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

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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 (sea ice-derived, sea ice-conditioned, non-sea 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 sea ice-derived and sea 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.

1. Introduction

Over the last four decades, sea ice has shown a rapid decline in areal coverage in polar regions. ~~the Arctic and parts of the Antarctic (e.g. Bellingshausen- and Amundsen Seas).~~ In the Arctic and parts of the Antarctic (e.g. Bellingshausen- and Amundsen Seas), ~~Here~~ sea ice concentrations are decreasinge 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 marine ecosystems 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 w~~W~~estern 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 led to ~~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. W~~Thus, w~~hile the former prevents phytoplankton blooms, the latter can promote them. Several processes associated with the seasonal retreat of sea ice are considered to 'condition' the upper water column for phytoplankton blooms (Smetacek and Nicol 2005). First, low-density meltwater can stabilize the surface layer and therefore enhance mean irradiance levels for phytoplankton (Smith and Nelson 1986). Second, the release of trace elements from melting sea ice can alleviate iron limitation, which is a common feature in the open Southern Ocean (Lannuzel et al. 2010). Third, some algae that thrive in sea ice also act as an inoculum for phytoplankton blooms (Smith and Nelson 1986). This explains why the marginal ice zone (MIZ) is, on

89 average, more productive than the permanently open waters of the Southern Ocean (Smith and Nelson
90 1986, Tréguer and Jacques 1992).

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

107 Dominant polar grazers such as calanoid copepods and euphausiids are adapted to the strong
108 seasonality in primary production and the dynamic interface between ice and water (Smetacek and
109 Nicol 2005). Postlarval stages of these species biosynthesise large lipid stores which enable them to
110 survive long periods without food (Hagen and Auel 2001). Some species remain active during winter
111 (e.g. the Antarctic copepod *Calanus propinquus* and the Antarctic krill *Euphausia superba*) and can be
112 found under sea ice feeding on ice algae or heterotrophs, if available (Atkinson and Shreeve 1995,
113 Flores et al. 2012a, Schmidt et al. 2014). In other species, e.g. the Arctic *Calanus hyperboreus* and *C.*
114 *glacialis* together with the Antarctic *Calanoides acutus*, the life cycle is closely coupled to the bloom
115 period: they overwinter at depth in dormancy, are able to fuel their gonad maturation from lipid reserves
116 and their offspring make the most of the brief productive season (Hagen and Auel 2001). However,
117 years with very early or very late ice retreat can lead to poor population development of these species
118 (Quetin and Ross 2003, Ward et al. 2006, Leu et al. 2011). Optimal conditions are reached when peak
119 times of food demand and food availability are tightly matched (Quetin and Ross 2003, Søreide et al.
120 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 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 declined significantly (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, sea ice-conditioned and non-~~-~~ sea ice~~-~~-associated primary production for~~carbon in~~ krill nutrition~~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 (Belt and Müller 2013~~Armand et al. 2017~~). Around Antarctica, mixtures of a di-unsaturated HBI (referred to as diene II in previous studies; see Fig. S1) and a tri-unsaturated HBI (referred to as triene III in previous studies, thereafter HBI III, Fig. S1) 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*.

Methods

~~*2.1 Phytoplankton bloom development*~~

2.1 Satellite-derived chlorophyll a data

To gain an overview of phytoplankton development during the year of our field season (2002/2003) and for comparison with other years, we used satellite-derived chlorophyll *a* (chl *a*) data. These provide large-scale, quasi-synoptic coverage of chl *a* concentrations in surface waters, but have the caveat that deep chl *a* maxima are not detected. Data 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 seasonal mean chl *a* concentration and bloom duration (number of weeks with chl $a \geq 0.5$ mg m^{-3}) were determined for the 2002/2003 season and compared with the 13-year average, 2002-2015.

2.2~~3~~ Sea ice cover

For the 2002/ 2003 season, m~~M~~onthly 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 cover 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 were 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 6.25 km. Further details are given in Cavalieri et al. (1996) and Spreen et al. (2008).

2.3~~2~~Station sampling of o~~O~~ceanographic parameters~~y~~

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. 1~~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 (~~0~~ 47 mm diameter), and analysed for chl *a* after extraction in 90% acetone (Korb et al. 2005).

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 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 lateral edge of the carapace to the posterior edge of the sixth abdominal segment (Standard 3 body length). ~~eye to the tip of the telson.~~ Three to fifteen individuals of the same body length (±1 mm) were selected for HBI analysis. Standard 3 lengths of selected krill ranged from 16 - 42 mm. If available, up to six different size classes each differing by at least -2 mm, were analysed per station. Then, ~~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 seawater 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 HBI~~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 selected~~ingle~~-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 seawater, 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 in krill from four sampling locations near the retreating ice edge (Stn. 5, 17, 31 and 47). Analysis was carried out 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 (CI-V: juveniles, CVI: adultsstage 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.

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. 23A). 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. 23B). 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. 23C). 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 13-yearlonger-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. 23D, 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 compared to than in the 2002-2015 average (Fig. 23E).

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. 34A). Thirty days One month before each station was occupied, the cruise, stations in the southern Scotia Sea wasere still ice covered by 50-75 % concentration (Fig. 34B), 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. 3~~4~~C). 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. 3~~4~~D). 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. 3~~4~~E, 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. 3~~4~~G,H).

Out of the 61 stations where suspended matter was analysed for HBIs, 6 contained $IPSO_{25}$ and 51 HBI III (Fig. 4~~5~~A, 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. 4~~5~~C]. In addition to suspended matter, krill from 47 stations were ~~also~~ analysed for HBIs. $IPSO_{25}$ was present in krill from 21~~, while of these, whereas~~ HBI III was found in krill from all 47 stations (Fig. 4~~5~~D, 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~~ was also ~~be~~ detected in krill from~~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 in krill occurred near the ice edge in the western– and central Scotia Sea [mean I/(I+H): 0.3±0.2, n=21; Fig. 4~~5~~F].

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

The carbon isotopic signature ($\delta^{13}C$) of $IPSO_{25}$ extracted from krill sampled at three different locations near the ice edge (Stn 5, 17, 31), ranged from -9.2 to -15.7 ‰ (mean: -12.5±3.2 ‰, Table 1). Such high $\delta^{13}C$ values are indicative of a depleted dissolved inorganic carbon pool as common in the semi-enclosed sea ice matrix (Wang et al. 2014). In line with a sea ice origin of $IPSO_{25}$, stations with high $IPSO_{25}$ concentrations in suspended matter (Stn 18, 19, 20, 31) were characterised by recent sea ice retreat, sub-zero surface temperatures, low surface salinity and relatively low chl *a* concentrations (Fig. 5). In contrast, HBI III extracted from the same krill showed much lower $\delta^{13}C$ values (-39.1 to -42.5 ‰,

Table 1), suggesting a production in open waters where the dissolved inorganic carbon pool is replete. Stations with high HBI III concentrations in suspended matter (Stn 45, 50, 51, 52) had been ice-free for ~1 month at the time of sampling. Here, higher temperatures, higher surface salinity and elevated chl *a* concentrations indicate a progression of upper water column processes since the ice melt (Fig. 5).

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. 3G,H, Fig. 4B). Oceanographically, this area was characterised by shallow upper mixed layers and a strong vertical gradient in salinity (Fig. 3C-F, Fig. S2). A comparison of the stations' history of ice cover shows that the vertical density gradient was driven by ice melt. Across the Scotia Sea, there was a highly significant linear relationship between density- and salinity gradients, with strongest density gradients at stations that had >30% ice cover one month before sampling (Fig. 6). This supports salinity as the main driver of sea water density and therefore stratification at polar temperatures (Smith and Nelson 1986).

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

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

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

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

The I/(I+H) ratio within the various krill body fractions can reveal recent and past feeding history (Fig. 79A-D). ~~Thus, the stomach, gut, faecal pellets and digestive gland showed similar I/(I+H) ratios within the same individual, indicative of their recent feeding history. In contrast, muscle and remaining body tissue often had different ratios as they integrate diet information over longer times. Highest~~ The I/(I+H) ratios in krill stomach content ~~s~~ were highest ~~found~~ at ~~5~~ stations closest to the ice edge in the western and central Scotia Sea, indicating that here the krill diet was mainly based on ~~were feeding on a diet enriched in~~ sea ice diatoms. At 4 stations near the ice edge and up to ~200 km further north, krill had moderate I/(I+H) ratios in their stomach contents~~s~~ suggesting a mixed diet of ice-derived diatoms and open water diatoms. Low I/(I+H) ratios in krill stomachs, but higher ratios in their muscle and rest of the body were found at 11 stations ~200-600 km north of the ice edge, suggesting that krill had been feeding on ice diatoms in the past, but had switched to open water diatoms by the time of sampling. At

26 mainly northern stations, krill did not contain any detectable $IPSO_{25}$ and may, therefore, not have fed on ice diatoms within the last few weeks~~at all~~.

