it detects only Mg incorporated into crystalline phase of the skeleton unlike other  
217 methods (e.g., AAS, ICP-MS) measuring all Mg present in a sample, including Mg contained  
218 in amorphous phase, Mg adsorbed on the skeletal surface and Mg bound to organic matter. The  
219 XRD analyses were conducted using high-precision Enraf-Nonius XRD with a position-  
220 sensitive detector (PSD). Operating conditions of a cobalt X-ray source were 40 kV and 40 mA.  
221 The linearity of the position sensitive detector was calibrated using Y<sub>2</sub>O<sub>3</sub> (99.9% BDH  
222 Laboratory Chemicals) and peak positions were calibrated on Y<sub>2</sub>O<sub>3</sub> data from Mitric et al.  
223 (1997). During each measurement, the sample was rotated to improve the grain orientation  
224 randomness in the X-ray beam. All bryozoan skeletons were powdered using an agate mortar  
225 and pestle and then affixed with a drop of acetone on a single quartz crystal substrate.  
226 Subsequently, samples were analysed to confirm their calcitic mineralogy and to determine the  
227 content of magnesium in the form of MgCO<sub>3</sub> (mol%). Peak shapes were fitted with a pseudo  
228 Voigt function using Highscore software. Concentration of MgCO<sub>3</sub> in skeletal calcite was  
229 calculated by measuring the d<sub>104</sub> peak position. It is assumed that there is a linear correlation  
230 between d<sub>104</sub> and MgCO<sub>3</sub> content existing between 0 and 17 mol% MgCO<sub>3</sub> in calcite (e.g.,  
231 Mackenzie et al., 1983), and all records in this study fall within this range. The time of each  
232 samples analysis was 15 minutes.

233 For characterization of seawater chemistry with respect to carbonates, the following  
234 factors were selected: pH, CO<sub>3</sub><sup>2-</sup>, CO<sub>2</sub> and calcite saturation state ( $\Omega_c$ ). Moreover,  $\Omega_c$  were also  
235 expressed as mean values  $\pm$  standard error along sampled seasons and depths. All variables  
236 measured at the sampled stations during winter and summer were gathered from literature  
237 (Fransson et al., 2016; Iglukowska et al., 2017a). Detailed descriptions of analytical procedures

238 related to seawater chemistry are included in Fransson et al. (2016) and Iglowska et al.  
239 (2017a).

240

## 241 **Statistics and data analysis**

242 We examined variation in skeletal  $\text{MgCO}_3$  content using permutational multivariate  
243 analysis of variance (PERMANOVA) carried out with 9999 random permutations. The  
244 univariate PERMANOVA design was performed based on untransformed data and a Euclidean  
245 resemblance matrix. We used ‘season’ and ‘depth’ as fixed factors, with two levels (winter and  
246 summer) and three levels (50, 100 and 150 m), respectively. Because we found statistically  
247 significant differences in skeletal  $\text{MgCO}_3$  among studied species (Kruskal-Wallis ANOVA and  
248 Dunn post-hoc test), the PERMANOVA analysis was conducted for each species separately.  
249 Furthermore, we used Kruskal-Wallis ANOVA and Mann-Whitney tests to examine differences  
250 in  $\text{MgCO}_3$  skeletal values found between studied sampling locations (see Fig. 1) and between  
251 specimens collected near the glaciers (stations 1W-3W, 7-9S and 12-14W) *versus* those from  
252 the open-sea stations (4-6S and 10-11W). All graphical displays and numerical analyses were  
253 carried out using STATISTICA 12 (Statsoft Inc., 2014), PRIMER (version 6.1.13) and  
254 PERMANOVA (version 1.0.3) software packages.

255

## 256 **Results**

257 Seawater calcite saturation states ( $\Omega_c$ ) showed lower values for winter (mean  $2.55 \pm 0.05$   
258 SD) than for summer ( $2.93 \pm 0.21$ ) (Fig. 3), with differences being statistically significant  
259 (Mann-Whitney  $U = 1.00$ ,  $p < 0.01$ ). However, differences in seawater calcite saturation states  
260 between studied depths appeared to be non-significant (Kruskal-Wallis  $H = 0.27$ ,  $p = 0.87$ ),  
261 with mean values for 50, 100 and 150 m at  $2.86 \pm 0.33$ ,  $2.66 \pm 0.21$  and  $2.66 \pm 0.19$ , respectively  
262 (Fig. 4).

