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Do pelagic grazers benefit from sea ice? Insights from the Antarctic sea ice proxy $IPSO_{25}$

Katrin Schmidt[1], Thomas A. Brown[1,2], Simon T. Belt[1], Louise C. Ireland[3], Kyle W.R. Taylor[4], Sally E. Thorpe[3], Peter Ward[3], Angus Atkinson[5]

[1]School of Geography, Earth and Environmental Sciences, University of Plymouth, Drake Circus, Plymouth, UK

[2] Marine Ecology and Chemistry, Scottish Association for Marine Science, Oban, UK

[3]British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge, UK

[4]Elementar UK Ltd, Isoprime House, Earl Road, Cheadle Hulme, Stockport, UK

[5]Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth, UK

Corresponding author: Katrin Schmidt (e-mail: katrin.schmidt@plymouth.ac.uk)

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ABSTRACT

Sea ice affects primary production in polar regions in multiple ways. It can dampen water column productivity by reducing light or nutrient supply, it provides a habitat for ice algae and on its seasonal retreat can condition the marginal ice zone (MIZ) for phytoplankton blooms. The relative importance of three different carbon sources (ice-derived, ice-conditioned, non-ice associated) for the polar food web is not well understood, partly due to the lack of methods that enable their unambiguous distinction. Here we analysed two highly branched isoprenoid (HBI) biomarkers to trace ice-derived and ice-conditioned carbon in Antarctic krill (*Euphausia superba*), and relate their concentrations to the grazers' body reserves, growth and recruitment. During our sampling in January/February 2003, the proxy for sea ice diatoms (a di-unsaturated HBI termed $IPSO_{25}$, $\delta^{13}C$ = -12.5±3.3‰) occurred in open waters of the western Scotia Sea, where seasonal ice retreat was slow. In suspended matter, $IPSO_{25}$ was present at a few stations close to the ice edge, but in krill the marker was widespread. Even at stations that had been ice-free for several weeks, $IPSO_{25}$ was found in krill stomachs, suggesting that they gathered the ice-derived algae from below the upper mixed layer. Peak abundances of the proxy for MIZ diatoms (a tri-unsaturated HBI termed HBI III, $\delta^{13}C$ = -42.2±2.4‰) occurred in regions of fast sea ice retreat and persistent salinity-driven stratification in the eastern Scotia Sea. Krill sampled in the area defined by the ice edge bloom likewise contained high amounts of HBI III. As indicators for the grazer's performance we used the mass-length ratio, size of digestive gland and growth rate for krill, and recruitment for the biomass-dominant calanoid copepods *Calanoides acutus* and *Calanus propinquus*. These indices consistently point to blooms in the MIZ as an important feeding ground for pelagic grazers. Even though ice-conditioned blooms are of much shorter duration than the bloom downstream of the permanently sea ice-free South Georgia, they enabled fast growth and offspring development. Our study shows two rarely considered ways that pelagic grazers may benefit from sea ice: Firstly, after their release from sea ice, suspended or sinking ice algae can supplement the grazers' diet if phytoplankton concentrations are low. Secondly, conditioning effects of seasonal sea ice can promote pelagic primary production and therefore food availability in spring and summer.

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1. Introduction

Over the last four decades, sea ice has shown a rapid decline in areal coverage in the Arctic and parts of the Antarctic (e.g. Bellingshausen- and Amundsen Seas). Here sea ice concentrations decrease during both summer (-10 to -13% per decade) and winter (-2% per decade) (Meier et al. 2017, Stammerjohn and Maksym 2017), and current trends towards later autumn sea ice advance and earlier spring sea ice retreat are likely to continue in both hemispheres (Stammerjohn et al. 2012). Ecosystem responses to the loss in sea ice and co-occurring warming and freshening include changes in primary productivity, alterations in phytoplankton community structure, range shifts for zooplankton, benthic organisms and fish, and decline in sea ice-dependent sea birds and mammals (Ducklow et al. 2007, Li et al. 2009, Grebmeier et al. 2010, Constable et al. 2014). Understanding such climate-related changes in structure and functioning of the polar ecosystem is imperative for the management of their resource exploitation (Smetacek and Nicol 2005).

Extended open-water seasons have been suggested to lead to higher primary production in the polar oceans (Arrigo and Thomas 2004, Arrigo 2017) and generate a negative feedback to climate change (Peck et al. 2010, Barnes and Tarling 2017). Some satellite-derived chlorophyll *a* -time series support this prediction (Arrigo et al. 2008), while others do not (Marchese et al. 2017). Along the Western Antarctic Peninsula, warming and a reduction in sea ice extent between 1978 and 2006 led to two very different scenarios (Montes-Hugo et al. 2009). In the southern part, perennial sea ice was replaced by seasonal sea ice and the ice-free summer days translated into more favourable conditions for phytoplankton growth (e.g. increased light). In contrast, in the northern part, loss of seasonal sea ice allowed a deepening of the upper mixed layer with less favourable light conditions for phytoplankton (Montes-Hugo et al. 2009). These observations illustrate the opposing effects that permanent- and seasonal sea ice can have on primary productivity. Thus, while the former prevents phytoplankton blooms, the latter can promote them. During seasonal ice retreat, meltwater can stabilize the surface layer and therefore enhance mean irradiance levels (Smith and Nelson 1986). Moreover, the release of trace elements from sea ice can alleviate nutrient limitation (Lannuzel et al. 2010, Schallenberg et al. 2015). This explains why the MIZ is, on average, more productive than the permanently open waters of the Southern Ocean (Smith and Nelson 1986, Tréguer and Jacques 1992).

Chlorophyll *a* concentrations in sea ice are not accessible to satellite observations and therefore primary production estimates rely on sparse *in situ* measurements and numerical models. Such data suggest that primary production in sea ice accounts for only small amounts of total annual production in

polar waters; typically 2-10% in the Arctic and ca. 1-3% in the Southern Ocean south of 50°S (Arrigo 2017). However, an important difference between phytoplankton and ice algae is that while the former is deeply mixed in the water column, sea ice provides a platform that retains the latter in the surface ocean where light levels can be sufficient for photosynthesis and net growth even during the dark season (Kottmeier and Sullivan 1987, Roukaerts et al. 2016). Therefore, ice algae supply an important autumn, winter and early spring carbon source to in-ice fauna, with subsequent transfer to the wider food web of ice-associated invertebrates, fish, seabirds and mammals (Ainley et al. 2017, Bluhm et al. 2017, Caron et al. 2017, Bester et al. 2017). Other merits of ice algae are their enrichment in polyunsaturated fatty acids that make them a high-quality food source (Søreide et al. 2010, Wang et al. 2014), while their tendency to aggregate and sink after being released from sea ice can be an important pathway of carbon export to the benthos (Riebesell et al. 1991, Renaud et al. 2007). Thus, the small contribution of ice algae to the overall primary production in the polar regions likely understates their ecological importance.

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

An exception is Antarctic krill that have been sampled extensively over the last 90 years due to their central role in Antarctic food webs and their commercial interest (Smetacek and Nicol 2005). The main

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habitat of Antarctic krill is the south-west Atlantic Sector of the Southern Ocean (Atkinson et al. 2008), which largely overlaps with areas of negative trends in sea ice concentrations (western Antarctic Peninsula, north-west Weddell Sea) (Stammerjohn and Maksym 2017). A long-term data set shows that krill stocks in this region have significantly declined (Atkinson et al. 2014), with consequences for populations of krill predators such as penguins and seals (Reid and Croxall 2001, Fraser and Hoffmann 2003, Trivelpiece et al. 2011, Forcada and Hoffmann 2014). Concurrent expansion and operational changes in Antarctic krill fisheries (Kawaguchi et al. 2009) make the krill decline a significant issue of Southern Ocean ecosystem management (Flores et al. 2012b). However, the key mechanism linking krill and sea ice remains elusive (Meyer et al. 2017). Some studies stress the crucial role of sea ice for overwinter survival of krill larvae by providing food and shelter (Daly 2004, Meyer et al. 2009, Kohlbach et al. 2017), while others point to sea ice as an important habitat for juvenile and adult krill during spring and summer (Marschall 1988, Brierley et al. 2002, Flores et al. 2012a) or emphasize indirect effects of seasonal ice cover due to its control on summer phytoplankton productivity and therefore krill recruitment (Quetin and Ross 2003, Saba et al. 2014).

To resolve some of this uncertainty it is essential to quantify the relative importance of sea ice-derived, ice-conditioned and non-ice associated carbon in krill diet, and to relate dietary differences to the performance of krill in terms of growth, recruitment and accumulation of body reserves. However, ice algae-produced carbon has rarely been traced through Southern Ocean food webs (Goutte et al. 2013, Jia et al. 2016, Kohlbach et al. 2017), as distinguishing it unambiguously from phytoplankton-produced carbon is difficult. Here we tackle this challenge by measuring two highly branched isoprenoid (HBI) biomarkers, which are metabolites of certain diatom species and established proxies for palaeo sea ice reconstructions (Armand et al. 2017). Around Antarctica, mixtures of a di-unsaturated HBI (referred to as diene II in previous studies; see Fig. 1) and a tri-unsaturated HBI (referred to as triene III in previous studies, thereafter HBI III, Fig. 1) have repeatedly been found in sediment cores, water column samples and Antarctic predators (Massé et al. 2011, Collins et al. 2013, Goutte et al. 2013, 2014a,b, Smik et al. 2016). The samples were obtained from the Atlantic-, Indian- and Pacific sector of the Southern Ocean, suggesting a widespread occurrence of these biomarkers. However, only diene II has been identified in sea ice samples, and its enrichment in ^{13}C ($\delta^{13}C$ = -5.7 to -17.8‰) is in line with a depleted dissolved inorganic carbon pool in the semi-enclosed sea ice matrix (Massé et al. 2011). This has led to the name 'Ice Proxy for the Southern Ocean with 25 carbon atoms' – $IPSO_{25}$, with the sympagic diatom *Berkeleya adeliensis* being recently identified as one of the source species (Belt et al. 2016). In contrast, HBI III is produced by certain pelagic diatom species, e.g. *Rhizosolenia*

spp. (Belt et al. 2017), and its significantly lighter stable isotopic signature ($\delta^{13}C$ = -35.0 to -41.6‰) indicates a replete carbon pool typical for open waters (Massé et al. 2011). Previous water column and sediment studies have shown relative enhancements in HBI III within the MIZ in the Arctic and Antarctic (Collins et al. 2013, Etourneau et al. 2013, Belt et al. 2015, Smik et al. 2016, Ribeiro et al. 2017), even when other productivity signatures were less revealing, possibly reflecting a preferred habitat for the HBI III-producing species within this setting (Belt et al. 2015). As such, measurements of these two HBIs provide an opportunity to distinguish between direct and indirect effects of sea ice: $IPSO_{25}$ indicates ice algae-produced carbon, while HBI III indicates phytoplankton-produced carbon in waters conditioned by sea ice (i.e. the MIZ). Importantly, both $IPSO_{25}$ and HBI III have been identified in body tissues of seabirds, seals and fish, which confirms their transfer across Antarctic food webs and supports their use as trophic markers (Goutte et al. 2013, 2014a,b). However, detailed interpretation of these biomarkers still lacks basic knowledge about (1) the oceanographic conditions (e.g. sea ice history, stratification, mixed layer depth, chl *a* concentration) that favour the abundance of $IPSO_{25}$ and HBI III-producing diatoms; (2) the subsequent uptake and turnover of $IPSO_{25}$ and HBI III by Antarctic grazers; and (3) the link between the ingested carbon-source and the performance of the grazers.

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

2. Methods

2.1 Phytoplankton bloom development

Chlorophyll *a* (chl *a*) concentrations were obtained from ocean colour radiometry (MODIS, 9 km standard product, 8-day composites, 6th of September – 30th of March, 2002-2015). The Scotia Sea (55-63°S, 25-60°W) and South Georgia region (52-55°S, 32-42°W) were divided into subareas of 1°Lat by 2.5°Lon. For each of these subareas the monthly- and annual mean chl *a* concentration and the annual bloom duration (number of weeks with chl $a \geq 0.5$ mg m^{-3}) were determined for the 2002/2003 season and compared to the longer-term average, 2002-2015.

2.2 Oceanography

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

2.3 Sea ice cover

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

2.4 Sampling of suspended matter, krill and faecal pellets

Suspended matter was sampled from the ship's non-toxic seawater supply located ~6 m below the sea surface. Seawater samples (3 L) were filtered onto pre-ashed GF/F filters and stored at -80°C until analysis. Krill swarms were identified in the vicinity of each station using a Simrad EK60 echosounder and sampled with a Rectangular Midwater Trawl (RMT 8). The RMT was equipped with two nets that were opened and closed remotely from the ship, allowing short duration hauls targeted on specific krill schools in the upper 50 m of the water column. One sub-sample of the freshly caught krill was immediately frozen at -80°C for subsequent analysis of HBIs. Another sub-sample of krill was kept

Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
Manuscript under review for journal Biogeosciences
Discussion started: 18 December 2017

alive to allow for defecation. These krill were placed into buckets filled with surface water and pellets were collected as soon as visible on the bottom of the buckets. The pellets were transferred into 1 ml Eppendorf tubes and rinsed repeatedly with GF/F-filtered seawater with a final brief rinse in deionised water. The supernatant water was removed and vials were stored at -80°C.

2.5 Krill dissections

In the laboratory, krill body length was measured from the anterior edge of the eye to the tip of the telson. Three to fifteen individuals of the same body length were selected for HBI analysis. If available, up to six different size classes were analysed per station and krill were dissected into stomach content, gut, digestive gland, third abdominal segment (muscle) and remaining body. A pooled sample of each of these components was placed in a pre-weighed vial, freeze-dried for 24 h and re-weighed on a Sartorius microbalance. The mass of the digestive gland was related to the total body mass.

2.6 HBI extraction and analysis

HBIs were extracted and analysed as described previously for filtered water samples and zooplankton tissue (Brown and Belt 2012, Smik et al. 2016, Belt et al. 2016). In brief, freeze-dried faecal pellets and krill body fractions were ground using a pestle and mortar. Following addition of an internal standard [9-octyl-8-heptadecene (10µl; 2 µg ml^{-1})] to facilitate HBI quantification, samples were saponified with 5% KOH (filters) or 20% KOH (krill tissue) (70°C; 60 min). Thereafter, non-saponifiable lipids were extracted with hexane (3 x 1 ml) and purified by open column chromatography (SiO_2). HBIs were eluted using hexane (5 column volumes) before being dried (N_2 stream, 25°C). The analysis of partially purified non-polar lipids containing $IPSO_{25}$ and triene III was carried out using an Agilent 7890A gas chromatograph, coupled to an Agilent 5975 mass selective detector, fitted with an Agilent HP-5ms column with auto-splitless injection and helium carrier gas. Identification of individual lipids was achieved by comparison of their retention index and mass spectrum with those obtained from purified standards. Quantification of $IPSO_{25}$ and HBI III was achieved by integrating individual ion ($IPSO_{25:}$ m/z 348.3; HBI III: *m/z* 346.3) responses in single-ion monitoring mode, and normalising these to the corresponding peak area of the internal standard and an instrumental response factor obtained from purified standards (Belt et al. 2012). The GC-MS-derived masses of both HBIs were converted to water column concentrations using the volume of filtered water, and to concentrations in krill body fractions using the mass of the sample extracted. For simplicity in representing biomarker ratios, we use

the terms I and H for $IPSO_{25}$ and HBI III, respectively. Thus, the proportion of $IPSO_{25}$ to the combined concentration of $IPSO_{25}$ and HBI III is given by I/(I+H).

