

1 **Do pelagic grazers benefit from sea ice?**
2 **Insights from the Antarctic sea ice proxy IPSO₂₅**
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27 ABSTRACT

28 Sea ice affects primary production in polar regions in multiple ways. It can dampen water column
29 productivity by reducing light or nutrient supply, it provides a habitat for ice algae and on its seasonal
30 retreat can condition the marginal ice zone (MIZ) for phytoplankton blooms. The relative importance of
31 three different carbon sources (sea ice-derived, sea ice-conditioned, non-sea ice-associated) for the polar
32 food web is not well understood, partly due to the lack of methods that enable their unambiguous
33 distinction. Here we analysed two highly branched isoprenoid (HBI) biomarkers to trace sea ice-derived
34 and sea ice-conditioned carbon in Antarctic krill (*Euphausia superba*), and relate their concentrations to
35 the grazers' body reserves, growth and recruitment. During our sampling in January/February 2003, the
36 proxy for sea ice diatoms (a di-unsaturated HBI termed IPSO₂₅, $\delta^{13}\text{C} = -12.5 \pm 3.3\text{‰}$) occurred in open
37 waters of the western Scotia Sea, where seasonal ice retreat was slow. In suspended matter, IPSO₂₅ was
38 present at a few stations close to the ice edge, but in krill the marker was widespread. Even at stations
39 that had been ice-free for several weeks, IPSO₂₅ was found in krill stomachs, suggesting that they
40 gathered the ice-derived algae from below the upper mixed layer. Peak abundances of the proxy for
41 MIZ diatoms (a tri-unsaturated HBI termed HBI III, $\delta^{13}\text{C} = -42.2 \pm 2.4\text{‰}$) occurred in regions of fast sea
42 ice retreat and persistent salinity-driven stratification in the eastern Scotia Sea. Krill sampled in the area
43 defined by the ice edge bloom likewise contained high amounts of HBI III. As indicators for the
44 grazer's performance we used the mass-length ratio, size of digestive gland and growth rate for krill,
45 and recruitment for the biomass-dominant calanoid copepods *Calanoides acutus* and *Calanus*
46 *propinquus*. These indices consistently point to blooms in the MIZ as an important feeding ground for
47 pelagic grazers. Even though ice-conditioned blooms are of much shorter duration than the bloom
48 downstream of the permanently sea ice-free South Georgia, they enabled fast growth and offspring
49 development. Our study shows two rarely considered ways that pelagic grazers may benefit from sea
50 ice: Firstly, after their release from sea ice, suspended or sinking ice algae can supplement the grazers'
51 diet if phytoplankton concentrations are low. Secondly, conditioning effects of seasonal sea ice can
52 promote pelagic primary production and therefore food availability in spring and summer.

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58 1. Introduction

59 Over the last four decades, sea ice has shown a rapid decline in areal coverage in polar regions. In
60 the Arctic and parts of the Antarctic (e.g. Bellingshausen- and Amundsen Seas), sea ice concentrations
61 are decreasing during both summer (-10 to -13% per decade) and winter (-2% per decade) (Meier et al.
62 2017, Stammerjohn and Maksym 2017), and current trends towards later autumn sea ice advance and
63 earlier spring sea ice retreat are likely to continue in both hemispheres (Stammerjohn et al. 2012).
64 Ecosystem responses to the loss in sea ice and co-occurring warming and freshening include changes in
65 primary productivity, alterations in phytoplankton community structure, range shifts for zooplankton,
66 benthic organisms and fish, and decline in sea ice-dependent sea birds and mammals (Li et al. 2009,
67 Grebmeier et al. 2010, Constable et al. 2014). Understanding such climate-related changes in structure
68 and functioning of polar marine ecosystems is imperative for the management of their resource
69 exploitation (Smetacek and Nicol 2005).

70 Extended open-water seasons have been suggested to lead to higher primary production in the polar
71 oceans (Arrigo 2017) and generate a negative feedback to climate change (Barnes and Tarling 2017).
72 Some satellite-derived chlorophyll *a* -time series support this prediction (Arrigo et al. 2008), while
73 others do not (Marchese et al. 2017). Along the western Antarctic Peninsula, warming and a reduction
74 in sea ice extent between 1978 and 2006 led to two very different scenarios (Montes-Hugo et al. 2009).
75 In the southern part, perennial sea ice was replaced by seasonal sea ice and the ice-free summer days
76 translated into more favourable conditions for phytoplankton growth (e.g. increased light). In contrast,
77 in the northern part, loss of seasonal sea ice led to a deepening of the upper mixed layer with less
78 favourable light conditions for phytoplankton (Montes-Hugo et al. 2009). These observations illustrate
79 the opposing effects that permanent- and seasonal sea ice can have on primary productivity. While the
80 former prevents phytoplankton blooms, the latter can promote them. Several processes associated with
81 the seasonal retreat of sea ice are considered to ‘condition’ the upper water column for phytoplankton
82 blooms (Smetacek and Nicol 2005). First, low-density meltwater can stabilize the surface layer and
83 therefore enhance mean irradiance levels for phytoplankton (Smith and Nelson 1986). Second, the
84 release of trace elements from melting sea ice can alleviate iron limitation, which is a common feature
85 in the open Southern Ocean (Lannuzel et al. 2010). Third, some algae that thrive in sea ice also act as an
86 inoculum for phytoplankton blooms (Smith and Nelson 1986). This explains why the marginal ice zone
87 (MIZ) is, on average, more productive than the permanently open waters of the Southern Ocean (Smith
88 and Nelson 1986, Tréguer and Jacques 1992).

89 Chlorophyll *a* concentrations in sea ice are not accessible to satellite observations and therefore
90 primary production estimates rely on sparse *in situ* measurements and numerical models. Such data
91 suggest that primary production in sea ice accounts for only small amounts of total annual production in
92 polar waters; typically 2-10% in the Arctic and ca. 1-3% in the Southern Ocean south of 50°S (Arrigo
93 2017). However, an important difference between phytoplankton and ice algae is that while the former
94 is deeply mixed in the water column, sea ice provides a platform that retains the latter in the surface
95 ocean where light levels can be sufficient for photosynthesis and net growth even during the dark
96 season (Kottmeier and Sullivan 1987, Roukaerts et al. 2016). Therefore, ice algae supply an important
97 autumn, winter and early spring carbon source to in-ice fauna, with subsequent transfer to the wider
98 food web of ice-associated invertebrates, fish, seabirds and mammals (Ainley et al. 2017, Bluhm et al.
99 2017, Caron et al. 2017, Bester et al. 2017). Other merits of ice algae are their enrichment in
100 polyunsaturated fatty acids that make them a high-quality food source (Søreide et al. 2010, Wang et al.
101 2014), while their tendency to aggregate and sink after being released from sea ice can be an important
102 pathway of carbon export to the benthos (Riebesell et al. 1991, Renaud et al. 2007). Thus, the small
103 contribution of ice algae to the overall primary production in the polar regions likely understates their
104 ecological importance.

105 Dominant polar grazers such as calanoid copepods and euphausiids are adapted to the strong
106 seasonality in primary production and the dynamic interface between ice and water (Smetacek and
107 Nicol 2005). Postlarval stages of these species biosynthesise large lipid stores which enable them to
108 survive long periods without food (Hagen and Auel 2001). Some species remain active during winter
109 (e.g. the Antarctic copepod *Calanus propinquus* and the Antarctic krill *Euphausia superba*) and can be
110 found under sea ice feeding on ice algae or heterotrophs, if available (Atkinson and Shreeve 1995,
111 Flores et al. 2012a, Schmidt et al. 2014). In other species, e.g. the Arctic *Calanus hyperboreus* and *C.*
112 *glacialis* together with the Antarctic *Calanoides acutus*, the life cycle is closely coupled to the bloom
113 period: they overwinter at depth in dormancy, are able to fuel their gonad maturation from lipid reserves
114 and their offspring make the most of the brief productive season (Hagen and Auel 2001). However,
115 years with very early or very late ice retreat can lead to poor population development of these species
116 (Quetin and Ross 2003, Ward et al. 2006, Leu et al. 2011). Optimal conditions are reached when peak
117 times of food demand and food availability are tightly matched (Quetin and Ross 2003, Søreide et al.
118 2010). A change towards earlier sea ice retreat has been suggested to cause severe mismatches (Søreide
119 et al. 2010). Whether this has already impacted the populations of polar grazers is largely unknown,

120 however, due to the paucity of adequate baseline data that allow us to distinguish interannual variability
121 from long-term trends (Wassmann et al. 2011).

122 An exception is Antarctic krill that have been sampled extensively over the last 90 years due to their
123 central role in Antarctic food webs and their commercial interest (Smetacek and Nicol 2005). The main
124 habitat of Antarctic krill is the south-west Atlantic Sector of the Southern Ocean (Atkinson et al. 2008),
125 which largely overlaps with areas of negative trends in sea ice concentrations (western Antarctic
126 Peninsula, north-west Weddell Sea) (Stammerjohn and Maksym 2017). A long-term data set shows that
127 krill stocks in this region have declined significantly (Atkinson et al. 2014), with consequences for
128 populations of krill predators such as penguins and seals (Fraser and Hoffmann 2003, Forcada and
129 Hoffmann 2014). Concurrent expansion and operational changes in Antarctic krill fisheries (Kawaguchi
130 et al. 2009) make the krill decline a significant issue of Southern Ocean ecosystem management (Flores
131 et al. 2012b). However, the key mechanism linking krill and sea ice remains elusive (Meyer et al. 2017).
132 Some studies stress the crucial role of sea ice for overwinter survival of krill larvae by providing food
133 and shelter (Meyer et al. 2009, Kohlbach et al. 2017), while others point to sea ice as an important
134 habitat for juvenile and adult krill during spring and summer (Marschall 1988, Flores et al. 2012a) or
135 emphasize indirect effects of seasonal ice cover due to its control on summer phytoplankton
136 productivity and therefore krill recruitment (Quetin and Ross 2003, Saba et al. 2014).

137 To resolve some of this uncertainty it is essential to quantify the relative importance of sea ice-
138 derived, sea ice-conditioned and non sea ice-associated primary production for krill nutrition, and to
139 relate dietary differences to the performance of krill in terms of growth, recruitment and accumulation
140 of body reserves. However, ice algae-produced carbon has rarely been traced through Southern Ocean
141 food webs (Goutte et al. 2013, Jia et al. 2016, Kohlbach et al. 2017), as distinguishing it unambiguously
142 from phytoplankton-produced carbon is difficult. Here we tackle this challenge by measuring two
143 highly branched isoprenoid (HBI) biomarkers, which are metabolites of certain diatom species and
144 established proxies for palaeo sea ice reconstructions (Belt and Müller 2013). Around Antarctica,
145 mixtures of a di-unsaturated HBI (referred to as diene II in previous studies; see Fig. S1) and a tri-
146 unsaturated HBI (referred to as triene III in previous studies, thereafter HBI III, Fig. S1) have repeatedly
147 been found in sediment cores, water column samples and Antarctic predators (Massé et al. 2011, Collins
148 et al. 2013, Goutte et al. 2013, 2014a,b, Smik et al. 2016). The samples were obtained from the
149 Atlantic-, Indian- and Pacific sector of the Southern Ocean, suggesting a widespread occurrence of
150 these biomarkers. However, only diene II has been identified in sea ice samples, and its enrichment in
151 ^{13}C ($\delta^{13}\text{C} = -5.7$ to -17.8%) is in line with a depleted dissolved inorganic carbon pool in the semi-

152 enclosed sea ice matrix (Massé et al. 2011). This has led to the name ‘Ice Proxy for the Southern Ocean
153 with 25 carbon atoms’ – IPSO₂₅, with the sympagic diatom *Berkeleya adeliensis* being recently
154 identified as one of the source species (Belt et al. 2016). In contrast, HBI III is produced by certain
155 pelagic diatom species, e.g. *Rhizosolenia* spp. (Belt et al. 2017), and its significantly lighter stable
156 isotopic signature ($\delta^{13}\text{C} = -35.0$ to -41.6‰) indicates a replete carbon pool typical for open waters
157 (Massé et al. 2011). Previous water column and sediment studies have shown relative enhancements in
158 HBI III within the MIZ in the Arctic and Antarctic (Collins et al. 2013, , Belt et al. 2015, Smik et al.
159 2016, Ribeiro et al. 2017), even when other productivity signatures were less revealing, possibly
160 reflecting a preferred habitat for the HBI III-producing species within this setting (Belt et al. 2015). As
161 such, measurements of these two HBIs provide an opportunity to distinguish between direct and indirect
162 effects of sea ice: IPSO₂₅ indicates ice algae-produced carbon, while HBI III indicates phytoplankton-
163 produced carbon in waters conditioned by sea ice (i.e. the MIZ). Importantly, both IPSO₂₅ and HBI III
164 have been identified in body tissues of seabirds, seals and fish, which confirms their transfer across
165 Antarctic food webs and supports their use as trophic markers (Goutte et al. 2013, 2014a,b). However,
166 detailed interpretation of these biomarkers still lacks basic knowledge about (1) the oceanographic
167 conditions (e.g. sea ice history, stratification, mixed layer depth, chl *a* concentration) that favour the
168 abundance of IPSO₂₅ and HBI III-producing diatoms; (2) the subsequent uptake and turnover of IPSO₂₅
169 and HBI III by Antarctic grazers; and (3) the link between the ingested carbon-source and the
170 performance of the grazers.

