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## Abrupt shifts of productivity and sea ice regimes at the western Barents Sea slope from the Last Glacial Maximum to the Bølling-Allerød interstadial

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### Abstract :

Advanced knowledge of spatio-temporal constraints on the Barents Sea Ice Sheet during the late Weichselian glaciation overshadows relatively limited understanding of seasonal sea ice (experiencing an annual advance-retreat cycle) and primary productivity trends accompanying massive, abrupt climate changes during glacial-deglacial cycles. Such paleo-reconstructions are crucial prerequisites for improved comprehension and prediction of current and future climate change. Here, we investigate sea ice and phytoplankton biomarker distributions in a Barents Sea sediment core covering ca. 25.8–15.4 cal kyr BP to elucidate abrupt shifts of spring–summer sea ice concentrations and relative sympagic–pelagic productivity trends at the southwestern continental slope. Despite significant presence of seasonal sea ice, the Last Glacial Maximum (LGM) and initial shelf edge deglaciation (SEDG) at the core site are characterised by occurrence of productive coastal polynya adjacent to the maximum ice sheet extent. The onset of perennial (i.e. multi-year) ice cover and near-zero productivity during Heinrich Stadial 1 (HS1; ca. 18.0–16.3 cal kyr BP) accompanies significant meltwater fluxes from ice sheet debuitressing and the consequent stagnation of thermohaline circulation. Rapid sea ice retreat and unprecedented pelagic productivity observed after 16.3 cal kyr BP coincides with areal ice sheet deglaciation and is potentially linked to the release of sub-surface heat and nutrient reservoirs, together with reinvigorated deep water circulation following millennial heating of the deep ocean during HS1. We find that a multivariate fingerprinting approach involving assessment of both downcore and surface biomarker distributions is able to distinguish relative ice-algal and pelagic diatom productivity driven by sea ice dynamics.

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## Highlights

▶ Seasonal sea ice and high sympagic productivity characterised the LGM. ▶ Abrupt decline of productivity coincided with perennial ice cover during the HS1. ▶ Unprecedented pelagic productivity dominated following the post-HS1 ice retreat. ▶ Multivariate HBI biomarker set can decouple sympagic and pelagic productivity.

**Keywords** : Arctic Ocean, Quaternary, Sea ice, Marine biomarkers, HBI, IP25, PIP25, Barents Sea, Coastal polynya, Classification tree

## 23 **1. Introduction**

24 Arctic sea ice cover is an integral component of the climate system and exhibits complex  
25 interactions with the ocean and the atmosphere. High albedo allows sea ice to effectively  
26 reflect incoming solar radiation during the spring and summer months, while extensive areal  
27 coverage during winter prevents excessive oceanic heat loss, thus regulating the heat budget  
28 across the ocean-atmosphere interface (e.g. Smedsrud et al., 2013). Oceanic convection from  
29 brine expulsion during ice formation contributes to the thermohaline overturning circulation  
30 (Berger and Jansen, 1995), while occurrence of leads, polynya and seasonal ice melting  
31 stratifies the water column, facilitating between 10–55 % of all primary productivity in the  
32 Arctic Ocean (Gosselin et al., 1997; Wassmann et al., 1999, 2006). The decline of seasonal  
33 sea ice extent (Fetterer et al., 2017), thickness (Lindsay and Schweiger, 2015), and perennial  
34 (multi-year) ice fraction (Smedsrud et al., 2017) evident since ca. 1850 AD (Walsh et al.,  
35 2017) has accelerated further over the last ca. 40 years. Such a precipitous decline is  
36 augmented via positive feedback (Smedsrud et al., 2013) and is likely caused by a  
37 combination of anthropogenic warming (Notz and Marotzke, 2012), as well as increasing  
38 inflow and temperature of Atlantic Water (AW) (Årthun et al., 2012). The latter is most  
39 evident in the seasonally ice-covered Barents Sea, where the North Atlantic Current (NAC)  
40 provides ample nutrients for spring-summer primary productivity blooms (e.g. Wassmann et  
41 al., 1999, 2006). Higher volume and temperature of AW and multi-decadal recession of the  
42 Barents Sea ice cover (Onarheim et al., 2018) are already contributing to earlier ice melt,  
43 increased lead/polynya incidence (Willmes and Heinemann, 2016), hastening of spring  
44 phytoplankton blooms (Stroeve et al., 2014), and northward intrusion of lower-energy,  
45 smaller pelagic species at the expense of ice-obligate algae (Hegseth and Sundfjord, 2008;  
46 Assmy et al., 2017; Hoppe et al., 2018) that likely affects survivability and biodiversity of  
47 pelagic and benthic communities in the region (Søreide et al., 2013). The motivation of

48 understanding such implications and forecasting development of high-latitude oceans in a  
49 warming climate implies paleo-reconstruction of sea ice conditions and associated responses  
50 of sympagic and pelagic biota over longer timescales.

51 Such paleo reconstructions can potentially be obtained through the analysis of proxy  
52 measures of sympagic and pelagic primary production in sedimentary records whose  
53 temporal coverage includes significant shifts in oceanographic and sea ice conditions. Sea ice  
54 reconstructions traditionally involve analysis of census data and isotopic composition of  
55 calcareous and siliceous microfossils, including foraminifer tests, dinocysts and diatom  
56 frustules (de Vernal et al., 2013, and references therein). However, microfossils are  
57 susceptible to carbonate and silicate dissolution in corrosive waters formed, for example, via  
58 brine rejection during ice formation (Zamelczyk et al., 2014). Such challenges may  
59 potentially be circumvented via analysis of certain geochemical lipid biomarkers, such as  
60 highly-branched isoprenoids (HBIs; Belt and Müller, 2013; Belt, 2018) and sterols (Volkman,  
61 1986), which are often more stable over geologically-significant timescales (e.g. Stein and  
62 Fahl, 2013) and can be source-specific (Belt and Müller, 2013; Belt, 2018). A suite of such  
63 biomarker proxies representing contrasting primary production sources (e.g. sympagic versus  
64 pelagic) may therefore be used to reconstruct environmental variability over temporal  
65 windows spanning significant climate shifts. For example, the LGM in the Barents Sea  
66 between ca. 26.5–19.0 cal kyr BP (Clark et al., 2009; Peltier and Fairbanks, 2006) and  
67 eventual collapse of the Barents Sea Ice Sheet (BSIS) between ca. 18.0–17.5 cal kyr BP  
68 (Bauch et al., 2001; Dokken and Jansen, 1999; Elverhøi et al., 1995; Knies et al., 2018) are  
69 relevant time intervals for investigating the interactions between AW inflow, Atlantic  
70 Meridional Overturning Circulation (AMOC), sea ice concentration, and primary  
71 productivity. Geochemical evidence suggests that the LGM and post-deglaciation intervals  
72 exhibited heavy seasonal sea ice and near ice-free conditions, respectively, and were

73 punctuated by the Heinrich Stadial 1 (HS1), when harsh glaciomarine conditions and  
74 weakened AW inflow prevented growth of biota (e.g. Jennings et al., 2018; Knies et al.,  
75 2018; Müller et al., 2009; Müller and Stein, 2014). Such contrasting conditions that  
76 characterised these time intervals, coupled with the direct interaction of AW inflow with both  
77 the maximum-extent BSIS and the adjacent sea ice margin, make the Late Weichselian  
78 Barents Sea key for elucidating the interactions between oceanographic conditions, the sea  
79 ice regime, and the associated interplay of sympagic and pelagic primary productivity. Such  
80 an investigation could also aid the understanding of potential consequences associated with  
81 the projected debuttressing of the contemporary West Antarctic Ice Sheet (WAIS) (Hulbe,  
82 2017), for which the Late Weichselian BSIS was previously suggested as a close paleo-  
83 analogue (Andreassen and Winsborrow, 2009; Bjarnadottir et al., 2014).

84 The focus of this study was, therefore, to reconstruct sea ice conditions and associated  
85 changes in primary productivity at the western Barents Sea continental slope throughout  
86 extreme climate shifts spanning ca. 25.8–15.4 cal kyr BP. To achieve this, we quantified a  
87 multivariate set of 10 geochemical biomarkers (**Table 1**) representing ice-algal and marine  
88 phytoplankton input (**Fig. 1**) in a marine sediment core (**Fig. 2b**) to assess the roles of ice  
89 cover and coastal polynya proximal to the BSIS in sustaining both sympagic and pelagic  
90 primary productivity from the LGM to the retreat of sea ice cover preceding the Bølling-  
91 Allerød (BA) interstadial. Downcore biomarker distributions were compared to those of  
92 proximal surface sediments to identify paleo-analogues of contemporary sea ice and  
93 productivity settings or, alternatively, determine whether certain intervals within the  
94 downcore record represent unique conditions not reproduced in the current climate.

95

## 96 **2. Biomarker background**

97 HBIs are unsaturated hydrocarbons produced exclusively by a relatively narrow range of  
98 marine and lacustrine diatoms (Belt and Müller, 2013; Belt, 2018). A C<sub>25</sub> HBI discovered in  
99 Canadian Arctic sea ice and labelled IP<sub>25</sub> (Belt et al., 2007) was confirmed as a seasonal sea  
100 ice proxy due to its accumulation during the spring diatom bloom in March–April (Brown et  
101 al., 2011) and Arctic sea ice diatom sources (*Pleurosigma* and *Haslea* spp.; Brown et al.,  
102 2014b), all of which also contribute to Barents Sea spring blooms (von Quillfeldt, 2000).  
103 Notably, at least certain productive sea-ice diatom species abundant in multi-year ice  
104 (Syvertsen, 1991; Boetius et al., 2013), such as *Melosira arctica*, do not produce IP<sub>25</sub> or any  
105 other HBIs. Accordingly, numerous analyses of surface sediments ( $n > 850$ ) spanning the  
106 Arctic Ocean showed near-ubiquitous presence of IP<sub>25</sub> in seasonally ice-covered locations,  
107 and either very low abundance or absence in regions of year-round open water or multi-year  
108 ice cover, such as that found in the central Arctic (Xiao et al., 2013). IP<sub>25</sub> has since been  
109 extensively used for reconstructing past sea ice variability throughout the Arctic Ocean and  
110 the Nordic Seas (Belt, 2018, and references therein). An HBI diene (HBI II; Table 1) is co-  
111 produced (Brown et al., 2014b) and usually highly correlated (e.g. Cabedo-Sanz et al., 2013;  
112 Xiao et al., 2013) with IP<sub>25</sub>. The latter is often combined with a marine phytoplankton  
113 biomarker (e.g. brassicasterol, dinosterol; Volkman, 1986) into the Phytoplankton–IP<sub>25</sub> index  
114 (PIP<sub>25</sub>; **Eq. 1** and **Fig. 1**) to obtain semi-quantitative descriptions of sea ice conditions (e.g.  
115 Müller et al., 2011; Stein et al., 2017; Xiao et al., 2015). More recently, the calculation of a  
116 P<sub>III</sub>IP<sub>25</sub> index using a tri-unsaturated HBI (HBI III; **Table 1** and **Fig. 1**) as the phytoplankton  
117 biomarker resulted in semi-quantitative spring sea ice concentration (SpSIC) estimates in the  
118 Barents Sea (Belt et al., 2015; Berben et al., 2017; Smik et al., 2016). Further, HBI III and its  
119 diastereoisomer (HBI IV; **Table 1** and **Fig. 1**) were recently detected in the pelagic diatom  
120 *Rhizosolenia setigera* near Western Svalbard (Belt et al., 2017). Indeed, *R. setigera* is likely  
121 the most cosmopolitan among identified producers of trienes III and IV (Belt et al., 2000;

122 Brown et al., 2014a), given its identification as one of most globally abundant diatoms  
123 (Leblanc et al., 2012) and the capacity of certain *Rhizosolenia* spp. for active buoyancy  
124 control (Joseph et al., 1997) and formation of macroscopic mats under nutrient-replete  
125 conditions (Yoder, 1994). Together with high correlation and clear enhancement of both  
126 biomarkers near the receding spring sea ice edge (Belt et al., 2015), this supports the use of  
127 HBIs III and IV as indicators of pelagic diatom productivity in the Barents Sea. Thus, the  
128 availability of a multivariate HBI biomarker set in Barents Sea surface sediments (IP<sub>25</sub>, HBIs  
129 II, III and IV; **Table 1** and **Fig. 1**) recently prompted the development of a classification tree  
130 (CT) model of HBI distributions (**Fig. 1**) in surface sediments as a viable method of  
131 categorising sea ice conditions over centennial to millennial timescales (Köseoğlu et al.,  
132 2018a, 2018b). These investigations showed clear enhancement of pelagic HBIs III and IV  
133 relative to sympagic IP<sub>25</sub> and HBI II in the productive Barents Sea MIZ, while the reverse  
134 was evident under heavy ice cover northeast off Svalbard. The database of HBI  
135 concentrations in Barents Sea surface sediments therefore provides an opportunity to  
136 determine whether, and to what extent, HBI distributions characteristic of different sea ice  
137 regimes in the modern Barents Sea are reproduced within the Late Weichselian sedimentary  
138 sequence.