2.7 Stable isotope determination

The stable carbon isotopic compositions ($\delta^{13}C$) of $IPSO_{25}$ and HBI III were determined by gas chromatography–isotope ratio mass spectrometry (GC–IRMS), using an IsoPrime100 IRMS with GC5 interface and Agilent 7890B GC installed with an Agilent HP-5MS column (30 m × 0.2m mm I.D., film thickness 0.25 μm). Samples in ca. 10–150 μl hexane were injected in splitless mode with the following inlet conditions: 250°C, purge flow 25 ml min^{-1}, purge time 0.75 min. GC carrier gas (He) 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}, then 13 minute hold. The combustion furnace consisted of a 0.7 mm I.D. quartz tube packed with CuO pellets, held at 850°C. GC–IRMS data were calibrated using the certified Indiana alkane standard mix A5 (Indiana University, Bloomington, IN, USA) and all results reported in delta notation ($\delta^{13}C$) relative to VPDB. $IPSO_{25}$ and HBI III were identified in GC–IRMS chromatograms by retention time comparison with corresponding GC–MS analyses. IonOS software (Elementar UK Ltd) was used to process GC–IRMS data; 'Peak Mapping' functionality was used to designate specific compound identifications across multiple injections. The A5 alkane mix was analysed in at least duplicate, and calibrations were constructed from at least three interspersed replicate measurements of the A5 mix. Reproducibility of all individual alkanes was always ≤ 0.35 ‰. Root mean standard error (RMSE) of each of the calibrations was usually ≤ 0.25 ‰, with an overall RMSE for all calibrations combined of ≤ 0.21 ‰, reflecting both the reliability of each calibration, and the long-term stability of the system (analyses were undertaken over a three week period in total). Samples containing $IPSO_{25}$ and HBI III were run in triplicate; precisions for both compounds were ≤ 0.27 (see Table 1).

2.8 Copepod abundance and stage composition

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

Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
Manuscript under review for journal Biogeosciences
Discussion started: 18 December 2017

3. Results

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

In October 2002, elevated chl *a* concentrations (>0.5 mg m^{-3}) were only found north of South Georgia (~53°S), and one month later in the north-eastern Scotia Sea (~56°S, Fig. 3A). With the rapid retreat of sea ice in December 2002, the bloom in the east extended south and reached the northern Weddell Sea in January 2003 (~62°S, Fig. 3B). In February 2003, chl *a* concentrations remained high in the eastern Scotia Sea and at South Georgia, but started to decline in March except for a local peak at the southern edge of our study area (~63°S, Fig. 3C). In the western and central Scotia Sea, chl *a* concentrations remained low throughout the summer, apart from slightly enhanced values across the South Orkney Plateau in January 2003. Compared to the longer-term average (2002-2015), there was a negative anomaly in phytoplankton abundance in the central Scotia Sea in 2002/2003, but a surplus in the east (Fig. 3D, E). At the East Scotia Ridge, mean annual chl *a* concentrations were up to 0.7 mg m^{-3} higher and the bloom lasted up to 16 weeks longer in 2002/2003 than in the 2002-2015 average (Fig. 3E).

3.2. Spatial distribution of oceanographic data and HBIs

During maximum sea ice extent the previous winter, about two-thirds of our sampling stations were ice covered (Fig. 4A). One month before the cruise, stations in the southern Scotia Sea were still ice covered by 50-75 % concentration (Fig. 4B), but values had dropped to < 6 % at the time of sampling. Surface temperatures ranged from -1.2°C at stations near the ice edge to 4.5°C at South Georgia (Fig. 4C). Surface salinity was likewise lowest near the retreating ice edge and highest within the Southern Antarctic Circumpolar Current Front (range: 33.1-34.4; Fig. 4D). Stations of the Scotia Sea that had been ice covered showed a stronger vertical density gradient and shallower mixed layer than northerly stations that remained ice free (Fig. 4E, F). Highest surface chl *a* concentrations in the eastern Scotia Sea and near South Georgia coincided with the dominance of large phytoplankton size classes (Fig. 4G,H).

Out of the 61 stations where suspended matter was analysed for HBIs, 6 contained $IPSO_{25}$ and 51 HBI III (Fig. 5A, B). Stations where $IPSO_{25}$ occurred in suspended matter were all located near the ice edge (Stn 6, 18, 19, 20, 31, 48), while stations with elevated HBI III concentrations were found near the ice edge (Stn 45, 46, 49-53) and further north (Stn 12, 25, 26, 37, 40). At stations where both HBIs co-occurred, $IPSO_{25}$ concentrations usually exceeded those of HBI III [mean I/(I+H): 0.6±0.3, n=6; Fig.

5C]. In addition to suspended matter, krill from 47 stations were also analysed for HBIs. $IPSO_{25}$ was present in 21 of these, whereas HBI III was found in all 47 (Fig. 5D, E). The spatial distribution of $IPSO_{25}$ in krill matched that found in suspended matter, with highest concentrations near the ice edge. However, $IPSO_{25}$ could also be detected in krill at stations further north, even though it was not identified in suspended matter from the upper mixed layer. Highest HBI III concentrations in krill were observed in the central Scotia Sea (Stn 13, 14, 22) and in the east (Stn 47, 52, 54), which only partly overlaps with locations of highest HBI III concentrations in suspended matter. However, as for suspended matter, maximum HBI III concentrations in krill exceeded those of $IPSO_{25}$ by an order of magnitude (ca. 4300 *vs* 450 ng g^{-1}), and highest I/(I+H) ratios occurred near the ice edge in the western– and central Scotia Sea [mean I/(I+H): 0.3±0.2, n=21; Fig. 5F].

3.3 The habitat of $IPSO_{25}$ vs. HBI III-producing diatoms

Highest $IPSO_{25}$ and HBI III concentrations in suspended matter were both found in the southern Scotia Sea near the retreating ice edge. However, the occurrence of $IPSO_{25}$ was restricted to the western and central Scotia Sea, while HBI III reached highest concentrations in the east (Fig. 5). The oceanographic conditions in those regions showed clear differences. At stations with high $IPSO_{25}$ concentrations (Stn 18, 19, 20, 31), ice cover had just retreated and re-appeared shortly after the stations were sampled (Fig. 6A). Sub-zero surface temperatures, a strong salinity gradient in the upper ~25 m water column, and relatively low chl *a* concentrations are in line with the recent sea ice melt (Fig. 6C-E). In contrast, the eastern stations with high HBI III concentrations (Stn 45, 50, 51, 52) had been ice-free for ~1 month at the time of sampling. Higher temperatures, higher surface salinity and elevated chl *a* concentrations suggest a progression of upper water column processes since the ice retreat (Fig. 6B-E).

To confirm the source environments of $IPSO_{25}$ and HBI III, we analysed their carbon isotopic signature after extraction from krill sampled at various locations. In each case, $IPSO_{25}$ had much higher $\delta^{13}C$ values than HBI III (-12.5±3.2 ‰ *vs* -42.2±3.0‰; Table 1), and their respective values are consistent with those reported for the same lipids isolated from sea ice, phytoplankton and sediment (Massé et al. 2011, Belt et al. 2016).

In the south-eastern Scotia Sea, there was a large area where high HBI III concentrations coincided with elevated chl *a* concentrations and high proportions of large phytoplankton (Fig. 4G, H, Fig. 5B). Oceanographically, this area was characterised by a strong vertical gradient in temperature and salinity

Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
Manuscript under review for journal Biogeosciences
Discussion started: 18 December 2017

342 (and therefore in water column density), and by shallow upper mixed layers (Fig. 4C-F, Fig. 7). A
343 comparison of the stations' history of ice cover shows that the vertical density gradient was driven by
344 ice melt. There was a highly significant linear relationship between density- and salinity gradients, with
345 strongest density gradients at stations that had >30% ice cover one month before sampling (Fig. 8). In
346 contrast, at more northerly stations that had been ice-free for longer, there was a mixed rather than
347 stratified surface layer and chl *a* concentrations were much lower (Fig. 7). Only at South Georgia were
348 surface temperatures high enough to co-influence the vertical density gradient.

349 In the western and central Scotia Sea, stations near the ice edge were also characterised by high
350 density gradients and shallow mixed layers. However, here high HBI III concentrations were only found
351 in krill (Fig. 5E, especially Stn 22), not in suspended matter (Fig. 4E-G, Fig. 5B).

352

353 *3.4 $IPSO_{25}$ and HBI III concentrations in krill – the role of body fraction and body size*

354 The analysis of krill body fractions shows that not all of the ingested $IPSO_{25}$ and HBI III was
355 absorbed into body tissue, but part remained in the intestine and was then egested via their faecal
356 pellets. Thus, $IPSO_{25}$ and HBI III concentrations in the stomach were, on average, three times higher
357 than in the digestive gland, over fifty-times higher than in the muscle, and about ten-times higher than
358 in the whole krill (Table 2).

359 The I/(I+H) ratio within the various krill body fractions can reveal recent and past feeding history
360 (Fig. 9A-D). Thus, the stomach, gut, faecal pellets and digestive gland showed similar I/(I+H) ratios
361 within the same individual, indicative of their recent feeding history. In contrast, muscle and remaining
362 body tissue often had different ratios as they integrate diet information over longer times. Highest
363 I/(I+H) ratios in krill stomachs were found at 5 stations closest to the ice edge in the western and central
364 Scotia Sea, suggesting that krill were feeding on a diet enriched in sea ice diatoms. At 4 stations near
365 the ice edge and up to ~200 km further north, krill had moderate I/(I+H) ratios in their stomachs
366 indicating a mixed diet of ice-derived diatoms and open water diatoms. Low I/(I+H) ratios in krill
367 stomachs, but higher ratios in their muscle and rest of the body were found at 11 stations ~200-600 km
368 north of the ice edge, suggesting that krill had been feeding on ice diatoms in the past, but had switched
369 to open water diatoms by the time of sampling. At 26 mainly northern stations, krill did not contain any
370 detectable $IPSO_{25}$ and may, therefore, not have fed on ice diatoms at all.

371 The overall concentration of $IPSO_{25}$ and HBI III in krill and their I/(I+H) ratios showed some
372 variability with body size. Small krill (≤ 0.1 g dry mass) contained lower concentrations of $IPSO_{25}$ and

Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
Manuscript under review for journal Biogeosciences
Discussion started: 18 December 2017

HBI III in their stomachs than larger krill (> 0.1 g dry mass) (mean: 806 *vs* 9822 ng g^{-1}, *t*-Test: -3.14, df = 23, $p = 0.005$). In their muscles, these differences were less pronounced (mean: 74.8 *vs* 195 ng g^{-1}, *t*-Test: -2.63, df = 34, $p = 0.013$). However, the I/(I+H) ratios in krill stomachs did not show any relationship with body mass (Fig. 9E). High I/(I+H) ratios were found in both small and large krill, indicating equal access to sea ice diatoms. Likewise, medium and low I/(I+H) ratios occurred across the sampled size range of krill suggesting that they switched simultaneously from feeding on sympagic to pelagic diatoms. In krill muscle, maximum I/(I+H) ratios were lower than in the stomach and ratios showed a linear drop with body size (Fig. 9F). A likely explanation is that krill had been feeding on sea ice diatoms for a relatively short time only. During this time, I/(I+H) ratios in their muscle did not equilibrate with values in their diet. This applies to small krill with fast turnover rates and even more so to large krill with longer integration times.

3.5 Krill performance under different feeding conditions

Based on our analysis, three groups of krill can be distinguished: those that had been feeding on ice diatoms (high $IPSO_{25}$ content), those that had been feeding on open-water diatoms favoured by conditions at the receding ice edge (high HBI III content) and those that did not feed substantially on either of these diatoms (no/ low $IPSO_{25}$ or HBI III content). To establish whether one of these feeding histories gave krill an advantage in their condition and performance, we tested three indicators: their mass-length-ratio, the size of their digestive gland and their growth rate. However, as each of these indicators correlates with krill body size, we present the residuals of the indicator-to-body size regression rather than absolute values (i.e. size of digestive gland-to-total mass regressions, growth rate-to-length regression and mass-to-length regression). Using this approach, we found that krill were in best condition near the ice edge in the eastern Scotia Sea (Stn 47) with positive residuals for all three indicators (Fig. 10A-C). Krill sampled at the ice edge in the central Scotia Sea (Stn 20, 31) and at South Georgia (Stn 56-61) showed positive residuals for at least two of these parameters. Overall, the residuals of the krill mass-length regression were mostly positive in the central and eastern Scotia Sea and at South Georgia, but negative in the western Scotia Sea. This is likely due to local differences in the food availability, as indicated by the significant positive relationship between mass-residual and *in situ* chl *a* concentration (Fig. 10D). On average, a high $IPSO_{25}$ content in krill was associated with low chl *a* concentrations and therefore 'below average' krill body mass, while a high HBI III content in krill co-occurred with medium chl *a* concentrations and more often with 'above average' body mass (Fig. 10D).

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405 *3.6 Recruitment of large calanoid copepods*

406 Another important group of pelagic grazers in the Southern Ocean are calanoid copepods, e.g. the
407 high-latitude species *Calanoides acutus* and *Calanus propinquus*. While HBIs have not been measured
408 in these species, their overall abundance and age structure gives some information about suitable
409 feeding grounds. For both species, abundances were highest at South Georgia and in the south-eastern
410 Scotia Sea (Fig. 11A). The latter site was dominated by young development stages (copepodite stages I-
411 III), which indicates recent successful recruitment (Fig. 11B). At South Georgia, the population was
412 older, but also dominated by new recruits (copepodite stage IV). In contrast, in the western Scotia Sea
413 copepod abundances were low, overall, and the population consisted of 'overwintered' copepodite stage
414 V and females, suggesting that recruitment was delayed or had failed.

415

416 **4. Discussion**

417 *4.1 Evaluating the HBI approach*

418 Knowledge about the role of ice algae- vs. phytoplankton-produced carbon for higher trophic levels
419 is central to our understanding of polar ecosystems. However, reliable estimates are difficult to achieve.
420 Firstly, traditional trophic markers such as fatty acids, accessory pigments or taxonomy are of limited
421 use as diatoms often dominate both communities with few species being obligate ice inhabitants
422 (Garrison et al. 1987, Lizotte 2001, Arrigo 2017). Secondly, approaches that allow the separation of the
423 two sources based on non-conservative tracers, including bulk- or compound-specific stable isotope
424 analysis, rely on numerous assumptions that are not always met in practice (Budge et al. 2008). An
425 example is isotopic fractionation, where the $\delta^{13}C$ values of fatty acids derived from diatoms, and not
426 produced *de novo* by the consumer [e.g. 16:4(n-1) or 20:5(n-3)] are usually assumed to remain
427 unchanged across trophic levels (e.g. Budge et al. 2008, Wang et al. 2015, Kohlbach et al. 2017).
428 However, laboratory and field studies have shown significant isotopic fractionation (-4 to -1‰) in
429 polyunsaturated fatty acids between diet and consumer, and a gradual depletion in the ^{13}C content of
430 fatty acids upward through the food chain (Bec et al. 2011, Gladyshev et al. 2012 and ref. therein). If
431 this isotopic fractionation remains unaccounted for, the contribution of the isotopically lighter source is
432 overestimated and this bias increases with shorter isotopic distance between the endmembers (Bec et al.
433 2011). Based on data obtained from Antarctic krill by Kohlbach et al. (2017), the ice algae source of
434 20:5(n-3) increased from 64 to 89% in larvae, from 46 to 70% in juveniles and from -18 to 7% in adults
435 if a fractionation of -1.5‰ between diatoms and grazer was implemented, according to Bec et al.