263 The content of  $\text{MgCO}_3$  determined for 232 bryozoan specimens (Appendix) in five  
264 selected species ranged from 4.7 to 12.5 mol%, with mean at  $7.0 \text{ mol}\% \pm 1.19$  (SD). The lowest  
265  $\text{MgCO}_3$  value (4.7 mol%) was observed in a *Myriozoa plana* specimen collected in January  
266 from the station 1W at 50 m depth, whereas the highest content (12.5 mol%) was found in  
267 *Stomacrustula pachystega* taken in January from 10W station at 100 m depth. *Hincksipora*  
268 *spinulifera* (Fig. 5), *Microporella klugei* (Fig. 6) and *M. plana* (Fig. 7) had mean  $\text{MgCO}_3$  mol%  
269 skeletal values of  $7.3 \pm 0.55$ ,  $6.7 \pm 0.71$  and  $5.7 \pm 0.57$ , respectively. Skeletons of remaining  
270 species, *S. pachystega* (Fig. 8) and *Smittina bella* (Fig. 9), had mean mol%  $\text{MgCO}_3$   
271 concentrations of  $8.1 \pm 0.90$  and  $8.4 \pm 0.79$ , respectively.

272 There were no statistically significant differences in MgCO<sub>3</sub> values for any species  
273 between depths and seasons separately, although interactions between those two variables were  
274 significant for *M. plana* (Table 2, Fig. 7). For *H. spinulifera*, *M. klugei*, *M. plana* and *S.*  
275 *pachystega*, the highest MgCO<sub>3</sub> contents were recorded at winter stations despite the fact that  
276 surrounding seawater showed significantly lower  $\Omega_c$  values compared to those from summer  
277 stations (Fig. 3).

278 In three species (*H. spinulifera*, *M. klugei* and *M. plana*), significant differences in  
279 skeletal MgCO<sub>3</sub> were observed among studied sampling locations (Fig. 1, Kruskal-Wallis H =  
280 14.27, p = 0.01; H = 9.32, p = 0.03 and H = 16.17, p = 0.01, respectively). However, the  
281 remaining species (*S. pachystega* and *S. bella*) did not follow this relationship (H = 1.61, p =  
282 0.45 and H = 2.42, p = 0.30, respectively). Furthermore, only *H. spinulifera* exhibited  
283 statistically significant differences in skeletal MgCO<sub>3</sub> levels in specimens collected near the  
284 glacier *versus* individuals taken from the open-sea stations (Kruskal-Wallis H = 6.72, p = 0.01).  
285 In *H. spinulifera*, slightly higher MgCO<sub>3</sub> content was found at the open-sea stations (7.66 mol%  
286  $\pm$  0.59) compared to those collected near the Kongsfjorden glaciers (7.23 mol%  $\pm$  0.48).

287

## 288 Discussion

289

290 Skeletal MgCO<sub>3</sub> concentration did not differ significantly between seasons or among  
291 depths for any of the five studied species. Only one species (*Myrionzoella plana*) showed a  
292 statistically significant interaction effect between season and depth on MgCO<sub>3</sub> content (Table  
293 2). Winter calcite saturation state ( $\Omega_c$ ) values showed slightly lower values (mean  $2.55 \pm 0.05$   
294 SD) compared to summer values ( $2.93 \pm 0.21$ ), yet overall water masses in the study area were  
295 saturated with respect to carbonates during both summer and winter. The lack of differences  
296 between summer and winter MgCO<sub>3</sub> levels in skeletons of bryozoans may indicate that Arctic  
297 bryozoans have physiological mechanisms which enable them to regulate MgCO<sub>3</sub> content  
298 despite observed, although small, differences in ambient seawater  $\Omega_c$ . Carbonate mineralogy of  
299 some organisms, including foraminifera, coccolithophores and calcifying algae, seems to be  
300 highly dependent on ambient environmental conditions, and, thus, these taxa may be more  
301 prone to impacts of variable pH of Arctic seawater (e.g., Erez, 2003; Long et al., 2014;  
302 Andersson et al., 2008). Bryozoans, however, may be thought of as “active mineralizers” (Smith  
303 et al., 2006) which exert strong biological control on Mg uptake and composition of their  
304 calcareous skeleton. Other invertebrates, such as corals, possess ion pumps controlling  
305 precipitation of the carbonate lattice through creation of favourable conditions for crystal