171 In this study, we contribute to the development of the HBI-based approach by analysing Antarctic
172 krill and suspended material during seasonal sea ice retreat in the Scotia Sea (Atlantic Sector of the
173 Southern Ocean) in January-February 2003. The suitability of different feeding grounds (MIZ,
174 permanently ice-free Scotia Sea, South Georgia) for pelagic grazers was established based on the mass-
175 length ratio, size of digestive gland and growth rate of krill, and recruitment of the biomass-dominant
176 calanoid copepods *Calanoides acutus* and *Calanus propinquus*.

177

178 **2. Methods**

179 *2.1 Satellite-derived chlorophyll *a* data*

180 To gain an overview of phytoplankton development during the year of our field season (2002/2003)
181 and for comparison with other years, we used satellite-derived chlorophyll *a* (chl *a*) data. These provide
182 large-scale, quasi-synoptic coverage of chl *a* concentrations in surface waters, but have the caveat that

183 deep chl *a* maxima are not detected. Data were obtained from ocean colour radiometry (MODIS, 9 km
184 standard product, 8-day composites, 6th of September – 30th of March, 2002-2015). The Scotia Sea
185 (55-63°S, 25-60°W) and South Georgia region (52-55°S, 32-42°W) were divided into subareas of 1°Lat
186 by 2.5°Lon. For each of these subareas the monthly- and seasonal mean chl *a* concentration and bloom
187 duration (number of weeks with chl *a* $\geq 0.5 \text{ mg m}^{-3}$) were determined for the 2002/2003 season and
188 compared with the 13-year average, 2002-2015.

189

190 *2.2 Sea ice cover*

191 For the 2002/ 2003 season, monthly sea ice edges were calculated using sea ice concentrations from
192 Nimbus-7 SMMR and DMSP SSM/I-SSMIS passive microwave data. Monthly composites were
193 calculated using the median of the daily grids for each month. These were then contoured at 15% to
194 extract a line indicating average position of the sea ice edge for each month. Timelines of sea ice cover
195 at each of our sampling stations were established within a 50km radius. Using these zones, we extracted
196 an average value of sea ice concentration on a daily basis. The input data were derived from Microwave
197 Scanning Radiometer-Earth Observation System (AMSR-E) aboard the NASA's Aqua satellite and the
198 Defense Meteorological Satellite Program SSM/I, which is at a higher spatial resolution of 6.25 km.
199 Further details are given in Cavalieri et al. (1996) and Spreen et al. (2008).

200

201 *2.3 Station sampling of oceanographic parameters*

202 Shipboard data were collected from the research vessel RRS 'James Clark Ross' cruise JR82
203 between 9 January and 16 February 2003. Fifty-five hydrographic stations were positioned at 110 km
204 intervals along 8 transects across the Scotia Sea, commencing north of Elephant Island and traversing
205 eastward. A further 6 stations were located to the north-west of South Georgia (Fig. 1). At each station,
206 vertical profiles of conductivity-temperature-depth (CTD) and blue light-stimulated chlorophyll
207 fluorescence were collected with a SeaBird 911+CTD and attached Aqua-Tracka Mk III fluorometer
208 (Chelsea Instruments) (Korb et al. 2005). Mixed-layer depths were calculated as the depth where the
209 density difference ($\Delta\sigma$) relative to the surface water is 0.05 kg m^{-3} (Venables et al. 2013). Size
210 fractionated chl *a* was measured from water samples collected at 20 m depth. Samples were filtered
211 sequentially onto a series of 12, 2 and 0.2 μm polycarbonate membrane filters (47 mm diameter), and
212 analysed for chl *a* after extraction in 90% acetone (Korb et al. 2005).

213

214 *2.4 Sampling of suspended matter, krill and faecal pellets*

215 Suspended matter was sampled from the ship's non-toxic seawater supply located ~6 m below the
216 sea surface. Seawater samples (3 L) were filtered onto pre-ashed GF/F filters and stored at -80°C until
217 analysis. Krill swarms were identified in the vicinity of each station using a Simrad EK60 echosounder
218 and sampled with a Rectangular Midwater Trawl (RMT 8). The RMT was equipped with two nets that
219 were opened and closed remotely from the ship, allowing short duration hauls targeted on specific krill
220 schools in the upper 50 m of the water column. One sub-sample of the freshly caught krill was
221 immediately frozen at -80°C for subsequent analysis of HBIs. Another sub-sample of krill was kept
222 alive to allow for defecation. These krill were placed into buckets filled with surface water and pellets
223 were collected as soon as visible on the bottom of the buckets. The pellets were transferred into 1 ml
224 Eppendorf tubes and rinsed repeatedly with GF/F-filtered seawater with a final brief rinse in deionised
225 water. The supernatant water was removed and vials were stored at -80°C.

226

227 *2.5 Krill dissections*

228 In the laboratory, krill body length was measured from the anterior lateral edge of the carapace to
229 the posterior edge of the sixth abdominal segment (Standard 3 body length). Three to fifteen individuals
230 of the same body length (± 1 mm) were selected for HBI analysis. Standard 3 lengths of selected krill
231 ranged from 16 - 42 mm. If available, up to six different size classes each differing by at least 2 mm,
232 were analysed per station. Then, krill were dissected into stomach content, gut, digestive gland, third
233 abdominal segment (muscle) and remaining body. A pooled sample of each of these components was
234 placed in a pre-weighed vial, freeze-dried for 24 h and re-weighed on a Sartorius microbalance. The
235 mass of the digestive gland was related to the total body mass.

236

237 *2.6 HBI extraction and analysis*

238 HBIs were extracted and analysed as described previously for filtered seawater samples and
239 zooplankton tissue (Brown and Belt 2012, Smik et al. 2016, Belt et al. 2016). In brief, freeze-dried
240 faecal pellets and krill body fractions were ground using a pestle and mortar. Following addition of an
241 internal standard [9-octyl-8-heptadecene (10 μ l; 2 μ g ml⁻¹)] to facilitate HBI quantification, samples
242 were saponified with 5% KOH (filters) or 20% KOH (krill tissue) (70°C; 60 min). Thereafter, non-
243 saponifiable lipids were extracted with hexane (3 x 1 ml) and purified by open column chromatography
244 (SiO₂). HBIs were eluted using hexane (5 column volumes) before being dried (N₂ stream, 25°C). The
245 analysis of partially purified non-polar lipids containing IPSO₂₅ and HBI III was carried out using an
246 Agilent 7890A gas chromatograph, coupled to an Agilent 5975 mass selective detector, fitted with an
247 Agilent HP-5ms column with auto-splitless injection and helium carrier gas. Identification of individual

248 lipids was achieved by comparison of their retention index and mass spectrum with those obtained from
249 purified standards. Quantification of IPSO₂₅ and HBI III was achieved by integrating individual ion
250 (IPSO₂₅: m/z 348.3; HBI III: m/z 346.3) responses in selected-ion monitoring mode, and normalising
251 these to the corresponding peak area of the internal standard and an instrumental response factor
252 obtained from purified standards (Belt et al. 2012). The GC-MS-derived masses of both HBIs were
253 converted to water column concentrations using the volume of filtered seawater, and to concentrations
254 in krill body fractions using the mass of the sample extracted. For simplicity in representing biomarker
255 ratios, we use the terms I and H for IPSO₂₅ and HBI III, respectively. Thus, the proportion of IPSO₂₅ to
256 the combined concentration of IPSO₂₅ and HBI III is given by $I/(I+H)$.

257

258 *2.7 Stable isotope determination*

259 The stable carbon isotopic compositions ($\delta^{13}\text{C}$) of IPSO₂₅ and HBI III were determined in krill from
260 four sampling locations near the retreating ice edge (Stn. 5, 17, 31 and 47). Analysis was carried out by
261 gas chromatography–isotope ratio mass spectrometry (GC–IRMS), using an IsoPrime100 IRMS with
262 GC5 interface and Agilent 7890B GC installed with an Agilent HP-5MS column (30 m \times 0.2 mm
263 I.D., film thickness 0.25 μm). Samples in ca. 10–150 μl hexane were injected in splitless mode with the
264 following inlet conditions: 250°C, purge flow 25 ml min^{-1} , purge time 0.75 min. GC carrier gas (He)
265 flow rate was 1 mL min^{-1} , oven program as follows: 1 minute hold at 50°C, ramp to 310°C at 10°C min^{-1} ,
266 then 13 minute hold. The combustion furnace consisted of a 0.7 mm I.D. quartz tube packed with
267 CuO pellets, held at 850°C. GC–IRMS data were calibrated using the certified Indiana alkane standard
268 mix A5 (Indiana University, Bloomington, IN, USA) and all results reported in delta notation ($\delta^{13}\text{C}$)
269 relative to VPDB. IPSO₂₅ and HBI III were identified in GC–IRMS chromatograms by retention time
270 comparison with corresponding GC–MS analyses. IonOS software (Elementar UK Ltd) was used to
271 process GC–IRMS data; ‘Peak Mapping’ functionality was used to designate specific compound
272 identifications across multiple injections. The A5 alkane mix was analysed in at least duplicate, and
273 calibrations were constructed from at least three interspersed replicate measurements of the A5 mix.
274 Reproducibility of all individual alkanes was always $\leq 0.35\%$. Root mean standard error (RMSE) of
275 each of the calibrations was usually $\leq 0.25\%$, with an overall RMSE for all calibrations combined of \leq
276 0.21 %, reflecting both the reliability of each calibration, and the long-term stability of the system
277 (analyses were undertaken over a three week period in total). Samples containing IPSO₂₅ and HBI III
278 were run in triplicate; precisions for both compounds were ≤ 0.27 (see Table 1).

279

280 *2.8 Copepod abundance and stage composition*

281 Copepods were collected at each station with a motion-compensating Bongo net of 200 μm mesh
282 size. The net was deployed to 400 m and hauled vertically back to the surface. The content of the net
283 was preserved in 10% (v:v) formalin in seawater. In the laboratory, samples were divided into
284 appropriate aliquots with a Folsom plankton splitter and examined under a binocular microscope.
285 *Calanoides acutus* and *Calanus propinquus* were identified to their copepodite stages (CI-V: juveniles,
286 CVI: adults). The mean age of the population was calculated as the sum of the products of each stage
287 number and its abundance, divided by the total abundance.