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

~~The overall concentration of $IPSO_{25}$ and HBI III in krill and their I/(I+H) ratios showed some variability with body size. Small krill (≤ 0.1 g dry mass) contained lower concentrations of $IPSO_{25}$ and 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. 8~~10~~A-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. 8~~10~~D). 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. 8~~10~~D).

3.6 Recruitment of large calanoid copepods

Another important group of pelagic grazers in the Southern Ocean are calanoid copepods, e.g. the high-latitude species *Calanoides acutus* and *Calanus propinquus*. While HBIs have not been measured in these species, their overall abundance and age structure gives some information about suitable feeding grounds. For both species, abundances were highest at South Georgia and in the south-eastern Scotia Sea (Fig. S3~~11A~~). The latter site was dominated by young development stages (CI-III~~copepodite stages I-III~~), which indicates recent successful recruitment (Fig. 8E,F~~11B~~). At South Georgia, the population was older, but also dominated by new recruits (C~~copepodite stage~~ IV). In contrast, in the western Scotia Sea copepod abundances were low, ~~overall,~~ and the population consisted of 'overwintered' copepodite stages (CV and females), suggesting that recruitment was delayed or had failed.

4. Discussion

4.1 Evaluating the HBI approach

Knowledge of~~about~~ the role of ice algae- vs. phytoplankton-produced carbon for higher trophic levels is central to our understanding of polar ecosystems. However, reliable estimates are difficult to achieve. Firstly, traditional trophic markers such as fatty acids, accessory pigments or taxonomy are of limited use as diatoms often dominate both communities with few species being obligate ice inhabitants (~~Garrison et al. 1987, Lizotte 2001,~~ Arrigo 2017). ~~-~~Secondly, approaches that allow the separation of the two sources based on non-conservative tracers, including bulk- or compound-specific stable isotope analysis, rely on numerous assumptions that are not always met in practice (Budge et al. 2008). An

example is isotopic fractionation, where the $\delta^{13}C$ values of fatty acids derived from diatoms, and not produced *de novo* by the consumer [e.g. 16:4(n-1) or 20:5(n-3)] are usually assumed to remain unchanged across trophic levels (e.g. Budge et al. 2008, Wang et al. 2015, Kohlbach et al. 2017). However, laboratory and field studies have shown significant isotopic fractionation (-4 to -1‰) in polyunsaturated fatty acids between diet and consumer, and a gradual depletion in the ^{13}C content of fatty acids upward through the food chain (Bec et al. 2011, Gladyshev et al. 2012 and ref. therein). If this isotopic fractionation remains unaccounted for, the contribution of the isotopically lighter source is overestimated and this bias increases with shorter isotopic distance between the endmembers (Bec et al. 2011). Based on data obtained from Antarctic krill by Kohlbach et al. (2017), the ice algae source of 20:5(n-3) increased from 64 to 89% in larvae, from 46 to 70% in juveniles and from -18 to 7% in adults 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. 7~~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 $IPSO_{25}$ (*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* also inhabiting 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. 5~~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. 4~~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. 7~~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

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

~~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 couple of hours before capture (Schmidt and Atkinson 2016), and therefore relates to the environment at the sampling location.~~ At five stations near the ice edge, krill stomachs contained a higher proportion of 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]. Up to 200 km north of the ~~current~~ ice edge, ~~krill still ingested~~ a mixture of ice algae and phytoplankton was found in krill stomachs [$I/(I+H)_{Stomach}$: 0.56±0.24], while $IPSO_{25}$ was not detected in suspended matter from surface waters. These observations suggest that krill fed preferentially on ice algae and sampled them below the upper mixed layer, either during their diurnal vertical migration or in special foraging trips towards the benthos (~~Clarke and Tyler 2008,~~ Schmidt et al. 2011). At Stn 8, for instance, a high I/(I+H) ratio coincided with lithogenic particles in krill stomachs, which may have been ingested at the seabed (Schmidt et al. 2011). About 200-600 km north of the ice edge, $IPSO_{25}$ was found in krill

muscle tissue, but not in their stomachs. ~~Lipids in krill muscle tissue have a much slower turnover rate than those in the stomach and can therefore give information about the feeding history within the last few weeks. Here, t~~These results indicate that krill had been feeding on ice algae in the past, but subsequently relied on phytoplankton. Overall, $IPSO_{25}$ was detected in krill from 21 stations across the western and central Scotia Sea, confirming the widespread uptake of ice algae as a food source.

We found different trends between krill body mass and their I/(I+H) ratios in stomach content and muscle, ~~Krill stomach and muscle showed different trends between body mass and the I/(I+H) ratio, suggesting that krill had only been feeding on ice algae for a relatively short period.~~ Small krill were equilibrated with the ice algae diet, having high I/(I+H) ratios in both stomach and muscle, while larger krill had high I/(I+H) ratios only in their stomachs and not in their muscles (Fig. 7~~9~~). This suggests that larger krill did not feed long enough on ice algae to reach equilibrium between diet and body tissue. Most likely, ice algae became more accessible to krill when the ice started to melt (Jia et al. 2016). The $IPSO_{25}$ extracted from krill was enriched in $\delta^{13}C$ (Table 1), as is typical for material from interior sea ice (McMinn et al. 1999, Wang et al. 2014) that is only within reach of krill when the algae are released into the water column. A carbon budget of ice algae in the Canadian Arctic in spring showed that >65% of the biomass, released from sea ice into the upper water column, remained suspended (Michel et al. 1996). However, the high variability in chl *a* residence time (mean: 31±33 days) and ~~-~~sinking rate (mean: 1.4±1.5 m d^{-1}) illustrates the dual fate of ice algae (Michel et al. 1996). W~~; w~~hile some algae rapidly sink out of the euphotic zone and efficiently transfers carbon to the benthos (e.g. Riebesell et al. 1991, Renaud et al. 2007~~, Amiraux et al. 2017~~), others remain suspended over several weeks and can aid the nutrition of pelagic grazers (Michel et al. 1996, Smik et al. 2016). In any case, the trophic importance of ice algae extends beyond the period of their maximum production in sea ice (Michel et al. 1996). Here, the ice proxy $IPSO_{25}$ revealed that ice algae can be an important food source for krill even several weeks after the ice cover has disappeared.

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. 3~~4~~, Korb et al. 2005). This may explain why krill continued feeding on ice algae even after the algae~~y~~ 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. 34, 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. 45), 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 13-year ~~longer-term~~ data set of satellite-derived chl *a* concentrations shows that the area where krill contained high amounts of HBI III (Fig. 45E) matches the region with exceptionally low surface chl *a* concentrations in the central Scotia Sea in the 2002/2003 season (Fig. 23E).

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's 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. 8C~~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 main 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 confirms ~~indicates~~ the~~an~~ essential role of phytoplankton blooms for krill performance in spring~~, as has been suggested previously~~ (Cuzin-Roudy et al. 1992, Schmidt et al. 2012).

4.3 The role of sea 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. 2008, 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, Lannuzel et al. 2010, 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. 2~~3~~; Park et al. 2010). Sea ice retreat can assist phytoplankton growth due to the freshness of the meltwater, following brine rejection during ice~~ts~~ formation. The low-salinity (hence low-density) 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 eastern Scotia Sea, phytoplankton blooms propagated behind the receding ice edge over hundreds of kilometres and for several months (Fig. 2). In contrast, i~~I~~n 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 and references therein). 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. 8C~~10c~~). The occurrence of HBI III in krill tissue often coincided with medium to high chl *a* concentrations in the water column (Fig. 8D~~10d~~). Therefore, enhanced krill performance in the east is most likely a result of higher food concentrations. A number of studies ha~~ves~~ 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.

A few copepod species inhabit Antarctic sea ice, but the biomass dominant copepod grazers in high latitudes, *Calanoides acutus* and *Calanus propinquus*, are only loosely associated with sea ice, if at all (Arndt and Swadling 2006). *C. acutus* shows reduced feeding activity within the ice and their offspring

only occur in the MIZ or open waters (Atkinson and Shreeve 1995, Burghart et al 1999). In contrast, *C. propinquus* have been found feeding on ice algae and spawning below sea ice, but their populations likewise expand mainly in open waters (Atkinson and Shreeve 1995, Burghart et al 1999). Both species can complete their life cycle at South Georgia (Atkinson and Peck~~et al.~~ 1988), which is permanently sea ice-free. During our study period, the occurrence and recruitment of these species showed similarities to feeding behaviour and performance of Antarctic krill. In the western and central Scotia Sea, *C. acutus* and C. *propinquus* had low abundances and the populations were dominated by females and late copepodite stages representing the 'old, overwintered' generation. This delay or failure of recruitment was likely caused by the lack of phytoplankton, as also indicated by krill feeding on sinking ice algae in open waters, and their below-average body mass. Highest copepod abundances in the south-east coincided with the dominance of early copepodite stages (i.e. the 'new' generation). This region of intensive copepod reproduction (Stn 45, 50, 51, 52) matches high HBI III concentrations in suspended matter and enhanced krill performance in the wake of retreating sea ice. We therefore suggest that the MIZ is an important nursery ground for these large copepod species, in line with previous findings (Atkinson and Shreeve 1995, Burghart et al. 1999). At South Georgia, the copepod populations of *C. acutus* and C. *propinquus* were further advanced in their seasonal development (dominated by medium copepodite stages of the 'new' generation), but the overall abundances were similar to those in the south.