139 To complement the HBI data, we also analysed several sterol lipids, which are ubiquitous  
140 components of eukaryotes (Volkman, 1986). In marine settings, the particular diversity of  
141 C<sub>27</sub>–C<sub>29</sub> sterols among microorganisms, including microalgae and plankton (Volkman, 2003),  
142 has facilitated their use as chemotaxonomic biomarkers of organic matter sources in paleo-  
143 environments, including high-latitude shelf seas (e.g. Belt et al., 2013; Knies, 2005). Despite  
144 this, few sterols are considered unambiguous biomarkers of specific algal groups as many  
145 classes of marine microorganisms contribute the same sterols to the sedimentary budget  
146 (Volkman, 1986). For instance, 24-methylcholesta-5,22*E*-dien-3β-ol (epibrassicasterol) and

147 24-methylcholesta-5,24(28)-dien-3 $\beta$ -ol (24-methylenecholesterol or chalinasterol) are often  
148 used as indicators of diatom primary production, despite the fact that the former is often not a  
149 major constituent of diatoms (Rampen et al., 2010) and is found in other clades of algae  
150 (Volkman, 1986; Volkman et al., 1999). Additionally, epibrassicasterol has been utilised as  
151 an indicator of pelagic phytoplankton productivity in ice-covered regions (e.g. Navarro-  
152 Rodriguez et al., 2013), in spite of its abundance in sea ice (Belt et al., 2013, 2018) and  
153 pennate diatoms (e.g. Rampen et al., 2010). Moreover, diatoms often produce C<sub>29</sub> sterols  
154 (Belt et al., 2013, 2018; Rampen et al., 2010), such as 24-ethylcholest-5-en-3 $\beta$ -ol ( $\beta$ -  
155 sitosterol) and 24-methylcholest-5-en-3 $\beta$ -ol (campesterol) traditionally associated with  
156 vascular plants (Huang and Meinschein, 1976), which makes distinguishing between marine  
157 and terrigenous organic matter in sediments challenging. Even 4-methyl C<sub>30</sub> sterols, such as  
158 4 $\alpha$ ,23,24-trimethyl-5 $\alpha$ -cholesta-22-en-3 $\beta$ -ol (dinosterol), traditionally considered to be  
159 exclusive to dinoflagellates (Boon et al., 1979) and more specific to marine productivity (e.g.  
160 Knies, 2005), have been detected in both sea ice (Nichols et al., 1990) and diatom cultures  
161 (*Navicula* spp.; Volkman et al., 1993). Such factors underline the need to consider more  
162 source-specific biomarkers, such as HBIs representative of sympagic and pelagic sources, in  
163 addition to sterols when decoupling ice-covered and open water conditions in paleo-records  
164 (Belt et al., 2015; Smik et al., 2016). Despite their wide distribution across different biota,  
165 sterols remain useful indicators of both marine and terrigenous sedimentation, as well as  
166 general marine primary productivity, provided such inferences are drawn from a multivariate  
167 sterol record further contextualised using other proxy data (Volkman, 1986) or more source-  
168 specific biomarkers (such as IP<sub>25</sub> and other HBIs). Here, we focus on downcore relative  
169 abundance distributions of a multivariate sterol set (**Table 1**), and compare these with surface  
170 sediment sterol distributions representative of contrasting sea ice (and productivity)  
171 conditions in the modern Barents and Norwegian seas.



### 172 **3. Modern regional setting**

173 The warm and saline NAC carries a significant amount of heat into the seasonally ice-  
174 covered Barents Sea (Smedsrud et al., 2010), which continues along the western and northern  
175 continental margins as the largely sub-surface West Spitsbergen Current (WSC), while the  
176 North Cape Current (NCaC) branches out towards Novaya Zemlya and the central Barents  
177 Sea (**Fig. 2a**). Fresher coastal water (CW) from the Baltic Sea flows inshore of the NAC with  
178 the Norwegian Coastal Current (NCC). Southwest-bound Arctic Water (ArW) enters the  
179 Barents Sea with the East Spitsbergen and Persey Currents (ESC and PC, respectively),  
180 forming a fresher and colder surface layer around Svalbard (Loeng et al., 1991; Smedsrud et  
181 al., 2013). Effective turbulent mixing of warm AW towards the surface during the winter  
182 (October–March), when over half of the Barents Sea may be ice-covered (Fetterer et al.,  
183 2017), facilitates selective thinning of the ice cover along the path of inflowing AW and  
184 keeps a significant portion of western and northern Svalbard shelves ice-free (Ivanov et al.,  
185 2012). Ice recession towards the northern shelf break occurs throughout the insolation-  
186 triggered melt season during spring and summer (April–September). The interplay of  
187 freshwater input and increased light penetration due to melting sea ice stabilises free-floating  
188 phytoplankton and AW-carried nutrients within the euphotic zone, developing extensive, but  
189 short-lived primary productivity blooms in the MIZ around the retreating ice margin  
190 (Wassmann et al., 1999, 2006). The resulting algal biomass fuels energy transfer to higher  
191 trophic levels (e.g. zooplankton) and eventually reaches the ocean floor, helping sustain  
192 benthic life (Søreide et al., 2013). Further, the development of leads and polynyas coupled  
193 with weak stratification from AW-induced melting of sea ice may trigger under-ice pelagic  
194 blooms even prior to the melt season (Assmy et al., 2017; Strass and Nöthig, 1996).  
195 Sympagic blooms of ice algae develop up to two months prior to seasonal ice retreat as they  
196 do not rely on stratification and are triggered by increasing solar insolation in March

197 (Signorini and McClain, 2009). Increasing temperature and volume of inflowing AW has  
198 already increased primary productivity by ca. 30% since the 1990’s by reducing sea ice  
199 extent and expanding that of the MIZ, prolonging and hastening the bloom season (Arrigo  
200 and van Dijken, 2015; Strong and Rigor, 2013). Nonetheless, average phytoplankton biomass  
201 at peak bloom is decreasing due to accelerated zooplankton grazing in a warming Barents Sea  
202 (Kvile et al., 2016).

## 203 **4. Materials and methods**

### 204 *4.1 Sediment material*

205 The 1384 cm long GS14-190-PC01 piston core (71.475° N, 16.165°E; 949 m water  
206 depth), hereafter GS14, was recovered aboard the RV “G.O. Sars” on June 3<sup>rd</sup>, 2014 at the  
207 southwestern Barents Sea slope (**Fig. 2b**). A detailed core chronology for the upper 694 cm  
208 of the core is available from Knies et al. (2018) and is based on six accelerator mass  
209 spectrometry (AMS) <sup>14</sup>C measurements of planktonic and benthic microfossils, including  
210 foraminifera and *Thyasira* spp. bivalves. This is supported by an additional six radiocarbon  
211 dates transferred to a common depth scale from the gravity core 33-GC08 (hereafter GC08)  
212 sampled from the same location as core GS14 using five tie-points inferred from XRF Ca  
213 records. The radiocarbon ages were calibrated to calendar ages (cal kyr BP) using the  
214 Marine13 curve (Reimer et al., 2013), and no local reservoir age correction was applied  
215 ( $\Delta R=0$ ). Finally, Bayesian accumulation age-depth modelling (Bacon 2.2) was used to create  
216 the age model (Blaauw and Christen, 2011).

217 In this study, core depths of 11.5–523 cm (ca. 25.8–15.4 cal kyr BP) were investigated,  
218 with the age model supported by four and five <sup>14</sup>C AMS dates from cores GS14 and GC08,  
219 respectively (**Fig. 3–5**). A total of 131 one centimetre sediment horizons were sampled with  
220 10 mL cut-barrel plastic syringes, freeze-dried for 24–48 hours (1  $\mu$ bar; -80°C) and frozen in  
221 plastic bags at -20°C to preserve sample integrity prior to lipid extraction. While HBIs were

222 extracted and analysed for all 131 horizons, sterol analysis was carried out separately using  
223 the same depth interval, but a lower sampling frequency (87 horizons) due to limited  
224 availability of material. Sedimentation rates ranged from 12.4 cm kyr<sup>-1</sup> to 148.9 cm kyr<sup>-1</sup>  
225 (Knies et al., 2018), resulting in a mean temporal resolution between analysed horizons of 81  
226 ± 62 yr for HBIs and 115 ± 74 yr for sterols.

227 To supplement the GS14 downcore analysis, Barents and Norwegian Sea surface  
228 sediments ( $n = 144$ ; **Fig. 2b**) representing contrasting contemporary sea ice conditions, and  
229 for a larger set of which ( $n = 198$ ) HBI data was recently reported (Köseoğlu et al., 2018a),  
230 were re-extracted to obtain sterol distributions. Barents and Norwegian Seas were delineated  
231 using the International Council for the Exploration of the Sea (ICES) Ecoregions shapefiles  
232 (<http://gis.ices.dk/geonetwork/srv/metadata/4745e824-a612-4a1f-bc56-b540772166eb>).  
233 Surface and downcore absolute biomarker concentrations (ng g<sup>-1</sup> dry sed.), downcore  
234 calibrated horizon ages (cal yr BP), and associated depths (cm) are available from Mendeley  
235 Data (doi: <https://doi.org/10.17632/jx97c9nv3k.1>).

#### 236 *4.2 Lipid extraction and analysis*

237 HBIs were extracted according to the methods of Belt et al. (2012), with certain  
238 modifications. Briefly, an internal standard (9-octylheptadec-8-ene; 0.1 µg) was added to  
239 freeze-dried and homogenized sediment (ca. 2 g), and the total organic extract (TOE) was  
240 obtained following repeated sonication and centrifugation with a DCM : MeOH solvent  
241 mixture (2:1 v/v; 3 × 2 mL). The solvent was evaporated to dryness at 25°C under N<sub>2</sub>, and the  
242 TOE was re-suspended in hexane (ca. 1 mL). Elemental sulphur was removed by repeatedly  
243 shaking the sample with ca. 1 mL of tetrabutylammonium sulphite reagent (3.39 g in 100 mL  
244 of milliQ water saturated with 25 g of anhydrous sodium sulphite) and 2 mL of isopropanol,  
245 followed by decanting the supernatant hexane layer into a separate vial (4 × 1 mL). The  
246 partially purified extracts were evaporated to dryness (N<sub>2</sub>; 25°C), re-suspended in hexane (1

247 mL) and transferred onto hexane-conditioned chromatography columns ( $3 \times 1$  mL of hexane;  
248 ca. 1 g of 60–200  $\mu\text{m}$  silica). A hydrocarbon fraction containing HBIs was eluted via hexane  
249 (ca. 7 mL), which was evaporated to dryness under  $\text{N}_2$ , re-suspended in hexane (ca. 300  $\mu\text{L}$ )  
250 and further fractionated into saturated and unsaturated hydrocarbons on Ag-ion  
251 chromatography columns (Discovery® Ag-Ion; ca. 0.1 g) by successive elution with hexane  
252 (ca. 1 mL) and acetone (ca. 2 mL), respectively. The HBI-containing acetone fractions were  
253 evaporated to dryness and transferred to gas chromatographic (GC) vials (300  $\mu\text{L}$ ) in hexane.

254 Sterols were extracted following internal standard addition to sediments ( $5\alpha$ -androstan-  
255  $3\beta$ -ol; 0.1  $\mu\text{g}$ ) and saponification with 5% (m/v) methanolic potassium hydroxide (KOH; 9:1  
256 v/v MeOH : milliQ water; 70°C for 60 min). Impurities were partially removed by elution via  
257 7:3 DCM : hexane (6 mL) on silica chromatography columns (ca. 1 g of hexane-conditioned  
258 silica) and sterols were subsequently collected using 4:1 (v/v) hexane : methyl acetate (ca. 7  
259 mL). Following  $\text{N}_2$  blowdown (25°C), sterol-containing fractions were derivatised with N,O-  
260 bis(trimethylsilyl)trifluoroacetamide (BSTFA; 100  $\mu\text{L}$ ; 70°C for 60 min) and transferred to  
261 GC vials (300  $\mu\text{L}$ ) in DCM.

262 Analysis of HBIs and sterols was carried out via gas chromatography–mass spectrometry  
263 (GC–MS) using established methods (Belt et al., 2012, 2013) with an Agilent 7890 gas  
264 chromatograph equipped with the HP<sub>5MS</sub> fused-silica column (30 m; 0.25 $\mu\text{m}$  film thickness;  
265 0.25 mm internal diameter) coupled to an Agilent 5975 series mass spectrometric detector.  
266 All biomarkers were identified in total ion current (TIC) mode by comparison of peak  
267 retention indices ( $\text{RI}_{\text{HP5-MS}} = 2081$  for IP<sub>25</sub>, 2082 for HBI II, 2044 for HBI III and 2091 for  
268 HBI IV) (Belt, 2018, and references therein) and mass spectra to authentic standards and, in  
269 the case of sterols, to published data (Boon et al., 1979; Combaut, 1986). Quantification was  
270 carried out in single ion monitoring (SIM) and TIC modes for HBIs and sterols, respectively.  
271 The resulting peak areas were corrected according to internal standard responses,

272 instrumental response factors (RFs), and sediment mass. Re-calibration of RF values allowed  
273 us to quantify additional sterols, updating and extending the GS14 dinosterol record of Knies  
274 et al. (2018).