288

289 **3. Results**

290 *3.1 Development of the Scotia Sea phytoplankton bloom in 2002/2003*

291 In October 2002, elevated chl *a* concentrations ($>0.5 \text{ mg m}^{-3}$) were found north of South Georgia
292 ($\sim 53^\circ\text{S}$), and one month later in the north-eastern Scotia Sea ($\sim 56^\circ\text{S}$, Fig. 2A). With the rapid retreat of
293 sea ice in December 2002, the bloom in the east extended south and reached the northern Weddell Sea
294 in January 2003 ($\sim 62^\circ\text{S}$, Fig. 2B). In February 2003, chl *a* concentrations remained high in the eastern
295 Scotia Sea and at South Georgia, but started to decline in March (Fig. 2C). In the western and central
296 Scotia Sea, chl *a* concentrations remained low throughout the summer, apart from slightly enhanced
297 values across the South Orkney Plateau in January 2003. Compared to the 13-year average (2002-2015),
298 there was a negative anomaly in phytoplankton abundance in the central Scotia Sea in 2002/2003, but a
299 surplus in the east (Fig. 2D, E). At the East Scotia Ridge, mean annual chl *a* concentrations were up to
300 0.7 mg m^{-3} higher and the bloom lasted up to 16 weeks longer in 2002/2003 compared to the 2002-2015
301 average (Fig. 2E).

302

303 *3.2. Spatial distribution of oceanographic data and HBIs*

304 During maximum sea ice extent the previous winter, about two-thirds of our sampling stations were
305 ice covered (Fig. 3A). Thirty days before each station was occupied, the southern Scotia Sea was still
306 ice covered by 50-75 % concentration (Fig. 3B), but values had dropped to $< 6 \%$ at the time of
307 sampling. Surface temperatures ranged from -1.2°C at stations near the ice edge to 4.5°C at South
308 Georgia (Fig. 3C). Surface salinity was likewise lowest near the retreating ice edge and highest within
309 the Southern Antarctic Circumpolar Current Front (range: 33.1-34.4; Fig. 3D). Stations of the Scotia
310 Sea that had been ice covered showed a stronger vertical density gradient and shallower mixed layer
311 than northerly stations that remained ice free (Fig. 3E, F). Highest surface chl *a* concentrations in the

312 eastern Scotia Sea and near South Georgia coincided with the dominance of large phytoplankton size
313 classes (Fig. 3G,H).

314 Out of the 61 stations where suspended matter was analysed for HBIs, 6 contained IPSO₂₅ and 51
315 HBI III (Fig. 4A, B). Stations where IPSO₂₅ occurred in suspended matter were all located near the ice
316 edge (Stn 6, 18, 19, 20, 31, 48), while stations with elevated HBI III concentrations were found near the
317 ice edge (Stn 45, 46, 49-53) and further north (Stn 12, 25, 26, 37, 40). At stations where both HBIs co-
318 occurred, IPSO₂₅ concentrations usually exceeded those of HBI III [mean I/(I+H): 0.6±0.3, n=6; Fig.
319 4C]. In addition to suspended matter, krill from 47 stations were analysed for HBIs. IPSO₂₅ was present
320 in krill from 21, while HBI III was found in krill from all 47 stations (Fig. 4D, E). The spatial
321 distribution of IPSO₂₅ in krill matched that found in suspended matter, with highest concentrations near
322 the ice edge. However, IPSO₂₅ was also detected in krill from stations further north, even though it was
323 not identified in suspended matter from the upper mixed layer. Highest HBI III concentrations in krill
324 were observed in the central Scotia Sea (Stn 13, 14, 22) and in the east (Stn 47, 52, 54), which only
325 partly overlaps with locations of highest HBI III concentrations in suspended matter. However, as for
326 suspended matter, highest I/(I+H) ratios in krill occurred near the ice edge in the western- and central
327 Scotia Sea [mean I/(I+H): 0.3±0.2, n=21; Fig. 4F].

328 329 *3.3 The habitat of IPSO₂₅ vs. HBI III-producing diatoms*

330 The carbon isotopic signature ($\delta^{13}\text{C}$) of IPSO₂₅ extracted from krill sampled at three different
331 locations near the ice edge (Stn 5, 17, 31), ranged from -9.2 to -15.7 ‰ (mean: -12.5±3.2 ‰, Table 1).
332 Such high $\delta^{13}\text{C}$ values are indicative of a depleted dissolved inorganic carbon pool as common in the
333 semi-enclosed sea ice matrix (Wang et al. 2014). In line with a sea ice origin of IPSO₂₅, stations with
334 high IPSO₂₅ concentrations in suspended matter (Stn 18, 19, 20, 31) were characterised by recent sea ice
335 retreat, sub-zero surface temperatures, low surface salinity and relatively low chl *a* concentrations (Fig.
336 5). In contrast, HBI III extracted from the same krill showed much lower $\delta^{13}\text{C}$ values (-39.1 to -42.5 ‰,
337 Table 1), suggesting a production in open waters where the dissolved inorganic carbon pool is replete.
338 Stations with high HBI III concentrations in suspended matter (Stn 45, 50, 51, 52) had been ice-free for
339 ~1 month at the time of sampling. Here, higher temperatures, higher surface salinity and elevated chl *a*
340 concentrations indicate a progression of upper water column processes since the ice melt (Fig. 5).

341 In the south-eastern Scotia Sea, there was a large area where high HBI III concentrations coincided
342 with elevated chl *a* concentrations and high proportions of large phytoplankton (Fig. 3G,H, Fig. 4B).
343 Oceanographically, this area was characterised by shallow upper mixed layers and a strong vertical

344 gradient in salinity (Fig. 3C-F, Fig. S2). A comparison of the stations' history of ice cover shows that
345 the vertical density gradient was driven by ice melt. Across the Scotia Sea, there was a highly
346 significant linear relationship between density- and salinity gradients, with strongest density gradients at
347 stations that had >30% ice cover one month before sampling (Fig. 6). This supports salinity as the main
348 driver of sea water density and therefore stratification at polar temperatures (Smith and Nelson 1986).
349

350 *3.4 IPSO₂₅ and HBI III concentrations in krill – the role of body fraction and body size*

351 The analysis of krill body fractions shows that not all of the ingested IPSO₂₅ and HBI III was
352 absorbed into body tissue, but part remained in the intestine and was then egested via their faecal pellets
353 (Table 2). Thus, IPSO₂₅ and HBI III concentrations were highest in the stomach content, followed by
354 the digestive gland and gut content, and lowest in muscle tissue.

355 The I/(I+H) ratio within the various krill body fractions can reveal recent and past feeding history
356 (Fig. 7A-D). The I/(I+H) ratios in krill stomach content were highest at stations closest to the ice edge
357 in the western and central Scotia Sea, indicating that here the krill diet was mainly based on sea ice
358 diatoms. At 4 stations near the ice edge and up to ~200 km further north, krill had moderate I/(I+H)
359 ratios in their stomach content suggesting a mixed diet of ice-derived diatoms and open water diatoms.
360 Low I/(I+H) ratios in krill stomachs, but higher ratios in their muscle and rest of the body were found at
361 11 stations ~200-600 km north of the ice edge, suggesting that krill had been feeding on ice diatoms in
362 the past, but had switched to open water diatoms by the time of sampling. At 26 mainly northern
363 stations, krill did not contain any detectable IPSO₂₅ and may, therefore, not have fed on ice diatoms
364 within the last few weeks.

365 The I/(I+H) ratios in krill stomach content did not show any relationship with body mass (Fig. 7E),
366 which suggests that both small and large krill had equal access to sea ice diatoms. However, maximum
367 I/(I+H) ratios were lower in muscle tissue than in the stomach content, and ratios dropped linearly with
368 body size (Fig. 7F). This suggest that especially the tissue of larger krill was not in equilibration with a
369 ice algae diet.

370 371 *3.5 Krill performance under different feeding conditions*

372 Based on our analysis, three groups of krill can be distinguished: those that had been feeding on
373 ice diatoms (high IPSO₂₅ content), those that had been feeding on open-water diatoms favoured by
374 conditions at the receding ice edge (high HBI III content) and those that did not feed substantially on
375 either of these diatoms (no/ low IPSO₂₅ or HBI III content). To establish whether one of these feeding

376 histories gave krill an advantage in their condition and performance, we tested three indicators: their
377 mass-length-ratio, the size of their digestive gland and their growth rate. However, as each of these
378 indicators correlates with krill body size, we present the residuals of the indicator-to-body size
379 regression rather than absolute values (i.e. size of digestive gland-to-total mass regressions, growth rate-
380 to-length regression and mass-to-length regression). Using this approach, we found that krill were in
381 best condition near the ice edge in the eastern Scotia Sea (Stn 47) with positive residuals for all three
382 indicators (Fig. 8A-C). Krill sampled at the ice edge in the central Scotia Sea (Stn 20, 31) and at South
383 Georgia (Stn 56-61) showed positive residuals for at least two of these parameters. Overall, the
384 residuals of the krill mass-length regression were mostly positive in the central and eastern Scotia Sea
385 and at South Georgia, but negative in the western Scotia Sea. This is likely due to local differences in
386 the food availability, as indicated by the significant positive relationship between mass-residual and *in*
387 *situ* chl *a* concentration (Fig. 8D). On average, a high IPSO₂₅ content in krill was associated with low
388 chl *a* concentrations and therefore ‘below average’ krill body mass, while a high HBI III content in krill
389 co-occurred with medium chl *a* concentrations and more often with ‘above average’ body mass (Fig.
390 8D).

391

392 *3.6 Recruitment of large calanoid copepods*

393 Another important group of pelagic grazers in the Southern Ocean are calanoid copepods, e.g. the
394 high-latitude species *Calanoides acutus* and *Calanus propinquus*. While HBIs have not been measured
395 in these species, their overall abundance and age structure gives some information about suitable
396 feeding grounds. For both species, abundances were highest at South Georgia and in the south-eastern
397 Scotia Sea (Fig. S3). The latter site was dominated by young development stages (CI-III), which
398 indicates recent successful recruitment (Fig. 8E,F). At South Georgia, the population was older, but also
399 dominated by new recruits (CIV). In contrast, in the western Scotia Sea copepod abundances were low,
400 and the population consisted of ‘overwintered’ copepodite stages (CV and females), suggesting that
401 recruitment was delayed or had failed.

402

403 **4. Discussion**

404 *4.1 Evaluating the HBI approach*

405 Knowledge of the role of ice algae- vs. phytoplankton-produced carbon for higher trophic levels is
406 central to our understanding of polar ecosystems. However, reliable estimates are difficult to achieve.
407 Firstly, traditional trophic markers such as fatty acids, accessory pigments or taxonomy are of limited

408 use as diatoms often dominate both communities with few species being obligate ice inhabitants (Arrigo
409 2017). Secondly, approaches that allow the separation of the two sources based on non-conservative
410 tracers, including bulk- or compound-specific stable isotope analysis, rely on numerous assumptions
411 that are not always met in practice (Budge et al. 2008). An example is isotopic fractionation, where the
412 $\delta^{13}\text{C}$ values of fatty acids derived from diatoms, and not produced *de novo* by the consumer [e.g.
413 16:4(n-1) or 20:5(n-3)] are usually assumed to remain unchanged across trophic levels (e.g. Budge et al.
414 2008, Wang et al. 2015, Kohlbach et al. 2017). However, laboratory and field studies have shown
415 significant isotopic fractionation (-4 to -1‰) in polyunsaturated fatty acids between diet and consumer,
416 and a gradual depletion in the ^{13}C content of fatty acids upward through the food chain (Bec et al. 2011,
417 Gladyshev et al. 2012 and ref. therein). If this isotopic fractionation remains unaccounted for, the
418 contribution of the isotopically lighter source is overestimated and this bias increases with shorter
419 isotopic distance between the endmembers (Bec et al. 2011). Based on data obtained from Antarctic
420 krill by Kohlbach et al. (2017), the ice algae source of 20:5(n-3) increased from 64 to 89% in larvae,
421 from 46 to 70% in juveniles and from -18 to 7% in adults if a fractionation of -1.5‰ between diatoms
422 and grazer was implemented, according to Bec et al. (2011). This illustrates that the interpretation of
423 fatty acid-specific stable isotope data can be severely skewed if possible 'digestive' ^{13}C depletion of
424 fatty acids is not considered (Gladyshev et al. 2012).