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

3. 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.

ACKNOWLEDGMENTS

We thank the officers, crew, and scientists onboard the RRS *James Clark Ross* for their professional support during JR82. We acknowledge the MODIS mission scientists and associated NASA personnel for the production of data in the Giovanni online data system. We thank R. Korb for providing size-fractionated chl *a* measurements, and P. Cabedo-Sanz and L. Smik for help with lab work. Comments from K. Bernard and one anonymous reviewer were much appreciated. This study was supported by a Research Project Grant (RPG-2014-021) awarded by the Leverhulme Trust (UK) to S.T.B. A.A. was part-funded by NERC and Department for Environment, Food and Rural Affairs (DEFRA) grant NE/L 003279/1 (Marine Ecosystems Research Program).

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Table 1. *Euphausia superba*: carbon isotopic signature ($\delta^{13}C$) of $IPSO_{25}$ and HBI III extracted from ~30 pooled, whole krill (mean ± SD, n=3) at four sampling locations near the retreating ice edge~~tations~~.

	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

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

Analysed stations ($IPSO_{25}$): Stn 5, 10, 13, 14, 17, 22, 31, 34, 54
Analysed stations (HBI III): Stn 5, 10, 13, 14, 17, 22, 31, 34, 47, 54, 60
Analysed stations [I/(I+H)]: Stn 5, 10, 13, 14, 17, 22, 31, 34, 54
Analysed stations, pellets ($IPSO_{25}$): Stn 21, 32
Analysed stations, pellets (HBI III): Stn 9, 10, 15, 21, 31, 32, 34, 42, 45, 47, 52, 54, 60, 61

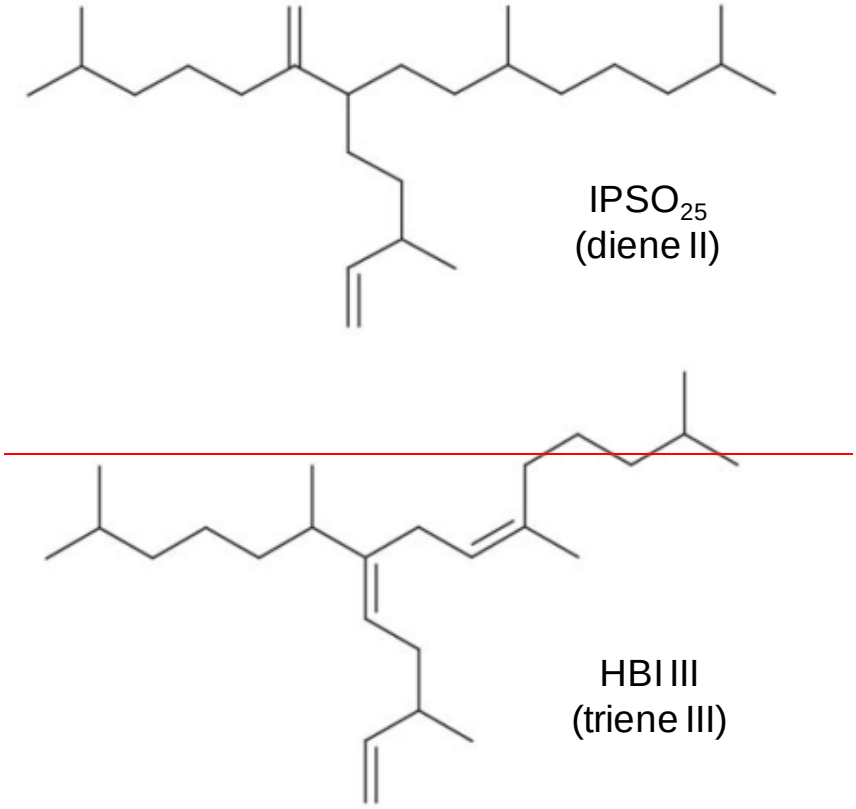

Fig. 1

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

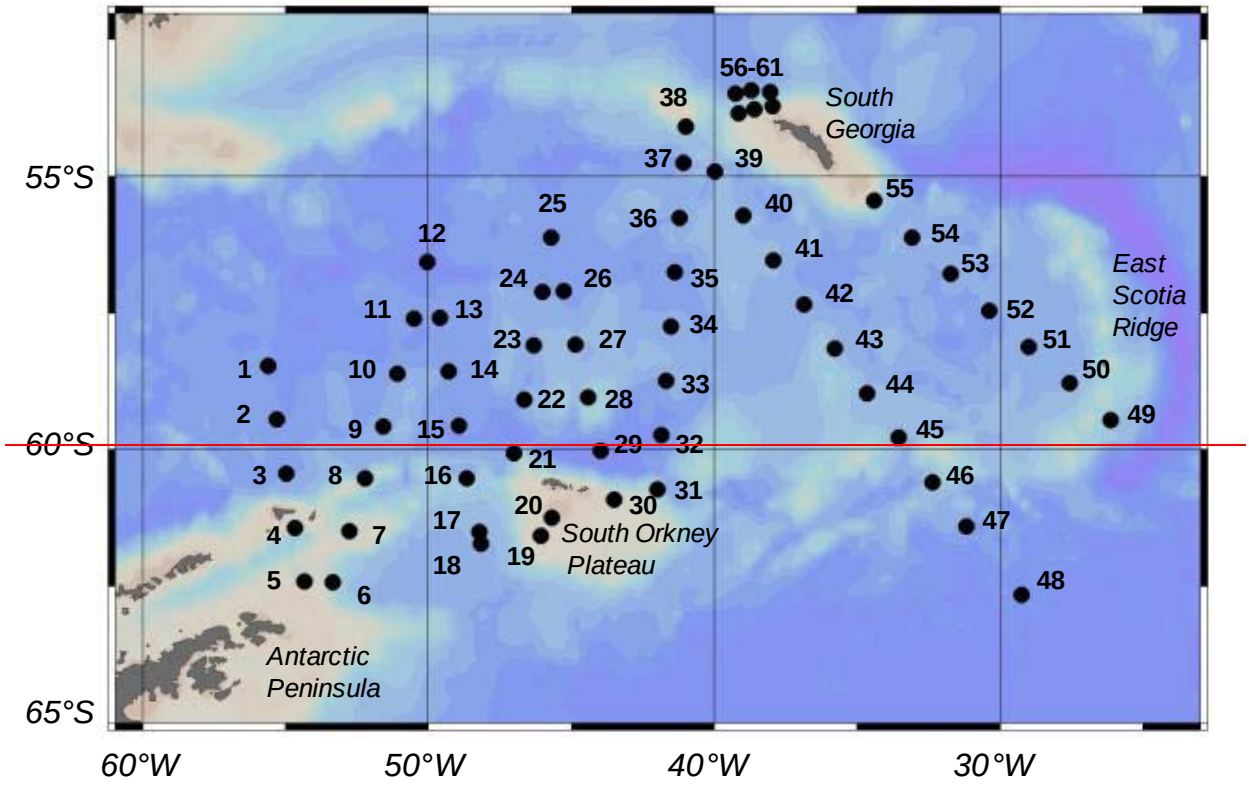

Fig. 2

Fig. 12. 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.

