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# Siliceous micro- and nanoplankton fluxes over the Northwind Ridge and their relationship to environmental conditions in the western Arctic Ocean

Jian Ren, Jianfang Chen, Hongliang Li, Martin Wiesner, Youcheng Bai, Marie-Alexandrine Sicre, Zhixiong Yao, Haiyang Jin, Yanpei Zhuang, Yangjie Li

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1 **Siliceous micro- and nanoplankton fluxes over the Northwind Ridge**  
2 **and their relationship to environmental conditions in the western**  
3 **Arctic Ocean**

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5 **Jian Ren<sup>a,b,c</sup>, Jianfang Chen<sup>a,b,d\*</sup>, Hongliang Li<sup>a,b</sup>, Martin G. Wiesner<sup>a,d</sup>, Youcheng Bai<sup>a,b</sup>,**  
6 **Marie-Alexandrine Sicre<sup>e</sup>, Zhixiong Yao<sup>b,d</sup>, Haiyan Jin<sup>a,b,d</sup>, Yanpei Zhuang<sup>a,b</sup>, Yangjie Li<sup>a,b</sup>**

7  
8 <sup>a</sup> *Key Laboratory of Marine Ecosystem Dynamics, Ministry of Natural Resources, Hangzhou*  
9 *310012, China*

10 <sup>b</sup> *Second Institute of Oceanography, Ministry of Natural Resources, Hangzhou 310012, China*

11 <sup>c</sup> *Southern Marine Science and Engineering Guangdong Laboratory (Zhuhai), Zhuhai 519000,*  
12 *China*

13 <sup>d</sup> *State Key Laboratory of Satellite Ocean Environment Dynamics, Second Institute of*  
14 *Oceanography, Ministry of Natural Resources, Hangzhou 310012, China*

15 <sup>e</sup> *Sorbonne Université, Campus Pierre et Marie Curie, LOCEAN, 4 place Jussieu, F-75005*  
16 *Paris, France*

17  
18  
19 \* Corresponding author at: Key Laboratory of Marine Ecosystem Dynamics, Second Institute  
20 of Oceanography, Ministry of Natural Resources, Hangzhou 310012, China.

21 \* E-mail: [jfchen@sio.org.cn](mailto:jfchen@sio.org.cn) (Jianfang Chen)

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27 **Abstract**

28

29 Siliceous planktons are valuable indicators of the environmental conditions in both  
30 modern and past marine settings. However, in contrast to diatoms and radiolarians, other  
31 siliceous micro- and nanoplankton in the Arctic Ocean have been rarely explored. In this study,  
32 silicoflagellates, endoskeletal dinoflagellate *Actiniscus pentasterias* and chrysophyte cysts  
33 were investigated in one-year mooring sediment trap material (from August 2008 to September  
34 2009) collected in the Northwind Ridge, western Arctic Ocean. The silicoflagellate assemblage  
35 was dominated by *Stephanocha speculum*, accounting for > 71% of the total silicoflagellate  
36 composition. While *S. speculum* was overwhelmingly abundant in summer, *S. medianoctisol*  
37 and *S. octonarius* were more frequent during winter. The export fluxes of endoskeletal  
38 dinoflagellate *A. pentasterias* did not show clear seasonal pattern except for a peak value in  
39 September 2009. We suggest that *A. pentasterias* reflects nutrient rich environment at sea ice  
40 edge rather than cold under sea ice conditions. High fluxes of chrysophyte cysts were recorded  
41 in summer 2009 peaking in late July and early August, ~10 times higher than in summer 2008.  
42 Peak of chrysophyte cysts and sea ice melting occurred simultaneously. In addition, observed  
43 encystment might be triggered by the population density, hence indicating a favorable  
44 environment for phytoplankton blooming. These siliceous micro- and nanoplankton provides  
45 information on the modern Arctic Ocean environment but requires further investigations to  
46 consolidate knowledge for robust use in paleoceanography.

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51 **Keywords:** Silicoflagellates, Endoskeletal dinoflagellate, Chrysophyte cysts, Siliceous  
52 micro- and nanoplankton, Arctic Ocean, Sediment trap

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## 54 1. Introduction

55 The Arctic sea ice extent has declined dramatically at a rate of -12% per decade since 1979  
56 (Comiso, 2012). Loss of the sea ice cover reduces the Arctic albedo and enhances heat exchange  
57 between the ocean and atmosphere, resulting in Arctic amplification on global climate change  
58 (Serreze et al., 2009). These changes have triggered fundamental transition in the Arctic marine  
59 ecosystem (e.g. Wassmann et al., 2011; Coupel et al., 2012; Lee et al., 2019; Nadaï et al., 2021).  
60 Decreasing size of phytoplanktons has been reported (Li et al., 2009; Morán et al., 2010), while  
61 annual net primary production (NPP) soared 30% in recent decades owing to prolonged ice-  
62 free period (Arrigo and Dijken, 2015). However, due to the lack of knowledge on the Arctic  
63 fauna and flora, our capacity to predict the future of the Arctic marine ecosystem is still limited.

64 Among siliceous planktons, Arctic diatoms and radiolarians are widely studied to  
65 understand their ecological niches and environmental preference (e.g. Katsuki et al., 2009;  
66 Ikenoue et al., 2015; Onodera et al., 2015; Lalande et al., 2019; Nadaï et al., 2021). The  
67 variability of diatom composition and fluxes derived from a sediment trap in the western Arctic  
68 during summer 2008 and 2009 have been related to surface currents change and sea ice  
69 distribution, showing their sensitivity to environmental alteration (Ren et al., 2020). However,  
70 other siliceous micro- and nanoplankton such as silicoflagellate, endoskeletal dinoflagellate  
71 *Actiniscus pentasterias* and chrysophyte cysts in the Arctic Ocean are sporadically reported  
72 (Zernova et al., 2000; Takahashi et al., 2009; Onodera et al., 2016), which has limited their use  
73 in monitoring Arctic environment changes. Knowledge on the ecology of siliceous micro- and  
74 nanoplankton is essential for interpreting paleoceanographic reconstructions.

75 The pioneering work on the geographic distribution of silicoflagellates in the surface  
76 sediments in the North Pacific has shown the close relationship between the silicoflagellate  
77 assemblages and sea surface temperature (Poelchau, 1976). Long sediment trap time series in  
78 the Bering and Chukchi Seas revealed that high relative abundances of *Stephanocha*  
79 *medianoetisol* are preferentially associated to colder conditions than *S. speculum* (Onodera and  
80 Takahashi 2005, 2012; Onodera et al., 2016), which is further supported by snapshot studies on  
81 the sea water and sea ice samples from the central and western Arctic Ocean (Takahashi et al.,  
82 2009; Onodera et al., 2016).

83 By contrast, the temporal and spatial distribution of modern endoskeletal dinoflagellate *A.*  
84 *pentasterias* and chrysophyte cysts are seldom reported in high latitudes. Only a few time series  
85 and *in situ* sea water studies of *A. pentasterias* were carried out in the northern North Pacific  
86 (Takahashi, 1987; Onodera and Takahashi, 2007) and the Arctic (Onodera et al., 2016).  
87 Chrysophyte cysts are mostly found in fresh waters while they are much less common in marine  
88 samples (Smol, 1988; Duff et al., 1995; Zeeb and Smol, 2001). Fossil chrysophyte cysts found  
89 in marine sediments and not related to modern species were assigned to the artificial family  
90 Archaeomonadaceae (Deflandre and Deflandre-Rigaud, 1969). They have been encountered in  
91 sediments as old as the Early Cretaceous (e.g. Harwood and Gersonde, 1990). A few studies on  
92 chrysophyte cysts in the surface sediments in polar region have linked their distribution to sea  
93 ice (Mitchell and Silver, 1982, 1986; Redmond Roche, 2019). Overall, these results show that  
94 our understanding of chrysophyte cysts in the modern Arctic Ocean is still very limited.