425 In contrast to fatty acids, where one marker [e.g. 20:5(n-3)] carries the mixed isotopic signal from
426 two food sources with additional fractionation within the grazer, the HBI approach is more straight-
427 forward. Here, two independent markers exist, one for ice algae (IPSO₂₅) and one for phytoplankton
428 (HBI III). Thus, if IPSO₂₅ occurred in krill in the present study, it unambiguously indicated their
429 consumption of ice algae. Moreover, the relative abundance of IPSO₂₅ and HBI III [I/(I+H)] remained
430 the same during transfer from krill stomach to the digestive gland (Fig. 7), which suggests that there
431 was no selective absorption or degradation within the grazer. This is in line with laboratory experiments
432 which showed near identical HBI ratios in the brine shrimp *Artemia* sp. and its food (Brown and Belt
433 2017). Thus, key advantages of the HBI approach are the existence of a sea ice proxy and its open water
434 counterpart, and minimal signature alterations by the consumer.

435 On the other hand, disadvantages of the HBI approach may arise from the generally lower abundance
436 of these markers. While fatty acids are ubiquitous to marine life, HBIs are only produced by certain
437 diatom species (Brown et al. 2014, Belt et al. 2017 and references therein). Four such species are
438 currently known to produce the Arctic sea ice proxy IP₂₅ (Brown et al. 2014), while in the Southern
439 Ocean so far only one diatom species has been identified as a source of IPSO₂₅ (*Berkeleya adeliensis*,

440 Belt et al. 2016). The four Arctic source species are considered omnipresent in sea ice, however, and the
441 application of IP₂₅ as a proxy for palaeo Arctic sea ice reconstructions is well established (Belt and
442 Müller 2013). In contrast, research effort on HBIs in the Southern Ocean started more recently and
443 initial findings require further confirmation. For instance, the known Antarctic source of IPSO₂₅, *B.*
444 *adeliensis*, is commonly associated with landfast ice and blooms in spring/ early summer, which may
445 limit its use as a sea ice proxy in oceanic settings or during winter (Belt et al. 2016). However, sediment
446 cores, sea ice samples, water samples and Antarctic predators indicate a widespread occurrence of
447 IPSO₂₅, including coastal- and open ocean regions, and samples obtained in summer and winter (this
448 study, Massé et al. 2011, Goutte et al. 2013, Collins et al. 2013). This suggests co-production of IPSO₂₅
449 by as yet unidentified source species or by *B. adeliensis* also inhabiting non-coastal sea ice.

450 The proportion of IPSO₂₅ in the combined IPSO₂₅ and HBI III pool [$I/(I+H)$ as presented in this
451 study] is only a relative indicator of ice algae- vs. phytoplankton produced carbon. A translation into
452 carbon values would require that the POC-to-HBI ratio is estimated for the local end-members (ice
453 algae, phytoplankton) and that $I/(I+H)$ ratios are calibrated with known proportions of these end-
454 members. Such calibration has been carried out for ratios of pelagic- vs. sympagic HBIs common in the
455 Arctic via the so-called HBI-fingerprint ('H-print'; Brown and Belt 2017), and subsequently applied to
456 obtain quantitative estimates of ice-derived carbon in Arctic amphipods (Brown et al. 2017). However,
457 in this study we did not assess the absolute amount of carbon that krill acquire from ice algae. Instead
458 we aimed for a mechanistic understanding of the role of sea ice for grazers such as krill, considering
459 both carbon-production within sea ice and conditioning effects of sea ice that promote phytoplankton
460 blooms.

461 After the initial application of HBIs as trophic markers in Southern Ocean food web studies by
462 Goutte et al. (2013, 2014a, 2014b), our results provide three lines of evidence for the robustness of this
463 approach: First, the carbon isotopic signatures ($\delta^{13}\text{C}$) of IPSO₂₅ and HBI III confirm their different
464 origins in sympagic vs. pelagic diatoms (Table 1). Second, given our open water set of sampling
465 stations, both HBIs occurred in highest concentrations in suspended matter near the retreating ice edge;
466 but they were associated with different oceanographic conditions. IPSO₂₅ coincided with sea ice cover
467 and low temperatures, while HBI III peaked where melt water-driven stratification and enhanced chl *a*
468 concentrations indicate favourable conditions for phytoplankton growth (Fig. 5). Third, there was a
469 spatial overlap in the occurrence of HBIs in suspended matter and krill, which points to a direct trophic
470 transfer (Fig. 4). The $I/(I+H)$ ratios in krill stomachs, and therefore the dietary role of ice diatoms,
471 decreased with the stations distance from the ice edge (Fig. 7). In conclusion, the HBI approach has

472 delivered plausible results and overcomes some of the limitations of other trophic markers. Therefore,
473 we consider it a suitable tool to assess the role of ice algae and ice-conditioned phytoplankton for
474 Southern Ocean grazers. However, given the different strengths and weaknesses of HBI, fatty acid-
475 specific stable isotopes and other trophic markers, their combined application is likely to increase the
476 robustness of the results and the amount of detail revealed (Schmidt et al. 2006).

477 478 *4.2 The role of ice algae-produced carbon for krill nutrition*

479 Trophic markers such as HBIs, fatty acids or stable isotopes have different residence times in the
480 various body compartments of consumers depending on their turnover- and growth rates (Schmidt and
481 Atkinson 2016). In the krill muscle, for instance, turnover is relatively slow and markers may be
482 conserved within this tissue for several weeks after their uptake. This allows us to gain information
483 about the consumer's feeding history. On the down side, time-integrated signals from muscle tissue
484 cannot be related to specific environmental conditions at the time of sampling or mobile features such
485 as the retreating ice edge. This is especially true in the Scotia Sea, where local retention as well as large-
486 scale advection of krill may occur (Meyer et al. 2017). We overcame this problem by analysing HBIs in
487 the krill stomach. The stomach content has a much faster turnover time than muscle tissue, varying
488 between 45 min and ~10 h in krill (Schmidt and Atkinson 2016). This 'snapshot' of their diet permits a
489 direct comparison between the uptake of IPSO_{25} and HBI III by krill and the occurrence of these
490 markers in the suspended matter of their sampling location.

491 At five stations near the ice edge, krill stomachs contained a higher proportion of ice algae
492 [$I/(I+H)_{\text{Stomach}}$: 0.93 ± 0.03] than the suspended matter in surface waters [$I/(I+H)_{\text{SM}}$: 0.68 ± 0.21]. Up to
493 200 km north of the ice edge, a mixture of ice algae and phytoplankton was found in krill stomachs
494 [$I/(I+H)_{\text{Stomach}}$: 0.56 ± 0.24], while IPSO_{25} was not detected in suspended matter from surface waters.
495 These observations suggest that krill fed preferentially on ice algae and sampled them below the upper
496 mixed layer, either during their diurnal vertical migration or in special foraging trips towards the
497 benthos (Schmidt et al. 2011). At Stn 8, for instance, a high $I/(I+H)$ ratio coincided with lithogenic
498 particles in krill stomachs, which may have been ingested at the seabed (Schmidt et al. 2011). About
499 200-600 km north of the ice edge, IPSO_{25} was found in krill muscle tissue, but not in their stomachs.
500 These results indicate that krill had been feeding on ice algae in the past, but subsequently relied on
501 phytoplankton. Overall, IPSO_{25} was detected in krill from 21 stations across the western and central
502 Scotia Sea, confirming the widespread uptake of ice algae as a food source.

503 We found different trends between krill body mass and their I/(I+H) ratios in stomach content and
504 muscle, Small krill were equilibrated with the ice algae diet, having high I/(I+H) ratios in both stomach
505 and muscle, while larger krill had high I/(I+H) ratios only in their stomachs and not in their muscles
506 (Fig. 7). This suggests that larger krill did not feed long enough on ice algae to reach equilibrium
507 between diet and body tissue. Most likely, ice algae became more accessible to krill when the ice started
508 to melt (Jia et al. 2016). The IPSO₂₅ extracted from krill was enriched in $\delta^{13}\text{C}$ (Table 1), as is typical for
509 material from interior sea ice (McMinn et al. 1999, Wang et al. 2014) that is only within reach of krill
510 when the algae are released into the water column. A carbon budget of ice algae in the Canadian Arctic
511 in spring showed that >65% of the biomass, released from sea ice into the upper water column,
512 remained suspended (Michel et al. 1996). However, the high variability in chl *a* residence time (mean:
513 31 ± 33 days) and sinking rate (mean: 1.4 ± 1.5 m d⁻¹) illustrates the dual fate of ice algae (Michel et al.
514 1996). While some algae rapidly sink out of the euphotic zone and efficiently transfers carbon to the
515 benthos (e.g. Riebesell et al. 1991, Renaud et al. 2007), others remain suspended over several weeks
516 and can aid the nutrition of pelagic grazers (Michel et al. 1996, Smik et al. 2016). In any case, the
517 trophic importance of ice algae extends beyond the period of their maximum production in sea ice
518 (Michel et al. 1996). Here, the ice proxy IPSO₂₅ revealed that ice algae can be an important food source
519 for krill even several weeks after the ice cover has disappeared.

520 In the western and central Scotia Sea, phytoplankton concentrations were low and the community
521 was dominated by small size classes (< 12 μm) during spring and summer 2002/2003 (Fig. 3, Korb et
522 al. 2005). This may explain why krill continued feeding on ice algae even after the algae had descended
523 out of surface waters. In some years, phytoplankton blooms seem not to take off in this region, and light
524 limitation, iron deficiency and grazing pressure have been discussed as potential reasons (Lancelot et al.
525 1993, Korb et al. 2005, Park et al. 2010). Our study period coincided with a negative phase of the
526 Southern Annular Mode (www.nerc-bas.ac.uk/public/icd/gjma/newsam.1957.2007.txt), which is
527 characterised by reduced strength and duration of wind mixing events (Saba et al. 2014). This led to
528 shallow mixed layers and deep euphotic depths, constituting favourable light conditions for
529 phytoplankton growth (Fig. 3, Korb et al. 2005). However, 2002/2003 was also a year of good krill
530 recruitment (Atkinson et al. 2014) and high krill densities occurred especially in the western and central
531 Scotia Sea (authors' unpubl. observations). At 7 stations in the central Scotia Sea, krill contained high
532 amounts of HBI III ($110\text{-}3460$ ng g⁻¹, esp. Stn 22, Fig. 4), even though there was little evidence of HBI
533 III in the suspended matter in surface waters at that time. This suggests that diatom species favoured
534 within the MIZ were produced in the central Scotia Sea, but did not accumulate, possibly due to high

535 grazing losses. A 13-year data set of satellite-derived chl *a* concentrations shows that the area where
536 krill contained high amounts of HBI III (Fig. 4E) matches the region with exceptionally low surface chl
537 *a* concentrations in the central Scotia Sea in the 2002/2003 season (Fig. 2E).