#### 275 4.3 Statistical analysis

276 We used divisive changepoint analysis from the R package ECP (James and  
277 Matteson, 2013; R Core Team, 2018) on individual biomarker timeseries to identify  
278 significant shifts ( $p = 0.005$ ) in biomarker profiles within the investigated temporal window  
279 (**Fig. 3** and **4**).  $P_{III}IP_{25}$  values for each horizon were derived using a regional concentration  
280 balance factor for the Barents Sea ( $c$ -factor = 0.63; **Eq. 1**) with non-zero absolute  
281 concentrations (ng g<sup>-1</sup> dry sed., shown in square brackets in all equations) of  $IP_{25}$  and HBI III.  
282 Semi-quantitative estimates of spring sea ice concentrations (SpSIC, %; April–June) were  
283 subsequently calculated using the Barents Sea SpSIC– $P_{III}IP_{25}$  calibration (**Eq. 2**) of Smik et  
284 al. (2016). The occurrence of summer sea ice (SuSIC, %; July–September) was tentatively  
285 inferred using a  $P_{III}IP_{25}$ -based SpSIC threshold of ca. 70% ( $P_{III}IP_{25} > 0.8$ ; Smik et al., 2016).  
286 Semi-quantitative SpSIC estimates were supplemented with categorical classification of each  
287 horizon into marginal (near ice-free waters; <10% SpSIC), intermediate (MIZ conditions with  
288 ca. 10–50% SpSIC), and extensive (heavy ice cover characteristic of north-eastern Svalbard;  
289 >50% SpSIC) sea ice conditions using the multivariate CT model of Köseoğlu et al. (2018a).  
290 CT predictions were derived from percentage contributions of each HBI ( $IP_{25}$ , HBIs II, III  
291 and IV) to the total (**Eq. 3**) and were not carried out for samples where no HBIs were  
292 detected.

$$293 \quad P_{III}IP_{25} = \frac{[IP_{25}]}{([IP_{25}] + [III] \times 0.63)} \#(1)$$

$$294 \quad SpSIC (\%) = \frac{(P_{III}IP_{25} - 0.0692)}{0.0107} \#(2)$$

$$HBI (\%) = \frac{[HBI]}{\sum([IP_{25}], [II], [III], [IV])} \times 100 \#(3)$$

In addition to examining downcore profiles (**Fig. 3** and **4**), the absolute concentration (ng g<sup>-1</sup> sed.) and compositional distributions (%; **Eq. 3**) of all biomarkers were examined to identify significant distributional shifts and further assess the general variability of each biomarker throughout the record (**Fig. 6**). Relative distributional changes were additionally compared to modern assemblages observed in Barents Sea surface sediments characterised by contrasting overlying SpSIC and annual open water duration (**Fig. 7**; Belt et al., 2015; Köseoğlu et al., 2018a). The SpSIC database represented April–June SIC spanning the 1988–2007 period, previously used to build the CT model (Köseoğlu et al., 2018a).

## 5. Results

### 5.1 Biomarker temporal profiles and distributions in core GS14

Following an initial increase from ca. 25.8 cal kyr BP, IP<sub>25</sub> and HBI II concentrations reached their respective peak values of 7.5 and 43.7 ng g<sup>-1</sup> by ca. 23.7 cal kyr BP (**Fig. 3a**). This coincided with a similar increase of all six sterols during the same period, which culminated between 24.7–23.7 cal kyr BP. Both sympagic HBIs (i.e. IP<sub>25</sub> and HBI II) and all sterols remained at relatively high, but variable concentrations until 18.0 cal kyr BP (**Fig. 3, 4, 6b**), while concentrations of HBI trienes III and IV remained low (0.7 ± 0.5 ng g<sup>-1</sup> and 0.6 ± 0.5 ng g<sup>-1</sup>, respectively; **Fig. 6a**). Accordingly, the HBI assemblage was dominated by IP<sub>25</sub> and HBI II, with respective percentage contributions of 13 ± 2% and 80 ± 5%, while HBIs III and IV were only minor constituents throughout the 25.8–18.0 cal kyr BP interval (**Fig. 7a**). This was accompanied by average P<sub>III</sub>IP<sub>25</sub> SpSIC estimates of 74 ± 9% and consistently extensive sea ice conditions predicted by the CT model (**Fig. 3c**). However, SpSIC values < 60% with sporadic summer sea ice occurrence ca. 19.2–18.7 cal kyr BP and CT predictions

318 of intermediate (MIZ-like) sea ice conditions accompanied slight, but abrupt decreases in  
319 sympagic HBI and sterol concentrations, with the more distinct changes also highlighted by  
320 changepoint analysis (**Fig. 3a, 4**). Finally, examination of the sterol distribution revealed the  
321 prevalence of  $\beta$ -sitosterol ( $23 \pm 6\%$ ) and epibrassicasterol ( $23 \pm 5\%$ ), with moderate  
322 cholesterol ( $18 \pm 3\%$ ) and chalinasterol ( $19 \pm 4\%$ ), as well as relatively minor campesterol  
323 ( $10 \pm 2\%$ ) and dinosterol ( $7 \pm 2\%$ ) until 18.0 cal kyr BP (**Fig. 7b**).

324 Precipitous and abrupt decreases of all biomarker concentrations characterised the  
325 18.0–16.3 cal kyr BP interval and were detected by changepoint analysis (**Fig. 3 and 4**).  
326 Thus, averaged HBI and sterol concentrations ranged from 0.2–2.2 ng g<sup>-1</sup> and 57–182 ng g<sup>-1</sup>,  
327 respectively (**Fig. 6**) despite brief increases in IP<sub>25</sub> and HBI II to ca. 2.9 ng g<sup>-1</sup> and 10.9 ng g<sup>-1</sup>,  
328 respectively (**Fig. 3a**). The interval was also characterised by the highest SpSIC estimates (ca.  
329 90%), summer sea ice occurrence, and CT predictions of extensive sea ice conditions (**Fig.**  
330 **3c**). Biomarker percentage distributions remained similar to those observed during the 25.8–  
331 18.0 cal kyr BP interval, albeit with more variability and, in case of sterols, prevalence of  $\beta$ -  
332 sitosterol alongside cholesterol (**Fig. 7**).

333 An abrupt increase of biomarker concentrations, with significant shifts in percentage  
334 distributions and sea ice conditions are evident after ca. 16.3 cal kyr BP. P<sub>III</sub>IP<sub>25</sub>-derived  
335 SpSIC values dropped to a minimum of  $4 \pm 11\%$ , and the CT model consistently predicted  
336 marginal ice cover or open water conditions (**Fig. 3c**). HBIs III and IV increased by ca. 2  
337 orders of magnitude to the highest values observed throughout the record ( $29.1 \pm 24.4$  ng g<sup>-1</sup>  
338 and  $48.2 \pm 41.8$  ng g<sup>-1</sup>, respectively), while IP<sub>25</sub> and HBI II remained at respective minimum  
339 values of  $0.6 \pm 0.3$  ng g<sup>-1</sup> and  $3.2 \pm 1.5$  ng g<sup>-1</sup> (**Fig. 6a**). Consequently, HBIs III and IV  
340 dominated the HBI distribution during this period, with relative abundances of  $33 \pm 8\%$  and  
341  $53 \pm 14\%$ , respectively (**Fig. 7a**). The sterols experienced a similar, but less pronounced  
342 resurgence, with most exhibiting concentrations similar to those observed prior to 18.0 cal

343 kyr BP (**Fig. 4** and **6c**). The greatest concentration increase was observed for cholesterol,  
344 which reached a mean value of ca.  $2957 \pm 930 \text{ ng g}^{-1}$  (**Fig. 4d** and **6b**), a factor ca. three  
345 higher than the 25.8–18.0 cal kyr BP average ( $904 \pm 302 \text{ ng g}^{-1}$ ). Cholesterol therefore  
346 dominated the sterol assemblage with  $36 \pm 1\%$  relative abundance instead of epibrassicasterol  
347 and  $\beta$ -sitosterol, which contributed  $22 \pm 2\%$  and  $12 \pm 1\%$ , respectively. Consistently with the  
348 remained of the record, chalinasterol abundance ( $21 \pm 2\%$ ) was comparable to that of  
349 epibrassicasterol, while campesterol ( $6 \pm 1\%$ ) and dinosterol ( $5 \pm 1\%$ ) remained minor  
350 components (**Fig. 7b**).

### 351 5.2 Surface sediment biomarker distributions

352 HBI distributions in surface sediments (**Fig. 7a**) characterised by extensive sea ice cover  
353 ( $>50\%$  SpSIC;  $n = 23$ ) were characterised by a distinct prevalence of IP<sub>25</sub> and HBI II within  
354 the assemblage ( $23 \pm 4\%$  and  $73 \pm 4\%$ , respectively), with minor contribution from HBIs III  
355 and IV ( $2 \pm 2\%$  and  $2 \pm 1\%$ , respectively). The contribution of sympagic biomarkers was  
356 lower and more variable in the central Barents Sea MIZ ( $\leq 50\%$  SpSIC;  $n = 36$ ), with  
357 respective percentage abundances of  $9 \pm 6\%$  and  $42 \pm 22\%$  observed for IP<sub>25</sub> and HBI II.  
358 Accordingly, pelagic HBIs III and IV comprised a higher  $31 \pm 19\%$  and  $18 \pm 9\%$  of the  
359 assemblage, respectively. Ice-free Barents ( $n = 119$ ) and Norwegian Sea ( $n = 20$ ) locations  
360 were characterised almost entirely by HBIs III ( $56 \pm 14\%$  and  $62 \pm 10\%$ , respectively) and IV  
361 ( $42 \pm 3\%$  and  $38 \pm 10\%$ , respectively), while only 4 locations close to the annual maximum  
362 sea ice edge in the Barents Sea exhibited non-zero IP<sub>25</sub> and HBI II.

363 Sterol distributions were mainly defined by the variability of  $\beta$ -sitosterol,  
364 epibrassicasterol, and cholesterol in all surface sediments. Conversely, chalinasterol,  
365 campesterol, and dinosterol remained minor components (**Fig. 7b**). Extensively ice-covered  
366 locations showed a prevalence of  $\beta$ -sitosterol ( $25 \pm 5\%$ ), with comparable, but slightly lower  
367 abundances of cholesterol ( $21 \pm 4\%$ ) and epibrassicasterol ( $22 \pm 5\%$ ). Conversely, MIZ and



368 ice-free Barents Sea locations ( $n = 26$  and  $n = 89$ , respectively) exhibited decreased  $\beta$ -  
369 sitosterol abundance ( $14\text{--}17 \pm 3\text{--}5\%$ ), with epibrassicasterol ( $32\text{--}37 \pm 5\text{--}7\%$ ) and cholesterol  
370 ( $28\text{--}29 \pm 5\text{--}11\%$ ) comprising most of the assemblage. Norwegian Sea sediments ( $n = 18$ )  
371 showed consistent prevalence of cholesterol ( $32 \pm 3\%$ ), with similar epibrassicasterol content  
372 ( $28 \pm 2\%$ ) and lower  $\beta$ -sitosterol ( $22 \pm 2\%$ ).

## 373 **6. Discussion**

374 Biomarker data presented herein allow us to reconstruct seasonal sea ice and productivity  
375 variability during climatically contrasting conditions encompassing both growth and decay of  
376 the BSIS. To facilitate paleo-interpretation and contextualisation, we delineate the GS14  
377 record into discrete time slices, and include a rationale for these in section 6.1. Paleo-  
378 interpretation for each time slice is then provided in section 6.2–6.4.

### 379 *6.1 Identification of time slices for core GS14*

380 Our record is delineated into three main time slices: (i) The LGM and initial shelf edge  
381 deglaciation (SEDG) following ice sheet destabilisation (ca. 26.0–18.0 cal kyr BP); (ii) HS1  
382 following final BSIS collapse (ca. 18.0–16.3 cal kyr BP); (iii) The retreat of sea ice cover (ca.  
383 16.3 cal kyr BP) preceding AMOC recovery and the onset of the Bølling-Allerød (BA)  
384 interstadial. The time slice definitions are based on a combination of clear changes of  
385 biomarker concentrations (**Fig. 3** and **4**) and percentage distributions (**Fig. 6** and **7**), and the  
386 agreement between the timing of these changes in core GS14 and paleoceanographic shifts  
387 previously identified in the Barents Sea and other Arctic regions. The definitions of the LGM,  
388 SEDG, and the HS1 onset are based on the study of Knies et al. (2018), who infer a BSIS  
389 advance to its LGM shelf-edge position at ca. 26.0 cal kyr BP from increased sedimentation  
390 rates and IRD deposition. This also agrees with previous global definitions of Peltier and  
391 Fairbanks (2006) and Clark et al. (2009), who propose LGM onset at 26 cal kyr BP and 26.5

392 cal kyr BP, respectively. An IRD spike marks the SEDG at ca. 19.5 cal kyr BP, while final  
393 BSIS collapse between ca. 18.0–17.7 cal kyr BP is associated with a rapid, meltwater-  
394 induced planktic  $\delta^{18}\text{O}$  depletion signifying the beginning of HS1 (**Fig. 5**) (Knies et al., 2018)  
395 and is also observed in various records from the Barents Sea, the Nordic Seas (Elverhøi et al.,  
396 1995; Dokken and Jansen, 1999; Bauch et al., 2001; Weinelt et al., 2003; Müller and Stein,  
397 2014), and other Arctic seas (e.g. Jennings et al., 2018). In our study, we additionally note the  
398 abrupt decreases of all biomarker concentrations by 18.0 cal kyr BP (**Fig. 3** and **4**), and use  
399 this date as the beginning of the HS1. Finally, the post-HS1 deglacial period is defined by  
400 significant and contemporaneous changes in biomarker concentrations (**Fig. 3b, 3c** and **4**) and  
401 relative abundances (**Fig. 6** and **7**) in core GS14 at ca. 16.3 cal kyr BP.