95 Here, we present a one-year sinking flux record of siliceous micro- and nanoplanktons  
96 (silicoflagellates, endoskeletal dinoflagellate *Actiniscus pentasterias* and chrysophyte cysts)  
97 obtained from a sediment trap deployed over the Northwind Ridge, western Arctic Ocean, from  
98 August 2008 to September 2009. Fluxes of siliceous micro- and nanoplankton combined with  
99 that of diatoms and biomarkers from the same sediment trap (Bai et al., 2019; Ren et al., 2020)  
100 were used to 1) document the temporal variation of siliceous micro- and nanoplanktons and 2)  
101 unravel the relationship between these siliceous planktons and surface ocean environmental  
102 conditions in the western Arctic Ocean.

## 103 **2. Regional setting**

104 The study area is located at the southern Northwind Ridge, western Arctic Ocean and  
105 characterized by seasonal sea ice. The sea ice cover starts to decrease in summer and retreats to  
106 a minimum over the northern Chukchi Sea in September, prior to an entire coverage of the study  
107 area from November to July (Fig. 1a; Fig. 2a-b). During the melting season, the study area sits  
108 in the marginal ice zone (MIZ), an interaction belt between sea ice and open ocean, where  
109 primary production is boosted (Kędra et al., 2015; Wassmann, 2015).

110 The region is also influenced by the surface water mass from different sources: the fresh  
111 and oligotrophic waters of the Beaufort Gyre (BG) driven by the Beaufort High (Proshutinsky  
112 and Johnson, 1997), the Pacific Water Inflow (PWI) transporting the saline and eutrophic  
113 Anadyr Water (AW), the fresher and nutrient-depleted Alaska Coastal Water (ACW) and the  
114 Bering Shelf Water (BSW) in the Chukchi Sea (Fig. 1a; Woodgate et al., 2005; Grebmeier et  
115 al., 2006). In addition, the Siberian Coastal Current (SCC) occasionally converges with the PWI  
116 and trespasses to the Chukchi Borderland (Weingartner et al., 1999).

117 In summer, the upper 10 m water column is composed of the relatively warm, fresher,  
118 nutrient depleted surface mixed layer overlying the colder, saline and nutrient-rich PWI  
119 consisting of Pacific Summer Water (PSW) in 50-100 m water depths and Pacific Winter Water  
120 (PWW) in 100-150 m that sometimes extends to deeper than 200 m (Woodgate, 2013). The  
121 PWI is thus a major source of nutrients for the western Arctic Ocean (Walsh et al., 1997;  
122 Grebmeier et al., 2006).

123 In summer 2008, the western Arctic was characterized by a strong BG inferred from the  
124 higher Arctic Ocean Oscillation (Proshutinsky et al., 2015), oligotrophic conditions associated  
125 with relatively low transport of eutrophic PWI (Woodgate et al., 2015; Woodgate, 2018),  
126 resulting in a reduced biogenic production (Ren et al., 2020). In summer 2009, by contrast,  
127 intensified PWI and weakened BG accounted for higher phytoplankton fluxes (Ren et al., 2020).  
128 Sea ice distribution pattern also influenced primary production in 2008 and 2009, respectively  
129 (Fig. 1b-c; Fig. 2c-d; Ren et al., 2020).

### 130 3. Material and Methods

#### 131 3.1 Sediment trap samples

132 A mooring system was deployed for one year at Station DM, Northwind Ridge, from August  
133 2008 to September 2009 (Fig. 1a; 74°24.0' N, 158°14.0' W, 1650 m water depth). The sediment  
134 trap (McLane Mark78H-21) equipped with 21 sampling cups was installed at ~870 m water  
135 depth. The cups were filled with artificial seawater (salinity≈35) and HgCl<sub>2</sub> as antiseptic before  
136 deployment. From July to November, the sampling interval was set around half month (15 or  
137 16 days) and to one month (28 to 31 days) between December and June (Table S1; Bai et al.,  
138 2019). After recovery of the sediment trap, all samples were sieved by a 1-mm mesh nylon  
139 sieve to remove swimmers. Particles <1 mm were then divided into equal aliquots with a  
140 McLane wet sample divider (WSD-10) and one aliquot was filtered onto a polycarbonate filter  
141 (47 mm diameter with 0.45 μm pore size). The filters were then dried in an oven at 45°C for 72  
142 h (Bai et al., 2019).

#### 143 3.2 Slides preparation and identification of siliceous planktons

144 Quantitative slides for siliceous micro- and nanoplankton were processed using the residue  
145 of the diatom slides prepared by Ren et al. (2020), following the standard method of Gersonde  
146 and Zielinski (2000). Residues were generated by treatment with HCl (~36%) and H<sub>2</sub>O<sub>2</sub> (~30%)  
147 of the subsamples of each cup (30 or 15 mg, dependent on sample amount). An aliquot of a  
148 known amount of the rinsed residue was then dropped on a cover glass (24 × 24 mm) by settling  
149 in a Petri dish. The permanent slides for siliceous micro- and nanoplankton were mounted with  
150 Naphrax ( $n_D \sim 1.7$ ). Only 1 mg of subsample was available for cup 14 (May 2009), but was  
151 analyzed in order to keep an intact record.

152 Around 100 skeletons of silicoflagellates (max. 137, min. 90) were counted for each slide  
153 with a Motic BA410E microscope at ×400 magnification. Fewer skeletons were found in cup  
154 14 (31 skeletons) and 16 (67 skeletons) due to low specimen content in the samples. Specimens  
155 of endoskeletal dinoflagellate *Actiniscus pentasterias* and chrysophyte cysts were counted  
156 meanwhile. Specimen numbers per slide ranged from 8 to 205 for *Actiniscus pentasterias*  
157 (mostly > 20 specimens) and from 22 to 1487 for chrysophyte cysts, respectively. Ebridians  
158 were found in a few slides but not reported here because of their low content (1-3 specimen per

159 sample). Only the specimens with intact main bodies were counted.

160 Silicoflagellates were identified to species level based primarily on the studies in the Arctic  
161 Ocean of Takahashi et al. (2009) and Onodera et al. (2016) as well as those in the subarctic  
162 Pacific of Takahashi (1987) and Onodera and Takahashi (2007, 2012). The illegitimate genus  
163 *Distephanus* has been replaced by *Stephanocha* according to Jordan and McCartney (2015).  
164 *Actiniscus pentasterias* was identified according to Orr and Conley (1976) and Onodera et al.  
165 (2016). Given the difficulties to identify chrysophyte cysts at a taxonomy level and the  
166 uncertainties to relate these cysts to their vegetative form, we only used chrysophyte cysts as  
167 the group of specimens represented by siliceous spheres, generally of ~5-10  $\mu\text{m}$  in diameter,  
168 with a single pore (Adam and Mahood, 1981; Mitchell and Silver, 1982). Because debates are  
169 still going on whether chrysophyte cysts and Archaeomonadaceae (marine fossil chrysophyte  
170 cysts that do not relate to modern vegetative forms) belong to the same taxonomy (Adam and  
171 Mahood, 1981; Mitchell and Silver, 1982), we only use chrysophyte cysts to avoid taxonomic  
172 difficulties. The taxonomy of chrysophyte cysts used herein refers to Duff et al. (1995) and  
173 Wilkinson et al. (2001). Most chrysophyte cysts, due to their diverse morphology and variable  
174 mature and immature ornamentation, have not been related to the vegetative cells that produce  
175 them (Zeeb and Smol, 2001). Therefore, we cannot robustly identify the original taxa of  
176 chrysophyte cysts of this study. Moreover, identification of chrysophyte cysts to subgroups was  
177 also limited owing to the small size of the cysts under light microscopy.