306 nucleation and growth (e.g., Weiner and Dove, 2003; Tambutté et al., 2011; Zoccola et al.,  
307 2015). Such compensatory ion pumps allow the organism to maintain the deposition of skeletal  
308 calcite even in undersaturated seawater conditions, although such a mechanism may be highly  
309 energy-demanding (e.g., Wood et al., 2008; Dupont et al., 2013). It is possible that bryozoans  
310 may use a similar mechanism to maintain certain ranges of  $\text{MgCO}_3$  in their skeletons, but this  
311 has not been well studied.

312         Bryozoans examined here have exclusively pure calcitic skeletons which is common for  
313 both Arctic and Antarctic species within this group (Kuklinski and Taylor, 2009; Krzeminska  
314 et al., 2016). In temperate and tropical areas bimineralic and aragonitic species have also been  
315 observed (e.g., Kuklinski and Taylor, 2009; Krzeminska et al., 2016). Calcitic skeletons are  
316 often considered as an adaptation against dissolution (Kuklinski and Taylor, 2009).  
317 Interestingly, two species examined in this study (*Stomacrustula pachystega* and *Smittina bella*)  
318 exceeded the skeletal  $\text{MgCO}_3$  content of 8 mol%, making their calcite less thermodynamically  
319 stable and thus prone to dissolution (Lebrato et al., 2016). Other Arctic calcite producing  
320 organisms, e.g. echinoderms, are characterized by even higher  $\text{MgCO}_3$  concentrations (5-18  
321 mol%) in skeletons (Iglikowska et al., 2017b, 2020). It is not clear why these organisms produce  
322 more soluble high-Mg calcite in Arctic cool waters. In the temperate bryozoan genus *Cellaria*,  
323 high concentrations of  $\text{MgCO}_3$  seem to be linked to ontogeny. In the flexible articulated colony  
324 of *Cellaria*, high-Mg calcite is precipitated within the internodes where new joints emerge  
325 (Smith et al., 2006). It is possible, then, that specific mechanical advantages of high-Mg calcite  
326 play a decisive role in the development of skeletal structures and mineralogies of Arctic  
327 bryozoans. Furthermore, encrusting cheilostome bryozoans possess a continuous external layer  
328 of organic periostracum which is variable in thickness (Tavener-Smith and Williams, 1972).  
329 Such layer might sufficiently protect an organism with an otherwise soluble skeleton against  
330 ambient corrosive conditions. All these potential mechanisms or adaptations allowing  
331 production of high-Mg calcite are still unstudied in Arctic bryozoans and need further, more  
332 comprehensive examination.

333         In this investigation we observed no differences in skeletal  $\text{MgCO}_3$  along a depth  
334 gradient. Other studies evaluating correlations between depth and skeletal  $\text{MgCO}_3$  of bryozoans  
335 (Borszcz et al., 2013; Figuerola et al., 2015) have also failed to find such relationship, despite  
336 examining a greater range of depths and potentially greater environmental differences (down to  
337 600 m in Figuerola et al., 2015). In our study, we demonstrate the lack of depth-related  
338 differences in skeletal  $\text{MgCO}_3$  in two different seasons: winter and summer. Borszcz et al.  
339 (2013) suggested that a historically young Arctic bryozoan community could have had too short

340 time to develop genetic adaptations to variable chemical seawater conditions related to depth.  
341 The Arctic is believed to have been recolonized by benthic organisms from lower latitudes after  
342 the last glaciation ~ 14 000 years ago (Dunton, 1992; Renaud et al., 2015). Yet the potential  
343 ancestors of today's Arctic benthos from lower temperate areas or polar refuges likely  
344 experienced the same water temperature variability at that time. Thus, the argument for possible  
345 lack of genetic adaptations to variable chemical seawater conditions related to depth or season  
346 by species inhabiting Arctic today does not seem to apply here.