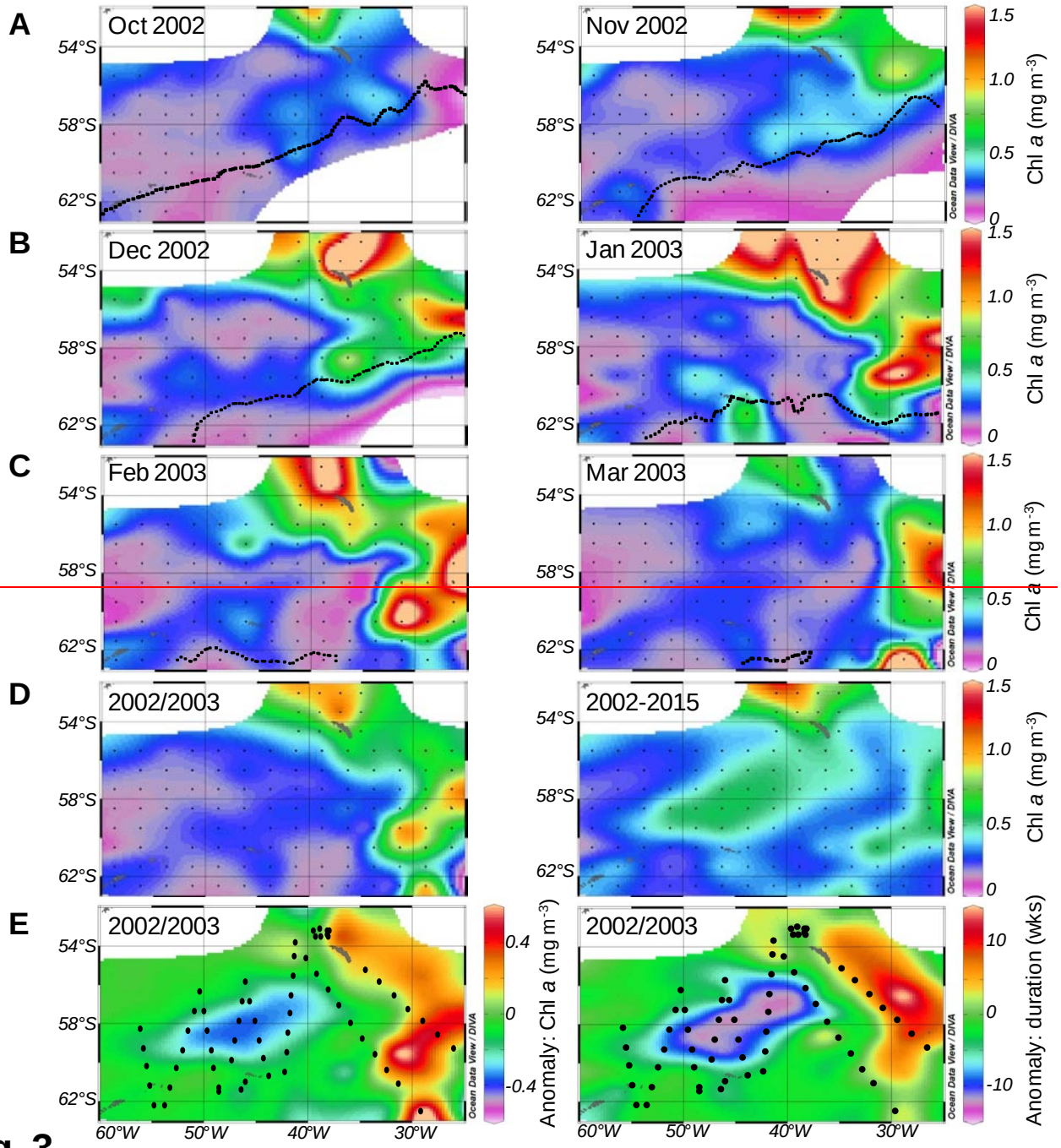

Fig. 3

Fig. 2~~3~~. Phytoplankton bloom development in the Scotia Sea~~, in 2002/2003 and on a longer-term average (2002-2015).~~ Monthly mean c~~C~~hl *a* concentrations in the 2002/2003 season; ~~the~~ **A)** the early season~~, (L: Oct. 2002; R: Nov. 2002),~~ **B)** the mid-season~~, (L: Dec. 2002; R: Jan. 2003)~~ and **C)** the late season~~. (L: Feb. 2003; R: Mar. 2003).~~ **D)** Seasonal ~~Average annual~~ mean chl *a* concentrations (Sept-Mar) in 2002/2003 and over the 13-year average of 2002-2015. ~~, Sept-Mar (L: 2002/2003; R: 2002-2015).~~ **E)** Anomaly in seasonal mean chl *a* concentration and bloom duration for ~~in~~ 2002/2003 ~~(Sept.-Mar.)~~ compared to the 13-year average of ~~longer-term average, 200~~2002-2015 ~~(L: chl *a* concentration;~~

~~R: bloom duration)~~. Chl *a* concentrations were derived from ocean colour radiometry (MODIS, 8-day composites, Sept-Mar). A bloom was defined as >0.5 mg Chl *a* m^{-3}. The dashed line represents the mean position of the 15% ice edge during each of the months. In panels E, the position of our sampling stations is given.

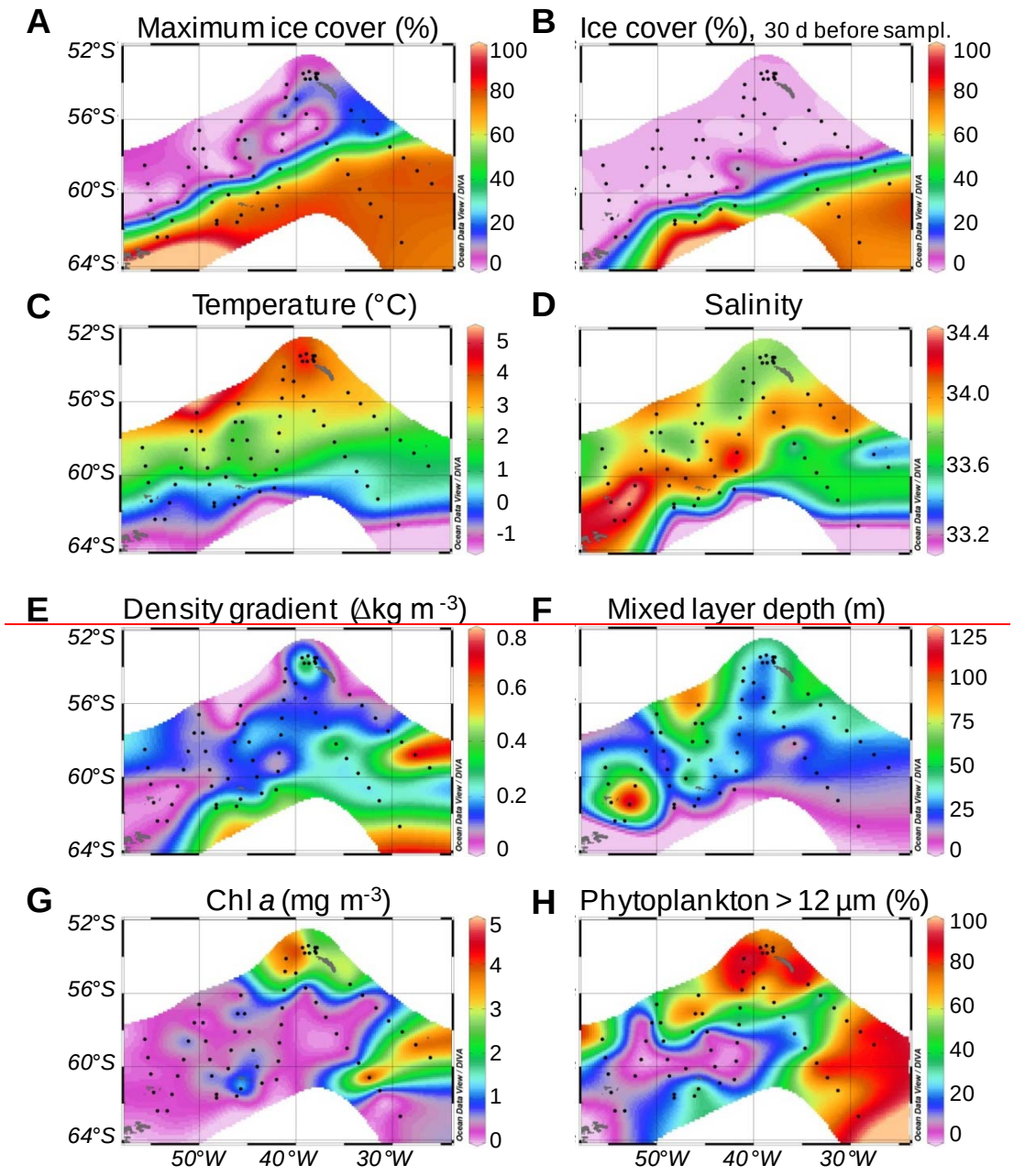

Fig. 4

Fig. 34. ~~-~~Oceanographic data: **A)** Maximum ice cover during the previous winter (Aug/ Sept/ Oct ~~within the~~ 2002)~~./2003 season.~~ **B)** Ice cover 30 days before each station was occupied~~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*).