### 178 3.3 Scanning electron microscope images

179 Diluted aliquots of the residues of the diatom slides were pipetted onto polycarbonate  
180 filters (0.45  $\mu\text{m}$  pore size, 47 mm in diameter). Part of the dried filters were mounted on the  
181 stubs of the scanning electron microscope (SEM) with double-sided adhesive tapes. The stubs  
182 were coated with platinum (Pt) for 2 minutes by a Hitachi MC1000 Ion Sputter Coater. A  
183 Hitachi SU8010 Field-Emission Scanning Electron Microscope (FE-SEM) at 3.0 kV was then  
184 used to take photomicrographs of siliceous micro- and nanoplankton.

### 185 3.4 Relative abundances and fluxes

186 The silicoflagellate counts were converted into relative abundances with respect to the  
187 total silicoflagellate assemblage.



188 The fluxes of siliceous micro- and nanoplankton were calculated using the equation given  
189 in Ren et al. (2020). First, the plankton concentrations (skeletons/cysts per milligram dry  
190 sample) were estimated with the following equation:

$$191 \quad \text{Concentration} = (1/dw) \times (csa/ta) \times (sv/split) \times (vn/tn)$$

192 where  $dw$  is the dried sample weight in milligrams,  $csa$  is the area of the cover slide (576  
193 mm<sup>2</sup>),  $ta$  is the area of one counted traverse (15 mm<sup>2</sup>),  $sv$  is the volume of processed  
194 suspension (6-15 ml),  $split$  is the volume of aliquot onto the cover slide (from 0.81 to 1.36  
195 ml),  $vn$  is the total counted micro- and nanoplankton skeleton/cyst number and the  $tn$  is the  
196 number of fully counted traverses.

197 Then fluxes (skeletons/cysts per square meters per day) were calculated using:

$$198 \quad \text{Flux} = \text{Total mass flux} \times \text{Concentration}$$

199 in which the *total mass flux* (milligram dry sample per square meters per day) are those  
200 of Bai et al. (2019) and *concentration* those obtained from the previous equation.

### 201 3.5 Biomarker and Environmental data

202 The fluxes of the biomarkers (IP<sub>25</sub>, HBI-III, brassicasterol, dinosterol) derived from the  
203 same sediment trap collected at Station DM were obtained from Bai et al. (2019).

204 Daily sea ice concentration and thickness data at Station DM for the studied period were  
205 retrieved from the National Centers for Environmental Prediction (NCEP)/Climate Forecast  
206 System Reanalysis (CFSR) 6-hourly dataset (Saha et al., 2010, 2014). In this study we consider  
207 July, August and September as summer months and November to April as winter months  
208 according to the sea ice concentration and thickness.

209 The Arctic Ocean Oscillation index used to indicate the strength of the Beaufort Gyre were  
210 the values of Proshutinsky et al. (2015).

211 Monthly transport volume of PWI were obtained from the “Bering Strait: Pacific Gateway  
212 to the Arctic” project (Woodgate et al., 2015; Woodgate, 2018).

## 213 4. Results

### 214 4.1 *Silicoflagellates*

215 Silicoflagellate fluxes were high ( $>20 \times 10^3$  skeletons  $\text{m}^{-2} \text{d}^{-1}$ ) for both summers, while  
216 much lower values were found in winter when Station DM was covered by sea ice (mostly  $<10$   
217  $\times 10^3$  skeletons  $\text{m}^{-2} \text{d}^{-1}$ ; Fig. 2a, b, f). The extreme peak flux of  $\sim 540 \times 10^3$  skeletons  $\text{m}^{-2} \text{d}^{-1}$  was  
218 encountered in late September 2009, synchronous with the maximum total mass flux (Fig. 2e,  
219 f). Late July 2009 saw an abrupt rise of silicoflagellate flux from  $\sim 2 \times 10^3$  to  $\sim 80 \times 10^3$  skeletons  
220  $\text{m}^{-2} \text{d}^{-1}$ , coinciding with the onset of sea ice decreasing (Fig. 2a, f).

221 The silicoflagellate assemblage was dominated by *Stephanocha speculum*, which on  
222 average accounted for more than 71% of total silicoflagellate composition (Fig. 3, 4a). The  
223 relative abundance of *S. speculum* showed clear seasonal variations. It reached over 80% during  
224 both summers and decrease to a minimum of 63% in winter (Fig. 3b). The second most  
225 abundant species, *S. medianoetisol*, contributed  $\sim 20\%$  of annual total silicoflagellate (Fig. 3b,  
226 4b). In contrast, *S. medianoetisol* was more abundant in winter ( $\sim 24\%$ ) than in summer ( $\sim 12\%$ ;  
227 Fig. 3b). Likewise, *S. octonarius* accounted for  $\sim 4\%$  of the total assemblage in winter (Fig. 3b,  
228 4c). Pentagonal *S. quinquangellus* was a minor component ( $<1\%$  on average). Only a few  
229 double skeletons were observed, most of which were *S. speculum* and occurred in summer.  
230 They were generally  $<2\%$  of the silicoflagellate assemblage.

### 231 4.2 *Endoskeletal dinoflagellate Actiniscus pentasterias*

232 *Actiniscus pentasterias* (Fig. 4d-f) fluxes were extremely high in summer 2009, especially  
233 in late September ( $71 \times 10^3$  skeletons  $\text{m}^{-2} \text{d}^{-1}$ ; Fig. 2g). The fluxes during other periods were  
234 mostly below  $6 \times 10^3$  skeletons  $\text{m}^{-2} \text{d}^{-1}$ . While higher values were found in October and  
235 November 2008 ( $\sim 7 \times 10^3$  skeletons  $\text{m}^{-2} \text{d}^{-1}$ ), minimum fluxes, lower than  $2 \times 10^3$  skeletons  $\text{m}^{-2}$   
236  $\text{d}^{-1}$ , were recorded in June and early July 2009. There was no clear seasonal pattern observed  
237 (Fig. 2g).

### 238 4.3 *Chrysophyte cysts*

239 Chrysophyte cysts (Fig. 4g-i) also showed marked seasonality. Fluxes for both summers  
240 exhibited high values, with chrysophyte cysts fluxes in summer 2009 at least twice as much as  
241 those of summer 2008 (Fig. 2h). Striking high fluxes peaked at  $\sim 932 \times 10^3$  and  $\sim 817 \times 10^3$  cysts  
242  $\text{m}^{-2} \text{d}^{-1}$  in late July and early August 2009, respectively, nearly 10 times higher than those of  
243 summer 2008. By contrast, winter fluxes were generally lower than  $20 \times 10^3$  cysts  $\text{m}^{-2} \text{d}^{-1}$ .

## 244 5. Discussion

### 245 5.1 *Silicoflagellates and their oceanographic features*

246 Our data at the Northwind Ridge revealed higher silicoflagellate fluxes in summer 2009  
247 than in 2008 and a seasonal pattern of the silicoflagellate assemblage (Fig. 3a). The relative  
248 abundance of the dominant species *S. speculum* was higher in summer, while that of *S.*  
249 *medianoetisol* and *S. octonarius* increased under sea ice cover (Fig. 3b). Similar seasonal  
250 pattern of silicoflagellate assemblage was also evidenced in the nearby sediment trap in the  
251 Northwind Abyssal Plain, western Arctic (NAP in Fig. 1a; Onodera et al., 2016), with *S.*  
252 *medianoetisol* and *S. octonarius* accounting for >30% of total silicoflagellate assemblage in  
253 summer 2010 (Onodera et al., 2016). These two species were reported as predominant in the  
254 central and the western Arctic, where sea ice prevailed (Melnikov, 1997; Melnikov et al., 2002;  
255 Takahashi et al., 2009). Highest relative abundance of *S. medianoetisol* in sediment traps from  
256 the subarctic Pacific were found to be correlated to colder conditions (Onodera and Takahashi,  
257 2012). It is thus likely that *S. medianoetisol* and *S. octonarius* tolerate sea ice and cold water  
258 and therefore that their high abundances in silicoflagellate assemblages are indicative of  
259 freezing conditions. This could explain that relative abundances of *S. medianoetisol* and *S.*  
260 *octonarius* were higher in summer 2009 when ice free conditions lasted approximately one  
261 month less than in 2008 (Fig. 2a, f, 3b). The biometry of *S. medianoetisol*, notably the spine  
262 length has been proposed as an indicator to discriminate sea ice and seawater habitats in the  
263 central Arctic (Tsutsui and Takahashi, 2009). However, this morphological parameter was not  
264 measured in this study. Further studies on the relationship between the biometry of  
265 silicoflagellate and their dwelling environment should be explored to refine this tool.