(2011). This illustrates that the interpretation of fatty acid-specific stable isotope data can be severely skewed if possible 'digestive' ^{13}C depletion of fatty acids is not considered (Gladyshev et al. 2012).

In contrast to fatty acids, where one marker [e.g. 20:5(n-3)] carries the mixed isotopic signal from two food sources with additional fractionation within the grazer, the HBI approach is more straight-forward. Here, two independent markers exist, one for ice algae ($IPSO_{25}$) and one for phytoplankton (HBI III). Thus, if $IPSO_{25}$ occurred in krill in the present study, it unambiguously indicated their consumption of ice algae. Moreover, the relative abundance of $IPSO_{25}$ and HBI III [I/(I+H)] remained the same during transfer from krill stomach to the digestive gland (Fig. 9), which suggests that there was no selective absorption or degradation within the grazer. This is in line with laboratory experiments which showed near identical HBI ratios in the brine shrimp *Artemia* sp. and its food (Brown and Belt 2017). Thus, key advantages of the HBI approach are the existence of a sea ice proxy and its open water counterpart, and minimal signature alterations by the consumer.

On the other hand, disadvantages of the HBI approach may arise from the generally lower abundance of these markers. While fatty acids are ubiquitous to marine life, HBIs are only produced by certain diatom species (Brown et al. 2014, Belt et al. 2017 and references therein). Four such species are currently known to produce the Arctic sea ice proxy IP_{25} (Brown et al. 2014), while in the Southern Ocean so far only one diatom species has been identified as a source of $IPSO_{25}$ (viz. *Berkeleya adeliensis*, Belt et al. 2016). The four Arctic source species are considered omnipresent in sea ice, however, and the application of IP_{25} as a proxy for palaeo Arctic sea ice reconstructions is well established (Belt and Müller 2013). In contrast, research effort on HBIs in the Southern Ocean started more recently and initial findings require further confirmation. For instance, the known Antarctic source of $IPSO_{25}$, *B. adeliensis*, is commonly associated with landfast ice and blooms in spring/ early summer, which may limit its use as a sea ice proxy in oceanic settings or during winter (Belt et al. 2016). However, sediment cores, sea ice samples, water samples and Antarctic predators indicate a widespread occurrence of $IPSO_{25}$, including coastal- and open ocean regions, and samples obtained in summer and winter (this study, Massé et al. 2011, Goutte et al. 2013, Collins et al. 2013). This suggests co-production of $IPSO_{25}$ by as yet unidentified source species or by *B. adeliensis* inhabiting also non-coastal sea ice.

The proportion of $IPSO_{25}$ in the combined $IPSO_{25}$ and HBI III pool [I/(I+H) as presented in this study] is only a relative indicator of ice algae- vs. phytoplankton produced carbon. A translation into carbon values would require that the POC-to-HBI ratio is estimated for the local end-members (ice

algae, phytoplankton) and that I/(I+H) ratios are calibrated with known proportions of these end-members. Such calibration has been carried out for ratios of pelagic- vs. sympagic HBIs common in the Arctic via the so-called HBI-fingerprint ('H-print'; Brown and Belt 2017), and subsequently applied to obtain quantitative estimates of ice-derived carbon in Arctic amphipods (Brown et al. 2017). However, in this study we did not assess the absolute amount of carbon that krill acquire from ice algae. Instead we aimed for a mechanistic understanding of the role of sea ice for grazers such as krill, considering both carbon-production within sea ice and conditioning effects of sea ice that promote phytoplankton blooms.

After the initial application of HBIs as trophic markers in Southern Ocean food web studies by Goutte et al. (2013, 2014a, 2014b), our results provide three lines of evidence for the robustness of this approach: First, the carbon isotopic signatures ($\delta^{13}C$) of $IPSO_{25}$ and HBI III confirm their different origins in sympagic *vs.* pelagic diatoms (Table 1). Second, given our open water set of sampling stations, both HBIs occurred in highest concentrations in suspended matter near the retreating ice edge; but they were associated with different oceanographic conditions. $IPSO_{25}$ coincided with sea ice cover and low temperatures, while HBI III peaked where melt water-driven stratification and enhanced chl *a* concentrations indicate favourable conditions for phytoplankton growth (Fig. 6). Third, there was a spatial overlap in the occurrence of HBIs in suspended matter and krill, which points to a direct trophic transfer (Fig. 5). The I/(I+H) ratios in krill stomachs, and therefore the dietary role of ice diatoms, decreased with the stations distance from the ice edge (Fig. 9). In conclusion, the HBI approach has delivered plausible results and overcomes some of the limitations of other trophic markers. Therefore, we consider it a suitable tool to assess the role of ice algae and ice-conditioned phytoplankton for Southern Ocean grazers. However, given the different strengths and weaknesses of HBI, fatty acid-specific stable isotopes and other trophic markers, their combined application is likely to increase the robustness of the results and the amount of detail revealed (Schmidt et al. 2006).

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

Krill feeding on ice algae is usually envisaged as larval krill accumulating under sea ice in search for winter food (Daly 2004), or juvenile and adult krill scraping off algae from the ice underside during the spring bloom (Marschall 1988) resulting in intensive downward flux of krill faecal pellets (Michels et al. 2008). However, here the ice proxy $IPSO_{25}$ revealed that ice algae can be an important food source for krill in early summer, even several weeks after the ice cover has disappeared. These considerations are based on the occurrence of $IPSO_{25}$ in the krill stomach, which contains food ingested within a

499 couple of hours before capture (Schmidt and Atkinson 2016), and therefore relates to the environment at
500 the sampling location. At five stations near the ice edge, krill stomachs contained a higher proportion of
501 ice algae [$I/(I+H)_{Stomach}$: 0.93±0.03] than the suspended matter in surface waters [$I/(I+H)_{SM}$: 0.68±0.21].
502 Up to 200 km north of the current ice edge, krill still ingested a mixture of ice algae and phytoplankton
503 [$I/(I+H)_{Stomach}$: 0.56±0.24], while $IPSO_{25}$ was not detected in suspended matter from surface waters.
504 These observations suggests that krill fed preferentially on ice algae and sampled them below the upper
505 mixed layer, either during their diurnal vertical migration or in special foraging trips towards the
506 benthos (Clarke and Tyler 2008, Schmidt et al. 2011). At Stn 8, for instance, a high I/(I+H) ratio
507 coincided with lithogenic particles in krill stomachs, which may have been ingested at the seabed
508 (Schmidt et al. 2011). About 200-600 km north of the ice edge, $IPSO_{25}$ was found in krill muscle tissue,
509 but not in their stomachs. Lipids in krill muscle tissue have a much slower turnover rate than those in
510 the stomach and can therefore give information about the feeding history within the last few weeks.
511 Here, the results indicate that krill had been feeding on ice algae in the past, but subsequently relied on
512 phytoplankton. Overall, $IPSO_{25}$ was detected in krill from 21 stations across the western and central
513 Scotia Sea, confirming the widespread uptake of ice algae as a food source.

514 Krill stomach and muscle showed different trends between body mass and the I/(I+H) ratio,
515 suggesting that krill had only been feeding on ice algae for a relatively short period. Small krill were
516 equilibrated with the ice algae diet, having high I/(I+H) ratios in both stomach and muscle, while larger
517 krill had high I/(I+H) ratios only in their stomachs and not in their muscles (Fig. 9). This suggests that
518 larger krill did not feed long enough on ice algae to reach equilibrium between diet and body tissue.
519 Most likely, ice algae became more accessible to krill when the ice started to melt (Jia et al. 2016). The
520 $IPSO_{25}$ extracted from krill was enriched in $\delta^{13}C$ (Table 1), as is typical for material from interior sea ice
521 (McMinn et al. 1999, Wang et al. 2014) that is only within reach of krill when the algae are released
522 into the water column. A carbon budget of ice algae in the Canadian Arctic in spring showed that >65%
523 of the biomass, released from sea ice into the upper water column, remained suspended (Michel et al.
524 1996). However, the high variability in chl *a* residence time (mean: 31±33 days) and -sinking rate
525 (mean: 1.4±1.5 m d^{-1}) illustrates the dual fate of ice algae; while some rapidly sink out of the euphotic
526 zone and efficiently transfers carbon to the benthos (e.g. Riebesell et al. 1991, Renaud et al. 2007,
527 Amiraux et al. 2017), others remain suspended over several weeks and can aid the nutrition of pelagic
528 grazers (Michel et al. 1996, Smik et al. 2016). In any case, the trophic importance of ice algae extends
529 beyond the period of maximum production in sea ice (Michel et al. 1996).

In the western and central Scotia Sea, phytoplankton concentrations were low and the community was dominated by small size classes (< 12 µm) during spring and summer 2002/2003 (Fig. 4, Korb et al. 2005). This may explain why krill continued feeding on ice algae even after they had descended out of surface waters. In some years, phytoplankton blooms seem not to take off in this region, and light limitation, iron deficiency and grazing pressure have been discussed as potential reasons (Lancelot et al. 1993, Korb et al. 2005, Park et al. 2010). Our study period coincided with a negative phase of the Southern Annular Mode (www.nerc-bas.ac.uk/public/icd/gjma/newsam.1957.2007.txt), which is characterised by reduced strength and duration of wind mixing events (Saba et al. 2014). This led to shallow mixed layers and deep euphotic depths, constituting favourable light conditions for phytoplankton growth (Fig. 4, Korb et al. 2005). However, 2002/2003 was also a year of good krill recruitment (Atkinson et al. 2014) and high krill densities occurred especially in the western and central Scotia Sea (authors' unpubl. observations). At 7 stations in the central Scotia Sea, krill contained high amounts of HBI III (110-3460 ng g^{-1}, esp. Stn 22, Fig. 5), even though there was little evidence of HBI III in the suspended matter in surface waters at that time. This suggests that diatom species favoured within the MIZ were produced in the central Scotia Sea, but did not accumulate, possibly due to high grazing losses. A longer-term data set of satellite-derived chl *a* concentrations shows that the area where krill contained high amounts of HBI III (Fig. 5E) matches the region with exceptionally low surface chl *a* concentrations in the central Scotia Sea in the 2002/2003 season (Fig. 3E).

The combination of high krill densities and low food availability can lead to competition-induced starvation (Ryabov et al. 2017). Such an effect may be seen in the krill' weight-to-length ratios: At most stations in the western and central Scotia Sea, krill were lighter than predicted from their body length, showing negative residuals from the mass-length regression (Fig. 10c). These stations largely coincided with those where krill contained the ice proxy $IPSO_{25}$. However, the presence of $IPSO_{25}$ in krill distant from the ice edge may simply indicate a shortage of their summer food – phytoplankton. More relevant is the link between $IPSO_{25}$ and krill performance at stations near the ice edge, where ice algae were prominent in their stomachs. Of these six stations, two provided good feeding conditions for krill (positive residuals, Stn 20, 31), while four did not (negative residuals, Stn 5, 6, 18, 30). This is in line with other studies showing high variability in food supply from sea ice (Marschall et al. 1988, Daly 2004, Michels et al. 2008, Schmidt et al. 2012, 2014, Meyer et al. 2017). Local differences in snow cover, ice thickness, ice rafting or time of ice formation can lead to different concentrations of ice algae in the bottom ice layer (Fritsen et al. 2008, Meiners et al. 2012). However, below-average krill body mass was even found in individuals that contained high concentrations of $IPSO_{25}$ (Stn. 5, 18), while krill

with positive residuals from the mass-length regression showed high concentrations of both $IPSO_{25}$ and HBI III (Stn 30) or mainly HBI III (Stn 20). This indicates an essential role of phytoplankton for krill performance in spring, as has been suggested previously (Cuzin-Roudy et al. 1992, Schmidt et al. 2012).

4.3 The role of ice-conditioned phytoplankton blooms

Off-shore regions of the Southern Ocean are often characterised by high-nitrate-low-chlorophyll (HNLC) conditions due to the shortage of iron. However, in the Scotia Sea primary and secondary production can be comparatively high (Atkinson et al. 2004, Park et al. 2010). In 2002/2003, late sea ice retreat coincided with a negative phase of the Southern Annular Mode, volcanic activity at Mount Belinda (~ 80 km east off Stn. 50) and high krill abundances (authors' unpublished observations, Patrick et al. 2005, Ward et al. 2006). This would have provided favourable light conditions and iron (Korb et al. 2005, Browning et al. 2014, Schallenberg et al. 2015), but also enhanced grazing impact and nutrient recycling (Schmidt et al. 2016). Perhaps as a consequence, the phytoplankton bloom was unusually long-lasting and intensive across the East Scotia Ridge, but weaker than average in the central Scotia Sea (Fig. 3; Park et al. 2010). Sea ice retreat can assist phytoplankton growth due to the freshness of the meltwater, following brine rejection during its formation. The low-salinity input enhances water column stability, thereby reducing vertical mixing and retaining phytoplankton in an optimal light environment (Smith and Nelson 1986). However, meltwater lenses do not always lead to ice edge blooms. In the western and central Scotia Sea, strong density gradients occurred upon ice retreat but phytoplankton did not accumulate. In contrast, in the east, blooms propagated behind the receding ice edge over hundreds of kilometres and for several months (Fig. 3). A reason for these differences may be the speed of ice retreat (Constable et al. 2003). Between mid December and mid February, ice retreated at ~1.7 km d^{-1} in the west and at 11.7 km d^{-1} in the east (authors' unpublished data). Rapid ice retreat enhances the volume and spatial extent of meltwater input and therefore the likelihood that stratification persists long enough for marked phytoplankton growth and accumulation (Smith and Nelson 1986, Smith et al. 2006). Other factors controlling phytoplankton development along the receding ice-edge include iron deficiency and grazing pressure by zooplankton (Tréguer and Jacques 1992, Lancelot et al. 1993).

Ice-edge phytoplankton blooms have been reported throughout the Arctic (Perrette et al. 2011) and from the Ross Sea, Weddell Sea, Scotia Sea, Prydz Bay and the Pacific sector of the Southern Ocean (e.g. Smith and Nelson 1986, Nelson et al. 1987, Sullivan et al. 1988, Comiso et al. 1993, Moore et al.