#### 402 *6.2 BSIS-adjacent productive ice margin during the LGM and SEDG (26–18 cal kyr BP)*

403 Based on high dinosterol and  $\text{IP}_{25}$  concentrations, Knies et al. (2018) previously  
404 provided direct evidence of highly-productive coastal polynyas at the GS14 site during the  
405 otherwise harsh glacial conditions of the LGM. Such polynyas initiated by AW upwelling  
406 and maintained by powerful katabatic winds from the BSIS were previously suggested to  
407 significantly influence Late Weichselian sea ice and primary productivity regimes across the  
408 western (Müller et al., 2009; Müller and Stein, 2014; Xiao et al., 2015) and northern Barents  
409 Sea margins (Chauhan et al., 2016; Knies et al., 1998, 2018; Nørgaard-Pedersen et al., 2003).  
410 Our findings of abundant sympagic biomarkers ( $\text{IP}_{25}$  and II; **Fig. 3a**) with presence of pelagic  
411 HBIs III and IV (**Fig. 3b**) and high sterol concentrations (**Fig. 4**) support the existence of  
412 extensive, but seasonal sea ice (**Fig. 3c**), high overall productivity, and vertical stabilisation  
413 necessary to maintain pelagic spring and summer blooms at the GS14 site (e.g. Falk-Petersen  
414 et al., 2000; Signorini and McClain, 2009; Wassmann et al., 1999). This is further  
415 corroborated by the similarity of both the overall HBI and sterol assemblages in our record  
416 during the LGM and SEDG to that of northern and north-eastern Svalbard (**Fig. 7**) – an ice-

417 covered region characterised by seasonally open waters during the summer (Fetterer et al.,  
418 2017; Köseoğlu et al., 2018a, 2018b; Vare et al., 2010), as well as WSC-mediated winter  
419 polynya (Ivanov et al., 2012) and a high overall lead fraction (Willmes and Heinemann,  
420 2016) facilitating light penetration and development of under-ice pelagic blooms (Assmy et  
421 al., 2017; Strass and Nöthig, 1996). Moreover, average LGM and SEDG concentrations of  
422 pelagic HBIs III and IV ( $0.7 \text{ ng g}^{-1}$  and  $0.6 \text{ ng g}^{-1}$ , respectively) and sterols ( $0.37\text{--}1.22 \text{ } \mu\text{g g}^{-1}$ )  
423 in our record (**Fig. 6**) are also similar to those we observe in surface sediments north and  
424 north-east off Svalbard ( $0.5\text{--}0.6 \text{ ng g}^{-1}$  and  $0.63\text{--}2.67 \text{ } \mu\text{g g}^{-1}$  for HBIs and sterols,  
425 respectively). Thus, we confirm the incidence of coastal polynya at the GS14 site throughout  
426 26–18 cal kyr BP, which is also potentially associated with previously inferred sub-surface  
427 AW inflow in the Nordic Seas throughout ca. 27–22.5 cal kyr BP, at least (Chauhan et al.,  
428 2016; Dokken and Hald, 1996; Hebbeln et al. 1994; Knies et al., 1999; Nørgaard-Pedersen et  
429 al., 2003; Rasmussen et al., 2007; Rørvik et al., 2013; Vogt et al., 2001). Additionally,  
430 several investigations report high primary productivity with seasonally open waters evident  
431 from coevally high pelagic and sympagic biomarker concentrations along western Svalbard,  
432 Yermak Plateau (e.g. Kremer et al., 2018a, 2018b; Müller et al., 2009; Müller and Stein,  
433 2014; Rasmussen et al., 2007) and other Arctic regions (Stein et al., 2017), presence of  
434 temperate benthic foraminifera west and north off Svalbard (Chauhan et al., 2016), and  
435 decreasing planktonic foraminiferal and IRD abundances from the Fram Strait towards the  
436 central Arctic Ocean (Nørgaard-Pedersen et al., 2003).

437 The insolation-induced BSIS destabilisation at the GS14 site began at ca. 19.5 cal kyr  
438 BP (Knies et al. 2018), as indicated by increased IRD input; surface meltwater influence was  
439 likely absent or limited at this time, as no planktic  $\delta^{18}\text{O}$  depletions were observed (**Fig. 5**).  
440 High IRD input could have diluted biogenic sedimentation, resulting in the slightly decreased  
441 sympagic (e.g. IP<sub>25</sub>) and pelagic (sterols) primary productivity at the core site (**Fig. 3a–b, 4**).

442 Nonetheless, seasonal sea ice conditions that characterised the earlier LGM (26.0–19.7 cal  
443 kyr BP) persisted, with frequent summer sea ice occurrence (**Fig. 3c**).

### 444 6.3 Productivity termination during Heinrich Stadial HS1 (18.0–16.3 cal kyr BP)

445 Precipitous decreases of all biomarker concentrations to minimum values observed  
446 throughout the record (**Fig. 3** and **4**) and maximum P<sub>III</sub>IP<sub>25</sub>-derived SpSIC with extensive sea  
447 ice conditions predicted by the CT model (**Fig. 3c**) support the presence of closed perennial  
448 sea ice cover with near-zero primary productivity at the core site between ca. 18–16.3 cal kyr  
449 BP (Knies et al., 2018). While a brief increase in sympagic HBIs to late LGM levels at 17.2  
450 cal kyr BP potentially indicates sufficient thinning of sea ice cover to initiate photosynthesis  
451 during the summer (**Fig. 3a**), the overall onset of harsh conditions agrees with the widespread  
452 collapse of NH ice sheets at ca. 17.5 cal kyr BP following continued increases of summer  
453 insolation and sea level (Yokoyama et al., 2000; Clark et al., 2009; Shakun et al., 2012),  
454 strong ice stream activity (Winsborrow et al., 2010) and AW-induced weathering of the BSIS  
455 grounding line (Hormes et al., 2013). Contemporaneous massive meltwater discharges from  
456 icebergs are evidenced between ca. 17.7–16.9 cal kyr BP by depleted planktic  $\delta^{18}\text{O}$  and  
457 dominance of *N. pachyderma* (sin.) across the Norwegian Sea (Hoff et al., 2016; Rasmussen  
458 and Thomsen, 2008; Thornalley et al., 2015), southwestern Barents Sea (Rasmussen et al.,  
459 2007) and Svalbard (Chauhan et al., 2016; Jessen et al., 2010; Koç et al., 2002). Accordingly,  
460 decreased planktic  $\delta^{18}\text{O}$  values observed in the GS14 record after ca. 18.0 cal kyr BP (**Fig. 5**)  
461 were previously attributed to meltwater-induced cooling and freshening of surface waters due  
462 to BSIS collapse (Knies et al., 2018), promoting stratification and sea ice re-expansion in the  
463 Barents Sea. Meltwater influence hampered the AMOC (McManus et al., 2004; Ritz et al.,  
464 2013), causing a reduction in NAC-bound AW inflow evident from depleted benthic  $\delta^{18}\text{O}$   
465 values across the Nordic Seas (Bauch et al., 2001; Knies et al., 2001; Rasmussen and  
466 Thomsen, 2008). Thus, our findings support the conclusions of Knies et al. (2018) that the

467 combined influence of cold, low-salinity surface waters, a strongly stratified water column,  
468 and a hindered AW inflow into the Barents Sea following BSIS disintegration facilitated  
469 perennial sea ice formation and limited the volume and upwelling of deep nutrient-rich  
470 waters to the photic zone (**Fig. 8b**). We argue that insufficient nutrient replenishment  
471 combined with reduced light penetration through thick multi-year ice following the closing of  
472 coastal polynya potentially caused a collapse of microalgal stocks – a scenario previously  
473 shown by modelling simulations (Schmittner, 2005) that likely resulted in near-zero  
474 biomarker concentrations in our dataset from ca. 18.0–16.3 cal kyr BP (**Fig. 3, 4 and 6**).  
475 Indeed, similarly to the LGM, the relative distributions of HBIs (**Fig. 7a**) remain consistent  
476 with modern assemblages indicative of extensive sea ice conditions North-East off Svalbard  
477 (Köseoğlu et al., 2018a), which suggests that primary productivity was still controlled by sea  
478 ice. The sterol distribution, however, slightly deviates from that of the north-eastern Svalbard  
479 surface sediments (**Fig. 7b**) due to dominance of cholesterol alongside  $\beta$ -sitosterol. The  
480 inhospitable conditions of thick ice cover during the HS1 likely reduced algal biodiversity – a  
481 trend observed at higher Arctic latitudes today (Falk-Petersen et al., 1998; Henderson et al.,  
482 1998). Thus, the change in sterol distribution probably reflects a shift in the algal assemblage,  
483 especially given their ubiquity (Belt et al., 2013; Belt, 2018; Volkman, 2003). For instance,  
484 spring blooms in the Central Arctic ocean are often dominated by the cold-adapted diatom *M.*  
485 *arctica* (Syvertsen, 1991; Boetius et al., 2013), while at least some *Melosirales* produce both  
486  $\beta$ -sitosterol and cholesterol as the two major sterols (Rampen et al., 2010). In any case, the  
487 presence of perennial ice overlying the study area is further substantiated by the absence of  
488 significant IRD input (**Fig. 5**) and low sedimentation rates of ca. 12 cm kyr<sup>-1</sup> throughout the  
489 18.0–16.3 cal kyr BP interval in core GS14 (Knies et al., 2018).

490 *6.4 Ice retreat and intense productivity after 16.3 cal kyr BP*

491           Considerable increases in absolute concentrations of pelagic HBIs (**Fig. 3b** and **6a**) and  
492 sterols (**Fig. 4** and **6b**), accompanied by shifts in respective percentage distributions (**Fig. 7**)  
493 indicated a general climate amelioration with enhanced primary productivity and SpSIC <  
494 10% (**Fig. 3c**) after 16.3 cal kyr BP. Low concentrations of sympagic IP<sub>25</sub> and HBI II  
495 therefore shift the relative distribution to favour HBIs III and IV, which agrees with the  
496 modern HBI assemblage representing nearly ice-free settings with prolonged open water  
497 duration (**Fig. 7a**). Together with decreased P<sub>III</sub>IP<sub>25</sub>-derived SpSIC with CT predictions of  
498 marginal sea ice conditions (**Fig. 3c**; Köseoğlu et al., 2018a; Smik et al., 2016) and an abrupt  
499 increase of IRD at ca. 16.3 cal kyr BP (Knies et al., 2018), our evidence suggests limited  
500 annual sea ice cover (<10% SpSIC) and sympagic productivity (e.g. Belt et al., 2007; Belt  
501 and Müller, 2013; Brown et al., 2014b), with favourable conditions for pelagic blooms and  
502 the GS14 site being close to the annual maximum ice edge (Belt et al., 2015, 2017). Rapid  
503 sea ice and areal BSIS retreat is also apparent throughout the Barents Sea continental shelves  
504 between ca. 16.5–15.5 cal kyr BP, inferred from the abundance of opportunistic benthic  
505 foraminifera characteristic of productive waters (Chauhan et al., 2016), increased IRD  
506 deposition and meltwater release from sea ice and icebergs (e.g. Chauhan et al., 2016; Jessen  
507 et al., 2010; Knies and Stein, 1998; Vogt et al., 2001), as well as high biomarker  
508 concentrations (e.g. Müller and Stein, 2014) around Svalbard. Since ca. 17.5 cal kyr BP, a  
509 gradual increase in insolation (Berger and Loutre, 1991; Laskar et al., 2004) probably  
510 contributed to the areal retreat of the BSIS and reinvigoration of the AMOC at ca. 16 cal kyr  
511 BP (McManus et al., 2004; Ritz et al., 2013) following a reduction of glacial meltwater flux  
512 also evident from modelling studies (e.g. Liu et al., 2009). The deglaciation was potentially  
513 also triggered by progressive aridification of the Arctic during HS1 due to limited ocean-  
514 atmosphere heat and moisture exchange through perennial ice cover (e.g. Hormes et al.,  
515 2013), which reduced the moisture supply for ice sheet build-up. Ice streams retreated from

516 the western Barents Sea margin due to a shifting BSIS mass balance after ca. 17 cal kyr BP  
517 (Winsborrow et al., 2010), which contributed to a separation of the BSIS and FIS in the  
518 central Barents Sea (Newton and Huuse, 2017). Thus, we suggest that precipitous sea ice  
519 retreat from the western Barents Sea continental slope at ca. 16.3 cal kyr BP coincided with  
520 the eastbound areal deglaciation of the BSIS (**Fig. 8c**).

521 Conspicuous enhancement of pelagic HBI concentrations (**Fig. 3b** and **6a**) towards  
522 values  $>140 \text{ ng g}^{-1}$  is unprecedented both within the GS14 record and the contemporary  
523 Barents Sea, where maximum sedimentary concentrations of HBIs III and IV detected in the  
524 highly-productive MIZ do not exceed ca. 47 and 22  $\text{ng g}^{-1}$ , respectively (Belt et al., 2015;  
525 Köseoğlu et al., 2018a). Such a remarkable increase in pelagic diatom productivity at the  
526 GS14 site after ca. 16.3 cal kyr is in broad agreement with Wollenburg et al. (2004), who also  
527 found that paleoproductivity in relatively fresh surface waters surpassed modern averages at  
528 the northern Svalbard margin during this period. Additionally, benthic foraminiferal  
529 assemblages along the continental margin adapted to warm AW and increased nutrient  
530 availability (e.g. Chauhan et al., 2016). Together, these data suggest the existence of  
531 significantly more productive post-HS1 conditions compared to those spanning at least the  
532 last several decades of sedimentation in the MIZ (Belt et al., 2015; Köseoğlu et al., 2018a),  
533 and are unlikely to be solely attributable to sea ice retreat and establishment of a productive  
534 seasonal ice margin following HS1.