347         The low variation of  $\Omega_c$  and/or other environmental factors which can influence the Mg  
348 content (i.e., pH, water temperature and salinity) may also explain why there was not any clear  
349 pattern in  $MgCO_3$  deposition in skeletons with depth. It is believed that water temperature  
350 influences  $MgCO_3$  concentration in bryozoan skeletons, with higher water temperatures leading  
351 to increased  $MgCO_3$  concentration (Kuklinski and Taylor, 2009; Krzeminska et al., 2016). In  
352 our study area, water temperature during sampling showed an overall range between 0.39-  
353 5.20°C (Table 1). Yet the observed temperature variability does not seem to correlate with  
354 depth, and there was no difference in the relationship of temperature with depth in summer  
355 *versus* winter. Admittedly our snapshot measurement did not cover the entire annual trend, the  
356 long-term literature data for the study area seem to confirm seasonal and depth-related  
357 differences in water temperature (Berge et al., 2015; Fransson et al., 2016; Tverberg et al.,  
358 2019). Although the existing variability (5°C) in seawater temperature may simply not be great  
359 enough to affect Mg-levels in skeletons of Arctic bryozoans. Schäfer and Bader (2008) reported  
360 higher concentrations of Mg in skeletons of the temperate bryozoan *Cellaria sinuosa* formed  
361 during summer compared to parts of the skeleton formed during winter where bottom  
362 temperatures ranged from 9.6°C in winter to 15.4°C in summer. This temperature range is  
363 similar to that experienced by the studied Arctic species. Our results may indicate that the  
364 concentration of  $MgCO_3$  in skeletons of the studied bryozoans is species-specific. Bryozoans  
365 may also exhibit species-specific response to temperature or show different response to  
366 temperature variability depending on latitude. And indeed high-latitude bryozoans generally  
367 have slower growth rates than those from warmer waters (Smith, 2007). Thus, there may be a  
368 hierarchy of factors leading to variability in bryozoan mineralogy, from a generally slower  
369 growth rate for bryozoans to species-specific adaptations leading generally low sensitivity to  
370 temperature changes, but with some species exhibiting seasonal shifts in  $MgCO_3$  content.

371         Some of the examined stations were kilometers apart which resulted in differences in  
372 local seawater properties, such as water temperature, carbonate saturation state (Table 1) and/or  
373 possible availability of Mg ions among these sites. Unfortunately, no *in situ* Mg/Ca data are

374 available, though it seems that the limiting factor(s) influencing skeletal precipitation of high-  
375 Mg calcite are more likely other parameters, including temperature and salinity (and  
376 consequently lower pH and  $\Omega$ ). The Mg/Ca ratio is generally high and considered to be  
377 relatively stable in the modern World's Ocean (Stanley and Hardie, 1998). In our study area  
378 locations closer to the open sea (Fig. 1) were characterized by higher water temperature, lower  
379  $\text{CO}_2$  and higher  $\text{CO}_3^{2-}$ , compared to stations located inside the fjord and closer to glacier (Table  
380 1). In the inner part of the fjord we found slightly lower pH (and  $\Omega$ ) values compared to middle  
381 part of the fjord. Both locations were under the influence of melting glaciers. It seems that  
382 higher  $\text{MgCO}_3$  levels observed in *Hincksipora spinulifera* at stations located near the open sea  
383 is correlated with higher seawater temperatures related to the influence of warm Atlantic water  
384 masses comparing to colder stations in inner fjord. Yet this trend was not exhibited by  
385 remaining species.