1999, Constable et al. 2003). However, the overall importance of primary production in the MIZ is still debated (Vancoppenolle et al. 2013). Originally, the MIZ was considered a major hotspot for autotrophic production in the Southern Ocean (Smith and Nelson 1986). Subsequent analysis of satellite data, however, suggests that phytoplankton blooms in the MIZ are largely suppressed at high wind speed, and even with lower winds, blooms occur only over one-third of the MIZ (Fitch and Moore 2007). Therefore, area-normalised primary production rates calculated from ocean colour are on average only slightly higher in the MIZ than in the permanently ice-free Southern Ocean (Arrigo et al. 2008). This has led to the conclusion that while the MIZ has the potential to be productive, physical conditions are seldom conducive to the development of intense, longer-lived phytoplankton blooms (Arrigo et al. 2008). On the other hand, high abundances of zooplankton, seabirds and whales are characteristic of the MIZ and confirm enhanced biological activity and the importance of this region for the food web (Brown and Lockyer 1984, Ichii et al. 1990, Ainley et al. 2017).

Antarctic krill sampled in the previously ice covered eastern Scotia Sea had high HBI III concentrations and above-average body mass (i.e. positive residuals in Fig. 10c). The occurrence of HBI III in krill tissue often coincided with medium to high chl *a* concentrations in the water column (Fig. 10d). Therefore, enhanced krill performance in the east is most likely a result of higher food concentrations. A number of studies has previously found chl *a* concentrations to represent a reliable predictor of krill growth and maturation (Ross et al. 2000, Atkinson et al. 2006, Schmidt et al. 2012, Meyer et al. 2017). Krill from the most southerly station of the eastern transects (Stn 47) were in similarly good conditions to those at South Georgia, showing high body mass, large digestive gland and exceptionally high growth rates when adjusted for their length. This is unexpected considering that, at the time of sampling, only 2 weeks of elevated chl *a* concentrations (>0.5 mg m^{-3}) were recorded at Stn. 47, but ~16 weeks at South Georgia (based on ocean colour data, Fig. 2). A previous study revealed that krill can engage in "superfluous" feeding when food is abundant (Schmidt et al. 2012). This way, the food concentration in their digestive tract remains high and nutrient absorption per unit time is maximised. Consequently, krill can rapidly improve their body condition and advance in maturation (Schmidt et al. 2012). $IPSO_{25}$ was not detected in krill from Stn. 47, but was found in low concentrations in suspended matter at the neighbouring station closer to the ice edge (Stn. 48). Station 47 had been ice free for ~20 days when krill were sampled, which is approximately the turnover-time of the Arctic sea ice proxy in zooplankton (Brown and Belt 2012). Therefore, krill may have been feeding on ice algae at this station, but any indication of this via $IPSO_{25}$ was lost following their switch to phytoplankton.

626 A few copepod species inhabit Antarctic sea ice, but the biomass dominant copepod grazers in high
627 latitudes, *Calanoides acutus* and *Calanus propinquus*, are only loosely associated with sea ice, if at all
628 (Arndt and Swadling 2006). *C. acutus* shows reduced feeding activity within the ice and their offspring
629 only occur in the MIZ or open waters (Atkinson and Shreeve 1995, Burghart et al 1999). In contrast, *C.*
630 *propinquus* have been found feeding on ice algae and spawning below sea ice, but their populations
631 likewise expand mainly in open waters (Atkinson and Shreeve 1995, Burghart et al 1999). Both species
632 can complete their life cycle at South Georgia (Atkinson et al. 1988), which is permanently sea ice-free.
633 During our study period, the occurrence and recruitment of these species showed similarities to feeding
634 behaviour and performance of Antarctic krill. In the western and central Scotia Sea, *C. acutus* and C.
635 *propinquus* had low abundances and the populations were dominated by females and late copepodite
636 stages representing the 'old, overwintered' generation. This delay or failure of recruitment was likely
637 caused by the lack of phytoplankton, as also indicated by krill feeding on sinking ice algae in open
638 waters, and their below-average body mass. Highest copepod abundances in the south-east coincided
639 with the dominance of early copepodite stages (i.e. the 'new' generation). This region of intensive
640 copepod reproduction (Stn 45, 50, 51, 52) matches high HBI III concentrations in suspended matter and
641 enhanced krill performance in the wake of retreating sea ice. We therefore suggest that the MIZ is an
642 important nursery ground for these large copepod species, in line with previous findings (Atkinson and
643 Shreeve 1995, Burghart et al. 1999). At South Georgia, the copepod populations of *C. acutus* and C.
644 *propinquus* were further advanced in their seasonal development (dominated by medium copepodite
645 stages of the 'new' generation), but the overall abundances were similar to those in the south.

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

(Vancoppenolle et al. 2013). The former attenuates light, whereas the latter efficiently transmits it to the underlying ocean.

5. Conclusion

Large parts of the Southern Ocean are characterised by low phytoplankton concentrations due to the lack of iron, strong vertical mixing or grazing and other losses. Our study suggests that in such areas, pelagic grazers may benefit from seasonal sea ice in two ways. Firstly, suspended or sinking ice algae can supplement their diet in spring and summer. Second, retreating sea ice enhances the likelihood of bloom formation due to shoaling of the mixed layer, supply of iron and/or release of a seeding population. Phytoplankton blooms initiated in the MIZ allow zooplankton to grow rapidly, gain body reserves and advance in their development. Therefore, current and future changes in sea ice will not only affect sympagic fauna, but also zooplankton species that inhabit open waters adjacent to it. The analysis of two source-specific highly branched isoprenoids provided a useful tool to trace ice-produced and ice-conditioned food sources within pelagic grazers. Essential for their further application will be to resolve the spatial and temporal occurrence of the ice proxy $IPSO_{25,}$ and to gauge the carbon-to-isoprenoid ratios of ice algae and phytoplankton. Development of the HBI trophic marker approach, alongside other methods, will help us to understand exactly how Arctic and Antarctic food webs depend on sea ice.

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REFERENCES

Ainley, D., Woehler, E.J., and Lescroël, A.: Birds and Antarctic sea ice, In: 'Sea Ice', ed. D. N. Thomas (Chichester: John Wiley & Sons, Ltd), 570–582, doi:10.1002/9781118778371.ch24, 2017.

689 Amiraux, R., Belt, S.T., Vaultiera, F., Galindoc, V., Gosselin, M., Bonina, P., Rontani, J.-F.:
690 Monitoring photo-oxidative and salinity-induced bacterial stress in the Canadian Arctic using
691 specific lipid tracers. Mar. Chem.,194, 89-99, doi: 10.1016/j.marchem.2017.05.006, 2017.
692 Armand, L., Ferry, A., and Leventer, A.: Advances in palaeo sea ice estimation, In: 'Sea Ice', ed. D. N.
693 Thomas (Chichester: John Wiley & Sons, Ltd), 600–629, doi: 10.1002/9781118778371.ch26, 2017.
694 Arndt, C.E., and Swadling, K.M.: Crustacea in Arctic and Antarctic sea ice: distribution, diet and life
695 history strategies, Adv. Mar. Biol., 51, 197-315, doi: 10.1016/S0065-2881(06)51004-1, 2006.
696 Arrigo, K.: Sea ice as a habitat for primary producers, In: 'Sea Ice', ed. D. N. Thomas (Chichester: John
697 Wiley & Sons, Ltd), 352–369, doi: 10.1002/9781118778371.ch14, 2017.
698 Arrigo, K. and Thomas, D.: Large scale importance of sea ice biology in the Southern Ocean, Ant. Sc.,
699 16, 471-486, doi: 10.1017/S0954102004002263, 2004.
700 Arrigo, K.R., van Dijken, LG.L., and Bushinsky, S.: Primary production in the Southern Ocean, 1997-
701 2006, J. Geophys. Res., 113, C08004, doi:10.1029/2007JC004551, 2008.
702 Atkinson, A. and Peck, J.M.: A summer-winter comparison of zooplankton in the oceanic area around
703 South Georgia. Polar Biol., 8, 463-473, doi: 10.1007/BF00264723, 1988.
704 Atkinson, A. and Shreeve, R.S.: Response of the copepod community to a spring bloom in the
705 Bellingshausen Sea, Deep-Sea Res. II, 42, 1291-1311, doi: 10.1016/0967-0645(95)00057-W, 1995.
706
707 Atkinson, A., Siegel, V., Pakhomov, E., and Rothery P.: Long-term decline in krill stock and increase in
708 salps within the Southern Ocean, Nature, 432, 100-103, doi:10.1038/nature02996, 2004.
709 Atkinson, A., Shreeve, R., Hirst, A.G., Rothery, P., Tarling, G., Pond, D., Korb, R.E., Murphy, E.J., and
710 Watkins, J.L.: Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models
711 based on food, temperature, body length, sex, and maturity stage, Limnol. Oceanogr., 51, 973-987,
712 doi: 10.4319/lo.2006.51.2.0973, 2006.
713 Atkinson, A., Siegel, V., Pakhomov, E.A., Rothery, P., Loeb, V., Ross, R.M., Quetin, L.B., Schmidt,
714 K., Fretwell, P., Murphy, E.J., Tarling, G.A., and Fleming, A.H.: Oceanic circumpolar habitats of
715 Antarctic krill, Mar. Ecol. Prog. Ser., 362, 1-32, doi: 10.3354/meps07498, 2008.
716 Atkinson, A., Hill, S.L., Barange, M., Pakhomov, E.A., Raubenheimer, D., Schmidt, K., Simpson, S.J.,
717 and Reiss, C.: Sardine cycles, krill declines, and locust plagues: Revisiting 'wasp-waist' food webs,
718 Trends Ecol Evol., 29, 309-316, doi: 10.1016/j.tree.2014.03.011, 2014.
719 Barnes, D.K.A. and Tarling, G.A.: Polar oceans in a changing climate, Current Biol., 27, 454-460, doi:
720 10.1016/j.cub.2017.01.045, 2017.

721 Bec, A., Perga, M-E., Koussoroplis, A., Bardoux, G., Desvilettes, C., Bourdier, G., and Mariotti, A.:
722 Assessing the reliability of fatty acid-speific stable isotope analysis for trophic studies. Meth. Ecol.
723 Evolut., 2, 651-659, doi: 10.111/j.2041-210X.2011.00111.x, 2011.
724 Belt, S.T., and Müller, J.: The Arctic sea ice biomarker IP_{25}: a review of current understanding,
725 recommendations for future research and applications in Palaeo sea ice reconstructions. Quat. Sci.
726 Rev., 79, 9-25, doi: 10.1016/j.quascirev.2012.12.001, 2013.
727 Belt, S.T., Brown, T.A., Navarro-Rodriguez, A., Cabedo-Sanz, P., Tonkin, A., and Ingle, R.: A
728 reproducible method for the extraction, identification and quantification of the Arctic sea ice proxy
729 IP_{25} from marine sediments. Analyt. Meth., 4, 705-713, doi: , 2012.
730 Belt, S.T., Cabedo-Sanz, P., Smik, L., Navarro-Rodriguez, A., Berben, S.M. P., Knies, J., and
731 Husum, K.: Identification of paleo Arctic winter sea ice limits and the marginal ice zone: optimised
732 biomarker-based reconstructions of the late Quaternary Arctic sea ice. Earth Planet. Sci. Lett., 431,
733 127-139, doi:10.1016/j.epsl.2015.09.020, 2015.
734 Belt, S.T., Smik, L., Brown, T.A., Kim, J.-H., Rowland, S.J., Allen, C.S., Gal, J.-K., Shin, K.-H., Lee,
735 J.I., and Taylor, K.W.R.: Source identification and distribution reveals the potential of the
736 geochemical Antarctic sea ice proxy $IPSO_{25}$, Nat. Comms., 7, 12655, doi:10.1038/ncomms12655,
737 2016.
738 Belt, S.T., Brown, T.A., Smik, L., Tatrek, A., Wiktor, J., Stowasser, G., Assmy, P., Allen, C.S., and
739 Husum, K.: Identification of C_{25} highly branched isoprenoid (HBI) alkenes in diatoms of the genus
740 *Rhizosolenia* in polar and sub-polar marine phytoplankton, Org. Geochem. 110, 65-72, doi:
741 10.1016/j.orggeochem.2017.05.007, 2017.
742 Bester, M.N., Bornemann, H., and McIntyre, T.: Antarctic marine mammals and sea ice. In: 'Sea Ice',
743 ed. D. N. Thomas (Chichester: John Wiley & Sons, Ltd), 534-555,
744 doi: 10.1002/9781118778371.ch22, 2017.
745 Bluhm, B., Swadling, K.M., and Gradinger, R.: Sea ice as habitat for macrograzers, In: 'Sea Ice', ed. D.
746 N. Thomas (Chichester: John Wiley & Sons, Ltd), 394–414, doi: 10.1002/9781118778371.ch16,
747 2017.
748 Brierley, A.S., Fernandes, P.G., Brandon, M.A., Armstrong, F., Millard, N.W., McPhail, S.D.,
749 Stevenson, P., Pebody, M., Perrett, J., Squires, M., Bone, D.G., and Griffiths, G.: Antarctic krill
750 under sea ice: Elevated abundance in a narrow band just south of the ice edge, Science, 295, 1890-
751 1892, doi:10.1126/science.1068574, 2002.
752 Brown, S.G. and Lockyer, C.H.: Whales. In: Laws, R.M. (ed) Antarctic Ecology, Vol 2.
753 Academic Press, London, p 717-781, 1984.

754 Brown, T.A. and Belt, S.: Closely linked sea ice-pelagic coupling in the Amundsen Gulf revealed by the
755 sea ice diatom biomarker IP_{25}, J. Plankton Res., 34, 647-654, doi:10.1093/plankt/fbs045, 2012.
756 Brown, T.A. and Belt, S.: Biomarker-based H-Print quantifies the composition of mixed sympagic and
757 pelagic algae consumed by *Artemia* sp., J. Exp. Mar. Biol. Ecol., 488, 32-37, doi:
758 10.1016/j.jembe.2016.12.007, 2017.
759 Brown, T.A., Belt, S., Tatarek, A. and Mundy, C.J.: Source identification of the Arctic sea ice proxy
760 IP25. Nat. Commun., 5, 4197, doi:10.1038/ncomms5197, 2014.
761 Brown, T.A., Assmy, P., Hop, H., Wold, A., and Belt, S.T.: Transfer of ice algae carbon to ice-
762 associated amphipods in the high-Arctic pack ice environment. J. Plankton Res., 39, 664-674,
763 doi:10.1093/plankt/fbx030, 2017.
764 Browning, T.J., Bouman, H.A., Henderson, G.M., Mather, T.A., Pyle, D.M., Schlosser, C., Woodward,
765 E.M.S., and Moore, C.M.: Strong responses of Southern Ocean phytoplankton communities to
766 volcanic ash, Geophys. Res. Lett., 41, 2851-2857, doi: 10.1002/2014GL059364, 2014.
767 Budge, S.M., Wooller, M.J., Springer, A.M., Iverson, S.J., McRoy, C.P., and Divoky, G.J.: Tracing
768 carbon flow in an arctic marine food web using fatty acid-stable isotope analysis, Oecologia, 157,
769 117-129, doi: 10.1007/s00442-008-1053-7, 2008.
770 Burghart, S.E., Hopkins, T.L., Vargo, G.A., and Torres, J.J.: Effects of rapidly receding ice edge on the
771 abundance, age structure and feeding of three dominant calanoid copepods in the Weddell Sea,
772 Antarctica, Polar Biol., 22, 279-288, doi: 10.1007/S003000050421, 1999.
773 Caron, D.A., Gast, R.J., and Garneau, M.-E.: Sea ice as habitat for micrograzers, In: 'Sea Ice', ed D. N.
774 Thomas (Chichester: John Wiley & Sons, Ltd), 370-393, doi: 10.1002/9781118778371.ch15, 2017.
775 Cavalieri, D. J., Parkinson, C.L., P. Gloersen,P., and Zwally, H.J.: Sea Ice Concentrations from
776 Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data, Version 1. [Indicate subset
777 used]. Boulder, Colorado USA. NASA National Snow and Ice Data Center Distributed Active
778 Archive Center. doi: 10.5067/8GQ8LZQVL0VL. 1996 (updated: 2014).
779 Clarke, A. and Tyler, P.A.: Adult Antarctic krill feeding at abyssal depths, Current Biol., 18 282-285,
780 doi:10.106/j.cub.2008.01.059, 2008.
781 Collins, L.G., Allen, C.S., Pike, J., Hodgson, D.A., Weckström, K., and Massé, M.: Evaluating highly
782 branched isoprenoid (HBI) biomarkers as a novel Antarctic sea-ice proxy in deep ocean glacial age
783 sediments, Quat. Sci. Rev., 79 87-98, doi:10.1016/j.quascirev.2013.02.004, 2013.
784 Comiso, J.C., McClain, C.R., Sullivan, C.W., Ryan, J.P., and Leonhard, C.L.: Coastal zone color
785 scanner pigment concentrations in the Southern Ocean and relationships to geophysical surface
786 features, J. Geophys. Res., 98, 2419-2451, doi: 10.1029/92JC02505, 1993.