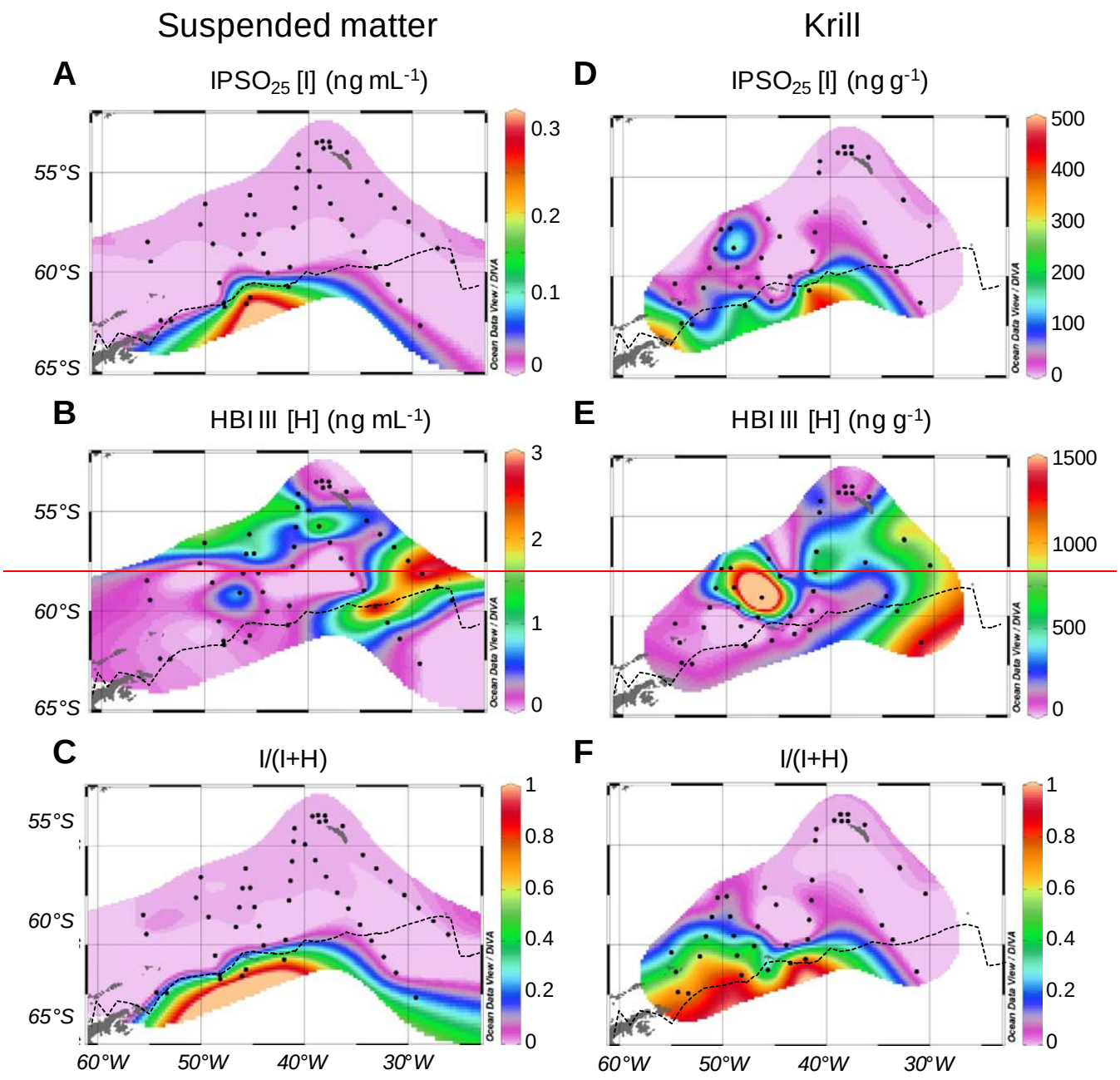

Fig. 5

Fig. 45. Highly branched isoprenoid (HBI) concentrations in suspended matter from surface waters (left) and whole krill (right): **A, D)** $IPSO_{25}$ concentrations. **B, E)** HBI III concentrations. **C, F)** $IPSO_{25}$ *vs* HBI III ratios. The dashed line represents the mean position of the 15% ice edge during January.

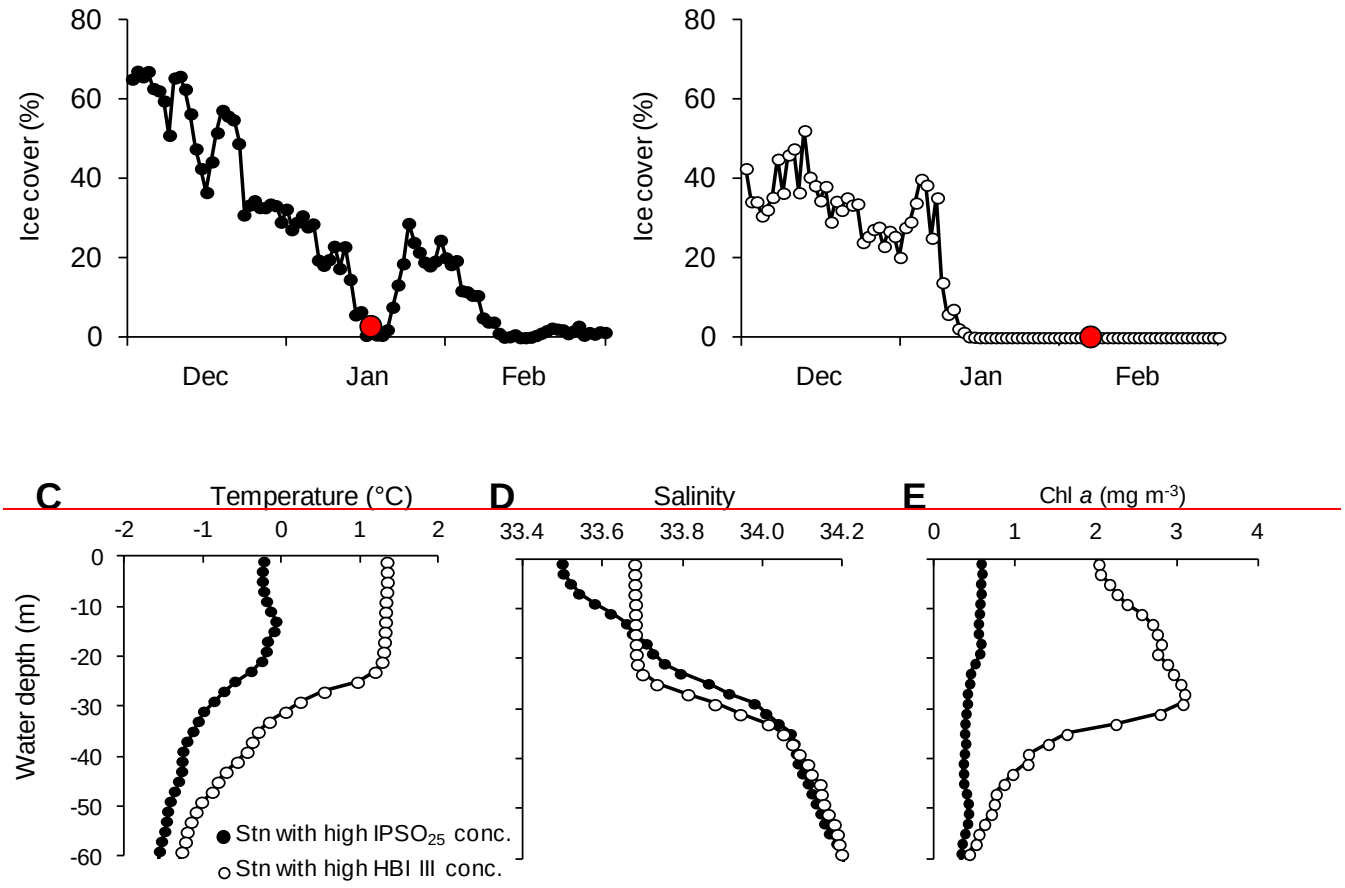

Fig. 6

Fig. ~~5~~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*.