266 The six-sided *S. speculum* represented less than 70% in winter except for one single sample  
267 in May 2009, most likely biased by insufficient sample amount (Fig. 3b). These results are in  
268 line with the silicoflagellate composition from the nearby NAP site (Onodera et al., 2016) and  
269 other studies, showing that *S. speculum* is a common species at high latitudes that dominates  
270 the silicoflagellate assemblage of sinking particles and sediments north of the Subarctic Front  
271 in the North Pacific (Poelchau, 1976; Takahashi, 1985, 1987; Onodera and Takahashi, 2005,  
272 2012). Based on its distribution in the North Pacific, Onodera et al. (2016) inferred that *S.*

273 *speculum* might be indicative of mesotrophic to eutrophic conditions. Higher *S. speculum* fluxes  
274 in summer 2009 than in 2008 (Fig. 3a) are in agreement with the high diatom fluxes (Ren et al.,  
275 2020) and enhanced PWI in 2009 entraining more nutrient to our site (Woodgate et al., 2012;  
276 Woodgate, 2018). If higher *S. speculum* is indeed related to increased productivity due to  
277 nutrient supply, this species could also be regarded as a productivity indicator as proposed by  
278 Takahashi (1989). Furthermore, *S. speculum* was found abundant in the Bering Sea (>60% in  
279 sediment; Poelchau, 1976; >80% in sediment trap; Onodera and Takahashi, 2012) and less  
280 frequent in the central Arctic (<29%; Takahashi et al., 2009), suggesting that it might reflect  
281 subarctic conditions in the area.

282 Most of double skeletons in our sediment trap material, though in low abundance, were  
283 encountered in summer, which could imply silicoflagellate reproduction and higher production  
284 during phytoplankton blooming when sea ice retreats (Takahashi et al., 2009; Onodera et al.,  
285 2016). However, the relative abundance of summer silicoflagellate double skeletons at Station  
286 DM (<2%) were much less than that of the nearby NAP site (>10%; Onodera et al., 2016). This  
287 difference could suggest interannual variability or regional difference although methodological  
288 bias cannot be ruled out. Slide preparation, which might damage organic coat of double  
289 skeletons and separate them into single skeletons, accounts at least in part for this discrepancy.

290 Only a few studies have used silicoflagellate assemblages to reconstruct  
291 paleoenvironmental conditions in the Pacific-Arctic region (Onodera et al., 2016; Teraishi et  
292 al., 2016). Past oceanographic variability of the Gulf of Alaska for the past 15000 years has  
293 been established partly based on fossil silicoflagellate assemblages (Barron et al., 2009). Higher  
294 abundances of *S. medianoetisol* were also reported in the Bering Shelf break sediments during  
295 glacial periods of the early- to mid-Pleistocene corresponding to the cold intervals (Teraishi et  
296 al., 2016). A close relationship between the sea surface temperatures (SSTs) and the ratio of *S.*  
297 *medianoetisol* to *S. speculum* was highlighted by Onodera and Takahashi (2012) and used in  
298 sediment cores to estimate semi-quantitatively temperature variability (e.g. Ciesielski and  
299 Weaver, 1974). Yet, longer observation time series would be required to consolidate this  
300 relationship.

301 *5.2 Endoskeletal dinoflagellate and productivity*

302 Higher fluxes of endoskeletal dinoflagellate *Actiniscus pentasterias* were found in winter  
303 in the Northwind Abyssal Plain, under sea ice conditions (NAP in Fig. 1a; Onodera et al., 2016).  
304 However, except for peaking value in summer 2009, the fluxes of *A. pentasterias* at Station DM  
305 did not show a clear seasonal variability (Fig. 2g). This species has also been found in the  
306 subarctic (Takahashi, 1987) and tropical Pacific (Takahashi, 1991) indicating a possible wider  
307 distribution range. Steidinger and Tangen (1997) further showed the cosmopolitan occurrence  
308 of *A. pentasterias* from subtropical to cold temperate oceans. Low fluxes of *A. pentasterias* at  
309 our site in winter suggest that this species does not dwell under the ice. Interestingly, in summer  
310 2010 living *A. pentasterias* occurred in high abundances close to the sea ice edge (Onodera et  
311 al., 2016) in accordance with high flux values in summer 2009 at Station DM during the ice  
312 melting season (Fig. 2g). Therefore, given its wide distribution, *A. pentasterias* is unlikely to  
313 be an indicator of cold conditions. On the contrary, as a heterotroph, *A. pentasterias* is likely to  
314 be more sensitive to phytoplankton seasonal blooming, as its food supply, than to cold or warm  
315 environmental conditions. Besides, the fluxes of *A. pentasterias* are highly correlated with those  
316 of silicoflagellate ( $r^2 = 0.97, p < 0.01$ ), as well as to cold water diatoms ( $r^2 = 0.65, p < 0.01$ )  
317 and open water phytoplankton biomarker brassicasterol ( $r^2 = 0.88, p < 0.01$ ), featuring the close  
318 relationship between *A. pentasterias* and its prey (Table 1). Therefore *A. pentasterias* thriving  
319 under fertile conditions favoring phytoplankton blooms would portray productive MIZ  
320 environment as also suggested by sediment traps data from northern North Pacific (Takahashi,  
321 1987).

### 322 5.3 Chrysophyte cysts as environmental indicators

323 Although most chrysophytes inhabit fresh water systems (Duff et al., 1995; Zeeb and Smol,  
324 2001 and references therein), they have also been described in marine settings (Peters and  
325 Andersen, 1993; Berard-Therriault et al., 1999). A few species of chrysophytes have been  
326 observed in the Arctic Ocean (Coupel et al., 2012; Lee et al., 2012; Ardyna et al., 2017; Assmy  
327 et al., 2017), whereas chrysophyte cysts are rarely detected. Yet fossil chrysophyte cysts have  
328 been found in Arctic sediments as old as Eocene (Stickley et al., 2008). According to the  
329 morphology and ornamentation of chrysophyte cysts, it is likely that the cysts at Station DM  
330 (Fig. 4g-i) are stomatocysts No. 381 and 382 as described by Wilkinson et al. (2001) in

331 sediments of a Canadian Arctic lake that corresponds to a marine period (Wilkinson et al., 2001).  
332 If so, chrysophyte cysts found in our sediment trap would be indicative of an Arctic marine  
333 origin rather than fresh water. The fluxes of chrysophyte cysts in summer 2009 were one order  
334 of magnitude higher than those of summer 2008 (Fig. 2h) with maximum fluxes in late July to  
335 early August 2009 that were ~4 to 5 times greater than the rest of that summer (Fig. 2h). In  
336 addition, according to *in situ* measurements the surface layer near Station DM was fresher in  
337 summer 2008 than in summer 2009 (Zhang, 2009; Kikuchi, 2009) and the freshwater volume  
338 of the upper 30 m layer did not vary much during the blooming season as calculated from  
339 NCEP/CFSR dataset (Saha et al., 2010, 2014). Consequently, the freshwater origin of  
340 chrysophyte cysts at our site can be excluded.