386 Surprisingly, different bryozoan species collected from the same depth, in close  
387 proximity to each other and influenced by similar environmental conditions exhibited  
388 differences in  $\text{MgCO}_3$  concentration in their skeletons (Figs 5 to 9). This strongly suggests  
389 biological control of  $\text{MgCO}_3$  levels in the bryozoan skeletons. Although the environmental  
390 factors presumed to influence calcification are measured in ambient seawater, many calcifiers  
391 (e.g., bivalves) carry out calcification in specific parts of the organism (e.g., in mantle fluid)  
392 where concentration of calcification solution is strictly controlled physiologically. This process  
393 is well studied in molluscs (e.g., Shirai et al., 2014), but not fully investigated in bryozoans.  
394 Thus, this may be one mechanism by which species control skeletal mineralogy. Calcite  
395 saturation state as measure of conditions enabling deposition of high-Mg calcite skeletons is  
396 debated because it does not account for magnesium concentration of the calcitic lattice  
397 influencing its solubility. Thus, instead of  $\Omega_c$ , species-specific  $\Omega_{\text{Mg-c}}$  is proposed to reflect more  
398 accurately seawater chemical conditions regarding high-Mg calcite deposition. The  $\Omega_{\text{Mg-c}}$  is  
399 estimated on the basis of equilibrium thermodynamic principles and allows to assess the level  
400 at which the net formation ( $\Omega_{\text{Mg-c}} > 1$ ) or dissolution ( $\Omega_{\text{Mg-c}} < 1$ ) of Mg-calcite is favoured  
401 (more details in: Morse et al., 2006; Lebrato et al., 2016).

402 The differences in  $\text{MgCO}_3$  concentration in skeletons among sites differing in physico-  
403 chemical parameters of seawater might be a sign of environmental control, while variability in  
404  $\text{MgCO}_3$  concentration in skeletons within sites characterized by the same environmental  
405 conditions indicate physiological control on the process of calcification. Both indicate that the  
406 mechanism of Mg incorporation into bryozoan skeleton is complex and not fully understood.  
407 Overall it is difficult to determine unequivocally whether a lack of  $\text{MgCO}_3$  concentration

408 differences with season or depth is a result of environmental conditions or an effect of  
409 physiological regulation by the organism.

410 For purposes of this study, we assumed that colonies of selected species of bryozoans  
411 have continuous growth throughout the year as life cycles of the majority of bryozoans,  
412 including Arctic species, are virtually unknown. It has been shown that some polar bryozoans  
413 have defined colony growth bands believed to be associated with pulses of seasonal primary  
414 production (Barnes, 1995; Smith, 2007; Barnes et al., 2011; Kuklinski et al., 2013). Other polar  
415 species do not appear to produce carbonate skeleton during periods of no phytoplankton supply,  
416 i.e. during the winter season (Smith, 2007). However, the species selected for this investigation  
417 do not exhibit any growth bands, suggesting continuous development. Additionally our long  
418 term observation on colonization and succession of benthic communities during winter period  
419 suggest that bryozoans colonies continue to grow year-round (unpublished data). Bryozoans  
420 have food preferences at which they perform better growth (Winston, 1977). Picoplankton,  
421 which can be utilized as a food source for bryozoans is present in the Arctic throughout the  
422 year, even in winter (Rokkan Iversen and Seuthe, 2011; Sørensen et al., 2012). Yet as  
423 knowledge about the biology of bryozoans is very limited, we cannot rule out that Arctic  
424 bryozoans have periods of no skeletal production and that we cannot conclusively assume the  
425 edge of the colony we sampled represents incorporation of the environmental signal measured  
426 at the same time.

427 In conclusion both of the hypotheses tested by this study were rejected. Our results  
428 indicate that environmental effects on skeletal chemistry can be masked by various biological  
429 processes, including relatively inflexible physiochemical pathways resulting in Mg content  
430 across a relatively narrow range per species. There is little doubt that the level of  $MgCO_3$  in  
431 skeletons of each of the studied species of bryozoan is an indication of biologically controlled,  
432 genetically programmed processes and/or physiologically controlled process. However,  
433 obtained results on station-related differences suggest that seawater properties can also to some  
434 extent affect the level of  $MgCO_3$  in skeletal calcite of Arctic bryozoans. Thus, the skeletal  
435 chemistry is likely shaped by both, biological and environmental factors, as has been suggested  
436 by other authors (e.g., Taylor et al., 2014; Figuerola et al., 2015).

437 This study indicates the complexity of factors influencing incorporation of  $MgCO_3$  into  
438 biota skeletons, showing that field studies might be not sufficient to pinpoint the particular  
439 factors influencing properties of skeletons and detailed experimental studies are needed to shed  
440 more light on the subject.