538 The combination of high krill densities and low food availability can lead to competition-induced
539 starvation (Ryabov et al. 2017). Such an effect may be seen in the krill's weight-to-length ratios. At
540 most stations in the western and central Scotia Sea, krill were lighter than predicted from their body
541 length, showing negative residuals from the mass-length regression (Fig. 8C). These stations largely
542 coincided with those where krill contained the ice proxy IPSO₂₅. However, the presence of IPSO₂₅ in
543 krill distant from the ice edge may simply indicate a shortage of their main summer food –
544 phytoplankton. More relevant is the link between IPSO₂₅ and krill performance at stations near the ice
545 edge, where ice algae were prominent in their stomachs. Of these six stations, two provided good
546 feeding conditions for krill (positive residuals, Stn 20, 31), while four did not (negative residuals, Stn 5,
547 6, 18, 30). This is in line with other studies showing high variability in food supply from sea ice
548 (Marschall et al. 1988, Michels et al. 2008, Schmidt et al. 2012, 2014, Meyer et al. 2017). Local
549 differences in snow cover, ice thickness, ice rafting or time of ice formation can lead to different
550 concentrations of ice algae in the bottom ice layer (Fritsen et al. 2008, Meiners et al. 2012). However,
551 below-average krill body mass was even found in individuals that contained high concentrations of
552 IPSO₂₅ (Stn. 5, 18), while krill with positive residuals from the mass-length regression showed high
553 concentrations of both IPSO₂₅ and HBI III (Stn 30) or mainly HBI III (Stn 20). This confirms the
554 essential role of phytoplankton blooms for krill performance in spring (Cuzin-Roudy et al. 1992,
555 Schmidt et al. 2012).

556 557 *4.3 The role of sea ice-conditioned phytoplankton blooms*

558 Offshore regions of the Southern Ocean are often characterised by high-nitrate-low-chlorophyll
559 (HNLC) conditions due to the shortage of iron. However, in the Scotia Sea primary and secondary
560 production can be comparatively high (Atkinson et al. 2008, Park et al. 2010). In 2002/2003, late sea ice
561 retreat coincided with a negative phase of the Southern Annular Mode, volcanic activity at Mount
562 Belinda (~ 80 km east off Stn. 50) and high krill abundances (authors' unpublished observations,
563 Patrick et al. 2005, Ward et al. 2006). This would have provided favourable light conditions and iron
564 (Korb et al. 2005, Lannuzel et al. 2010, Browning et al. 2014), but also enhanced grazing impact and
565 nutrient recycling (Schmidt et al. 2016). Perhaps as a consequence, the phytoplankton bloom was
566 unusually long-lasting and intensive across the East Scotia Ridge, but weaker than average in the central
567 Scotia Sea (Fig. 2; Park et al. 2010). Sea ice retreat can assist phytoplankton growth due to the freshness

568 of the meltwater, following brine rejection during ice formation. The low-salinity (hence low-density)
569 input enhances water column stability, thereby reducing vertical mixing and retaining phytoplankton in
570 an optimal light environment (Smith and Nelson 1986). However, meltwater lenses do not always lead
571 to ice edge blooms. In the eastern Scotia Sea, phytoplankton blooms propagated behind the receding ice
572 edge over hundreds of kilometres and for several months (Fig. 2). In contrast, in the western and central
573 Scotia Sea, strong density gradients occurred upon ice retreat but phytoplankton did not accumulate. A
574 reason for these differences may be the speed of ice retreat (Constable et al. 2003). Between mid
575 December and mid February, ice retreated at $\sim 1.7 \text{ km d}^{-1}$ in the west and at 11.7 km d^{-1} in the east
576 (authors' unpublished data). Rapid ice retreat enhances the volume and spatial extent of meltwater input
577 and therefore the likelihood that stratification persists long enough for marked phytoplankton growth
578 and accumulation (Smith and Nelson 1986,). Other factors controlling phytoplankton development
579 along the receding ice-edge include iron deficiency and grazing pressure by zooplankton (Tréguer and
580 Jacques 1992, Lancelot et al. 1993).

581 Ice-edge phytoplankton blooms have been reported throughout the Arctic (Perrette et al. 2011) and
582 from the Ross Sea, Weddell Sea, Scotia Sea, Prydz Bay and the Pacific sector of the Southern Ocean
583 (e.g. Smith and Nelson 1986, Constable et al. 2003 and references therein). However, the overall
584 importance of primary production in the MIZ is still debated (Vancoppenolle et al. 2013). Originally,
585 the MIZ was considered a major hotspot for autotrophic production in the Southern Ocean (Smith and
586 Nelson 1986). Subsequent analysis of satellite data, however, suggests that phytoplankton blooms in the
587 MIZ are largely suppressed at high wind speed, and even with lower winds, blooms occur only over
588 one-third of the MIZ (Fitch and Moore 2007). Therefore, area-normalised primary production rates
589 calculated from ocean colour are on average only slightly higher in the MIZ than in the permanently
590 ice-free Southern Ocean (Arrigo et al. 2008). This has led to the conclusion that while the MIZ has the
591 potential to be productive, physical conditions are seldom conducive to the development of intense,
592 longer-lived phytoplankton blooms (Arrigo et al. 2008). On the other hand, high abundances of
593 zooplankton, seabirds and whales are characteristic of the MIZ and confirm enhanced biological activity
594 and the importance of this region for the food web (Brown and Lockyer 1984, Ichii et al. 1990, Ainley
595 et al. 2017).

596 Antarctic krill sampled in the previously ice covered eastern Scotia Sea had high HBI III
597 concentrations and above-average body mass (i.e. positive residuals in Fig. 8C). The occurrence of HBI
598 III in krill tissue often coincided with medium to high chl *a* concentrations in the water column (Fig.
599 8D). Therefore, enhanced krill performance in the east is most likely a result of higher food

600 concentrations. A number of studies have previously found chl *a* concentrations to represent a reliable
601 predictor of krill growth and maturation (Ross et al. 2000, Atkinson et al. 2006, Schmidt et al. 2012,
602 Meyer et al. 2017). Krill from the most southerly station of the eastern transects (Stn 47) were in
603 similarly good conditions to those at South Georgia, showing high body mass, large digestive gland and
604 exceptionally high growth rates when adjusted for their length. This is unexpected considering that, at
605 the time of sampling, only 2 weeks of elevated chl *a* concentrations ($>0.5 \text{ mg m}^{-3}$) were recorded at Stn.
606 47, but ~16 weeks at South Georgia (based on ocean colour data, Fig. 2). A previous study revealed that
607 krill can engage in “superfluous” feeding when food is abundant (Schmidt et al. 2012). This way, the
608 food concentration in their digestive tract remains high and nutrient absorption per unit time is
609 maximised. Consequently, krill can rapidly improve their body condition and advance in maturation
610 (Schmidt et al. 2012). IPSO₂₅ was not detected in krill from Stn. 47, but was found in low
611 concentrations in suspended matter at the neighbouring station closer to the ice edge (Stn. 48). Station
612 47 had been ice free for ~20 days when krill were sampled, which is approximately the turnover-time of
613 the Arctic sea ice proxy in zooplankton (Brown and Belt 2012). Therefore, krill may have been feeding
614 on ice algae at this station, but any indication of this via IPSO₂₅ was lost following their switch to
615 phytoplankton.

616 A few copepod species inhabit Antarctic sea ice, but the biomass dominant copepod grazers in high
617 latitudes, *Calanoides acutus* and *Calanus propinquus*, are only loosely associated with sea ice, if at all
618 (Arndt and Swadling 2006). *C. acutus* shows reduced feeding activity within the ice and their offspring
619 only occur in the MIZ or open waters (Atkinson and Shreeve 1995, Burghart et al 1999). In contrast, *C.*
620 *propinquus* have been found feeding on ice algae and spawning below sea ice, but their populations
621 likewise expand mainly in open waters (Atkinson and Shreeve 1995, Burghart et al 1999). Both species
622 can complete their life cycle at South Georgia (Atkinson and Peck 1988), which is permanently sea ice-
623 free. During our study period, the occurrence and recruitment of these species showed similarities to
624 feeding behaviour and performance of Antarctic krill. In the western and central Scotia Sea, *C. acutus*
625 and *C. propinquus* had low abundances and the populations were dominated by females and late
626 copepodite stages representing the ‘old, overwintered’ generation. This delay or failure of recruitment
627 was likely caused by the lack of phytoplankton, as also indicated by krill feeding on sinking ice algae in
628 open waters, and their below-average body mass. Highest copepod abundances in the south-east
629 coincided with the dominance of early copepodite stages (i.e. the ‘new’ generation). This region of
630 intensive copepod reproduction (Stn 45, 50, 51, 52) matches high HBI III concentrations in suspended
631 matter and enhanced krill performance in the wake of retreating sea ice. We therefore suggest that the

632 MIZ is an important nursery ground for these large copepod species, in line with previous findings
633 (Atkinson and Shreeve 1995, Burghart et al. 1999). At South Georgia, the copepod populations of *C.*
634 *acutus* and *C. propinquus* were further advanced in their seasonal development (dominated by medium
635 copepodite stages of the ‘new’ generation), but the overall abundances were similar to those in the
636 south.

637 The weak, sporadic link between large calanoid copepods and ice algae in the Antarctic contrasts
638 with conditions in the Arctic. Here ice algae serve as an important food source for spawning females of
639 *Calanus glacialis* (Søreide et al. 2010, Durbin and Casas 2013) and the early developmental stages of *C.*
640 *hyperboreus* (Conover 1988). Average primary production rates in sea ice are considered lower in the
641 Southern Ocean than in the Arctic (Arrigo 2017). In the Antarctic, ~85% of sea ice is annual and needs
642 to be newly inhabited every year (Stammerjohn and Maksym 2017). However, as much of this sea ice
643 forms over deep ocean, re-colonisation from the benthos or via lateral dispersion from perennial sea ice
644 is unlikely, leaving the water column as the sole source (Arndt and Swadling 2006). In contrast, Arctic
645 sea ice covers comparatively shallow waters, and traditionally has a larger proportion of perennial sea
646 ice, which increases the chances of re-colonisation. Another factor influencing productivity in sea ice is
647 the level of irradiance available to primary producers (Meiners et al. 2012). Antarctic pack ice
648 experiences some of the largest snowfall rates on Earth, while melt ponds are widespread in the Arctic
649 (Vancoppenolle et al. 2013). The former attenuates light, whereas the latter efficiently transmits it to the
650 underlying ocean.

651

652 **Conclusion**

653 Large parts of the Southern Ocean are characterised by low phytoplankton concentrations due to
654 the lack of iron, strong vertical mixing or grazing and other losses. Our study suggests that in such
655 areas, pelagic grazers may benefit from seasonal sea ice in two ways. Firstly, suspended or sinking ice
656 algae can supplement their diet in spring and summer. Second, retreating sea ice enhances the likelihood
657 of bloom formation due to shoaling of the mixed layer, supply of iron and/or release of a seeding
658 population. Phytoplankton blooms initiated in the MIZ allow zooplankton to grow rapidly, gain body
659 reserves and advance in their development. Therefore, current and future changes in sea ice will not
660 only affect sympagic fauna, but also zooplankton species that inhabit open waters adjacent to it. The
661 analysis of two source-specific highly branched isoprenoids provided a useful tool to trace ice-produced
662 and ice-conditioned food sources within pelagic grazers. Essential for their further application will be to
663 resolve the spatial and temporal occurrence of the ice proxy IPSO₂₅, and to gauge the carbon-to-

664 isoprenoid ratios of ice algae and phytoplankton. Development of the HBI trophic marker approach,
665 alongside other methods, will help us to understand exactly how Arctic and Antarctic food webs depend
666 on sea ice.

667

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978 **Table 1.** *Euphausia superba*: carbon isotopic signature ($\delta^{13}\text{C}$) of IPSO₂₅ and HBI III extracted from ~30
 979 pooled, whole krill (mean \pm SD, n=3) at four sampling locations near the retreating ice edge.