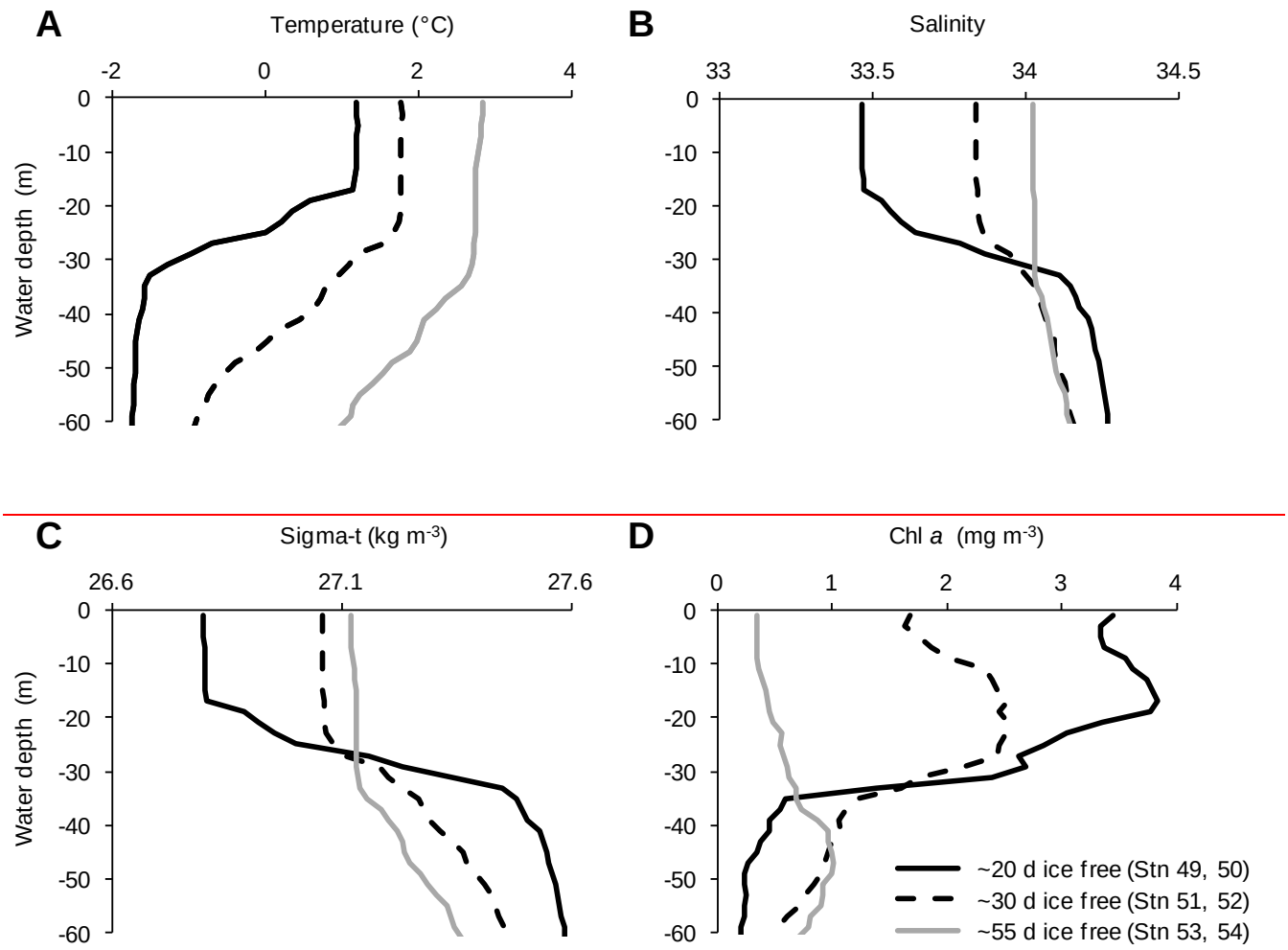

Fig. 7

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).

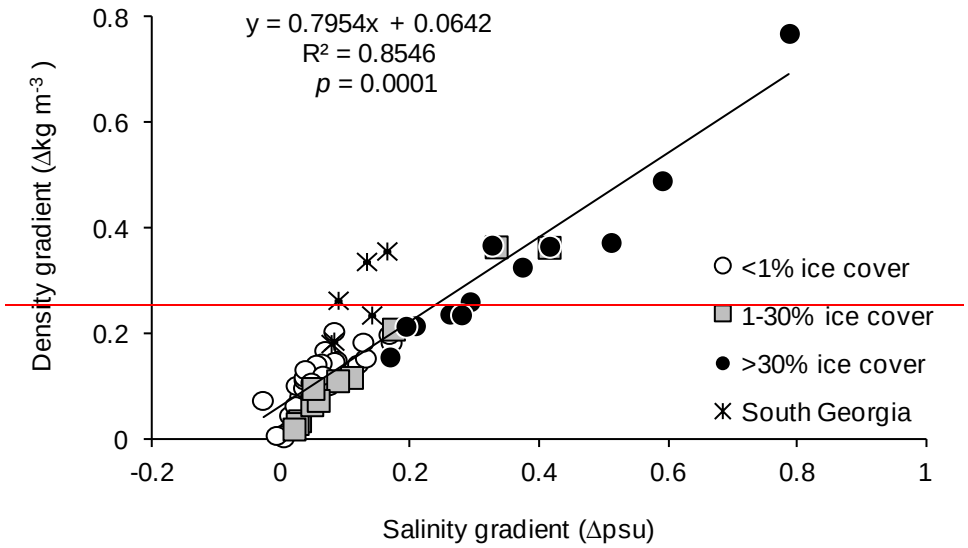

Fig. 8

Fig. ~~6~~8. The role of seasonal ice melt for water column stratification. During spring/summer 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; $R^2 = 0.9889$).

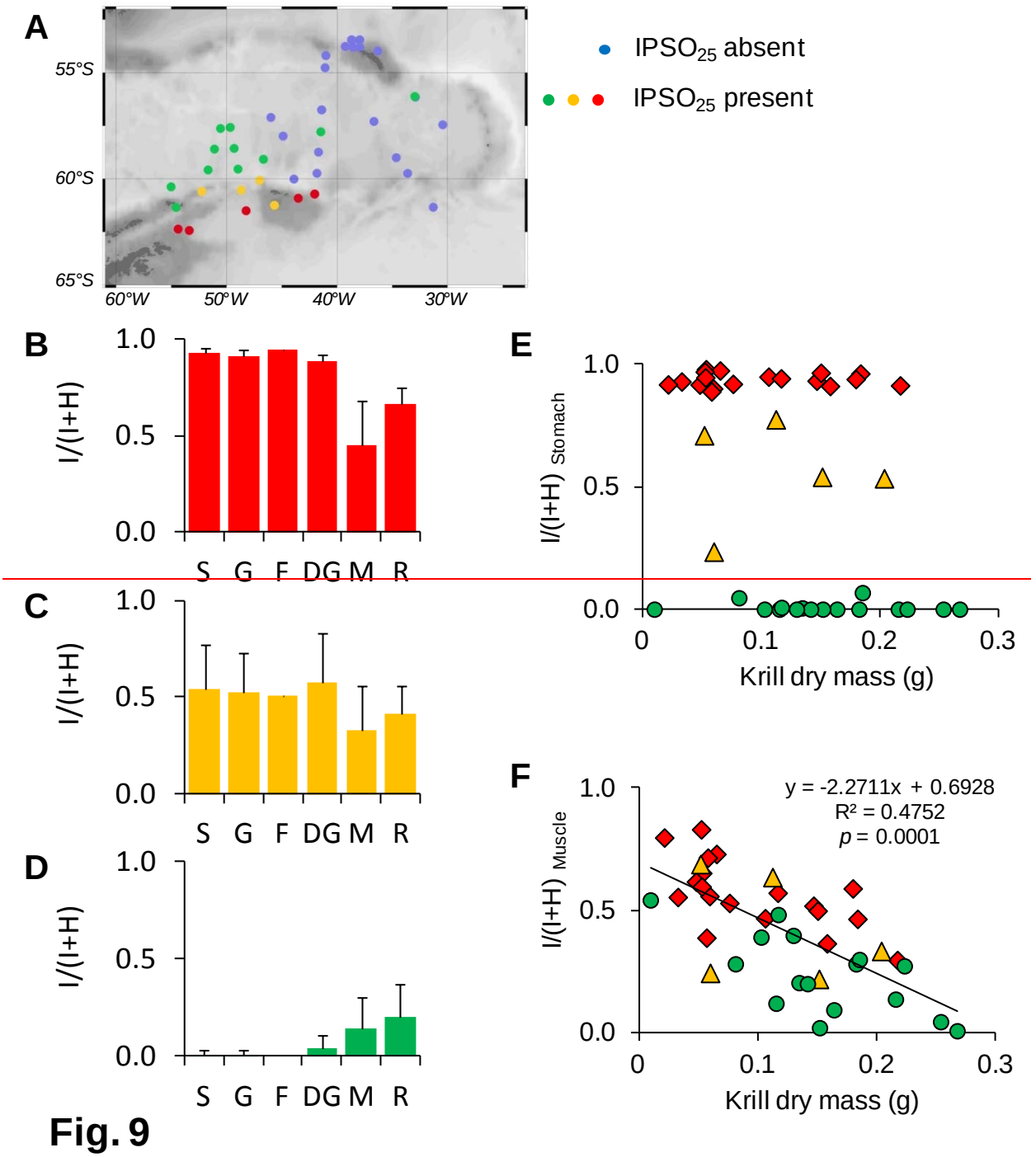

Fig. 9

Fig. 7~~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 (purple~~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. The regression line indicates the overall negative relationship between $I/(I+H)_{Muscle}$ and krill body weight. 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 Sstandard 3 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.