787 Conover, R.J.: Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the
788 Northern Hemisphere. Hydrobiologia, 167, 127-142, doi:10.1007/BF00026299, 1988.
789 Constable, A.J., Nicol, S., and Strutton, P.G.: Southern Ocean productivity in relation to spatial and
790 temporal variation in the physical environment. J. Geophys. Res.,108,1-10, doi:
791 10.1029/2001JC001270, 2003.
792 Constable, A.J. et al.: Climate change and Southern Ocean ecosystems I: how changes in physical
793 habitats directly affect marine biota. Glob. Change Biol., 20, 3004-3025, doi:10.1111/gcb.12623,
794 2014.
795 Cuzin-Roudy, J. and Labat, J.P.: Early summer distribution of Antarctic krill sexual development in the
796 Scotia-Weddell region: A multivariate approach. Polar Biol.,12, 65-74, 1992.
797 Daly, K.: Overwintering growth and development of larval *Euphausia superba*: an interannual
798 comparison under varying environmental conditions west of the Antarctic Peninsula. Deep-Sea
799 Res.II, 51, 2139-2168, doi:10.1016/j.dsr2.2004.07.010, 2004.
800 Ducklow, H.W., Baker, K., Martinson, D.G., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E.,
801 Vernet, M., and Fraser, W.: Marine pelagic ecosystems: the West Antarctic Peninsula, Philos. Trans.
802 R. Soc. Lond. B. Biol. Sci., 362, 67-94, doi: 10.1098/rstb.2006.1955, 2007.
803 Durbin, E.G. and Casas, M.: Early reproduction by Calanus glacialis in the Northern Bering Sea: the
804 role of ice algae as revealed by molecular analysis. J. Plank. Res, 36, 523-541,
805 doi:10.1093/plankt/fbt121, 2013.
806 Etourneau, J., Collins, L.G., Willmott, V., Kim, J.-H., Barbara, L., Leventer, A., Schouten, S.,
807 Sinninghe Damsté, J.S., Bianchini, A., Klien, V., Crosta, X., and Massé, G.: Holocene climate
808 variations in the western Antarctic Peninsula: evidence for sea ice extent predominantly controlled
809 by changes in insolation and ENSO variability, Climate of the Past, 9, 1431-1446, doi: 10.5194/cp-
810 9-1431-2013, 2013.
811 Fitch, D.T. and Moore, J.K.: Wind speed influence on phytoplankton bloom dynamics in the Southern
812 Ocean marginal ice zone, J. Geophys. Res., 112, C08006, doi: 10.1029/2006JC004061, 2007.
813 Flores, H., van Franeker, J.A., Siegel, V., Haraldsson, M., Strass, V., Meester, E.H., Bathmann,U., and
814 Wolff, W.J.: The association of Antarctic krill *Euphausia superba* with the under-ice habitat. PloS
815 ONE, 7, e31775, doi:10.1371/journal.pone.0031775, 2012a.
816 Flores, H. et al.: Impact of climate change on Antarctic krill. Mar. Ecol. Prog. Ser., 458, 1-19, doi:
817 10.3354/meps09831, 2012b.
818 Forcada, J. and Hoffman, J.I.: Climate change selects for heterozygosity in a declining fur seal
819 population, Nature, 511, 462-465, doi:10.1038/nature13542. 2014.

Fraser, W. and Hoffmann, E.: A predator's perspective on causal links between climate change, physical forcing and ecosystem response, Mar. Ecol. Prog. Ser., 265, 1-15, doi: 10.3354/meps265001, 2003.

Fritsen, C.H., Memmott, J., and Stewart, F.J.: Inter-annual sea-ice dynamics and micro-algal biomass in winter pack ice of Marguerite Bay, Antarctica, Deep-Sea Res. II, 55, 2059-2067, doi: 10.1016/j.dsr2.2008.04.034, 2008.

Garrison, D.L., Buck, K.R., and Fryxell, G.A.: Algal assemblages in Antarctic pack-ice and in ice-edge plankton, J. Phycol., 23, 564-572, doi: 10.1111/j.1529-8817.1987.tb04206.x, 1987.

Gladyshev, M.I., Sushchik, N.N., Kalachova, G.S. and Makhutova, O.N.: Stable isotope composition of fatty acids in organisms of different trophic levels in the Yenisei River, PloS ONE, 7, e34059, doi: 10.1371/journal.pone.0034059, 2012.

Goutte, A., Cherel, Y., Houssais, M-N., Klein, V., Ozouf-Costaz, C., Raccut, M., Robineau, C., and Massé, G.: Diatom-specific highly branched isoprenoids as biomarkers in Antarctic consumers, PloS ONE, 8, e56504, doi:10.1371/journal.pone.0056504, 2013.

Goutte, A., Charrassin, J-B., Cherel, Y. Carravieri, A, De Grissac, S., and Massé, G.: Importance of ice algal production for top predators: new insights using sea-ice biomarkers, Mar. Ecol. Prog. Ser., 513, 269-275, doi:10.3354/meps10971, 2014a.

Goutte, A., Cherel, Y., Ozouf-Costz, C., Robineau, C., Lanshere, J. and Massé, G.: Contribution of sea ice organic matter in teh diet of Antarctic fishes: a diatom-specific highly branched isoprenoid approach. Polar Biol., 37, 903-910, doi:10.1007/s00300-014-1489-7, 2014b

Grebmeier, J.M., Moore, S.E., Overland, J.E., Frey, K.E, and Gradinger, R.: Biological responses to recent Pacific Arctic sea ice retreat, Trans. Am. Geophys. Union, 91, 161-162, doi: 10.1029/2010EO180001, 2010.

Hagen, W., and Auel, H.: Seasonal adaptations and the role of lipids in oceanic zooplankton, Zoology, 104, 313-326, doi: 10.1078/0944-2006-00037, 2001.

Ichii, T.: Distribution of Antarctic krill concentrations exploited by Japanese krill trawlers and mink whales, Proc. NIPR Symp. Polar Biol., 3, 36-56, 1990.

Jia, Z., Swadling, K.M., Meiners, K.M., Kawaguchi, S., and Virtue, P.: The zooplankton food web under East Antarctic pack ice – A stable isotope study, Deep-Sea Res. II, 131, 189-202, doi: 10.1016/j.dsr2.2015.10.010, 2016.

Kawaguchi, S., Nicol, S., and Press, A.J.: Direct effects of climate change on the Antarctic krill fishery, Fish. Manag. Ecol., 16, 424-427, doi: 10.1111/j.1365-2400.2009.00686.x, 2009.

852 Kohlbach, D., Lange, B.A., Schaafsma, F.L., David, C., Vortkamp, M., Graeve, M., van Franeker, J.A.,
853 Krumpen, T., and Flores, H.: Ice algae-produced carbon is critical for overwintering of Antarctic
854 krill *Euphausia superba.* Front. Mar. Sci., 4, 310, doi: 10.3389/fmars.2017.00310, 2017.
855 Korb, R.E., Whitehouse, M.J., Thorpe, S.E., and Gordon M.: Primary production across the Scotia Sea
856 in relation to the physic-chemical environment, J. Mar. Syst., 57, 231-249, doi:
857 10.1016/j.jmarsys.2005.04.009, 2005.
858 Kottmeier, S.T. and Sullivan, C.W., Late winter primary production and bacterial production in sea ice
859 and seawater west of the Antarctic Peninsula, Mar. Ecol. Prog. Ser., 36, 287–298,
860 doi:10.3354/meps036287,1987.
861 Lancelot, C., Mathot, S., Veth, C., and de Baar, H.: Factors controlling phytoplankton ice-edge blooms
862 in the marginal ice-zone of the northwestern Weddell Sea during sea ice retreat 1988: field
863 observations and mathematical modelling, Polar Biol., 13, 377-387, 1993.
864 Lannuzel, D., Schoemann, V., de Jong, J., Pasquer, B., van der Merwe, P., and Bowie, A.R.:
865 Distribution of dissolved iron in Antarctic sea ice: spatial, seasonal and inter-annual variability, J.
866 Geophys. Res, 115, G03022, doi:10.1029/2009JG001031, 2010.
867 Leu, E., Søreide, J.E., Hessen, D.O., Falk-Petersen, S., and Berge, J.: Consequences of changing sea-
868 ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity,
869 and quality, Prog. Oceanogr. 90, 18-32, doi: 10.1016/j.pocean.2011.02.004, 2011.
870 Li, W.K.W., McLaughlin, F.A., Lovejoy, C., and Carmack, E.C.: Smallest algae thrive as the Arctic
871 Ocean freshens, Science, 326, 539, doi:10.1126/sciece.1179798, 2009.
872 Lizotte, M.P.: The contribution of sea ice algae to Antarctic marine primary production, Am. Zoolog.,
873 41, 57-73, doi:10.1093/icb/41.1.57, 2001.
874 Marchese, C., Albouy, C., Tremblay, J-E., Dumont, D., D'Ortenzio, F., Vissault, S., and Bélanger, S.:
875 Changes in phytoplankton bloom phenology over the North Water (NOW) polynya: a response to
876 changing environmental conditions, Polar Biol., doi: 10.1007/s00300-017-2095-2, 2017.
877 Marschall, P.: The overwintering strategy of Antarctic krill under the pack ice of the Weddell Sea, Polar
878 Biol., 34, 1887-1900, doi: 10.1007/BF00442041, 1988.
879 Massé, G., Belt, S.T., Crosta, X., Schmidt, S., Snape, I., Thomas, D.N., and Rowland, S.J.: Highly
880 branched isoprenoids as proxies for variable sea ice conditions in the Southern Ocean. Ant. Sci., 23,
881 487-498, doi: 10.1017/S0954102011000381, 2011.
882 McMinn, A., Skerratt, J., Trull, T., Ashworth, C., and Lizotte, M.: Nutrient stress gradient in the bottom
883 5 cm of fast ice, McMurdo Sound, Antarctica. Polar. Biol., 21, 220-227,
884 doi: 10.1007/s003000050356, 1999.

885 Meier, W.N.: Losing Arctic sea ice: observations of the recent decline and the long-term context. In:
886 'Sea Ice', ed. D. N. Thomas (Chichester: John Wiley & Sons, Ltd), 290–303,
887 doi: 10.1002/9781118778371.ch11, 2017.
888 Meiners, K.M., Vancoppenolle, M., Thanassekos, S., Dieckmann, G.S., Thomas, D.N., Tison, J.-L.,
889 Arrigo, A.R., Garrison, D., McMinn, A., Lannuzel, D., van der Merwe, P., Swadling, K., Smith,
890 W.O. Jr., Melnikov, I, and Raymond, B.: Chlorophyll a in Antarctic sea ice from historical ice core
891 data, Geophys. Res., Lett., 39, L21602, doi: 10.1029/2012GL053478, 2012.
892 Meyer, B., Fuentes, V, Guerra, C., Schmidt, K., Atkinson, A., Spahic, S., Cisewski, B, Freier, U,
893 Olariaga, A. and Bathmann, U.: Physiology, growth, and development of larval krill *Euphausia*
894 *superba* in autumn and winter in the Lazarev Sea, Antarctica, Limnol. Oceanogr., 54, 1595-1614,
895 doi:10.4319/lo.2009.54.5.1595, 2009.
896 Meyer, B. et al.: The winter pack-ice zone provides a sheltered but food-poor habitat for larval Antarctic
897 krill, Nature Ecol. Evol., doi:10.1038/s41559-017-0368-3, 2017.
898 Michel, C., Legendre, L., Ingram, R.G., Gosselin, M., and Levasseur, M.: Carbon budget of sea-ice
899 algae in spring: Evidence of a significant transfer to zooplankton grazers, J. Geophys. Res., 101,
900 18345-18360, doi:10.1029/96JC00045, 1996.
901 Michels, J., Dieckmann, G.S., Thomas, D.N., Schnack-Schiel, S.B., Krell, A., Assmy, P., Kennedy, H.,
902 Papadimitriou, S., Cisewski, B.: Short-term biogenic particle flux under late spring sea ice in the
903 western Weddell Sea, Deep-Sea Res. II, 55, 1024-1039, doi: 10.1016/j.dsr2.2007.12.019, 2008.
904 Montes-Hugo, M., Doney, S.C., Ducklow, H.W., Fraser, W., Martinson, D., Stammerjohn, S.E., and
905 Schofield, O.: Recent changes in phytoplankton communities associated with rapid regional climate
906 change along the western Antarctic Peninsula, Science, 323, 1470-1473,
907 doi:10.1126/science.1164533, 2009.
908 Moore, J.K., Abbott, M.R., Richman, J.G., Smith, W.O. Jr., Cowles, T.J., Coale, K.H., Gardner, W.D.,
909 and Barber, R.T.: SeaWiFS satellite ocean colour data at the U.S. Southern Ocean JGOFS line along
910 170°W, Geophys. Res. Let., 26, 1465-1468, doi: 10.1029/1999GL900242, 1999.
911 Nelson, D.M., Smith, W.O. Jr., Gordon, L.I., and Huber, B.A.: Spring distribution of density, nutrients,
912 and phytoplankton biomass in the ice edge zone of the Weddell-Scotia Sea, J. Geophys. Res. Ocean,
913 92, 7181-7190, doi: 10.1029/JC092iC07p07181, 1987.
914 Patrick, M.R., Smellie, J.L., Harris, A.J.L., Wright, R., Dean, K., Izbekov, P., Garbeil, H., and Pilger,
915 E.: First recorded eruption of Mount Belinda volcano (Montagu Island), South Sandwich Islands,
916 Bull Volcanol, 67, 415-422, doi: 10.1007/300445-004-0382-6, 2005.