	Stn 5	Stn 17	Stn 31	Stn 47	Mean
$\delta^{13}\text{C}$ - IPSO ₂₅ (‰)	-15.75 \pm 0.15	-12.63 \pm 0.15	-9.21 \pm 0.02	-	-12.53 \pm 3.27
$\delta^{13}\text{C}$ - HBI III (‰)	-42.54 \pm 0.27	-	-39.09 \pm 0.16	-45.05 \pm 0.07	-42.23 \pm 2.44

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984 **Table 2.** *Euphausia superba*: concentrations of IPSO₂₅ and HBI III in different body fractions. Average
 985 stomach values are used as baseline for comparisons across body fractions, 'Ratio (stomach/X)'. X –
 986 digestive gland, gut, muscle, rest or whole krill. The I/(I+H) ratio was calculated as the ratio of means
 987 for those stations where both IPSO₂₅ and HBI III had been detected in at least one of the body fractions.
 988 r - range

	IPSO ₂₅			HBI III			I/(I+H)
	Mean (\pm SD) (ng g ⁻¹)	Maximum (ng g ⁻¹)	Ratio (stomach/X)	Mean (\pm SD) (ng g ⁻¹)	Maximum (ng g ⁻¹)	Ratio (stomach/X)	Ratio of Means
Stomach	2875 \pm 5277	14337		14358 \pm 18844	58902		0.17 r: 0.00-0.95
Digestive gland	958 \pm 1609	4523	3	5018 \pm 6043	19686	3	0.16 r: 0.00-0.92
Gut	812 \pm 1414	3601	3.5	52027 \pm 167732	584461	0.3	0.02 r: 0.00-0.91
Muscle	51 \pm 46	125	56	245 \pm 238	861	59	0.17 r: 0.01-0.51
Rest	188 \pm 160	387	15	804 \pm 731	2340	18	0.19 r: 0.00-0.62
Whole krill	219 \pm 222	618	13	1393 \pm 1638	3221	10	0.14 r: 0.00-0.73
Pellets	1549 \pm 379	1973		1263 \pm 410	4419		

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990 Analysed stations (IPSO₂₅): Stn 5, 10, 13, 14, 17, 22, 31, 34, 54

991 Analysed stations (HBI III): Stn 5, 10, 13, 14, 17, 22, 31, 34, 47, 54, 60

992 Analysed stations [I/(I+H)]: Stn 5, 10, 13, 14, 17, 22, 31, 34, 54

993 Analysed stations, pellets (IPSO₂₅): Stn 21, 32

994 Analysed stations, pellets (HBI III): Stn 9, 10, 15, 21, 31, 32, 34, 42, 45, 47, 52, 54, 60, 61

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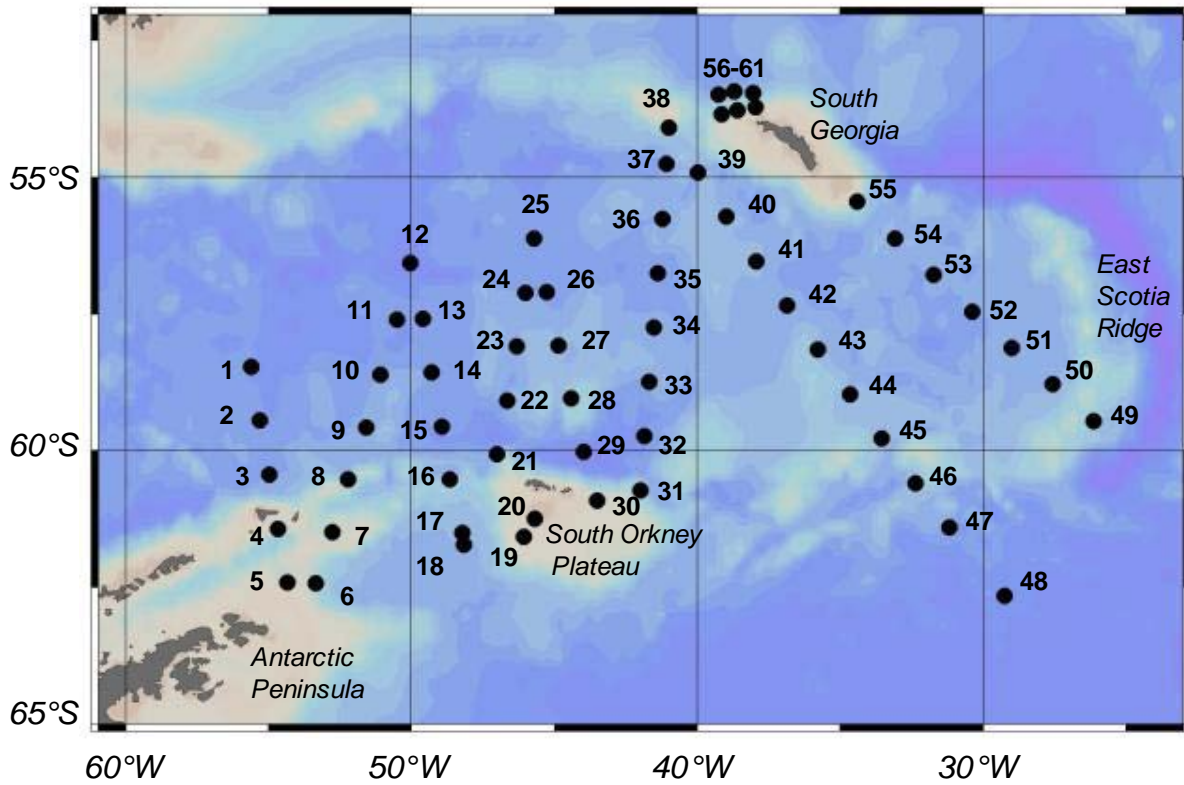


Fig. 1

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998 **Fig. 1.** Scotia Sea and South Georgia: sampling locations during austral summer 2003. The date of
 999 sampling progressed from January, 9th (Station 1) to February 16th (Station 61). Shelf areas (≤ 1000 m)
 1000 are presented in light brown colour.

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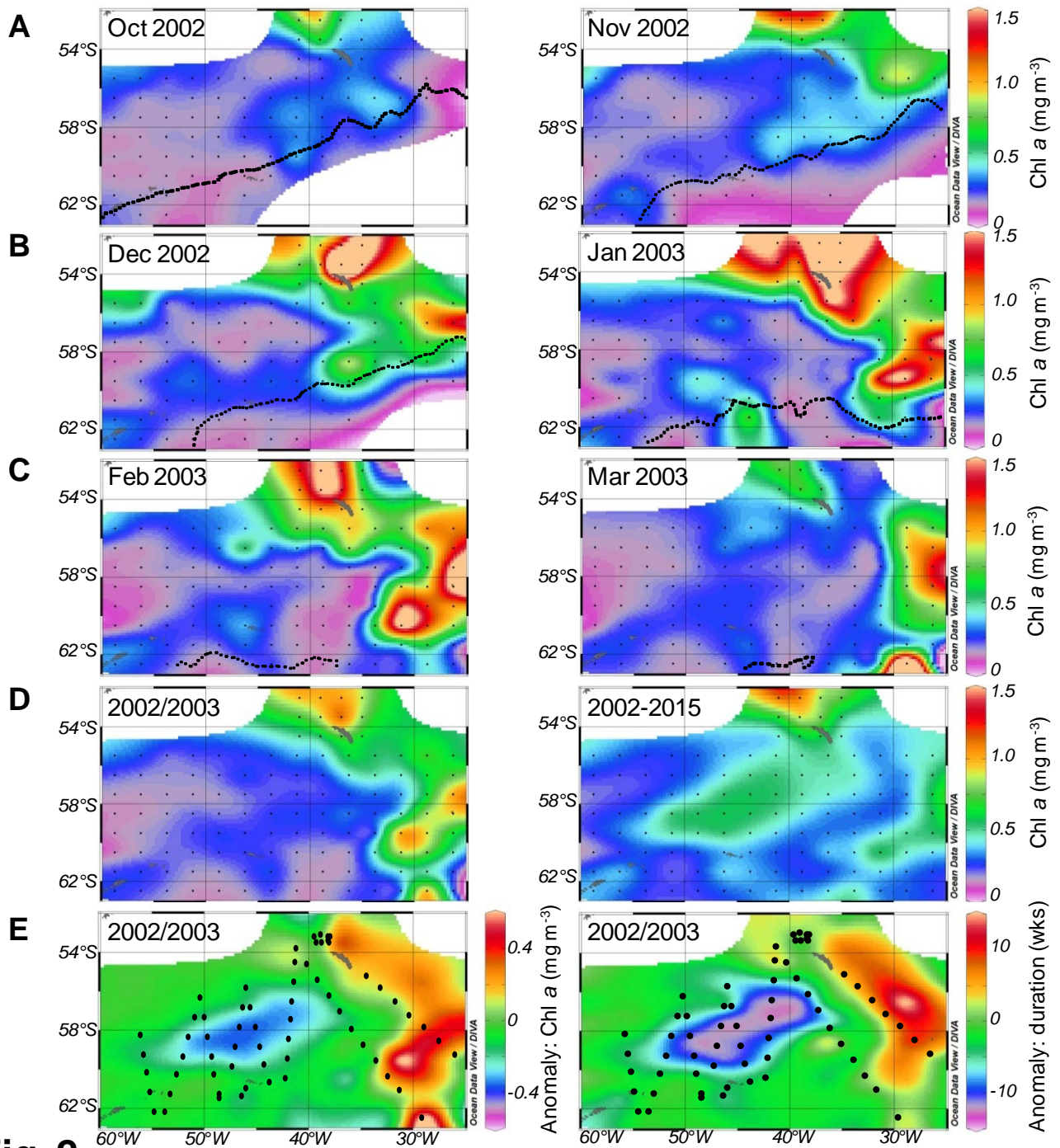


Fig. 2

Fig. 2. Phytoplankton bloom development in the Scotia Sea. Monthly mean chl *a* concentrations in the 2002/2003 season; **A)** the early season, **B)** the mid-season, and **C)** the late season. **D)** Seasonal mean chl *a* concentrations (Sept-Mar) in 2002/2003 and over the 13-year average of 2002-2015. **E)** Anomaly in seasonal mean chl *a* concentration and bloom duration for 2002/2003 compared to the 13-year average of 2002-2015. Chl *a* concentrations were derived from ocean colour radiometry (MODIS, 8-day composites, Sept-Mar). A bloom was defined as $>0.5 \text{ mg Chl } a \text{ m}^{-3}$. The dashed line represents the

1015 mean position of the 15% ice edge during each of the months. In panels E, the position of our sampling
1016 stations is given.

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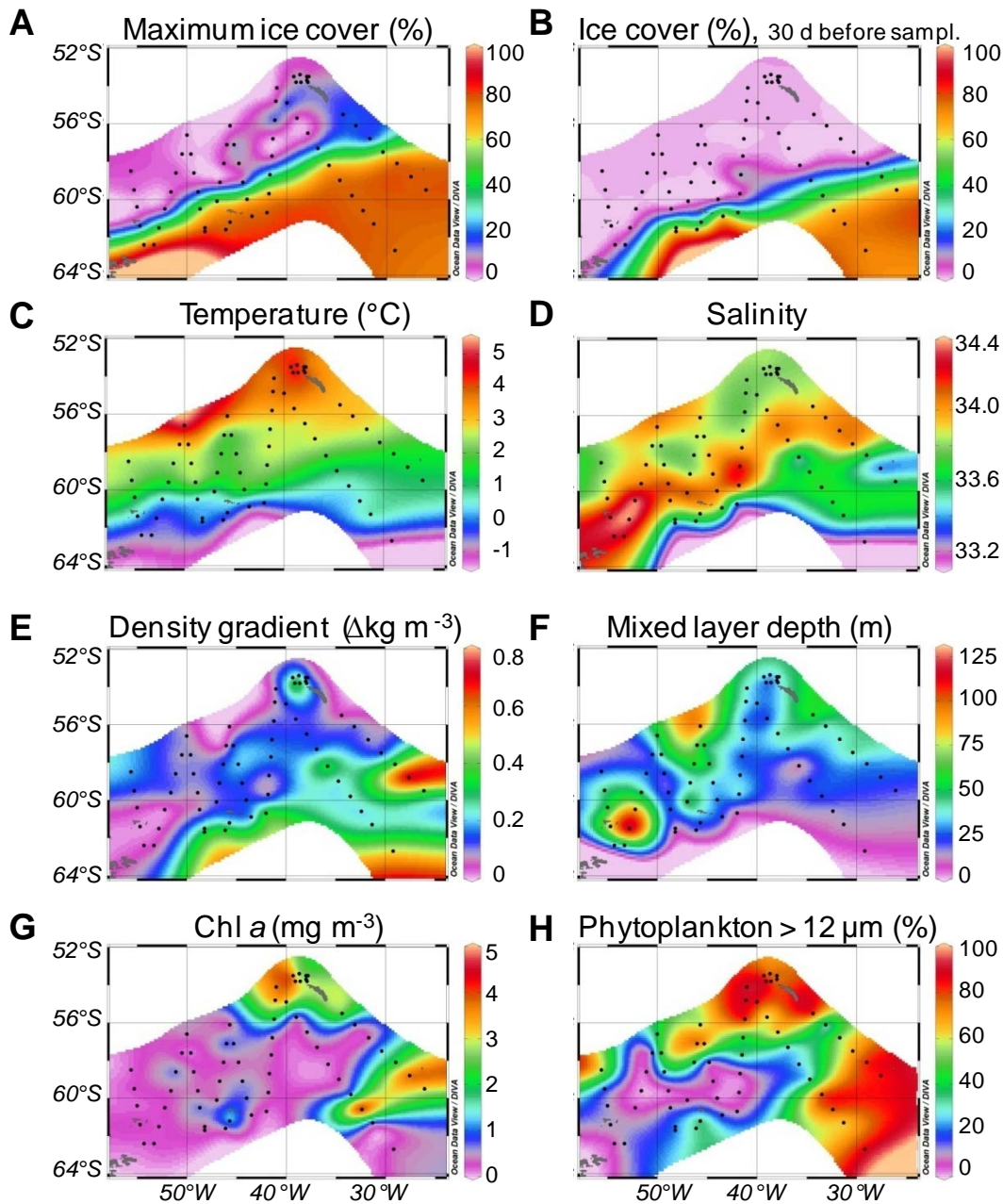