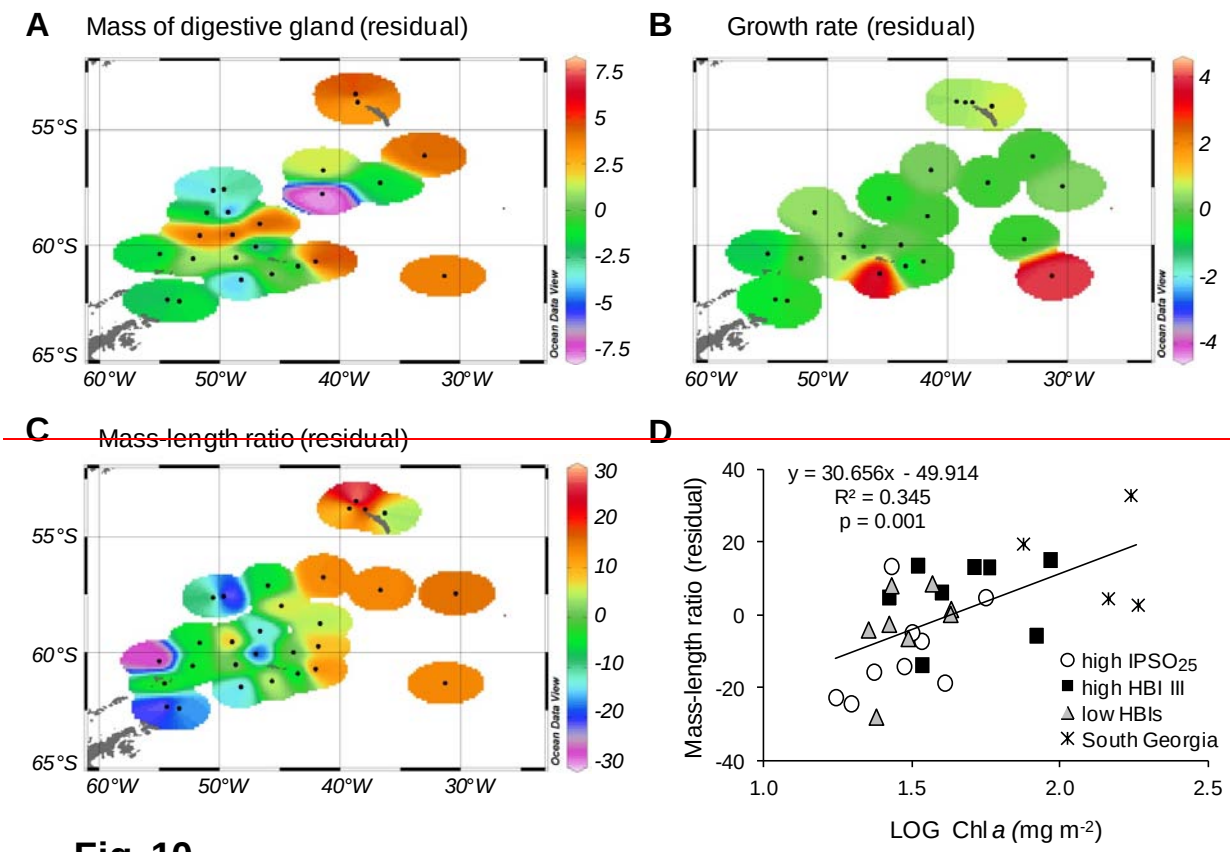

Fig. 10

Fig. 8~~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)** Overall l~~L~~inear regression between the residuals of the krill mass-length ratio (panel C) and the availability of food, indicated by the integrated chl *a* concentration in the upper 100 m-water column. Krill from different locations are distinguished by their $IPSO_{25}$- 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.

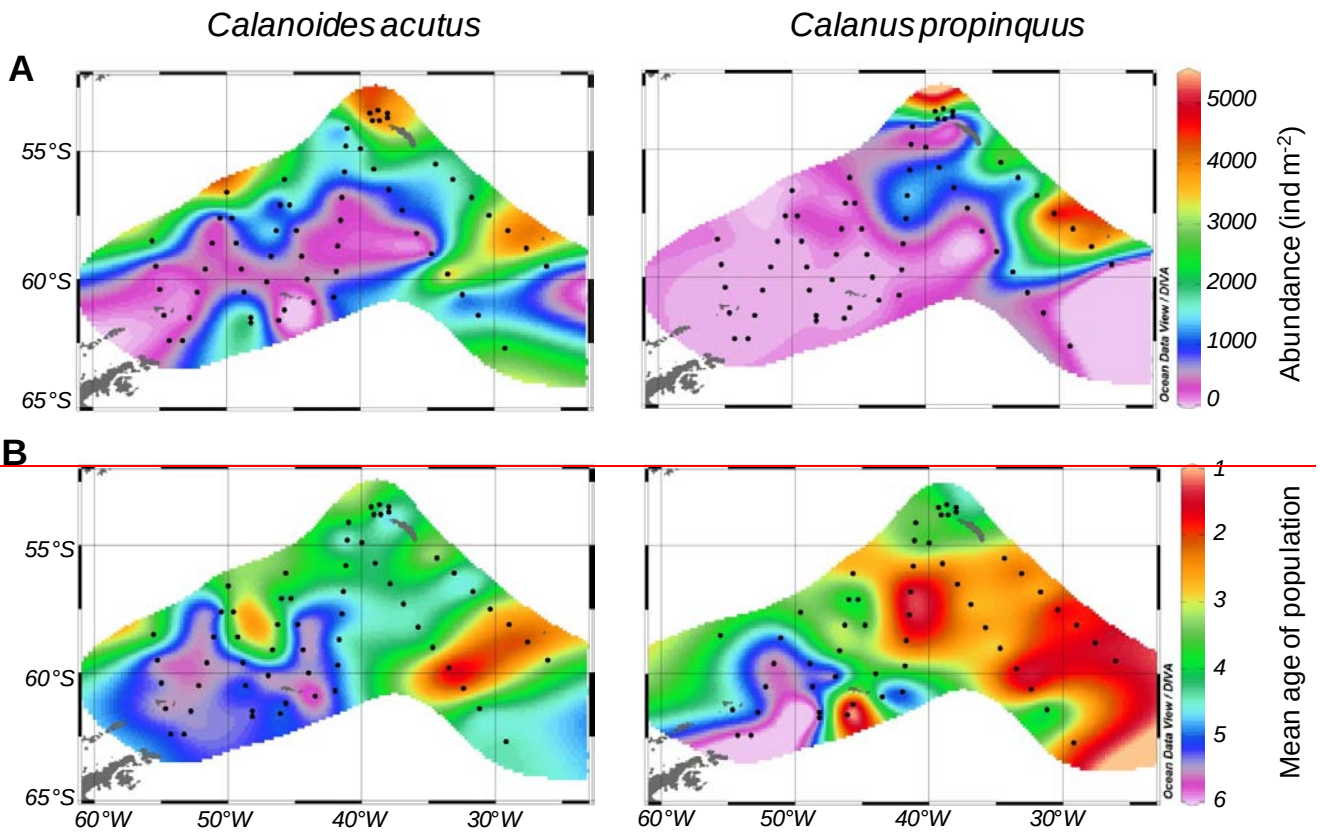

Fig. 11

~~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.~~

Major changes in response to reviewers comments

- Reduction of number of figures from 11 to 8 (3 figures were moved to 'Supplement')
- Reduction of text in the Result section by 20 lines
- Reduction of 20 references in text and reference list
- Insertion of short additional text paragraphs in the Introduction and Discussion section

Reply to comments by Ref #1 (Kim Bernard)

Review for Biogeosciences paper by Schmidt et al. 2018

General Comments:

This is an exceptionally well-written manuscript describing a study making use of a relatively novel technique (highly branched isoprenoid - HBI - biomarkers) to assess the role of ice algae and iceconditioned phytoplankton blooms in the summer diet and condition of Antarctic krill. The study serves two primary purposes as I see it. First, it provides validation for the use of IPSO25 (an ice proxy HBI biomarker) to infer food web transfer and the role of ice-derived nutrition in Southern Ocean pelagic grazers. Second, it demonstrates the importance of sea ice in the Marginal Ice Zone (MIZ) to the diet and condition of Antarctic krill, and biomass-dominant copepods - either through the provision of ice algae, or
through conditioning of the water column to promote phytoplankton blooms. The methods have been described clearly and in sufficient detail. The results are well-structured and are
presented in effective figures and tables. The results are discussed within the context of the broader literature, both in the Antarctic and Arctic pelagic ecosystems. Overall, I think this is an excellent paper that provides valuable new knowledge on the ecology of Antarctic
krill, as well as novel methods to improve our understanding of the role of sea ice in both the Arctic and Antarctic. I would highly recommend publication after a few very minor edits.

General reply: We would like to thank Kim Bernard for her very positive comments on our manuscript. We are glad that she values the purposes of our study, recognises the importance of our results and the quality of their presentation in this manuscript.

Action: None.

Specific Comments:

I only really have one specific comment, and that is that some of the discussion around the results assumes that the krill collected at each station had been there for a while. For instance, when I/I+H values are explained as a function of time since ice was last present at a particular station. This implies that the krill sampled were still at that station when the ice was last there. This might not necessarily be the case, since krill may be advected into and out of regions by ocean currents.