535 Several factors could have renewed pelagic productivity. The stratified water column in  
536 the Arctic throughout HS1 was initially salinity-controlled due to deglacial meltwater input  
537 since ca. 20–19 cal kyr BP (e.g. Chauhan et al., 2016; Hoff et al., 2016; Jennings et al., 2018;  
538 Jessen et al., 2010; Rasmussen et al., 2007; Rasmussen and Thomsen, 2008), which  
539 hampered the AMOC and NADW formation (Gherardi et al., 2009; McManus et al., 2004),  
540 slowing deep water ventilation in the North Atlantic and the Nordic Seas (Thiagarajan et al.,

2014; Thornalley et al., 2015). Thus, a combination of reduced convective heat loss from northbound bottom waters due to strong salinity-driven stratification, and geothermal heating (e.g. Adkins et al., 2005) potentially caused a basin-wide increase of subsurface water temperatures according to proxy-based (Cronin et al., 2012; Thiagarajan et al., 2014) and modelling studies (Liu et al., 2009). Indeed, millennial sub-surface warming of 2–3°C since ca. 19 cal kyr BP is supported by foraminiferal transfer function reconstructions (Rørvik et al., 2013),  $\Delta_{47}$  clumped isotope data, increased Mg/Ca ratios (Cronin et al., 2012; Thiagarajan et al., 2014; Thornalley et al., 2015), and benthic  $\delta^{18}\text{O}$  depletions (e.g. Rasmussen and Thomsen, 2004) across the Nordic Seas. Similar warming along the Barents Sea and Svalbard margins is indicated by intrusion of temperate benthic foraminifera adapted to reduced productivity immediately prior to the HS1 (Chauhan et al., 2016; Rasmussen et al., 2007; Wollenburg et al., 2004), which potentially affected the GS14 site and contributed to BSIS debuttressing, triggering glacial conditions at the onset of HS1 (e.g. Hormes et al., 2013; Marcott et al., 2011). Such accumulation of sub-surface heat in a salinity-stratified water column lowers the density of deep waters – a thermobaric effect which positively scales with pressure – and gradually destabilises the column by reducing the depth threshold at which the cold surface waters become denser than the warm, saline waters below. Once the depth threshold is breached, overturning resumes as the cold surface waters accelerate downwards, while the heat and salt accumulated in the deep waters is rapidly released to the surface ocean (e.g. Adkins et al., 2005). Such phenomena have been recorded in the Norwegian Sea, where subsurface temperatures rapidly decreased between ca. 18–15 cal kyr BP following a period of millennial warming (Rørvik et al., 2013; Thornalley et al., 2015). We therefore suggest that intense, instability- or buoyancy-driven upwelling of warm and saline subsurface waters at the GS14 site could have made massive surface reservoirs of heat and nutrients available (**Fig. 8c**) for seasonal ice melting (**Fig. 3c**) and unprecedented pelagic productivity (**Fig. 3b**)



566 after 16.3 cal kyr BP. Increased nutrient availability and efficient surface enrichment  
567 activated by this overturning resumption was potentially maintained by the deepening and  
568 intensification of the AMOC towards the Bølling-Allerød warming at ca. 15 cal kyr BP  
569 (McManus et al., 2004; Ritz et al., 2013; Shakun et al., 2012). Additionally, in contrast to the  
570 slow development of stratification and pelagic productivity in the ice-free southwestern  
571 Barents Sea today due to strong NAC- and wind-driven vertical mixing (Wassmann et al.,  
572 1999), the post-HS1 productive season at the GS14 site could have been prolonged and  
573 hastened by earlier stratification due to meltwater input from sea ice and BSIS retreat  
574 (Hormes et al., 2013). Influx of ice and iceberg-entrained terrigenous material from coastal  
575 erosion could have provided an additional nutrient supply, as previously noted for the  
576 postglacial western (Aagaard-Sørensen et al., 2010) and northern Barents Sea (Knies and  
577 Stein, 1998). Thus, a combination of marginal seasonal sea ice, surface warming, hastened  
578 meltwater-fuelled stratification, and an augmented nutrient input from terrigenous material  
579 and intense upwelling potentially stabilised pelagic species longer in the photic zone and  
580 reduced nutritional limitation during the peak bloom, explaining the GS14 productivity trends  
581 (**Fig. 8c**). Although it is not feasible to decouple the relative influences of individual factors,  
582 the core site was probably characterised by a significantly different productivity regime  
583 relative to the ephemeral, nutrient-limited blooms that occur in the modern Barents Sea  
584 (Signorini and McClain, 2009), where the phytoplankton productivity increase of recent years  
585 is mainly driven by a strengthening AW inflow (Årthun et al., 2012) and reducing sea ice  
586 extent (Arrigo and van Dijken, 2015; Assmy et al., 2017), and is not influenced by increased  
587 meltwater and terrigenous matter fluxes.

588 High sterol concentrations after ca. 16 cal kyr BP resemble the trend of abruptly  
589 increasing pelagic HBI concentrations (**Fig. 3b, 4**) and support our assumption of renewed  
590 primary productivity at the core site following precipitous ice retreat (**Fig. 3c, 8c**). While

591 most sterols only reach pre-HS1 values at the core site, cholesterol concentrations increase by  
592 a factor of 3 relative to LGM values and dominate the percentage distribution at 36% relative  
593 abundance instead of  $\beta$ -sitosterol (**Fig. 6b, 7b**). Similarly to HS1, this could simply be  
594 attributable to a switch in the algal assemblage to favour cholesterol production (e.g. by  
595 centric diatoms; Rampen et al., 2010). Another explanation is the efficient conversion of algal  
596 sterols to cholesterol by auxotrophic consumers, including zooplankton, which potentially  
597 flourished after the HS1 due to resumed deep circulation (Gherardi et al., 2009; McManus et  
598 al., 2004; Ritz et al., 2013) and global atmospheric-oceanic warming (Shakun et al., 2012).  
599 Zooplankton at lower trophic levels extensively feed on pelagic and sympagic algae for  
600 growth and reproduction, with increased grazing rates characteristic of warm and highly-  
601 productive conditions with large phytoplankton stocks (Falk-Petersen et al., 2000;  
602 Tamelander et al., 2008). Contemporary zooplankton communities in the Barents Sea MIZ  
603 during peak blooms are dominated by crustaceans, including copepods and krill (e.g. Eriksen  
604 et al., 2017), which require a continuous source of cholesterol to maintain their phospholipid  
605 membranes and produce offspring (Hassett and Crockett, 2009). Accordingly, cholesterol is  
606 invariably the major constituent (usually >50%) of sterol distributions in Arctic and Antarctic  
607 crustaceans (Hamm et al., 2001; Mühlebach et al., 1999). Herbivorous and omnivorous  
608 arthropods largely rely on chemical conversion of phytosterols to cholesterol, which they  
609 cannot biosynthesize (Goad, 1981; Martin-Creuzburg and von Elert, 2009) or obtain in  
610 sufficient quantity from an algal diet. Therefore, it is possible that the nutrient-replete and  
611 diatom-rich conditions inferred from high pelagic HBI (III and IV) concentrations at the  
612 GS14 site after HS1 (**Fig. 3b**) revitalised zooplankton production and phytosterol to  
613 cholesterol bioconversion, leading to the proportionally larger increases of the latter sterol  
614 (**Fig. 4**). Additionally, our suggestion of a warming water column due to intensive post-HS1  
615 circulation of sub-surface heat could have accelerated zooplankton metabolism, switching

616 from temperature-limited to nutrient-limited growth with increased nutritional and  
617 reproductive cholesterol requirements (Hassett and Crockett, 2009). Overall, increased  
618 phytosterol conversion rates and zooplankton stocks following the post-HS1 climate  
619 amelioration represent one plausible mechanism for the switch from a phytosterol- to  
620 cholesterol-defined sterol assemblage after 16 cal kyr BP. Notably, however, such a  
621 cholesterol-dominated sterol distribution is not reproduced in the contemporary Barents Sea,  
622 where epibrassicasterol abundances increase alongside those of cholesterol, and are often  
623 higher. Consistent cholesterol prevalence is only observed in the warmer Norwegian Sea  
624 (**Fig. 7b**) characterised by significant transport of copepods and krill with the NAC (Falk-  
625 Petersen et al., 2000), contributing to their role as major pelagic food web components in the  
626 Barents Sea (Aarflot et al., 2017; Eriksen et al., 2017). These observations potentially  
627 indicate that the highly-productive post-HS1 interval in the GS14 record is unique and not  
628 reproduced in the contemporary Barents Sea, supporting similar suggestions based on the  
629 unprecedented increase of pelagic HBIs III and IV, which overshadows that of cholesterol  
630 (**Fig. 3b, 4d, and 7**).

631

## 632 **Conclusions**

633 Geochemical biomarkers in a marine sediment core provided new insights into the  
634 abruptly shifting seasonal sea ice conditions and primary productivity regimes on the  
635 southwestern Barents Sea slope throughout ca. 26–15 cal kyr BP. We draw the following  
636 main outcomes:

- 637 1) The LGM interval and initial SEDG were characterised by extensive sea ice covering the  
638 site, with seasonal occurrence of highly-productive coastal polynya. Overall marine  
639 productivity was variable, but generally high until 18.0 cal kyr BP.

- 640 2) The onset of perennial sea ice cover during HS1 coincides with widespread NH ice sheet  
641 collapse and large meltwater influx at ca. 18.0 cal kyr BP as a result of AW-induced basal  
642 melting, atmospheric aridification and increased iceberg calving due to sea level rise.  
643 Thus, overall productivity plummeted until ca. 16.3 cal kyr BP as a result of a pan-Arctic  
644 meltwater-induced pycnocline, abrupt AMOC weakening and reduced light penetration  
645 through newly-formed perennial sea ice.
- 646 3) Coincident with a rapid sea ice retreat to values <10% SpSIC between ca. 16.3–16.1 cal  
647 kyr BP, primary productivity exceeded the most productive contemporary conditions in  
648 the Barents Sea MIZ. This feature is likely uniquely deglacial and attributable to heat and  
649 nutrients released to the surface waters due to thermobaric and/or buoyancy-triggered  
650 instabilities following sub-surface warming under weak thermohaline circulation of the  
651 HS1. Meltwater input and coastal erosion from the BSIS could have provided an  
652 additional nutrient supply to the pelagic environment. We tentatively infer a revitalisation  
653 of marine fauna due to vast increases of algal biomass and surface warming.
- 654 4) We note some consistency of relative biomarker distributions downcore with those  
655 observed in contrasting sea ice and primary productivity regimes of the contemporary  
656 Barents Sea. We are able to decouple sympagic and pelagic primary production using  
657 source-specific HBI biomarkers characteristic of ice algal and pelagic diatoms, which  
658 indicate that LGM productivity was predominantly ice-based, while post-HS1 production  
659 conversely relied on free-floating pelagic algae with minor contribution from sympagic  
660 sources. In contrast, sterol concentrations remained similar under seasonal sea ice  
661 conditions of the LGM and the post-HS1 deglaciation, and likely represent a mixed algal  
662 source.

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668 **Data availability**

669 Datasets related to this article can be found at doi: <http://dx.doi.org/10.17632/jx97c9nv3k.1>,  
670 hosted at Mendeley Data.

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1205 **Figure legends**

1206 Figure 1: Structures of IP<sub>25</sub> and HBI II (representing sea ice diatom productivity), as well as  
1207 HBIs III and IV (indicative of pelagic diatom productivity). The combined use of HBIs  
1208 within proxies for sea ice reconstruction (including P<sub>III</sub>IP<sub>25</sub> and CT models) is illustrated.

1209 Figure 2: Maps of the Barents Sea showing: (a) The main inflow currents carrying AW (via  
1210 the NAC, NCaC, and WSC), ArW (PC and ESC), and CW (NCC); (b) Surface and downcore  
1211 sample locations. Green and orange circles correspond to surface sediment locations where  
1212 HBI with or without additional sterol data were available for comparison with downcore  
1213 records, respectively. Both the investigated site and referenced downcore locations are shown  
1214 by numbered diamond markers: (1) GS14-190-PC01 (this study and Knies et al., 2018); (2)  
1215 JM11-F1-19PC (Hoff et al., 2016); (3) MD95-2010 (Marcott et al., 2011); (4) JM05-85-GC  
1216 (Aagaard-Sørensen et al., 2010); (5) JM02-460 GC/PC (Rasmussen et al., 2007); (6)  
1217 MSM5/5-712-2 (Müller and Stein, 2014); (7) PS93/006-1 (Kremer et al., 2018a); (8) PS2837-  
1218 5 (Wollenburg et al., 2004; Müller et al., 2009); (9) PS92/039-2 (Kremer et al., 2018b); (10)  
1219 HH11-09GC (Chauhan et al., 2016); (11) PS2138-1 (e.g. Knies and Stein, 1998; Nørgaard-  
1220 Pedersen et al., 2003). Maximum BSIS extent throughout the LGM (at ca. 21 cal kyr BP) is  
1221 shown by a filled white area (Hughes et al., 2016). In both maps, dashed and solid black lines  
1222 correspond to averaged SpSIC contours (April–June; 1988–2017) of 0% and 15%,  
1223 respectively.