Fig. 3

Fig. 3. Oceanographic data: **A)** Maximum ice cover during the previous winter (Aug/ Sept/ Oct 2002). **B)** Ice cover 30 days before each station was occupied. **C)** Surface temperature, **D)** Surface salinity, **E)** Maximum density gradient per 10 m water column, **F)** Mixed layer depth, **G)** Total chlorophyll *a* (Chl *a*) concentration of cells >0.2 μm , **H)** Proportion of large phytoplankton (>12 μm) based on size-fractionated Chl *a* measurements (% of total Chl *a*).

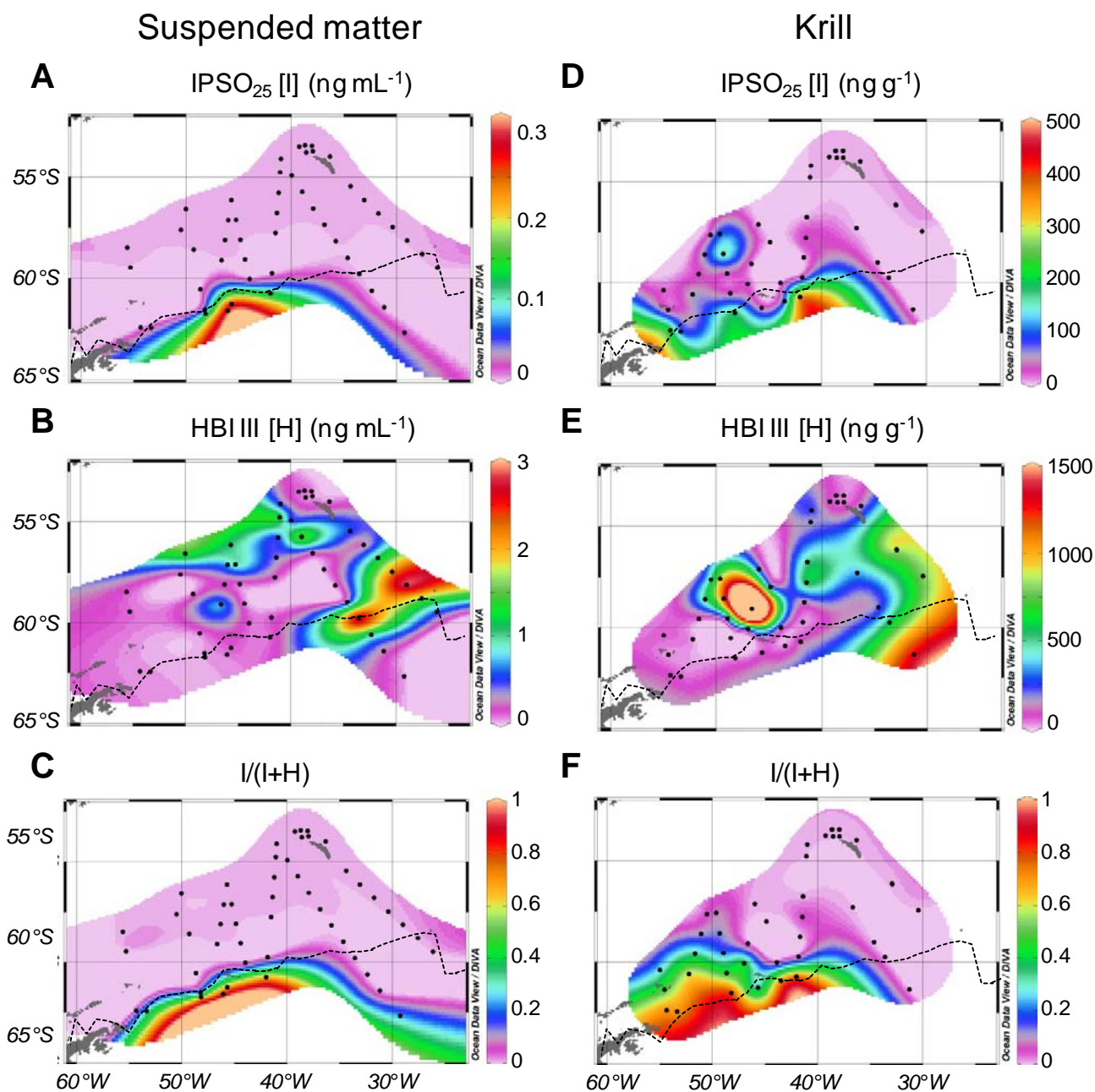


Fig. 4

Fig. 4. Highly branched isoprenoid (HBI) concentrations in suspended matter from surface waters (left) and whole krill (right): **A, D**) IPSO_{25} concentrations. **B, E**) HBI III concentrations. **C, F**) IPSO_{25} vs HBI III ratios. The dashed line represents the mean position of the 15% ice edge during January.

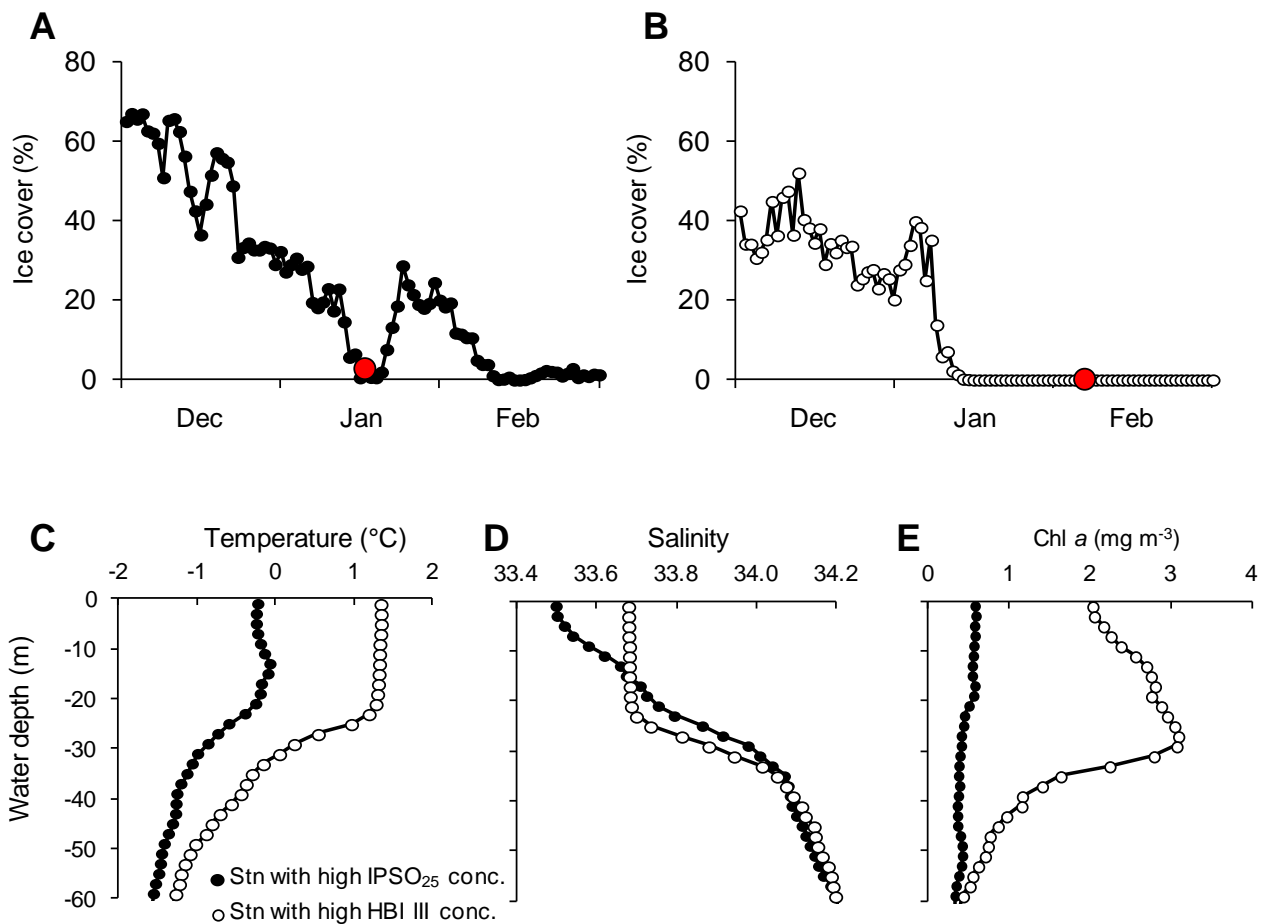


Fig. 5

Fig. 5. Oceanographic differences between stations with high IPSO₂₅ vs. high HBI III concentrations in suspended matter. **A)** Time line of sea ice cover at stations with high IPSO₂₅ concentrations (mean of Stn 18, 19, 20, 31). The red dot indicates the time of sampling. **B)** Time line of sea ice cover at stations with high HBI III concentrations (mean of Stn 45, 50, 51, 52). **C)** Vertical profiles of temperature, **D)** salinity and **E)** chlorophyll *a*.

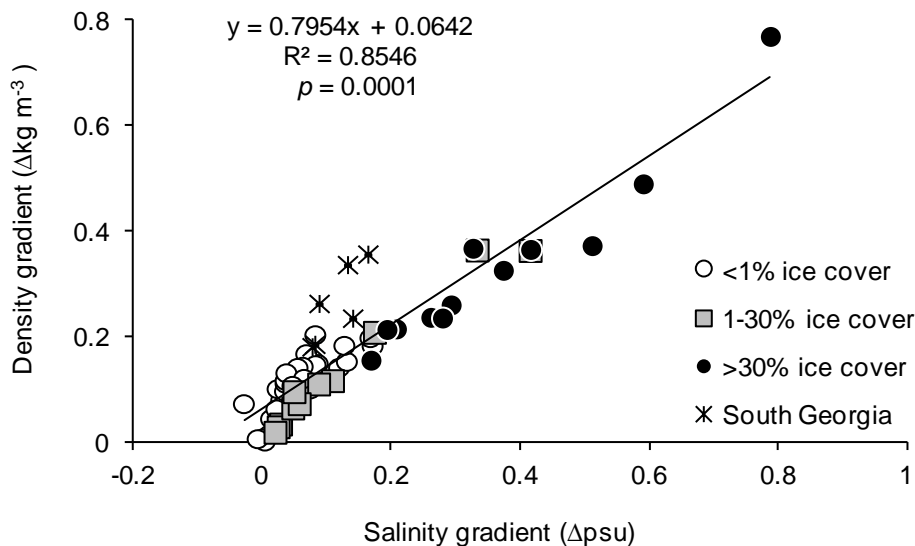


Fig. 6

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1064 **Fig. 6.** The role of seasonal ice melt for water column stratification. During spring/summer 2003, the
 1065 maximum density gradient per 10 m water column was a linear function of the co-occurring salinity
 1066 gradient, with strongest density gradients at stations that had been ice covered by >30% one month
 1067 before sampling. The remaining variability in the density gradient is explained by temperature (GLM:
 1068 density gradient = 0.00254 + 0.7255 salinity gradient + 0.07828 temperature gradient; $R^2 = 0.9889$).