341 It is also unlikely that chrysophyte cysts were transported by currents from brackish  
342 coastal areas. Higher fluxes of allochthonous diatoms (e.g. *Chaetoceros* resting spores and  
343 *Paralia sulcata*) and terrestrial biomarkers (campesterol and  $\beta$ -sitosterol) were recorded in  
344 summer 2009 and attributed to enhanced PWI bringing coastal material from the shallow  
345 Chukchi shelf region to the Northwind Ridge (Ren et al., 2020). Allochthonous material showed  
346 high fluxes over the entire summer 2009. In contrast, chrysophyte cysts were massively  
347 abundant from late July and early August of 2009 ( $>800 \times 10^3$  cysts  $m^{-2} d^{-1}$ ) and dropped by 4  
348 fold the following summer (Fig. 2h), which does not match with the high transport of PWI in  
349 2009 (Fig. 2d; Woodgate et al., 2015; Woodgate, 2018). Sea ice may have played a role in the  
350 transport of the cysts to the study site but the high fluxes in ice free waters in late August and  
351 September make this hypothesis improbable (Fig. 2a, h). It is thus very likely that chrysophyte  
352 cysts underwent *in situ* encystment after blooming at our site. Besides, the echinate spines on  
353 the surface of chrysophyte cysts were mostly intact and unbroken (Fig. 4g-i) in agreement with  
354 gentle rather than stirring surface current transport.

355 As earlier mentioned, peaking fluxes coincide with enhanced sea ice melting in summer  
356 (Fig. 2a, b, h). It is thus possible that chrysophyte cysts are associated to sea ice, akin to some  
357 sea ice diatoms as suggested by Mitchell and Silver (1982, 1986). Most reports linking  
358 chrysophyte cysts to sea ice are from the Southern Ocean (e.g. Silver et al., 1980; Takahashi et  
359 al., 1986; Riaux-Gobin and Stumm, 2006; Riaux-Gobin et al., 2011), and may therefore relate

360 to different species from our study. Nevertheless, the response of chrysophyte cysts to sea ice  
361 decline does not parallel that of sea ice diatoms (Ren et al., 2020). Although both increased  
362 abruptly late July 2009, the diatoms fluxes fluctuated much less than the cysts (Fig. 5; Ren et  
363 al. 2020). The correlation between the fluxes of chrysophyte cysts and sea ice diatoms is hence  
364 not significant ( $r^2 = 0.31$ ,  $p < 0.01$ ; Table 1). Comparison between the fluxes of chrysophyte  
365 cysts and sea ice biomarker IP<sub>25</sub> from the same sediment trap material does not show similar  
366 seasonal variability (Table 1; Bai et al., 2019). Neither does the cysts and sea ice margin  
367 biomarker HBI-III (Table 1). It is thus hard to conclude on the exact link between the  
368 chrysophyte cysts and sea ice. Surface sediments from the northern North Atlantic have shown  
369 that chrysophyte cysts mainly occurred between the winter maximum and summer minimum  
370 sea ice boundaries, where MIZ lies (Redmond Roche, 2019). According to light microscopic  
371 determination, this species is similar to that found at our site (Redmond Roche, 2019)  
372 suggesting that chrysophyte cysts are related at least to chilly environment.

373 Chrysophyte cysts are formed either asexually or sexually (Sandgren, 1991; Duff et al.,  
374 1995 and references therein). Although sexually induced cysts are still poorly studied, previous  
375 studies demonstrated that the sexual formation of cysts, as least for the investigated species, are  
376 possibly triggered by population density rather than environmental stress (Sandgren, 1991; Duff  
377 et al., 1995). Therefore, the maximum fluxes of chrysophyte cysts in late July and early August  
378 might be a consequence of specific environmental conditions that promoted the growth of  
379 chrysophyte vegetative cells and initiated the encystment when the cells number exceeded the  
380 population threshold. It is likely that peaking chrysophyte cysts in summer 2009 witnessed  
381 favorable conditions for phytoplankton blooming stimulated by enhanced light penetration  
382 caused by sea ice thinning and melting at the MIZ (Fig. 2a, b) together with increased nutrient  
383 supply from strengthened PWI (Fig. 2d; Ren et al., 2020). Therefore, high abundances of  
384 chrysophyte cysts might indicate a propitious environment for phytoplankton thriving (e.g. high  
385 nutrients) under cold condition.

#### 386 *5.4 Relationship between siliceous plankton and environmental conditions*

387 The fluxes of silicoflagellate, endoskeletal dinoflagellate *A. pentasterias* and chrysophyte  
388 cysts show no significant correlation with sea ice proxies, i.e. sea ice diatom and IP<sub>25</sub> (Table 1).



389 They instead seem to be more tightly associated to cold water diatoms and phytoplankton  
390 biomarkers (brassicasterol and dinosterol; Table 1). This implies that these siliceous planktons  
391 are more akin to MIZ rather than permanent ice zone. However, due to the temporal and spatial  
392 limitation of this times series, it is hard to unravel whether these siliceous planktons are sea ice  
393 inhabitants. Significant correlations between the fluxes of silicoflagellate and *A. pentasterias*  
394 ( $r^2 = 0.97, p < 0.01$ ) as well as between chrysophyte cysts and dinosterol, a biomarker produced  
395 by dinoflagellates ( $r^2 = 0.56, p < 0.01$ ; Table 1) suggest the food web relationship between preys  
396 and predators.

397

398

399 **6. Summary and Conclusions**

400 The one-year flux record of siliceous micro- and nanoplankton acquired at the Northwind  
401 Ridge, western Arctic Ocean, between August 2008 and September 2009 highlights the strong  
402 seasonality of the production and export of silicoflagellates, endoskeletal dinoflagellates  
403 *Actiniscus pentasterias* and chrysophyte cysts. The dominant silicoflagellate *Stephanocha*  
404 *speculum* prevailed in summer, while *S. medianoctisol* and *S. octonarius* were more frequent  
405 in winter. These findings suggest that *S. speculum* might reflect subarctic conditions and  
406 influence of Pacific waters through the Bering Strait while *S. medianoctisol* and *S. octonarius*  
407 would closely link to sea ice and associated cold conditions. Abundances of *A. pentasterias*  
408 were found to be manifesting productive conditions at the MIZ. Similarly, chrysophyte cysts  
409 were overwhelming abundant during ice melting suggesting favorable conditions for  
410 phytoplankton blooming. Overall, these groups of siliceous micro- and nanoplankton provide  
411 environmental information, complementary to diatoms, depicting modern and past changes in  
412 the Arctic Ocean. We suggest to explore further the potential of these siliceous micro- and  
413 nanoplankton for paleoceanographic studies in the western Arctic as they require fewer species  
414 identification compared to diatoms, while sharing similar processing methodology. A deeper  
415 understanding of their ecology will entail investigation of their long-term temporal variability  
416 and spatial distribution both in water column and surface sediments.

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418

419

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2 **and their relationship to environmental conditions in the western**  
3 **Arctic Ocean**

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8 **Table 1**

9 **Table 1.**

10  
 11 **Table 1.** Matrix of coefficient of determination ( $r^2$ ) between fluxes of chrysophyte cysts, silicoflagellate and endoskeletal dinoflagellate *Actiniscus pentasterias*, fluxes of sea  
 12 ice diatom and cold water diatom group, fluxes of brassicasterol and dinosterol and fluxes of IP<sub>25</sub> and HBI-III from August 2008 to September 2009 at Station DM. Significant  
 13 correlations are bold and underlined.