1224 Figure 3: HBI concentration profiles for core GS14: (a) IP<sub>25</sub> and HBI II, indicative of  
1225 sympagic diatom productivity; (b) HBIs III and IV, showing pelagic diatom productivity. A  
1226 zoomed-in version of the profile spanning ca. 25–18 cal kyr BP is also shown; (c) P<sub>III</sub>IP<sub>25</sub>-  
1227 based SpSIC (%) estimates with confidence limits (grey lines) corresponding to the standard  
1228 error of calibration (ca. ±11%; Smik et al., 2016), and superimposed categorical CT

1229 predictions of marginal (ca. <10% SpSIC), intermediate (ca. 10–50% SpSIC), and extensive  
1230 (>50% SpSIC) sea ice regimes denoted by red diamonds, yellow triangles, and green circles,  
1231 respectively. The threshold for summer sea ice occurrence is shown by the horizontal dashed  
1232 line. In all plots, coloured background bands constrain the LGM and SEDG (25.8–18.0 cal  
1233 kyr BP), HS1 (18.0–16.3 cal kyr BP) and Deglacial (after 16.3 cal kyr BP) intervals – a  
1234 rationale for dividing the GS14 record into time slices is provided in the Discussion.  
1235 Changepoints significant at a 99.5% confidence level ( $p < 0.005$ ) are shown by vertical red  
1236 lines, where upward-pointing dashed arrows apply to the left y-axis only, while a solid line  
1237 applies to both the left and right y-axes. Red and blue crosses highlight GS14 and GC08  $^{14}\text{C}$   
1238 AMS dates on the age scale, respectively.

1239 Figure 4: Sterol concentration profiles for core GS14: (a) Brassicasterol and chalinasterol; (b)  
1240 Campesterol and  $\beta$ -sitosterol; (c) Dinosterol; (d) Cholesterol. In all plots, coloured  
1241 background bands constrain the LGM and SEDG (25.8–18.0 cal kyr BP), HS1 (18.0–16.3 cal  
1242 kyr BP) and Deglacial (after 16.3 cal kyr BP) time slices. Changepoints significant at a 99.5%  
1243 confidence level ( $p < 0.005$ ) are shown by vertical red lines, where upward or downward  
1244 pointing dashed arrows apply to the left and right y-axis, respectively, while a solid line  
1245 applies to both left and right y-axes. Red and blue crosses highlight GS14 and GC08  $^{14}\text{C}$   
1246 AMS dates on the age scale, respectively.

1247 Figure 5: Planktic  $\delta^{18}\text{O}$  of *N. pachyderma* sin. (black line with circle markers) and IRD data  
1248 (green line) for core GS14, obtained from Knies et al. (2018). Red and blue crosses highlight  
1249 GS14 and GC08  $^{14}\text{C}$  AMS dates on the age scale, respectively.

1250 Figure 6: Concentration distributions during the LGM (with SEDG), HS1, and Deglacial for:  
1251 (a) HBIs; (b) Sterols. Error bars denote  $\pm 1$  sample SD in each case. Blue and red boxes with  
1252 outgoing arrows show plot areas zoomed in for clarity for HBIs and sterols, respectively.

1253 Figure 7: Relative abundance distributions during the LGM (with SEDG), HS1, and  
1254 Deglacial for: (a) HBIs, with comparisons to modern distributions reported in Barents and  
1255 Norwegian Sea surface sediments characterised by contrasting sea ice regimes (**Fig. 1b**); (b)  
1256 Sterols, with comparisons to surface sedimentary distributions analogous to those in (a). Error  
1257 bars denote  $\pm 1$  sample SD for each biomarker, while the sample size  $n$  is shown in red above  
1258 each distribution.

1259 Figure 8: Conceptual representation of sea ice and productivity conditions at the southwestern  
1260 Barents Sea continental slope throughout: (A) The LGM and SEDG (25.8–18.0 cal kyr BP);  
1261 (B) The HS1 (18.0–16.3 cal kyr BP); (C) The Deglacial (16.3 cal kyr BP onwards). Seasonal  
1262 sea ice conditions inferred from SpSIC (%) and the CT model are illustrated during winter  
1263 (October–March), spring (April–June) and summer (July–September). Red and blue arrows  
1264 correspond to AW and meltwater fluxes, respectively, where line width increases with flow  
1265 strength. Orange arrows represent solar insolation.

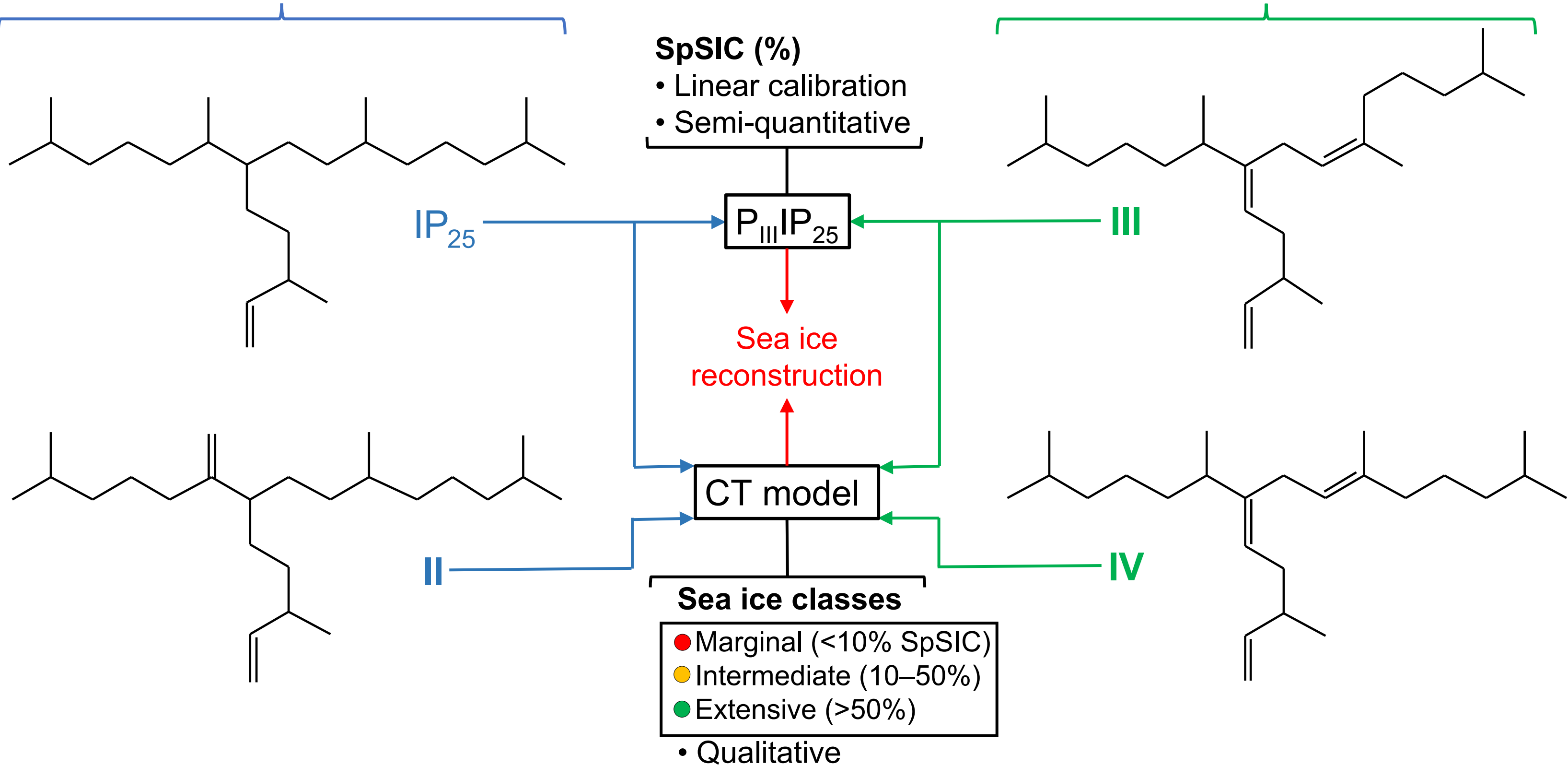
## 1266 **Tables**

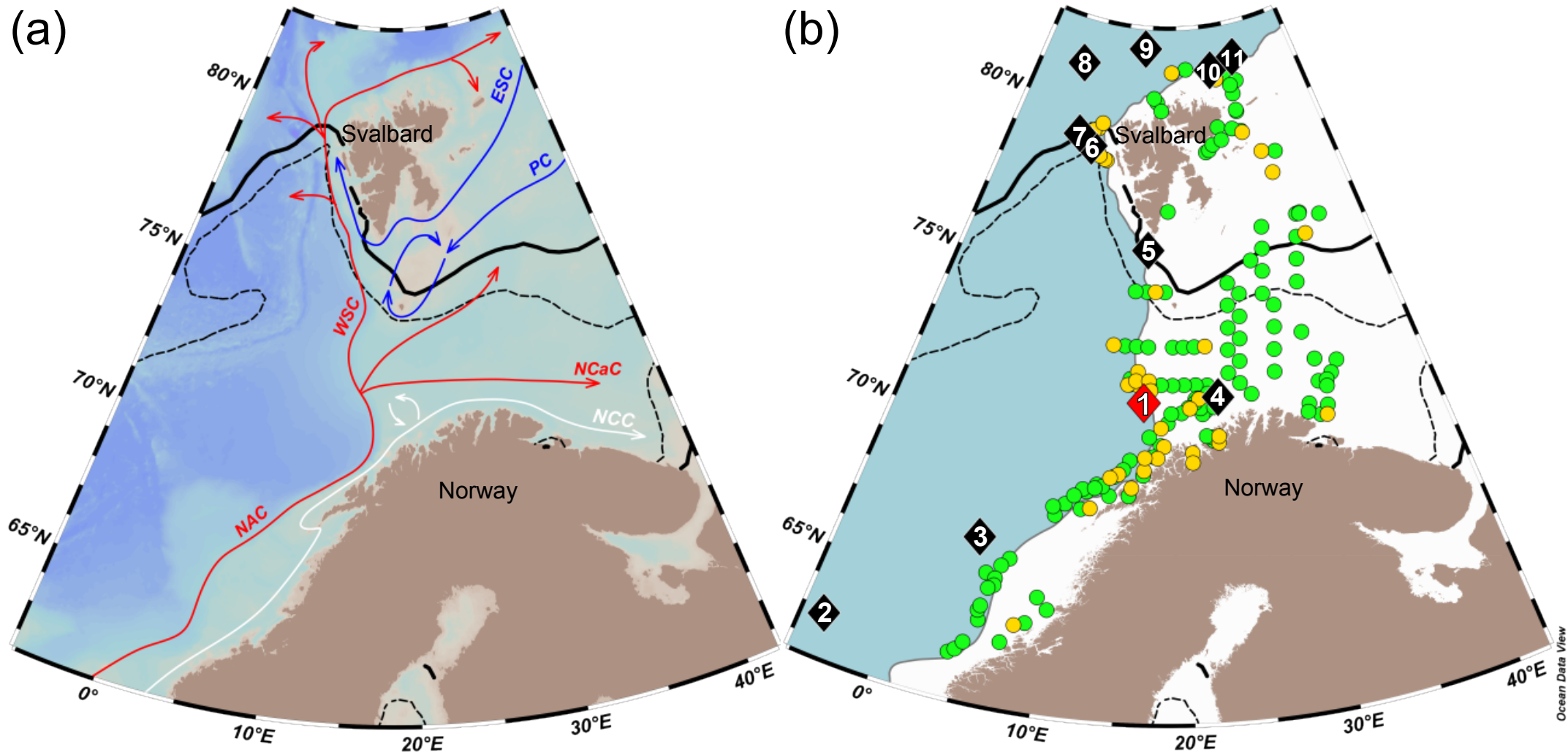
1267 Table 1: Uses and potential limitations of HBI and sterol lipids utilized as biomarkers of sea  
1268 ice and primary productivity regimes in the current study.