441

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### 686 **Figure captions**

687 **Figure 1.** Study area with sampling locations and site names identified (W = winter stations in  
688 blue, S = summer stations in red).

689 **Figure 2.** Scanning electron microscope images of studied cheilostome bryozoan species.  
690 *Hincksipora spinulifera* A-B, *Microporella klugei* C-D, *Myriozoella plana* E-F,  
691 *Stomacrustula pachystega* G-H, *Smittina bella* I-J.

692 **Figure 3.** Mean  $\pm$  standard error (box = mean  $\pm$  SE, whiskers = mean  $\pm$  1.96xSE) of seawater  
693 calcite saturation states at studied stations – comparison between seasonal values (data  
694 from Fransson et al. 2016 and Iglukowska et al. 2017a).

695 **Figure 4.** Mean  $\pm$  standard error (box = mean  $\pm$  SE, whiskers = mean  $\pm$  1.96xSE) of seawater  
696 calcite saturation states at studied stations – comparison between depths (data from  
697 Fransson et al. 2016 and Iglukowska et al. 2017a).

698 **Figure 5.** Seasonal variation of MgCO<sub>3</sub> concentrations (box = mean  $\pm$  SE, whiskers = mean  $\pm$   
699 1.96xSE) in skeletal calcite of *Hincksipora spinulifera*, comparison between three  
700 examined depths (50, 100 and 150 m) and two seasons (winter: blue, summer: red) (N  
701 = number of individuals analyzed, T = mean temperature,  $\Omega_c$  = mean calcite saturation  
702 state). Mann-Whitney test for differences between seasons at 50 m: U = 15.0, p = 0.03;  
703 100 m: U = 57.5, p = 0.20; 150 m: U = 47.0, p = 0.88.

704 **Figure 6.** Seasonal variation of MgCO<sub>3</sub> concentrations (box = mean  $\pm$  SE, whiskers = mean  $\pm$   
705 1.96xSE) in skeletal calcite of *Microporella klugei*, comparison between three examined  
706 depths (50, 100 and 150 m) and two seasons (winter: blue, summer: red) (N = number  
707 of individuals analyzed, T = mean temperature,  $\Omega_c$  = mean calcite saturation state). Too  
708 few records to carry out Mann-Whitney test for differences between seasons.

709 **Figure 7.** Seasonal variation of  $\text{MgCO}_3$  concentrations (box = mean  $\pm$  SE, whiskers = mean  $\pm$   
710 1.96xSE) in skeletal calcite of *Myriozoella plana*, comparison between three examined  
711 depths (50, 100 and 150 m) and two seasons (winter: blue, summer: red) (N = number  
712 of individuals analyzed, T = mean temperature,  $\Omega_c$  = mean calcite saturation state).  
713 Mann-Whitney test for differences between seasons at 50 m: U = 29.0, p = 0.03; 100 m:  
714 U = 54.0, p = 0.22; 150 m: U = 30.0, p = 0.15.

715 **Figure 8.** Seasonal variation of  $\text{MgCO}_3$  concentrations (box = mean  $\pm$  SE, whiskers = mean  $\pm$   
716 1.96xSE) in skeletal calcite of *Stomacrustula pachystega*, comparison between three  
717 examined depths (50, 100 and 150 m) and two seasons (winter: blue, summer: red) (N  
718 = number of individuals analyzed, T = mean temperature,  $\Omega_c$  = mean calcite saturation  
719 state). Mann-Whitney test for differences between seasons at 50 m: U = 10.0, p = 0.13;  
720 100 m: U = 20.0, p = 1.00; 150 m: U = 10.0, p = 0.08.

721 **Figure 9.** Seasonal variation of  $\text{MgCO}_3$  concentrations (box = mean  $\pm$  SE, whiskers = mean  $\pm$   
722 1.96xSE) in skeletal calcite of *Smittina bella*, comparison between two examined depths  
723 (100 and 150 m) and two seasons (winter: blue, summer: red) (N = number of  
724 individuals analyzed, T = mean temperature,  $\Omega_c$  = mean calcite saturation state). Mann-  
725 Whitney test for differences between seasons at 100 m: U = 40.0, p = 0.77, too few  
726 records for 50 and 150 m.