Park, J., Oh, I-S., Kim, H-C., and Yoo, S.: Variability of SeaWiFs chlorophyll-a in the southwest Atlantic sector of the Southern Ocean: Strong topography effects and weak seasonality, Deep-Sea Res. I, 57, 604-620, doi: 10.1016/j.dsr.2010.01.004, 2010.

Peck, L.S., Barnes, D.K.A., Cook, A.J., Fleming, A,H., and Clarke, A.: Negative feedback in the cold: ice retreat produces new carbon sinks in Antarctica, Global Change Biol., 16, 2614-2623, doi: 10.1111/j.1365-2486.2009.02071.x, 2010.

Perrette, M., Yool, A., Quartly, G.D., and Popova, E.E.: Near-ubiquity of ice-edge blooms in the Arctic, Biogeosciences, 8, 515-524, doi: 10.5194/bg-8-515-2011, 2011.

Quetin, L. and Ross, R.: Episodic recruitment in Antarctic krill *Euphausia superba* in the Palmer LTER study region, Mar. Ecol. Prog. Ser., 259, 185-200, doi:10.3354/meps259185, 2003.

Reid, K. and Croxall, J.P.: Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem, Proc. R. Soc. Lond. B, 268, 377-384, doi: 10.1098/rspb.2000.1371, 2001.

Renaud, P.E., Riedel, A., Michel, C., Morata, N., Gosselin, M., Juul-Pedersen, T., Chiuchiolo, A.: Seasonal variations in the benthic community oxygen demand: a response to an ice algal bloom in the Beaufort Sea, Canadian Arctic. J. Mar. Syst., 67, 1-12, doi: 10.1016/j.jmarsys.2006.07.00, 2007.

Ribeiro, S., Sejr, M.K., Limoges, A., Heikkilä, M., Andersen, T.J., Tallberg, P., Weckström, K., Husum, K., Forwick, M., Dalsgaard, T., Massé, G., Seidenkrantz, M.-S., Rysgaard, S., 2017. Sea ice and primary production proxies in surface sediments from a High Arctic Greenland fjord: spatial distribution and implications for palaeo-environmental studies. Ambio 46 (Suppl. 1), S106–S118. doi.:10.1007/s13280-016-0894-2, 2017.

Riebesell, U., Schloss, I., and Smetacek, V.: Aggregation of algae released from melting sea ice: implications for seeding and sedimentation, Polar Biol., 11, 239-248, 1991.

Ross, R.M., Quetin, L.B., Baker, K.S., Vernet, M., and Smith, R.C.: Growth limitation in young *Euphausia superba* under field conditions. Limnol. Oceanogr., 45, 31-43, doi: 10.4319/lo.2000.45.1.0031, 2000.

Roukaerts, A., Cavagna, A-J., Fripiat, F., Lannuzel, D., Meiners, K.M., and Dehairs, F.: Sea-ice algal primary production and nitrogen uptake off East Antarctica, Deep-Sea Res. II, 131, 140-149, doi: 10.1016/j.dsr2.2015.08.007, 2016.

Ryabov, A.B., de Ross, A.M., Meyer, B., Kawaguchi, S., and Blasius, B.: Competition-induced starvation drives large-scale population cycles in Antarctic krill, Nat. Ecol. Evol., 1, 0177, doi: 10.1038/s41559-017-0177, 2017.

Saba, G.K., Fraser, W.R., Saba, V.S., Iannuzzi, R.A., Coleman, K.E., Doney, S.C., Ducklow, H.W., Martinson, D.G., Miles, T.N., Patterson-Fraser, D.L., Stammerjohn, S.E., Steinberg, D.K., and Schofield, O.M.: Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula, Nat. Comms., 5, 4318, doi:10.1038/ncomms5318, 2014.

Schallenberg, C., van der Merwe, P., Chever, F., Cullen, J.T., Lannuzel, D., and Bowie, A.R.: Dissolved iron and iron(II) distributions beneath the pack ice in the East Antarctic (120°E) during the winter/spring transition, Deep-Sea Res. II, 131, 96-110, doi: 10.1016/j.dsr2.2015.02.019, 2015.

Schlitzer, R.: Ocean Data View http://odv.awi.de (2017).

Schmidt, K., and Atkinson, A.: Feeding and food processing in Antarctic krill (*Euphausia superba* Dana), in V. Siegel (ed.), Biology and Ecology of Antarctic krill, Adv. Polar Ecol., doi:10.1007/978-3-319-29279-3_5, 2016.

Schmidt, K., Atkinson, A., Petzke, K.J., Voss, M. and Pond, D.W.: Protozoans as a food source for Antarctic krill, *Euphausia superba*: complementary insights from stomach content, fatty acids, and stable isotopes, Limnol. Oceanogr., 51, 2409-2427, doi: 10.4319/lo.2006.51.5.2409, 2006.

Schmidt, K., Atkinson, A., Steigenberger, S., Fielding, S., Lindsay, M.C.M., Pond, D.W., Tarling, G.A., Klevjer, T.A., Allen, C.S., Nicol, S., and Achterberg, E.P.: Seabed foraging by Antarctic krill: Implications for stock assessment, bentho-pelgic coupling and the vertical transfer of iron, Limnol. Oceanogr., 56, 1411-1428, doi: 10.4319/lo.2011.56.4.1411, 2011.

Schmidt, K., Atkinson, A., Venables, H.J., and Pond, D.W.: Early spawning of Antarctic krill in the Scotia Sea is fuelled by 'superfluous' feeding on non-ice associated phytoplankton blooms. Deep-Sea Res. II, 59-60, 159-172, doi: 10.1016/j.dsr2.2011.05002, 2012.

Schmidt, K., Atkinson, A., Pond, D.W., and Ireland, L.C.: Feeding and overwintering of Antarctic krill across its major habitats: The role of sea ice cover, water depth, and phytoplankton abundance, Limnol. Oceanogr., 59, 17-36, doi: 10.4319/lo.2014.59.1.0017, 2014.

Schmidt, K., Schlosser, C., Atkinson, A., Fielding, S., Venables, H.J., Waluda, C.M., and Achterberg, E.P.: Zooplankton gut passage mobilizes lithogenic iron for ocean productivity, Current Biol, 26, 1-7, doi: 10.1016/j.cub.2016.07.058, 2016.

Smetacek, V. and Nicol, S.: Polar ocean ecosystems in a changing world, Nature, 437, 363-368, doi:10.1038/nature04161, 2005.

Smik, L., Belt, S.T., Lieser, J.L., Armand, L.K., and Leventer, A.: Distributions of highly branched isoprenoid alkenes and other algal lipids in surface waters from East Antarctica: Further insights for biomarker-based paleo sea-ice reconstruction. Org. Geochem., 95, 71-80, doi: 10.1016/j.orggeochem.2016.02.011, 2016.

Smith, W.O., Jr., and Nelson, D.M.: The importance of ice-edge blooms in the Southern Ocean, Biosciences, 36, 251-257, doi: 10.2307/1310215, 1986.

Smith, W.O., Jr., Shields, A.R., Peloquin, J.A., Catalano, G., Tozzi, S., Dinniman, M.S., and Asper, V.A., Biogeochemical budgets in the Ross Sea: Variations among years, Deep-Sea Res. II, 53, 815-833, doi: 10.1016/j. dsr2.2006.02.014, 2006.

Søreide, J.E., Leu, E., Berge, J., Graeve, M., and Falk-Petersen, S.: Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic, Glob. Change Biol. 16, 3154-3163, doi: 10.1111/j.1365-2486.2010.02175.x, 2010.

Spreen, G., Kaleschke, L., and Heygster, G.: Sea ice remote sensing using AMSR-E 89 GHz channels, J. Geophys. Res.,113, C02S03, doi:10.1029/2005JC003384, 2008.

Stammerjohn, S., Massom, R., Rind, D., and Martinson, D.: Regions of rapid sea ice change: An inter-hemispheric seasonal comparison, Geophys. Res. Lett, 39, L06501, doi:10.1029/2012GL050874, 2012.

Stammerjohn, S., and Maksym, T.: Gaining (and losing) Antarctic sea ice: variability, trends and mechanisms, In: 'Sea Ice', ed. D. N. Thomas (Chichester: John Wiley & Sons, Ltd), 261–289, doi: 10.1002/9781118778371.ch10, 2017.

Sullivan, C.W., McClain, C.R., Comiso, J.C., and Smith, W.O. Jr., Phytoplankton standing crops within an Antarctic ice edge, J. Geophys. Res., 93, 12487-12498, doi: 10.1029/JC093iC10p12487, 1988.

Tréguer, P., and Jacques, G.: Dynamics of nutrients and phytoplankton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. Polar Biol., 12, 149-169, 1992.

Trivelpiece, W., Hinke, J., Miller, A., Reiss, C., Trivelpiese, S., Watters, G.: Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. Proc. Nat. Acad. Sc. Unit. St. Am., 108, 7625-7628, doi:10.1073/pnas.1016560108, 2011.

Vancoppenolle, M., Meiners, K.M., Michel, C., Bopp, L., Brabant, F., Carbat, G., Delille, B., Lannuzel, D., Madec, G., Moreau, S., Tison, J-L., and van der Merwe, P.: Role of sea ice in global biogeochemical cycles: emerging views and challenges, Quat. Sci. Rev., 79, 207-230, doi:10.1016/j.quascirev.2013.04.011, 2013.

Venables, H.J., Clarke, A., Meredith, M.P.: Wintertime controls on summer stratification and productivity at the western Antarctic Peninsula, Limnol. Oceanogr., 58, 1035-1047, doi: 10.4319/lo.2013.58.1035, 2013.

Wang, S.W., Budge, S.M., Gradinger, R.R., Iken, K., and Wooller, M.J., Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: tools for

estimating sea ice algal contribution to Arctic food web production, Oecolog., 174, 699-712, doi:10.1007/s00442-013-2832-3, 2014.

Wang, S.W., Budge, S.M., Iken, K., Gradinger, R.R., Springer, A.M., and Wooller, M.J., Importance of sympagic production to Bering Sea zooplankton as revealed from fatty acid-carbon stable isotope analyses, Mar. Ecol. Prog. Ser., 518, 31-50, doi:10.3354/meps11076, 2015.

Ward, P., Shreeve, R., Atkinson, K., Korb, R., Whitehouse, M., Thorpe, S., Pond, D., and Cunnigham, N.: Plankton community structure and variability in the Scotia Sea: austral summer 2003, Mar. Ecol. Prog. Ser., 309, 75-91, doi:10.3354/meps309075, 2006.

Wassmann, P., Duarte, C.M., Agusti, S., and Sejr, M.K.: Footprints of climate change in the Arctic marine ecosystem, Glob. Change Biol., 17, 1235-1249, doi: 10.1111/j.1365-2486.2010.02311.x, 2011.

Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
Manuscript under review for journal Biogeosciences
Discussion started: 18 December 2017

1039 **Table 1.** *Euphausia superba*: carbon isotopic signature ($\delta^{13}C$) of $IPSO_{25}$ and HBI III extracted from ~30
1040 pooled, whole krill (mean ± SD, n=3) at four stations.

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

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1045 **Table 2.** *Euphausia superba*: concentrations of $IPSO_{25}$ and HBI III in different body fractions. Average
1046 stomach values are used as baseline for comparisons across body fractions, 'Ratio (stomach/X)'. X –
1047 digestive gland, gut, muscle, rest or whole krill. The I/(I+H) ratio was calculated as the ratio of means
1048 for those stations where both $IPSO_{25}$ and HBI III had been detected in at least one of the body fractions.
1049 r - range

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

1050
1051 Analysed stations ($IPSO_{25}$): Stn 5, 10, 13, 14, 17, 22, 31, 34, 54
1052 Analysed stations (HBI III): Stn 5, 10, 13, 14, 17, 22, 31, 34, 47, 54, 60
1053 Analysed stations [I/(I+H)]: Stn 5, 10, 13, 14, 17, 22, 31, 34, 54
1054 Analysed stations, pellets ($IPSO_{25}$): Stn 21, 32
1055 Analysed stations, pellets (HBI III): Stn 9, 10, 15, 21, 31, 32, 34, 42, 45, 47, 52, 54, 60, 61
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Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
Manuscript under review for journal Biogeosciences
Discussion started: 18 December 2017

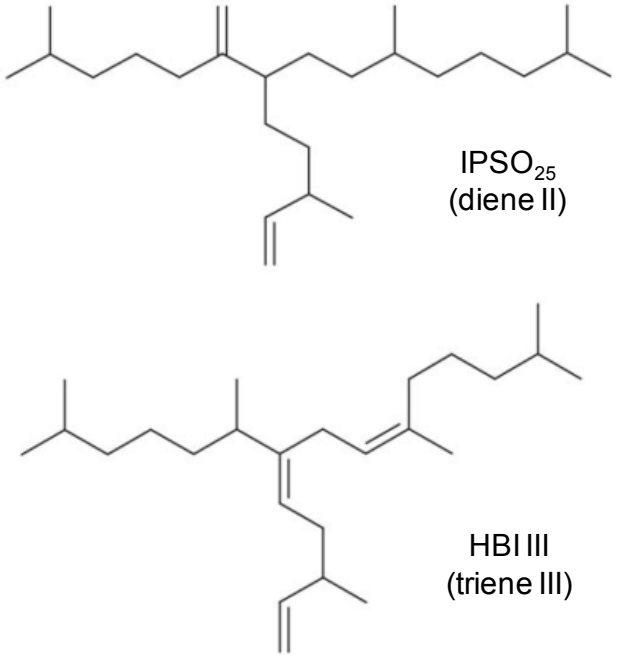

Fig. 1

Fig. 1. Chemical structures of diatom highly branched isoprenoid (HBI) biomarkers described in this study.

Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
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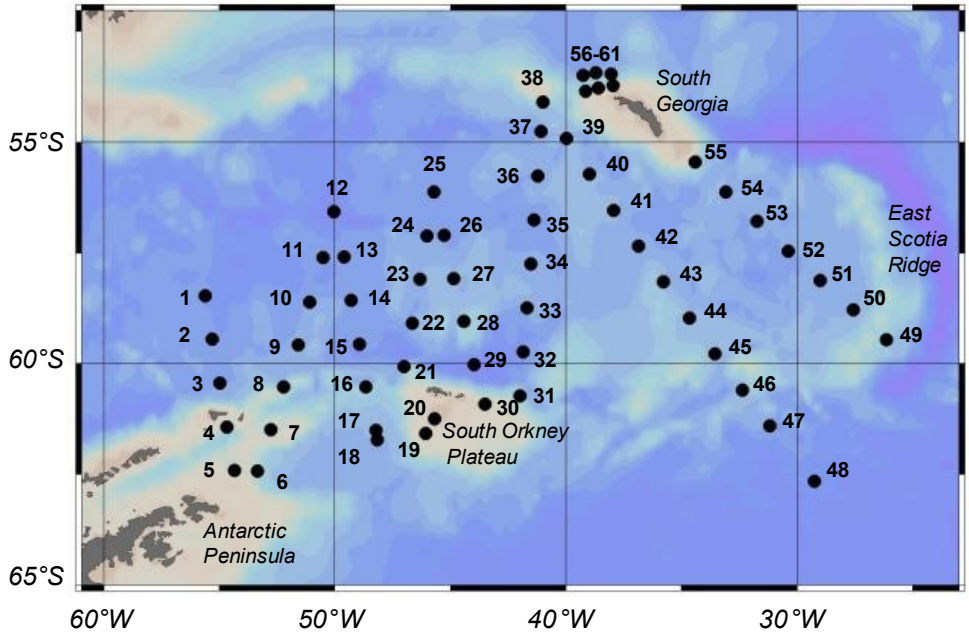

Fig. 2

Fig. 2. Scotia Sea and South Georgia: sampling locations during austral summer 2003. The date of sampling progressed from January, 9th (Station 1) to February 16th (Station 61). Shelf areas (≤ 1000 m) are presented in light brown colour.

Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
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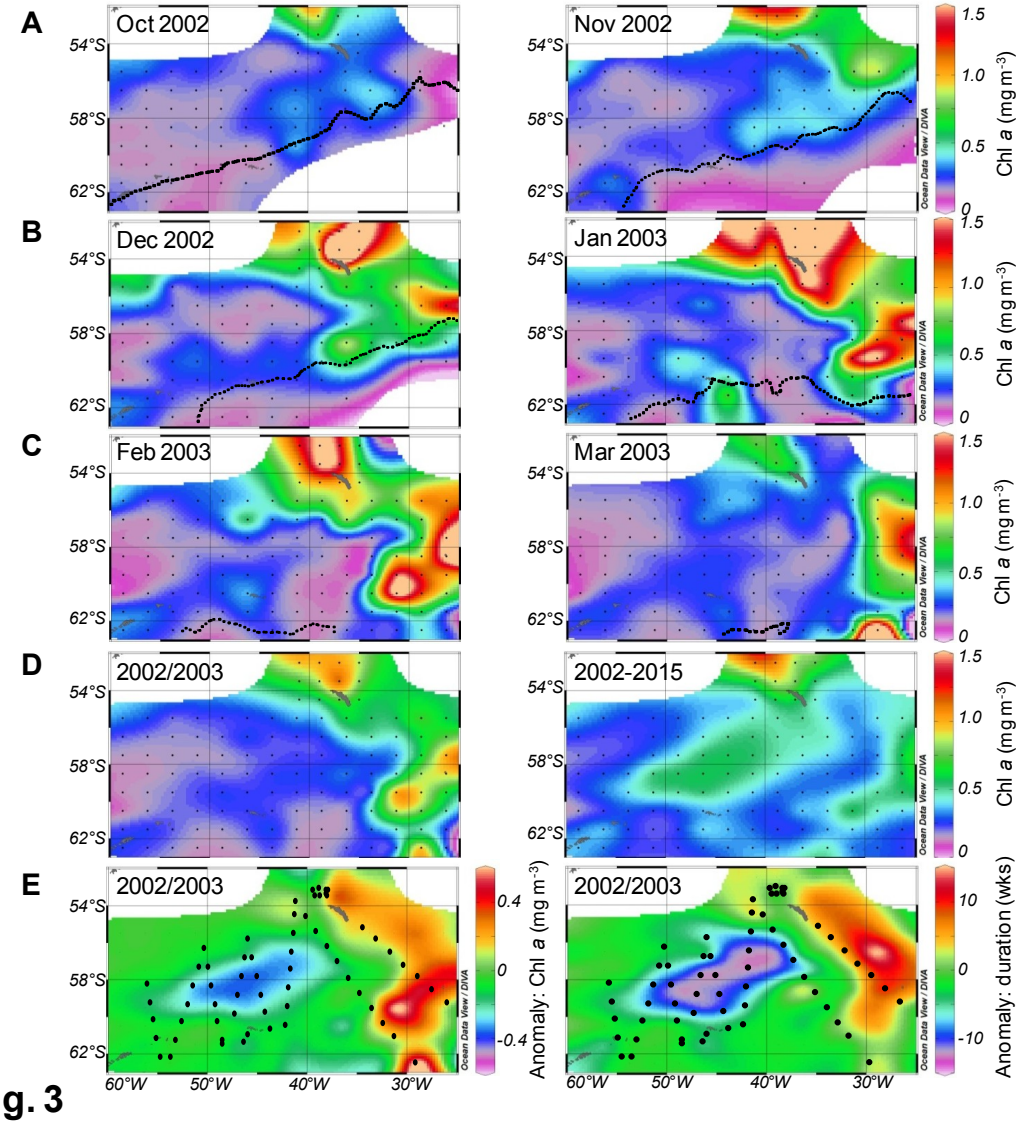

Fig. 3

Fig. 3. Phytoplankton bloom development in the Scotia Sea in 2002/2003 and on a longer-term average (2002-2015). Chl *a* concentrations in the **A)** early season (L: Oct. 2002; R: Nov. 2002), **B)** mid-season (L: Dec. 2002; R: Jan. 2003) and **C)** late season (L: Feb. 2003; R: Mar. 2003). **D)** Average annual chl *a* concentrations, Sept-Mar (L: 2002/2003; R: 2002-2015). **E)** Anomaly in 2002/2003 (Sept.–Mar.) compared to the longer-term average, 2002-2015 (L: chl *a* concentration; R: bloom duration). Chl *a* concentrations were derived from ocean colour radiometry (MODIS, 8-day composites). A bloom was

1087 defined as >0.5 mg Chl *a* m^{-3}. The dashed line represents the mean position of the 15% ice edge during
1088 each of the months. In panels E, the position of our sampling stations is given.

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Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
Manuscript under review for journal Biogeosciences
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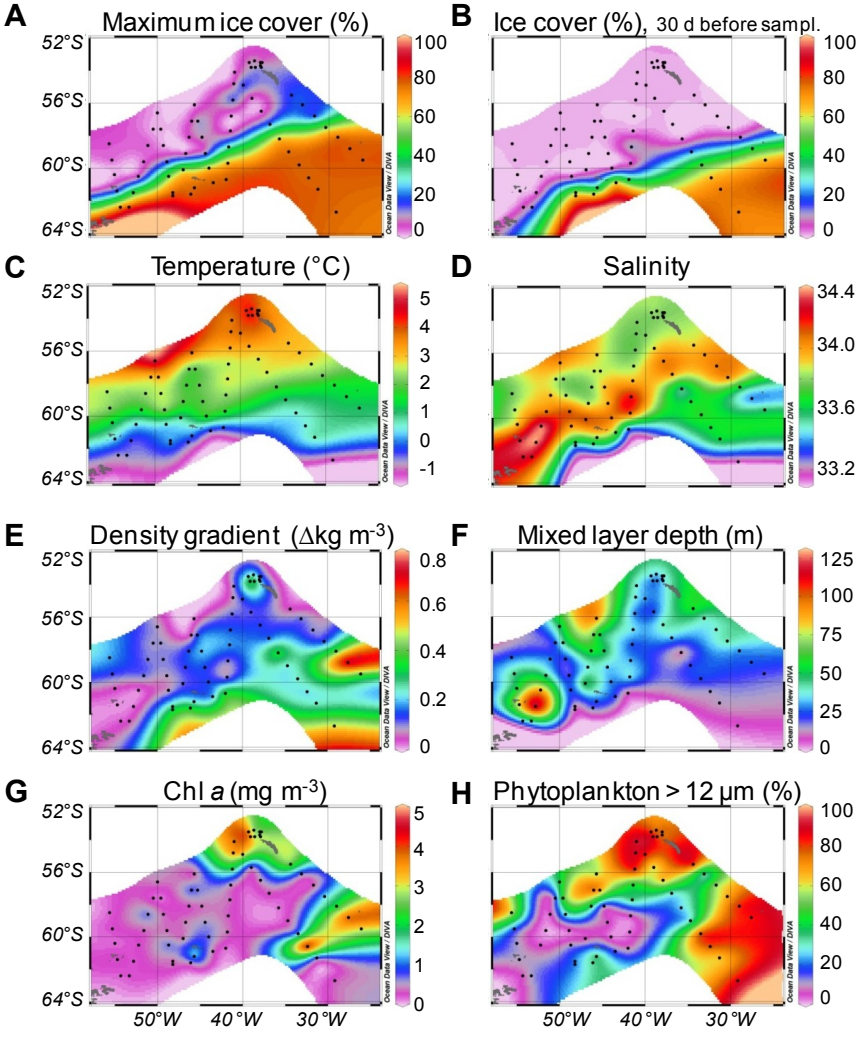

Fig. 4

Fig. 4. Oceanographic data: **A)** Maximum ice cover within the 2002/2003 season. **B)** Ice cover 30 days before each station was sampled. **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*).

Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
Manuscript under review for journal Biogeosciences
Discussion started: 18 December 2017

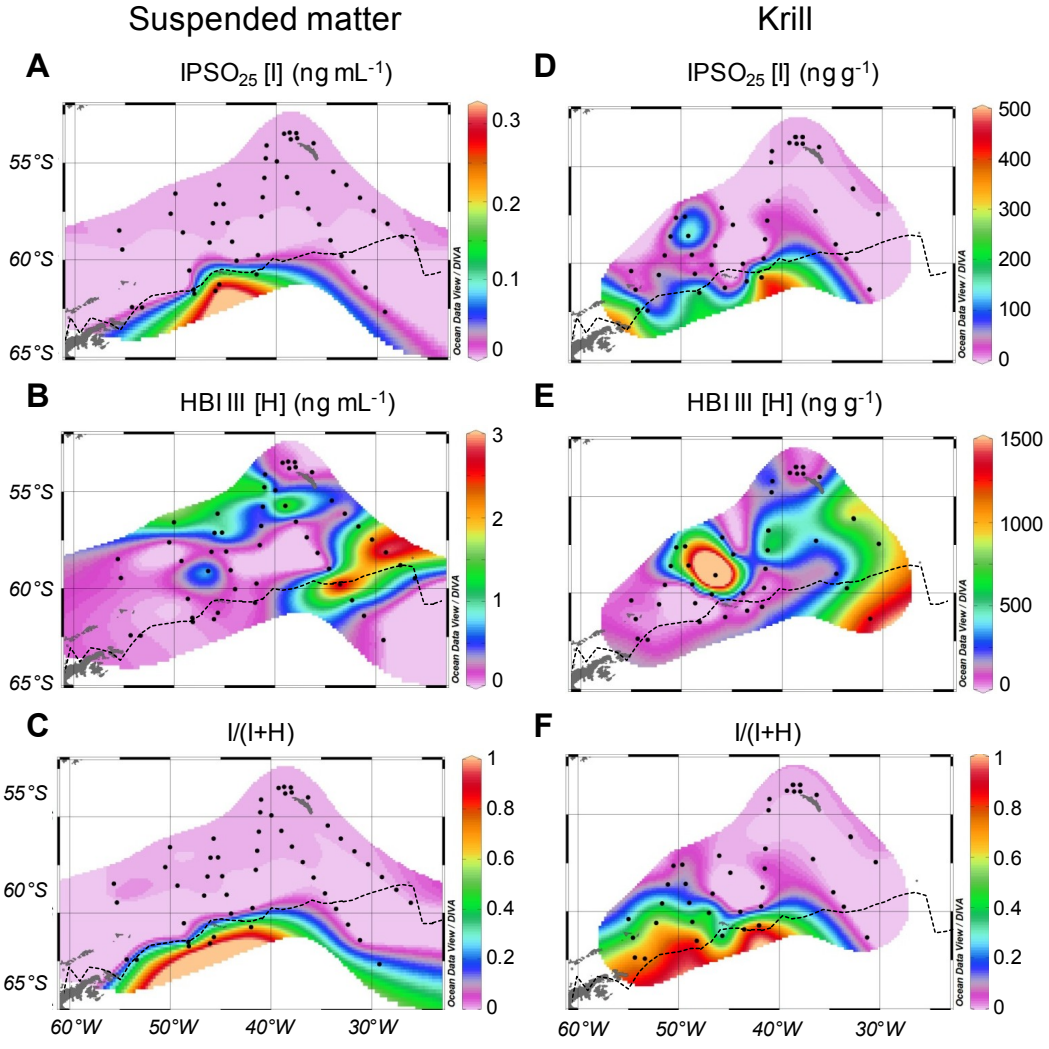

Fig. 5

Fig. 5. 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.

Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
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Discussion started: 18 December 2017

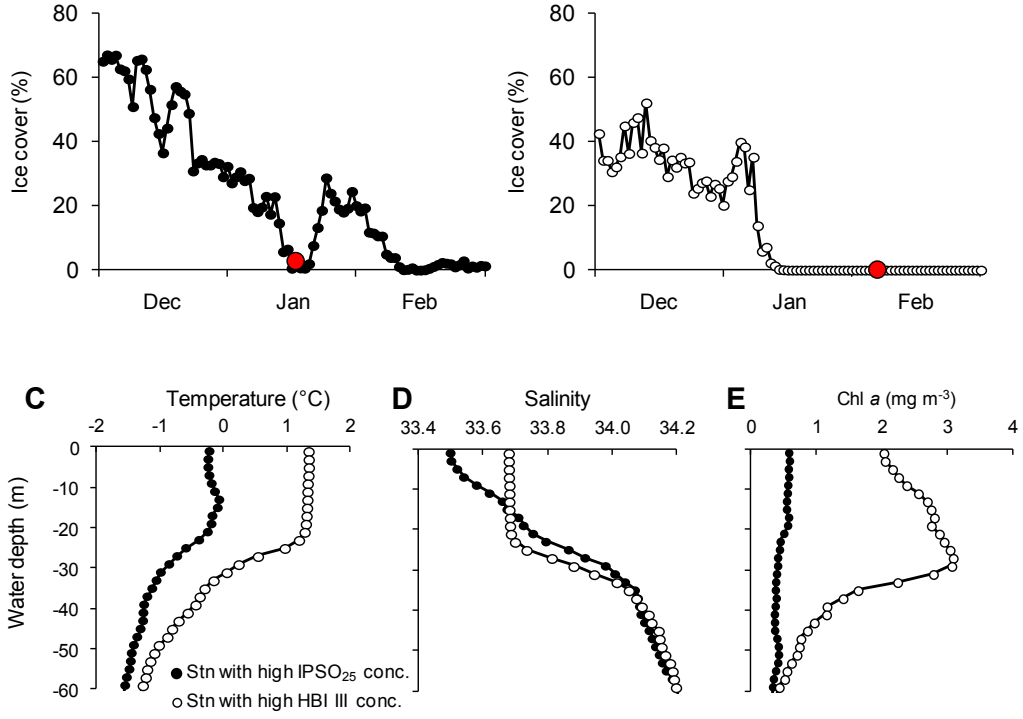

Fig. 6

Fig. 6. Oceanographic differences between stations with high $IPSO_{25}$ *vs.* high HBI III concentrations in suspended matter. **A)** Time line of sea ice cover at stations with high $IPSO_{25}$ 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*.

Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
Manuscript under review for journal Biogeosciences
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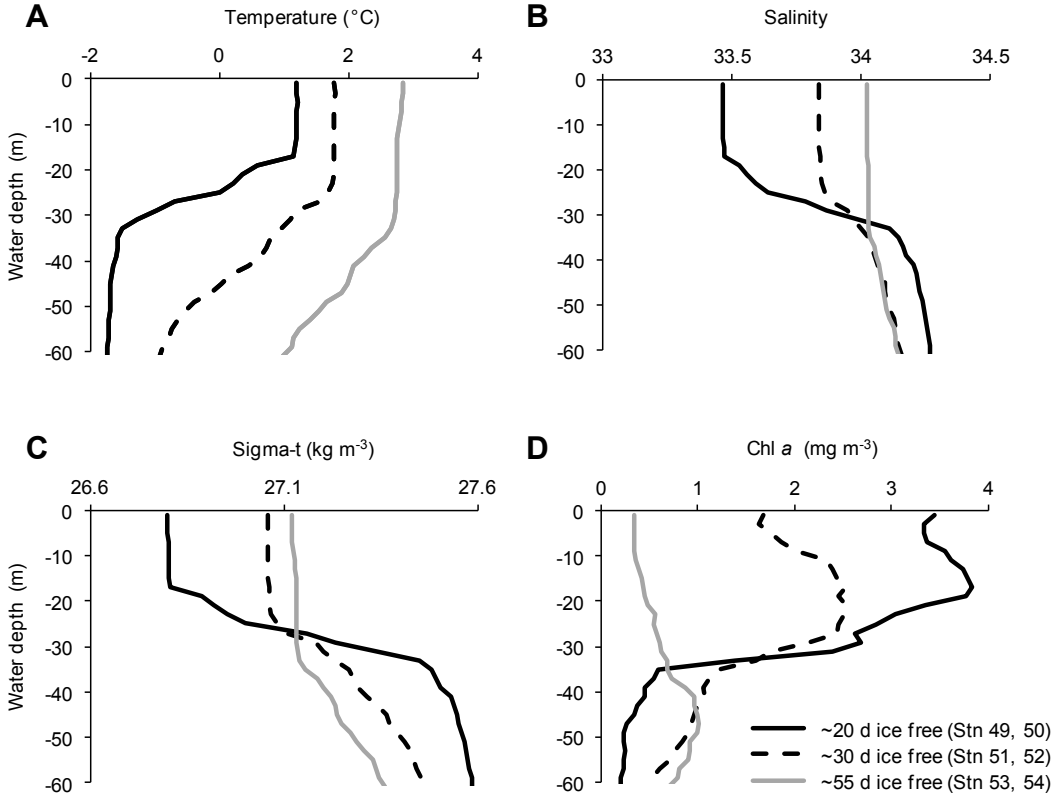

Fig. 7

Fig. 7. Oceanographic characteristics along the gradient in HBI III concentrations in the eastern Scotia Sea. **A)** Vertical profiles of temperature, **B)** salinity, **C)** density and **D)** chl *a* for the mean of two neighbouring stations. The HBI III content of the suspended matter was highest at stations which had been ice free for ~30 days (3.4±0.6 ng mL^{-1}, Stn 51 & 52), but lower for stations that had become ice free more recently (1.3±0.9 ng mL^{-1}, Stn 49 & 50) or longer ago (0.9±1.0 ng mL^{-1}, Stn 53 & 54).

Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
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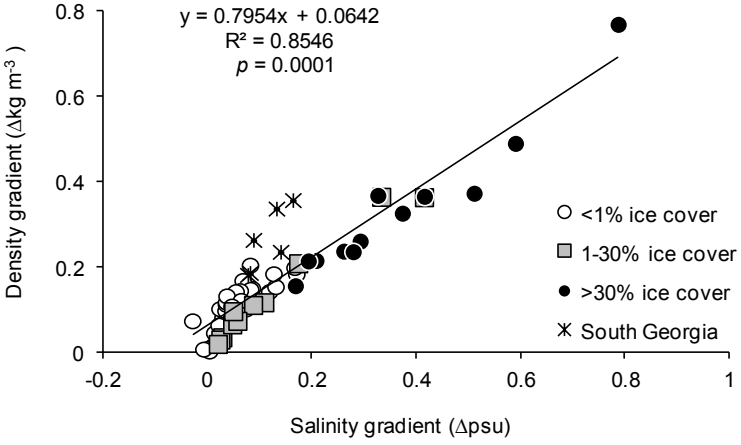

Fig. 8

Fig. 8. The role of seasonal ice melt for water column stratification. During spring 2003, the maximum density gradient per 10 m water column was a linear function of the co-occurring salinity gradient, with strongest density gradients at stations that had been ice covered by >30% one month before sampling. The remaining variability in the density gradient is explained by temperature (GLM: density gradient = 0.00254 + 0.7255 salinity gradient + 0.07828 temperature gradient; $R^2 = 0.9889$).

Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-535
Manuscript under review for journal Biogeosciences
Discussion started: 18 December 2017

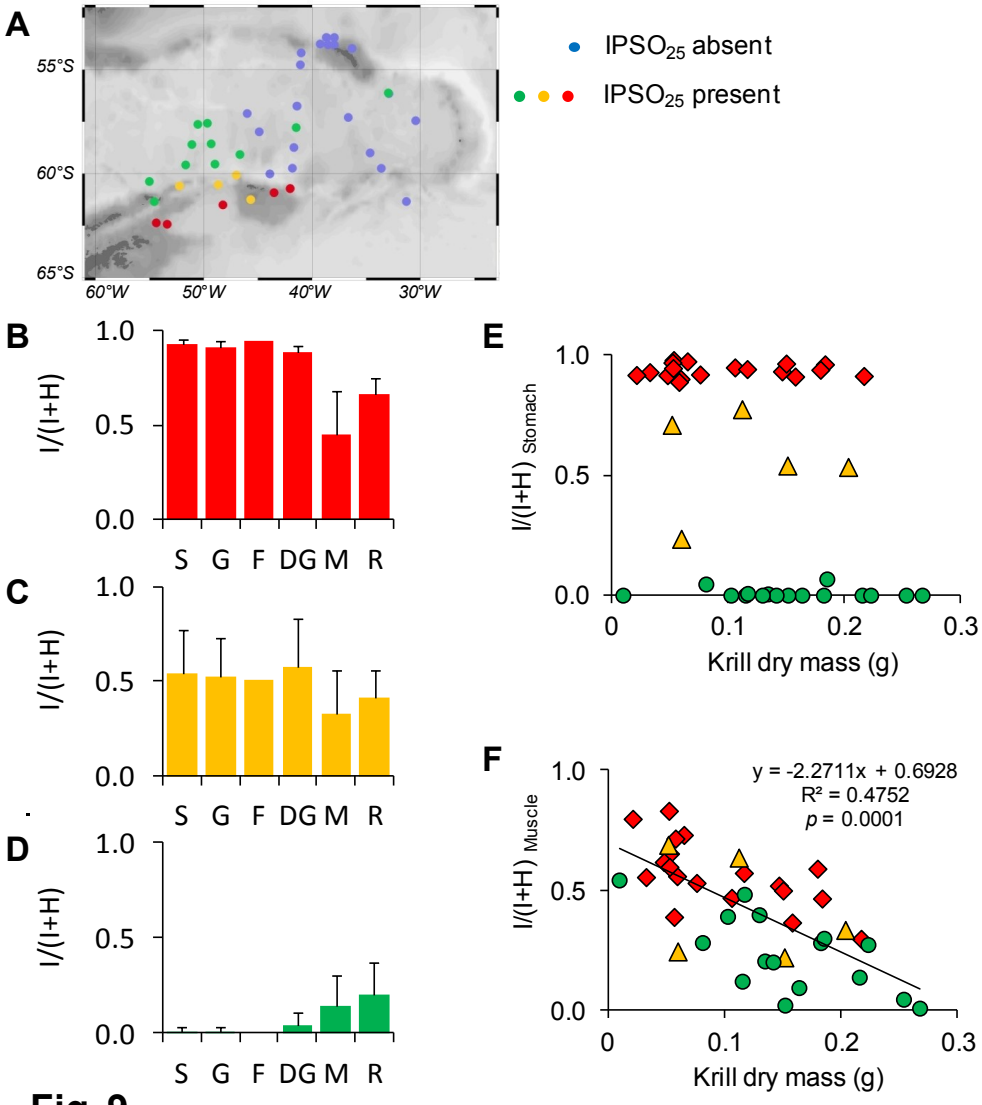

Fig. 9

Fig. 9. *E. superba*: multiple scenarios of krill feeding history on ice diatoms. **A)** Location of stations where $IPSO_{25}$ was present in krill (red – Scenario 1, amber – Scenario 2, green – Scenario 3) or absent (blue). **B)** Scenario 1: Krill are mainly feeding on ice diatoms. I/(I+H) ratios are high (>0.9) in stomach (S), gut (G), faecal pellets (F) and digestive gland (DG), but lower (0.4-0.7) in muscles (M) and rest of the body (R). **C)** Scenario 2: Krill are feeding on a mixture of ice diatoms and open water diatoms. I/(I+H) ratios are moderate (~0.5) in stomach, gut, faecal pellets and digestive gland, but lower (0.3-0.4)

in muscles and rest of the body. **D)** Scenario 3: Krill are feeding on open water diatoms, but fed on ice diatoms in the past. I/(I+H) ratios are very low (<0.1) in stomach, gut and digestive gland, but higher (0.1-0.2) in muscles and rest of the body. **E, F)** The effect of krill body size on their feeding on ice diatoms. I/(I+H) ratios are presented separately for krill stomach content and muscle. Colour of symbols in accordance with panels B-D: Red – krill that fed currently on ice diatoms, yellow – krill that fed currently on a mixture of ice- and open water diatoms, green – krill that fed currently on open water diatoms. Individuals ranged from 16-42 mm in standard body length [L] and 0.01-0.27 g in dry mass [M] ($M = 1*10^{-6} L^{3.2452}$, $R^2 = 0.9707$). Each symbol represents 3-15 pooled individuals of the same body length.

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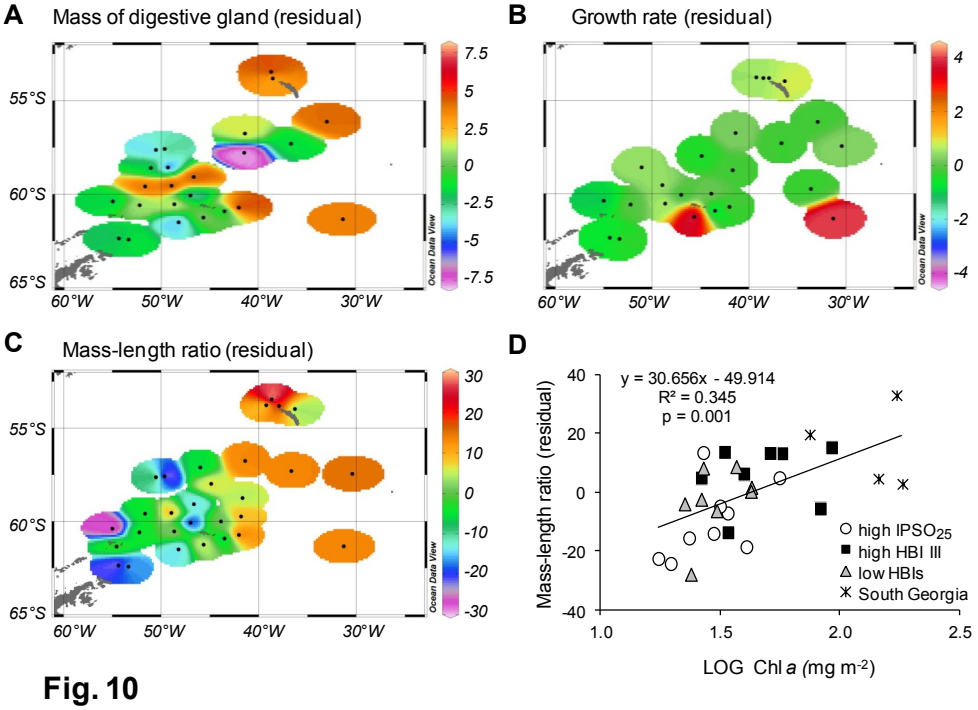

Fig. 10

Fig. 10. *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)** Linear regression between the residuals of 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 $IPSO_{25}$- or HBI III content: 'high $IPSO_{25}$' (>30 ng g^{-1}), 'high HBI III' (>100 ng g^{-1}), 'low $IPSO_{25}$ 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.

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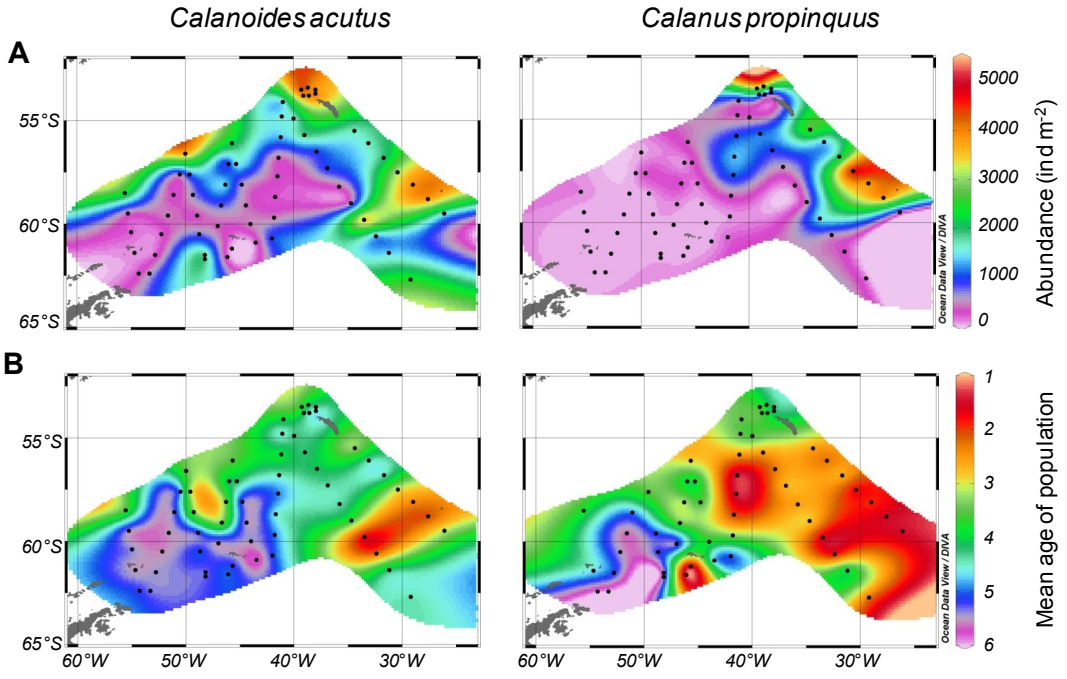

Fig. 11

Fig. 11. Large calanoid copepods, *Calanoides acutus* and *Calanus propinquus*. **A)** Species abundance and **B)** mean age of the population. Six copepodite stages of increasing age were considered: 1st, 2nd, 3nd, 4th, 5th and 6th. Low numbers indicate a young age of the population, dominant by new recruits (stage 1-3). Late copepodite stages (stage 5-6) represent the old, overwintered generation.