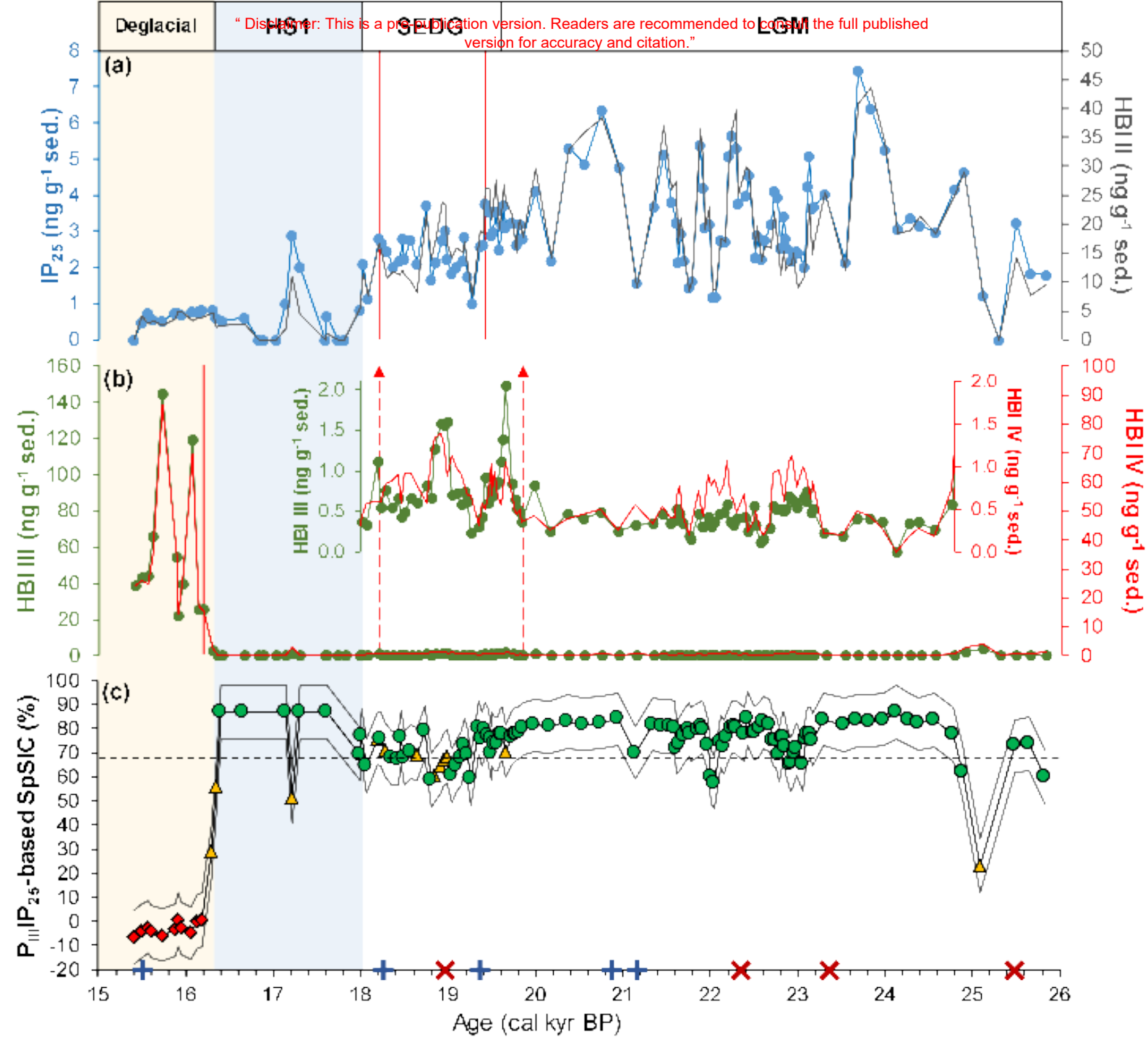


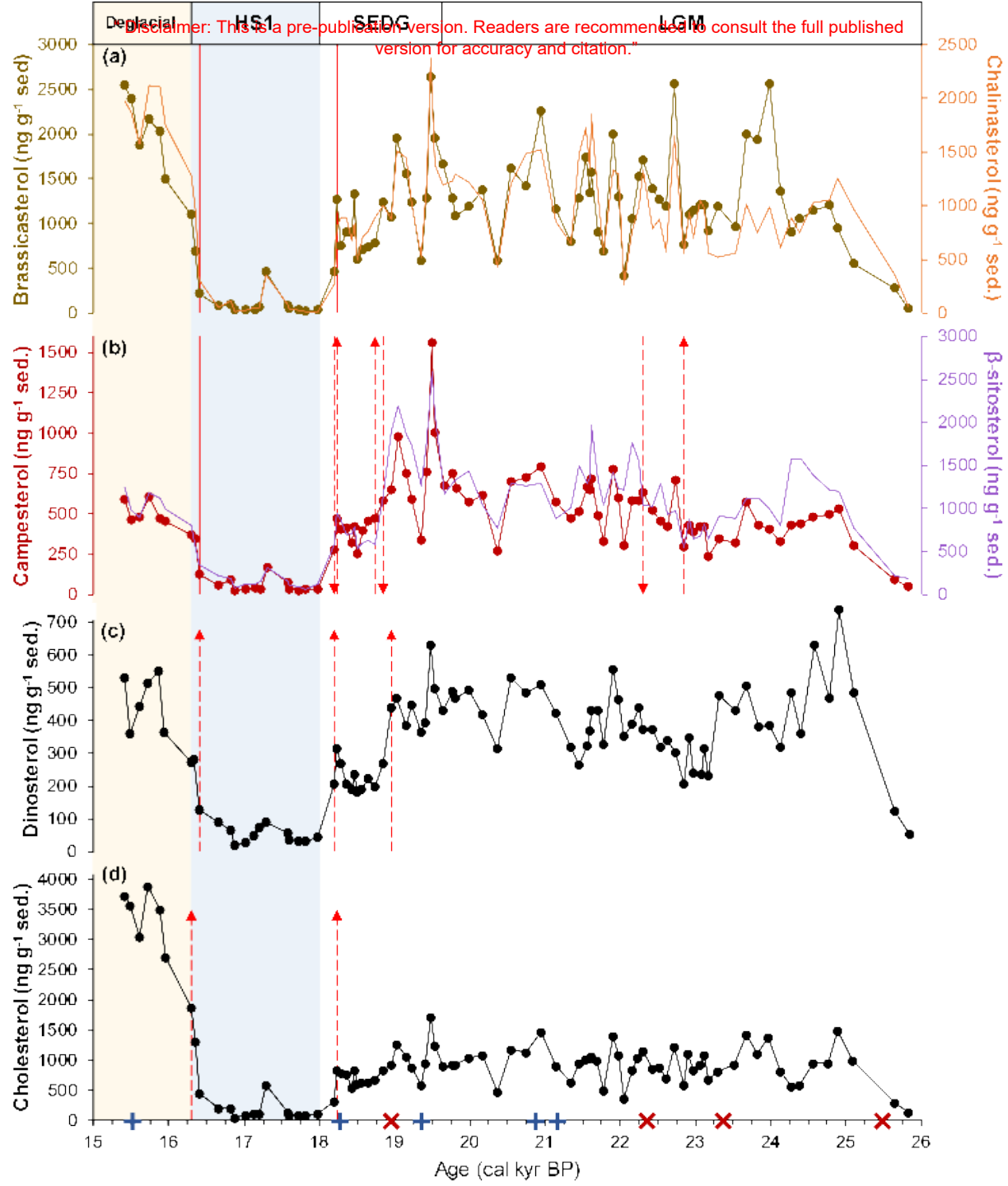
## Sympagic biomarkers (sea ice algal productivity)

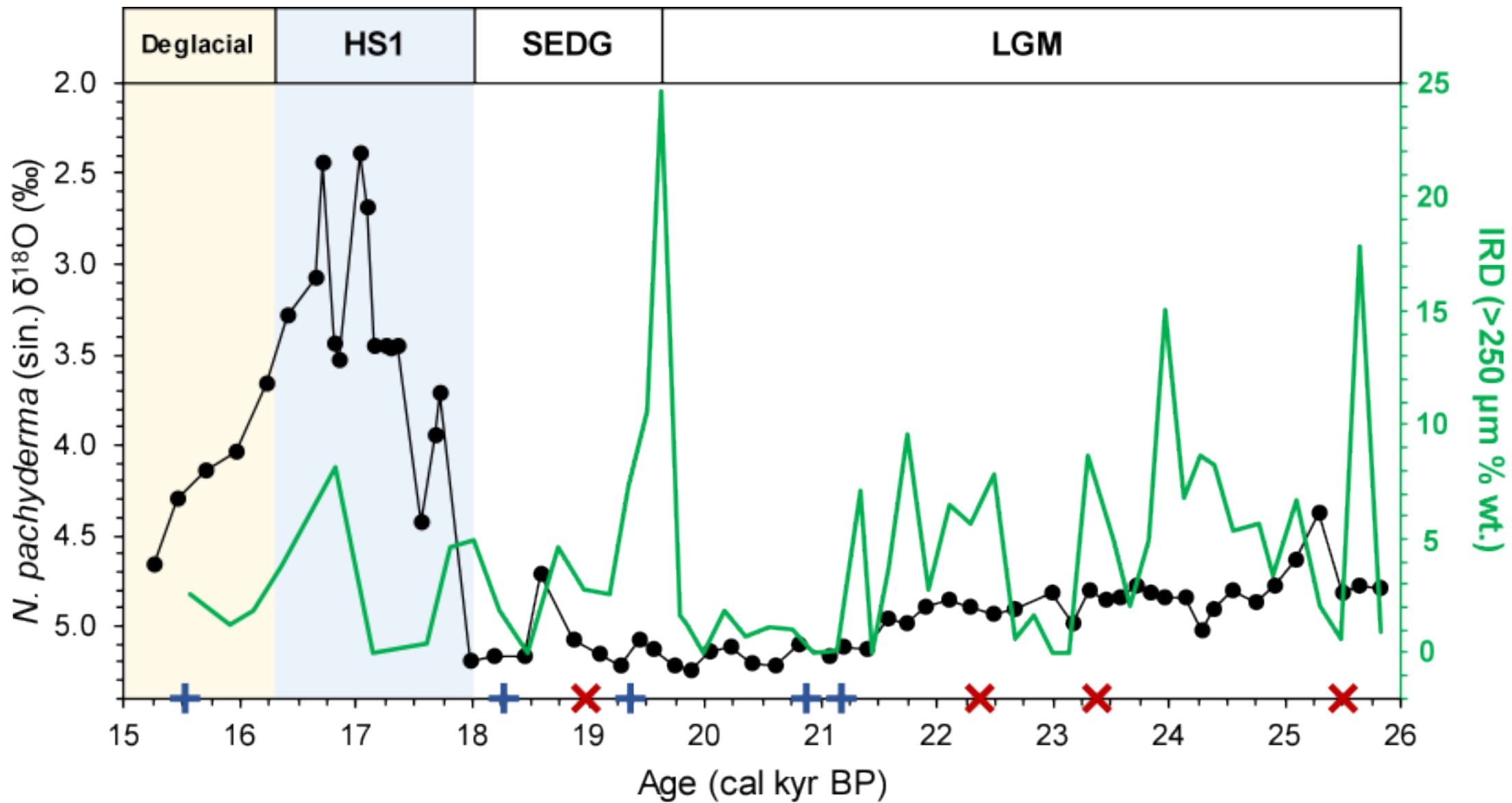
## Pelagic biomarkers (open water productivity)



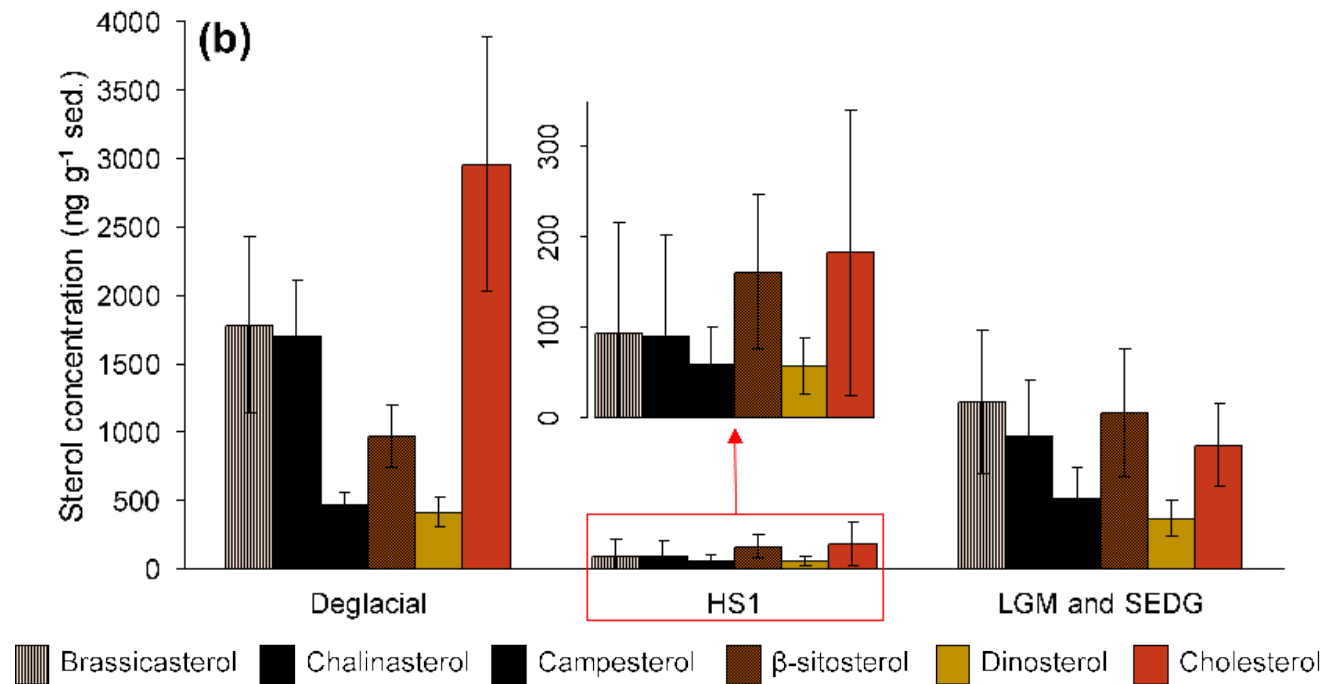
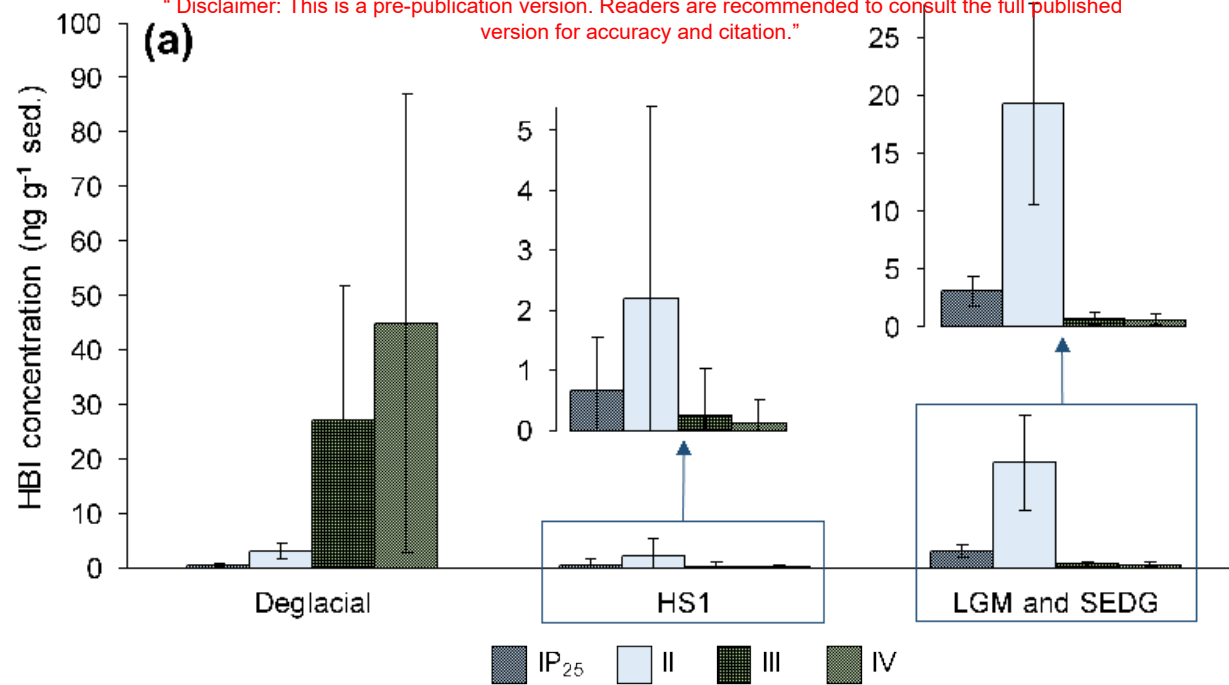