	Chrysophyte cyst flux	Silicoflagellate flux	<i>Actiniscus</i> <i>pentasterias</i> flux	Sea ice diatom flux	Cold water diatom flux	Brassicasterol flux	Dinosterol flux	IP <sub>25</sub> flux	HBI-III flux
Chrysophyte cyst flux <sup>a</sup>	1.00								
Silicoflagellate flux <sup>a</sup>	0.04	1.00							
<i>Actiniscus pentasterias</i> flux <sup>a</sup>	0.02	<b><u>0.97</u>*</b>	1.00						
Sea ice diatom flux <sup>b</sup>	0.31*	0.33*	0.24**	1.00					
Cold water diatom flux <sup>b</sup>	0.40*	<b><u>0.71</u>*</b>	<b><u>0.65</u>*</b>	<b><u>0.64</u>*</b>	1.00				
Brassicasterol flux <sup>c</sup>	0.14	<b><u>0.91</u>*</b>	<b><u>0.88</u>*</b>	0.44*	<b><u>0.83</u>*</b>	1.00			
Dinosterol flux <sup>c</sup>	<b><u>0.56</u>*</b>	0.43*	0.40*	<b><u>0.56</u>*</b>	<b><u>0.77</u>*</b>	<b><u>0.67</u>*</b>	1.00		
IP <sub>25</sub> flux <sup>d</sup>	0.14	0.01	<0.001	<b><u>0.64</u>*</b>	0.16	0.03	0.08	1.00	
HBI-III flux <sup>d</sup>	<0.003	0.01	<0.001	0.48*	0.03	0.01	0.02	<b><u>0.75</u>*</b>	1.00

14 <sup>a</sup> in 10<sup>3</sup> cysts/skeletons m<sup>-2</sup> d<sup>-1</sup>

15 <sup>b</sup> in 10<sup>5</sup> valves m<sup>-2</sup> d<sup>-1</sup>

16 <sup>c</sup> in µg m<sup>-2</sup> d<sup>-1</sup>

17 <sup>d</sup> in ng m<sup>-2</sup> d<sup>-1</sup>

18 \*  $p$ -value < 0.01

19 \*\*  $p$ -value < 0.05

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8 **Figure captions**

9 **Figure 1.** (a) Station DM (red circle) and surface currents (grey arrows) in the study area. The  
10 white dash line represents the average multi-year sea ice minimum for 1979-2017 (20% of sea  
11 ice concentration) (from Cavalieri et al., 1996). The other site for discussion is also presented  
12 (yellow circle). Major currents system: PWI- Pacific Water Inflow; ACW-Alaska Coastal Water;  
13 AW-Anadyr Water; BSW-Bering Shelf Water; BG-Beaufort Gyre; SCC-Siberia Coastal Current.  
14 Topography: NR-Northwind Ridge; NAP-Northwind Abyssal Plain; CP-Chukchi Plateau;  
15 CAP-Chukchi Abyssal Plain. The inset figure in the upper right indicates the study area in the  
16 Arctic Ocean. (b) and (c) demonstrate the surface currents and sea ice distribution near Station  
17 DM in summer 2008 and 2009, respectively (modified from Ren et al., 2020). The black dash  
18 line indicates the 20% isoline of summer sea ice concentration (July, August and September).  
19 Stronger currents are shown by thicker arrows. Sea ice data were obtained from Nimbus-7  
20 SMMR and DMSP SSM/I-SSMIS passive microwave data (Cavalieri et al., 1996).

21

22 **Figure 2.** Sea ice and sea surface environment variability and siliceous micro- and  
23 nanoplankton fluxes measured in the sediment trap at Station DM from August 2008 to  
24 September 2009. (a) Sea ice concentration (%); (b) Sea ice thickness (m); (c) Arctic Ocean  
25 Oscillation Index, indicating the strength of the Beaufort Gyre (from Proshutinsky et al., 2015);  
26 (d) Transport of the Pacific Water Inflow (Sv; Woodgate et al., 2015; Woodgate 2018).  
27 Maximum transport of 2008 and 2009 is also indicated; (e) Total mass flux ( $\text{mg m}^{-2} \text{d}^{-1}$ ; from  
28 Bai et al., 2019); (f) Total silicoflagellate fluxes ( $10^3$  skeletons  $\text{m}^{-2} \text{d}^{-1}$ ); (g) *Actiniscus*  
29 *pentastarias* fluxes ( $10^3$  skeletons  $\text{m}^{-2} \text{d}^{-1}$ ); (h) Chrysophyte cyst fluxes ( $10^3$  cysts  $\text{m}^{-2} \text{d}^{-1}$ ).

30

31 **Figure 3.** (a) Stacked fluxes of main silicoflagellate species ( $10^3$  skeletons  $\text{m}^{-2} \text{d}^{-1}$ ); (b) Relative  
32 abundance of main silicoflagellate species (%).

33

34 **Figure 4.** Scanning Electron Microscope (SEM) photomicrographs of silicoflagellates (a-c),  
35 endoskeletal dinoflagellate *Actiniscus pentastarias* (d-f) and chrysophyte cysts (g-i) obtained  
36 from the samples of Station DM. (a) *Stephanocha speculum*; (b) *S. medianoctisol* (internal  
37 view); (c) *S. octonarius*; (d) Apical view of *A. pentastarias*; (e) Oblique basal view of *A.*  
38 *pentastarias*; (f) Side view of *A. pentastarias*; (g) chrysophyte cyst type 1 (stomatocyst 382 in  
39 Wilkinson et al., 2001); (h) chrysophyte cyst type 2 (stomatocyst 381 in Wilkinson et al., 2001);  
40 (i) cluster of chrysophyte cyst type 1. Scale bars are 10  $\mu\text{m}$  for a-c and 5  $\mu\text{m}$  for d-i.

41

42 **Figure 5.** Fluxes of chrysophyte cysts ( $10^3$  cysts  $\text{m}^{-2} \text{d}^{-1}$ ) and sea ice diatom ( $10^5$  valves  $\text{m}^{-2} \text{d}^{-1}$ ).  
43 Sea ice concentration is also shown.

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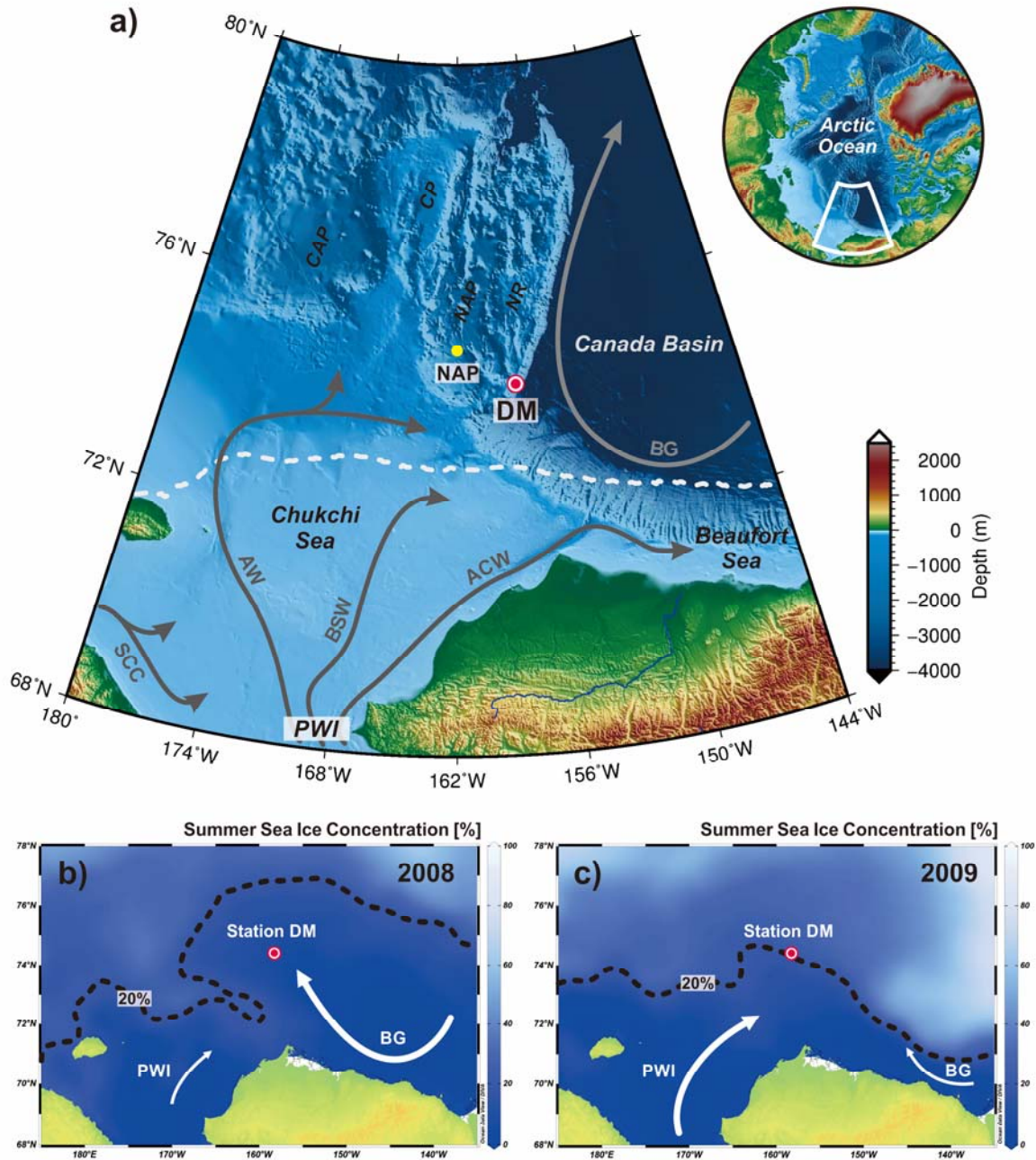
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54 **Figures 1-5**