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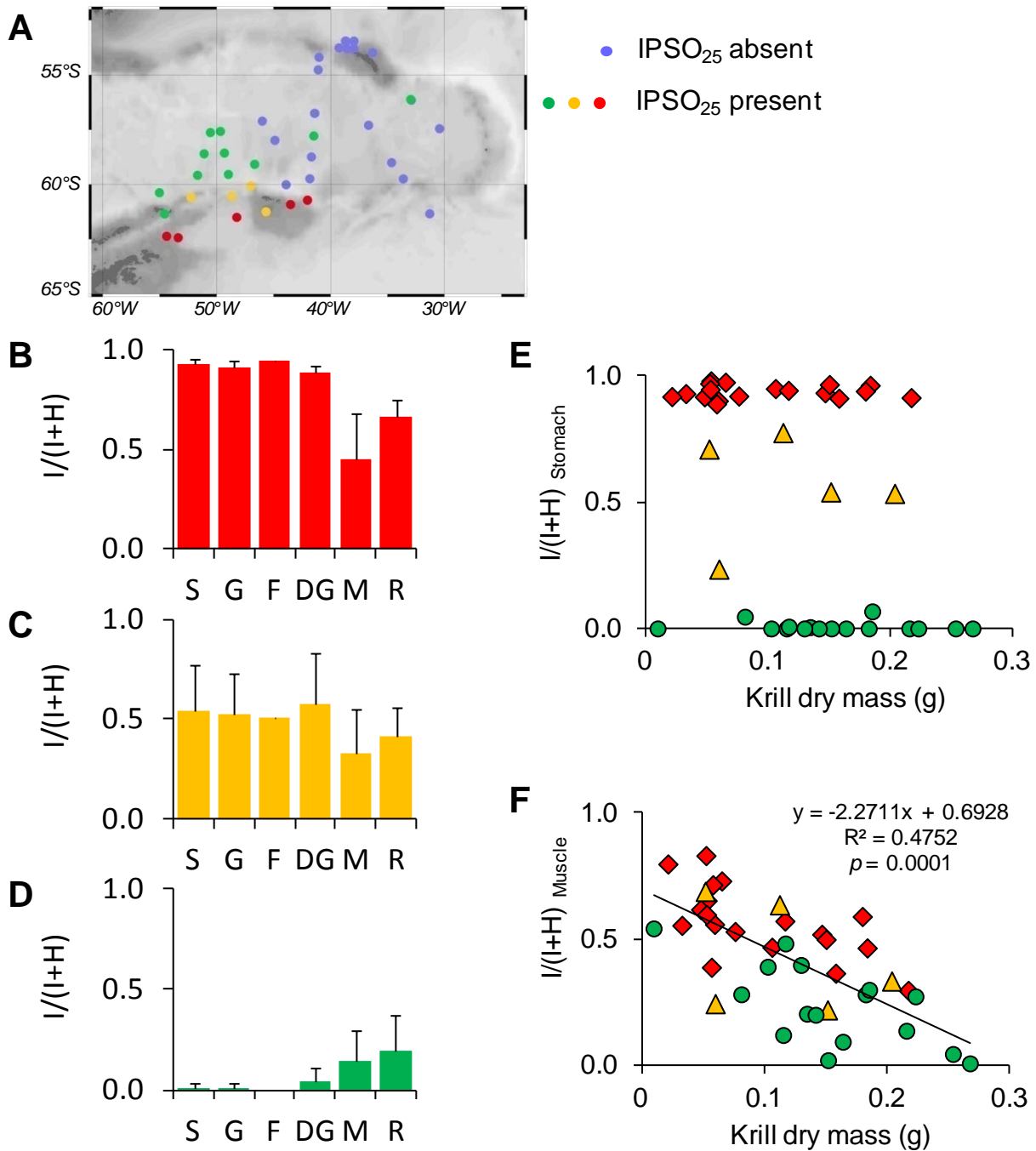


Fig. 7

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1079 **Fig. 7.** *E. superba*: multiple scenarios of krill feeding history on ice diatoms. **A)** Location of stations
 1080 where IPSO₂₅ was present in krill (red – Scenario 1, amber – Scenario 2, green – Scenario 3) or absent
 1081 (purple). **B)** Scenario 1: Krill are mainly feeding on ice diatoms. $I/(I+H)$ ratios are high (>0.9) in
 1082 stomach (S), gut (G), faecal pellets (F) and digestive gland (DG), but lower (0.4-0.7) in muscles (M)
 1083 and rest of the body (R). **C)** Scenario 2: Krill are feeding on a mixture of ice diatoms and open water
 1084 diatoms. $I/(I+H)$ ratios are moderate (~0.5) in stomach, gut, faecal pellets and digestive gland, but lower

1085 (0.3-0.4) in muscles and rest of the body. **D**) Scenario 3: Krill are feeding on open water diatoms, but
1086 fed on ice diatoms in the past. $I/(I+H)$ ratios are very low (<0.1) in stomach, gut and digestive gland, but
1087 higher (0.1-0.2) in muscles and rest of the body. **E, F**) The effect of krill body size on their feeding on
1088 ice diatoms. $I/(I+H)$ ratios are presented separately for krill stomach content and muscle. The regression
1089 line indicates the overall negative relationship between $I/(I+H)_{\text{Muscle}}$ and krill body weight. Colour of
1090 symbols in accordance with panels B-D: Red – krill that fed currently on ice diatoms, yellow – krill that
1091 fed currently on a mixture of ice- and open water diatoms, green – krill that fed currently on open water
1092 diatoms. Individuals ranged from 16-42 mm in Standard 3 body length [L] and 0.01-0.27 g in dry mass
1093 [M] ($M = 1 \cdot 10^{-6} L^{3.2452}$, $R^2 = 0.9707$). Each symbol represents 3-15 pooled individuals of the same body
1094 length.

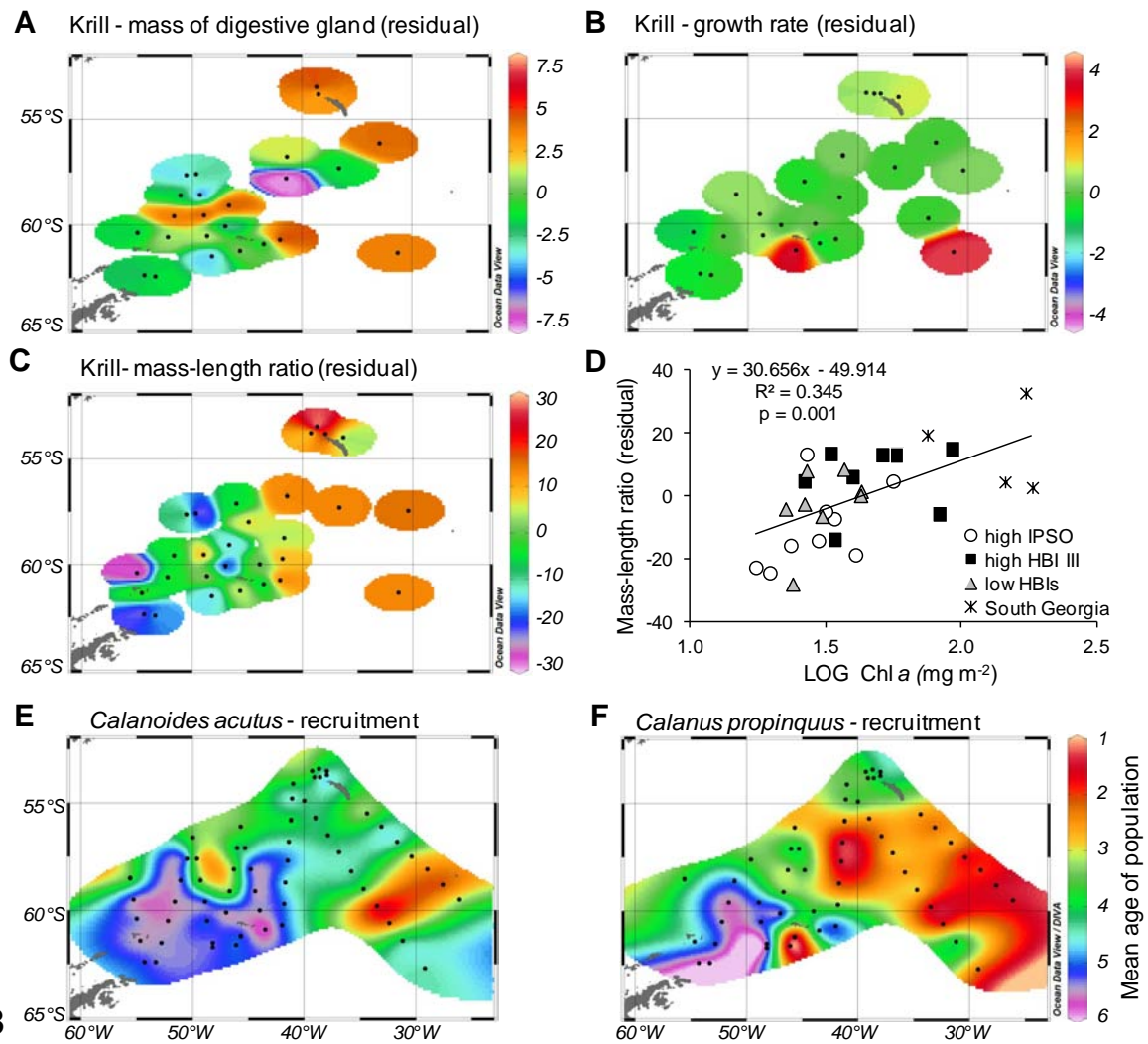


Fig. 8

Fig. 8. *E. superba*: local differences in krill body conditions as indicated by the size of their digestive gland, their growth rate or mass-length ratio. To account for differences in krill body length, residuals rather than absolute values are presented. Residuals were calculated as positive or negative deviations from the relationship between the index of body condition (y) and krill length (x). Positive values denote ‘above-average’ body conditions for their size, negative values suggest ‘below-average’ body conditions.

A) Mass of the digestive gland. $y = 85.234 x + 2.5386$; $R^2 = 0.7271$, $n = 25$. **B)** Krill growth rate in mass, based on original data from Atkinson et al. (2006). $y = 65586 x^{-3.069}$; $R^2 = 0.3265$, $n = 24$. **C)** Krill mass-length ratio. $y = 0.0016 x^{3.2479}$, $R^2 = 0.8627$, $n = 29$. **D)** Overall linear regression between the residuals of the krill mass-length ratio (panel C) and the availability of food, indicated by the integrated chl *a* concentration in the upper 100 m-water column. Krill from different locations are distinguished by their IPSO₂₅- or HBI III content: ‘high IPSO₂₅’ (>30 ng g⁻¹), ‘high HBI III’ (>100 ng g⁻¹), ‘low IPSO₂₅ and HBI III’ (< 100 ng g⁻¹), ‘South Georgia’ (< 100 ng g⁻¹). Each symbol represents 3-15 pooled individuals of the same body length.