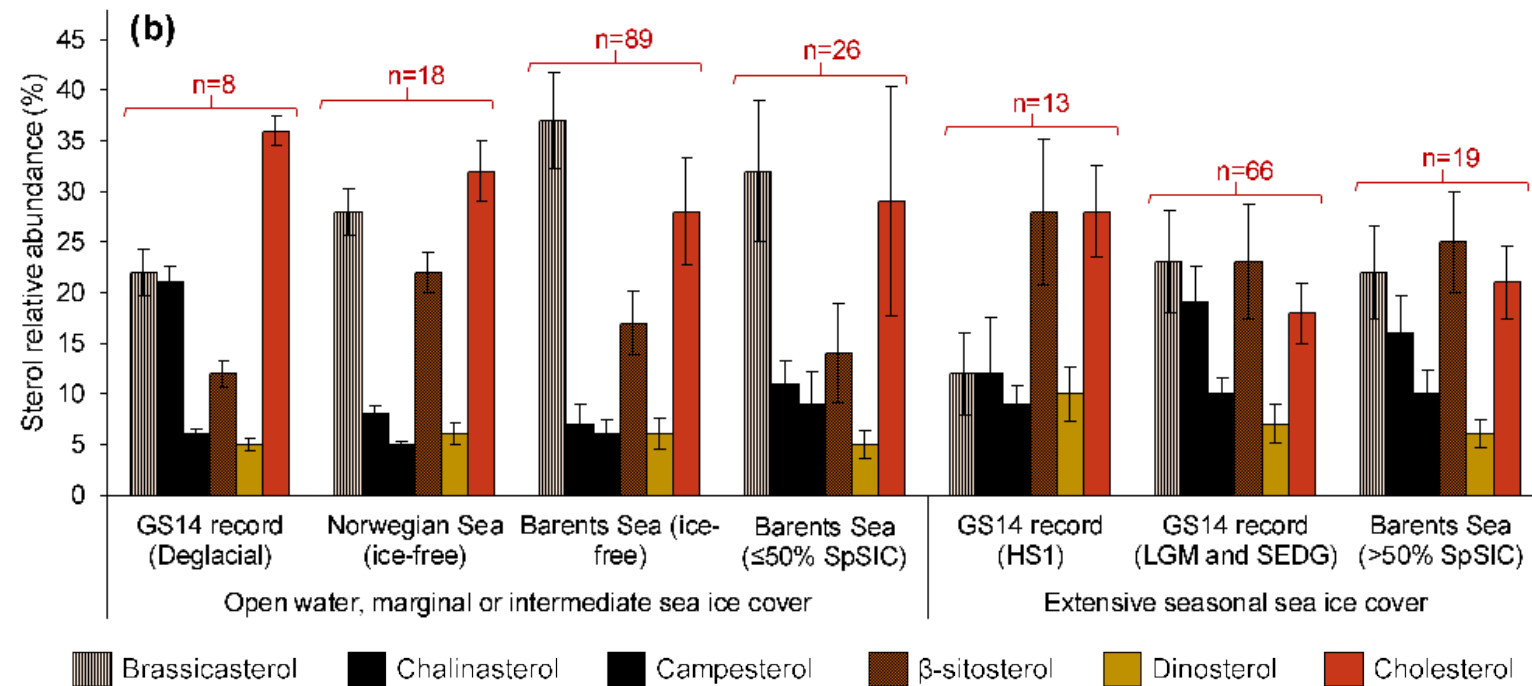
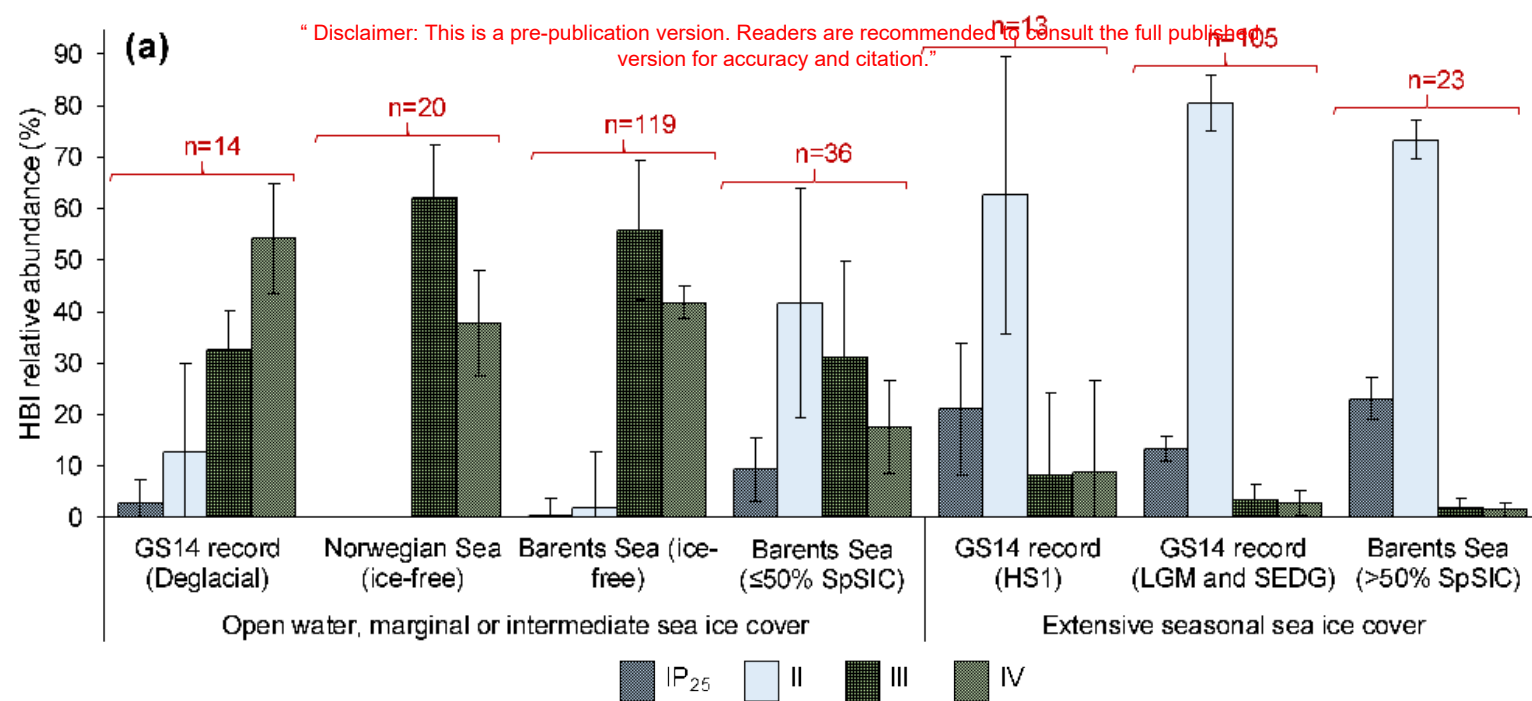






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HBIs	Common use(s)	Potential limitation(s)	Present interpretation	References
IP <sub>25</sub> and II	Source-specific, co-produced diatom proxies of seasonal Arctic sea ice <sup>1, 2</sup> .  Stable within sedimentary record and resistant to photodegradation and autoxidation <sup>3</sup> .	Require concurrent analysis of an open-water biomarker(s) to distinguish perennial ice and open water settings <sup>4, 5, 6, 7</sup> .  Only represent productivity of minor sympagic diatoms <sup>1, 2</sup> .	Used as indicators of sympagic diatom productivity within sea ice, where absolute concentrations and relative abundances increase with longer seasonal sea ice duration.	Belt et al. (2015 <sup>5</sup> , 2016 <sup>2</sup> , 2017 <sup>9</sup> ) Brown et al. (2014b) <sup>1</sup> Köseoğlu et al. (2018a,b) <sup>7</sup> Müller et al. (2011) <sup>4</sup> Ringrose (2012) <sup>8</sup> Rontani et al. (2011, 2014b) <sup>3</sup> Smik et al. (2016) <sup>6</sup>
III and IV	Ubiquitous pelagic diatom proxies vastly enhanced during the spring MIZ phytoplankton bloom, and limited under extensive ice conditions <sup>5, 6, 7</sup> .  III used to derive P <sub>III</sub> IP <sub>25</sub> -based SpSIC estimates <sup>5, 6</sup> , and IV used for CT predictions of sea ice cover <sup>7</sup> .	Increased degradation rates relative to IP <sub>25</sub> and II, at least under laboratory conditions <sup>3</sup> .  IV (<10%) detected in sea ice, while all but one <i>in-situ</i> sources in the Arctic ( <i>Rhizosolenia setigera</i> ) are still unknown <sup>9</sup> .	Used as indicators of pelagic diatom productivity in the photic zone of the water column. Absolute concentrations and relative abundances increase under highly-productive conditions.	<b>Reviews:</b> Belt and Müller (2013) Belt (2018)
<b>Sterols</b>				
Brassicasterol	A major constituent of marine algae and indicative of general productivity <sup>10</sup> .	Present in sea ice <sup>11</sup> .	Due to their reduced source-specificity, variability of all absolute sterol concentrations was interpreted as a general indicator of changes in marine productivity.	Belt et al. (2013, 2018) <sup>11</sup> Boon et al. (1979) <sup>15</sup> Hassett and Crockett (2009) <sup>19</sup> Huang and Meinschein (1976) <sup>14</sup> Mühlebach et al. (1999) <sup>18</sup> Nichols et al. (1990) <sup>16</sup> Rampen et al. (2010) <sup>10</sup> Rontani et al. (2014a, 2016) <sup>12</sup> Volkman et al. (1993) <sup>17</sup>
Chalinasterol	An indicator of marine diatom productivity as the dominant sterol in many centric and pennate diatoms <sup>10</sup> .	Susceptible to photodegradation and autoxidation <sup>12</sup> ; Found in other algae (e.g. cryptomonads), and in sea ice <sup>11, 13</sup> .	Comparison of sterol relative abundance distributions downcore to those of surface sediments was used to identify similarities and differences between paleo and more recent/contemporary settings characterised by contrasting sea ice and/or productivity conditions.	<b>Review:</b> Volkman (1986) <sup>13</sup>
Campesterol and $\beta$ -sitosterol	Commonly associated with terrigenous input from vascular plants <sup>14</sup> .	Found in many diatoms, where $\beta$ -sitosterol often dominates the sterol assemblage <sup>10</sup> .		
Dinosterol	A common biomarker of dinoflagellate productivity <sup>15</sup> .	Detected as a minor constituent of diatoms (including sympagic) in polar settings <sup>16</sup> and cultures <sup>17</sup> .		
Cholesterol	High proportional abundance can indicate increased marine faunal productivity <sup>13</sup> .	Ubiquitous amongst vertebrates <sup>18, 19</sup> and diatoms <sup>10</sup> .		