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56 **Figure 1**

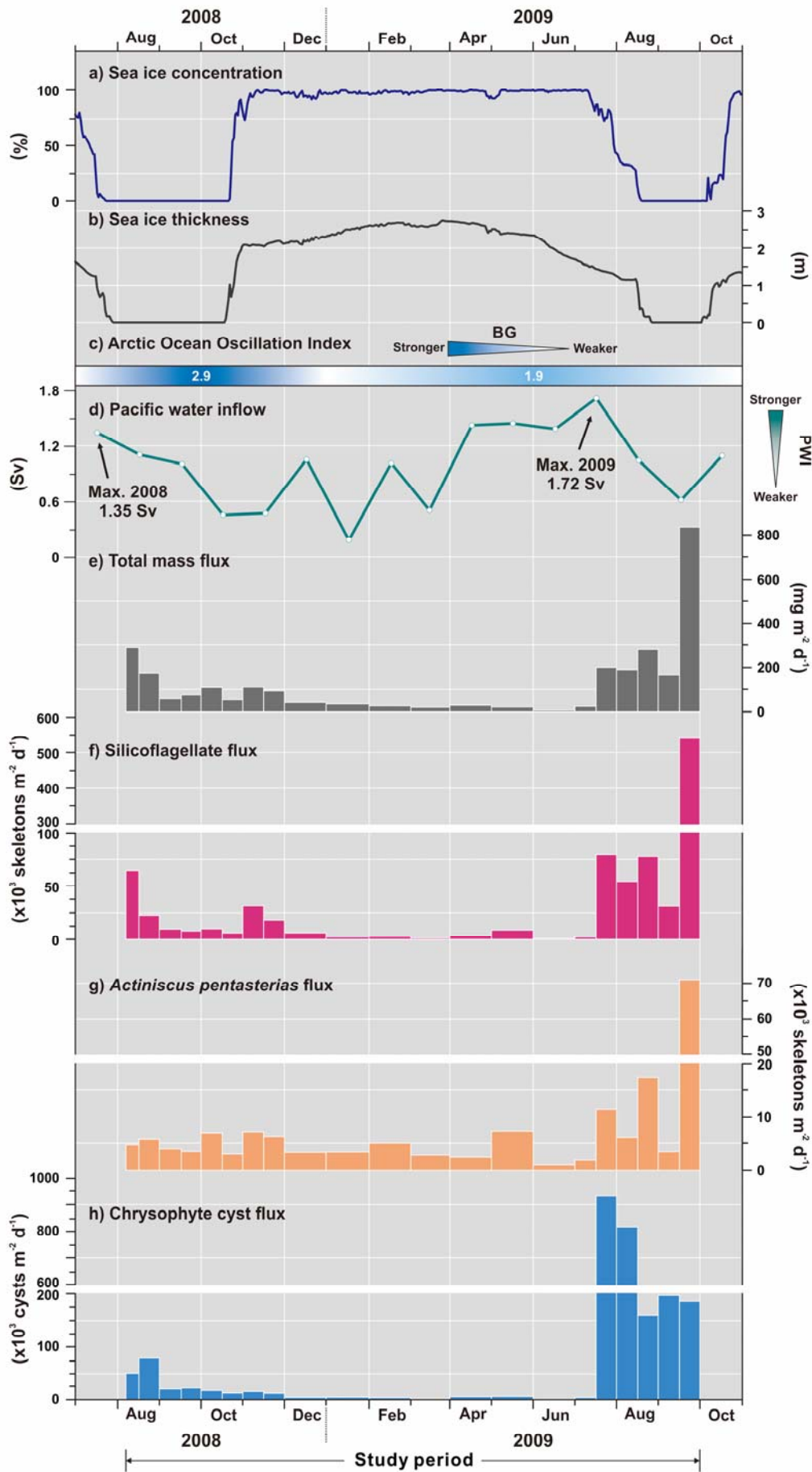


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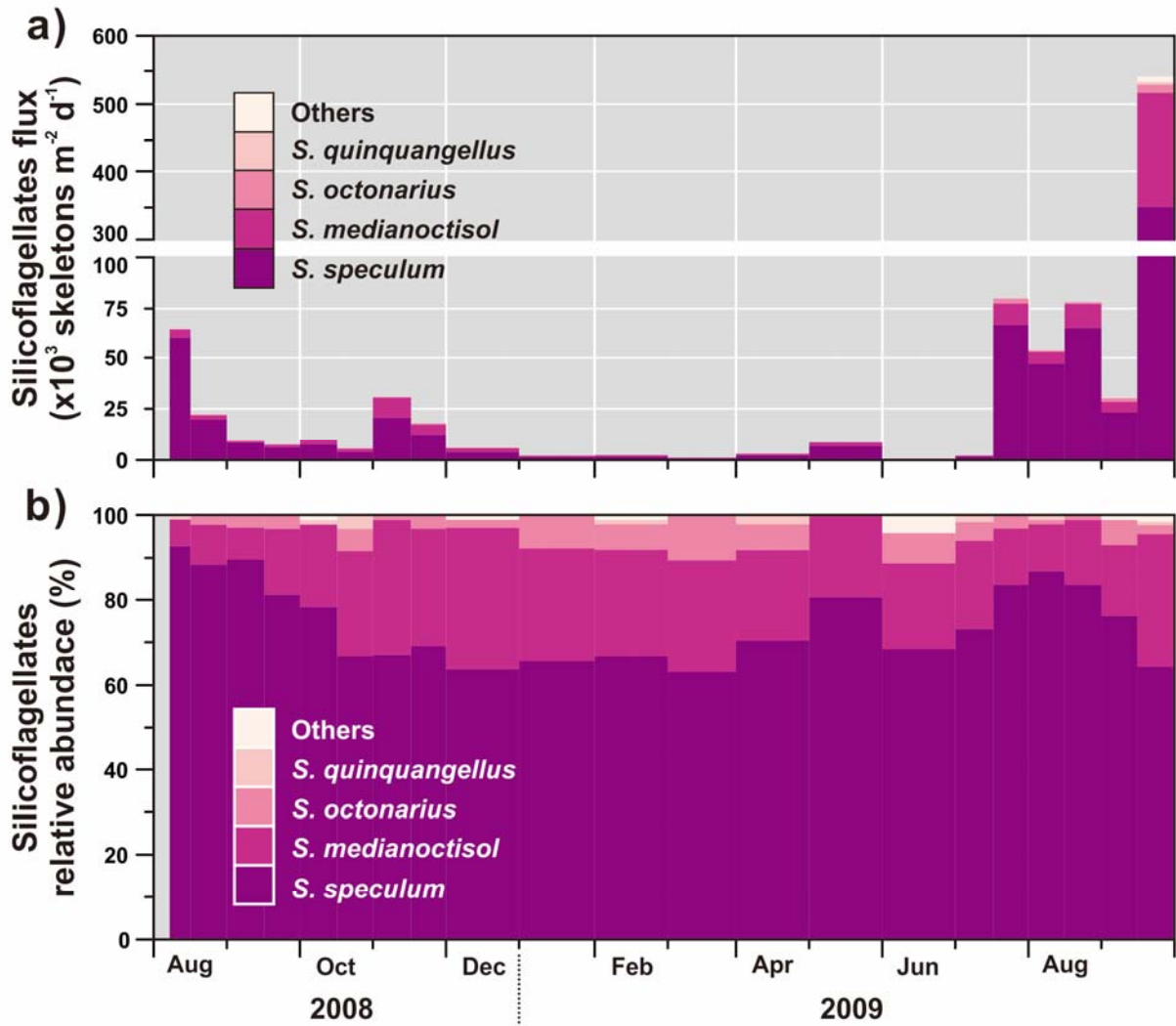
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59 Figure 2

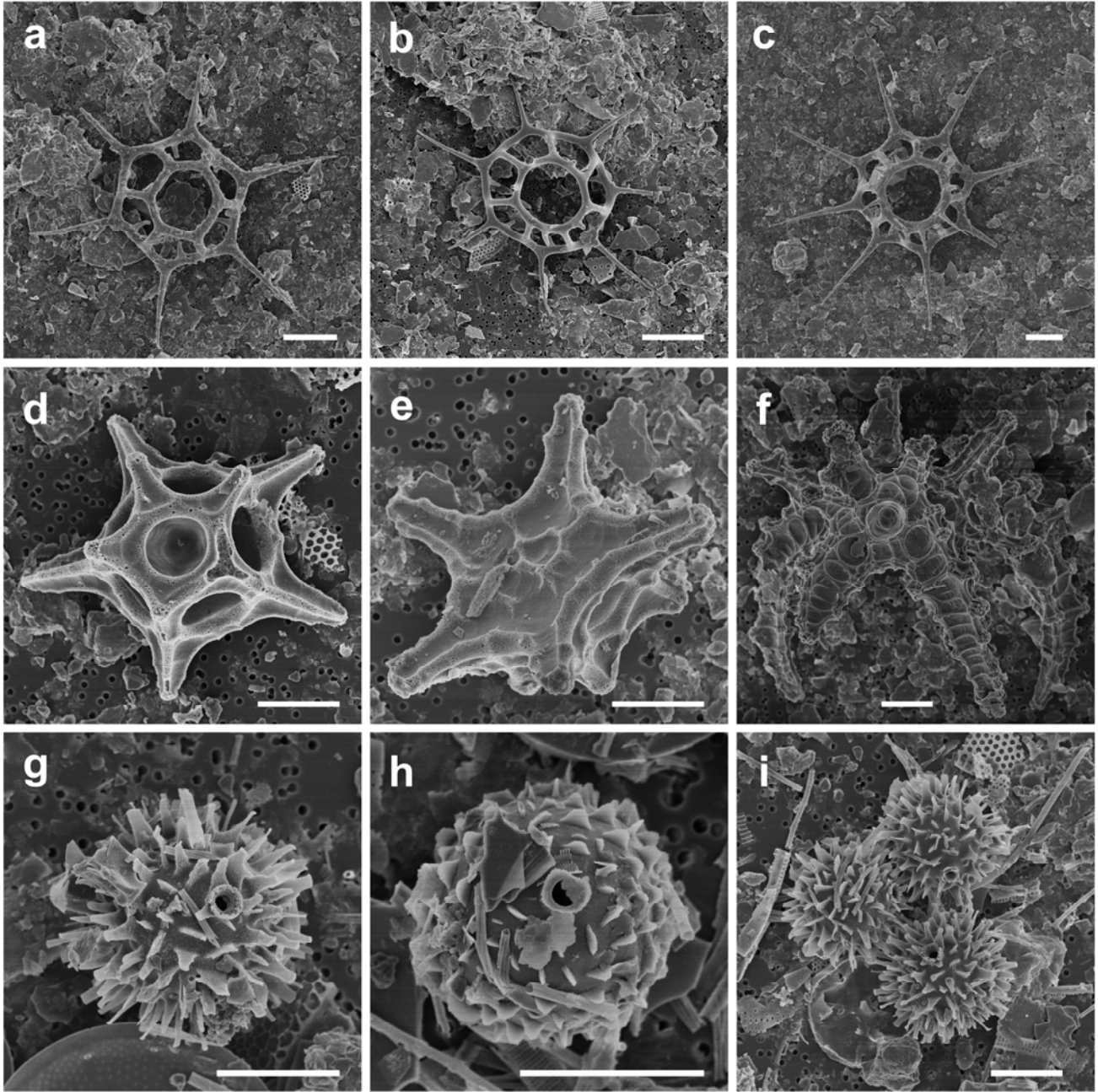


60 Figure 3



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62 **Figure 4**

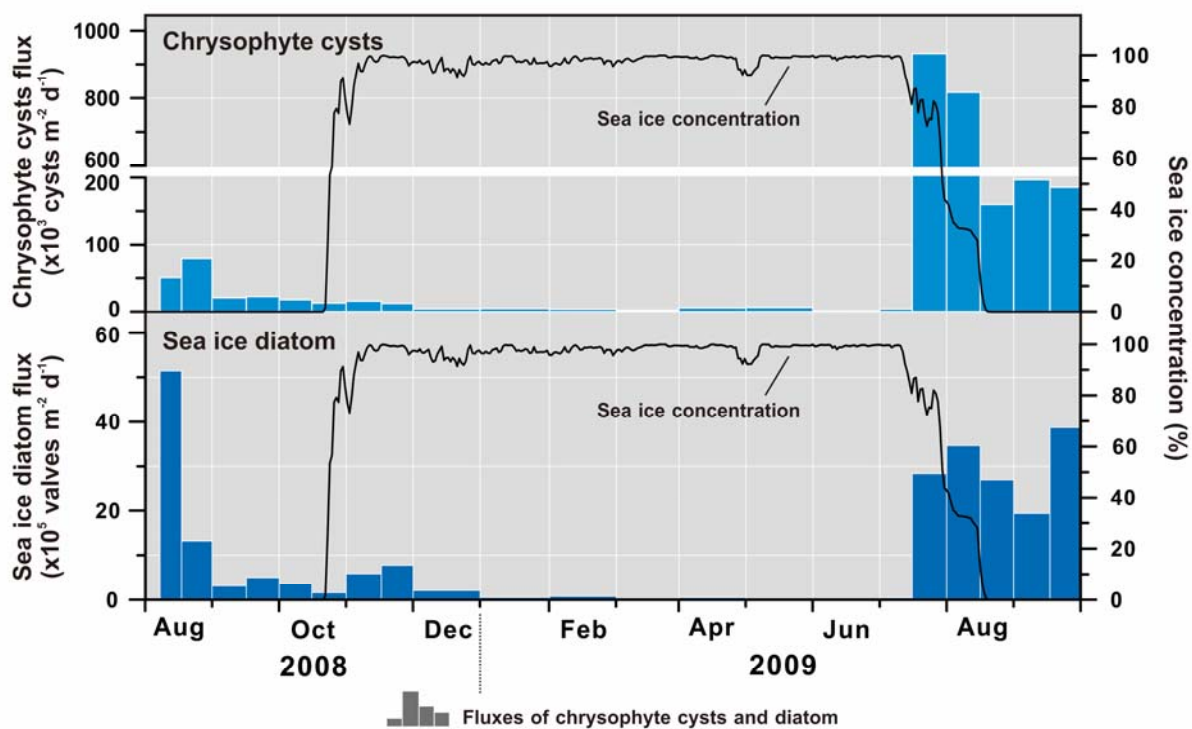


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66 **Figure 5**



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