Reply: We agree with the reviewer that the interpretation of trophic marker signals from muscle tissue or whole animals can be confounded by advection when related to features such as the retreating ice edge or the food availability at the time of sampling.

Action: We have now included the following text at the beginning of the Discussion section '*4.2 The role of ice algae-produced carbon for krill nutrition*': 'Trophic markers such as HBIs, fatty acids or stable isotopes have different residence times in the various body compartments of consumers depending on their turnover- and growth rates (Schmidt and Atkinson 2016). In the krill muscle, for instance, turnover is relatively slow and markers may be conserved within this tissue for several weeks after their uptake. This allows us to gain information about the consumer's feeding history. On the down side, time-integrated signals from muscle tissue cannot be related to specific environmental conditions at the time of sampling or mobile features such as the retreating ice edge. This is especially

true in the Scotia Sea, where local retention as well as large-scale advection of krill may occur (Meyer et al. 2017). We overcame this problem by analysing HBIs in the krill stomach. The stomach content has a much faster turnover time than muscle tissue, varying between 45 min and ~10 h in krill (Schmidt and Atkinson 2016). This 'snapshot' of their diet permits a direct comparison between the uptake of $IPSO_{25}$ and HBI III by krill and the occurrence of these markers in the suspended matter of their sampling location.

Technical Corrections:
The following is a list of line-by-line technical corrections:

Line 60: Where is "Here", do you mean both the Arctic and Antarctic, or just the Antarctic?
Reply: We mean both Arctic and Antarctic.
Action: We replaced the word 'Here' with 'In the Arctic and parts of the Antarctic (e.g. Bellingshausen- and Amundsen Seas) ...'

Line 68: I would change "…of the polar ecosystem…" to "…of polar marine ecosystems…"
Reply: We agree.
Action: We changed '... of the polar ecosystem' to '... of polar marine ecosystems'

Line 83: I would include the word "melting" as in "…trace elements from melting sea ice…"
Reply: We agree.
Action: We inserted the word 'melting'.

Line 84: I would write MIZ out in full here. I know it's in full with the abbreviation in the abstract, but I think it would be good to have it here too.
Reply: We agree.
Action: We inserted 'marginal ice zone'.

Line 106: "…and the krill *Euphausia superba*…", I would specify the krill as Antarctic krill here.
Reply: We agree.
Action: We included the word 'Antarctic'.

Line 122: "western Antarctic Peninsula" is used here, but "Western Antarctic Peninsula" has been used in other sections of the manuscript.
Reply: We agree.
Action: We now use 'western Antarctic Peninsula' throughout the manuscript.

Line 136: It would be useful to the reader if you could define "ice-conditioned" here.
Reply: We agree that the term 'sea ice-conditioned' should be defined. However, rather than at this place, we define it when first mentioned in the 'Introduction' on Line 81.
Action: We now write 'A number of processes associated with the seasonal retreat of sea ice are considered to 'condition' the upper water column for phytoplankton blooms (Smetacek and Nicol 2005). First, low-density meltwater can stabilize the surface layer and therefore enhance mean irradiance levels for phytoplankton (Smith and Nelson 1986). Second, the release of trace elements from melting sea ice can alleviate iron limitation that often occurs in the open Southern Ocean (Lannuzel et al. 2010). Third, some ice algae species may act as an inoculum for phytoplankton blooms (Smith and Nelson 1986)...'.

Line 202: "Timelines of sea ice over" should be "Timelines of sea ice cover".

Reply: We agree.
Action: We corrected to ‘sea ice cover’.

Line 204: Should be “the data were” rather that “the data was”.
Reply: We agree.
Action: We corrected to ‘the data were’.

Line 225: What were the size classes used? Were they in 1mm increments, or something else? I think it would be useful to state that here.
Reply: We agree that more detail would be useful here.
Action: We now state: ‘Three to fifteen individuals of the same body length (±1 mm) were selected for HBI analysis. Standard 3 lengths of selected krill ranged from 16 - 42 mm. If available, up to six different size classes each differing by at least 2 mm, were analysed per station.’

Line 225: There should be a comma after “per station”.
Reply: We agree.
Action: As we added ‘with a minimum increment of 2 mm’ to this sentence (see previous ‘Comment’), there is now a full-stop after ‘per station’, and the new sentence starts with ‘Then, krill were dissected ...’.

Line 231: Although it’s obvious, “filtered water” should be “filtered seawater”.
Reply: We agree.
Action: We added ‘sea’.

Line 238: You refer to HBI III as triene III here, but the rest of the paper uses HBI III. To avoid confusion for readers, I would change this to HBI III.
Reply: We agree.
Action: We changed to ‘HBI III’.

Line 246: “seawater” rather than “water”.
Reply: We agree.
Action: We added ‘sea’.

Line 334: “There was a highly…” - the “a” is typed in a blue font for some reason.
Reply: Thanks.
Action: We changed to a black font.

Line 370: “and may, therefore, not have fed on ice diatoms at all.” - should this rather say “and may, therefore, not have fed on ice diatoms within the last XX days.”. Because, presumably it is possible that they had fed on ice diatoms at some much earlier stage.
Reply: We agree.
Action: We added ‘within the last few weeks.’

Line 502: “…north of the current ice edge…”, I would remove “current”.
Reply: We agree.
Action: We removed ‘current’.

Line 532: "…even after they had descended…", "they" is ambiguous here, do you mean the krill or the ice algae? I'm assuming you mean the ice algae, but the sentence structure could suggest that you mean the krill.
Reply: We agree.
Action: We changed 'they' to 'the algae'.

Line 549: I believe that "…krill'…" should be "…krill's…".
Reply: We agree.
Action: We changed 'krill'' to 'krill's'.

Line 549: Please replace the colon at the end of the sentence with a period.
Reply: We agree.
Action: We replaced the colon with a period.

Line 610: "…studies has…" should be "…studies have…"
Reply: We agree.
Action: We changed 'studies has ...'' to 'studies have ...'

Line 1111 (Fig. 4): "…within the 2002/2003 season." - in the text, this figure is referred to as showing ice cover from the previous winter, so should this rather be "…within the winter 2002 season."?
Reply: We agree.
Action: We changed "…within the 2002/2003 season." to '.... during the previous winter (Aug/ Sept/ Oct 2002).'

Lines 1111-1112: "Ice cover 30 days before each station was sampled." - in the text, this figure is referred to as showing ice cover 1 month before the cruise, which is different from 30 days before each station was occupied, given that the stations would have been occupied on different days. Please verify which is correct and change either the figure title or the text accordingly.
Reply: We agree. The figure caption is correct, while the text on line 297 (original manuscript) is incorrect.
Action: We changed the text from 'One month before the cruise, ...' to 'Thirty days before each station was occupied, ...'.

Figure 6: Sub-figures A and B need to have "A" and "B" typed next to them, these are missing.
Reply: We agree.
Action: We added 'A' and 'B' to the corresponding figure panels.

Line 1139 (Fig. 7): "…or longer ago…" - please rather use the amount of time, i.e. ~55 days prior, or something like that.
Reply: We agree.
Action: We inserted '~20 days ago' and '~55 days' into the sentence.

Line 1147 (Fig. 8): "During spring…" - do you rather mean during summer?
Reply: In 2002/ 2003 season, sea ice retreat was late. Thus, even January is usually considered summer in the Southern Ocean, it was like spring in the sense that ice was just retreating.
Action: We changed 'During spring 2003, ...' to 'During spring/ summer 2003, ...'.

Figure 9: The $IPSO_{25}$ absent stations are purple in sub-figure A, rather than blue.
Reply: We agree.

Action: We changed ‘blue’ to ‘purple’.

Line 1213 (Fig. 11): “…population, dominant by new…” should be “…population, dominated by new…”.

Reply: We agree.

Action: We changed ‘…population, dominant by new…’ to ‘…population, dominated by new…

Reply to comments to Ref #2

Title: Do pelagic grazers benefit from sea ice? Insights from the Antarctic sea ice proxy IPSO25

By: Katrin Schmidt et al

In this study the relative importance of three different carbon sources (ice-derived, ice-conditioned and non-ice associated) for Antarctic krill (*Euphausia superba*) is estimated with the use of the sea ice diatom proxy IPSO25 (a di-unsaturated highly branched isoprenoid (HBI), δ13C=-12.5 ‰) and the proxy for marginal ice zone (MIZ) diatoms (phytoplankton bloom) a tri-unsaturated HBI termed HBI III, δ13C=-42.2 ‰). The relative importance of sea ice diatoms in krill was related to the performance in krill (mass-length ratio, size of digestive gland and growth rate).

General comment:

This study is of broad scientific interest since the sea ice conditions in the Arctic and Antarctic are significantly changing without us knowing the impacts on marine ecosystems. This is mainly due to methodological challenges and in this study the authors present the use of the sea ice proxy IPSO25 to trace/estimate the importance of sea ice diatoms for krill and krill performance in the Scotia Sea, Atlantic sector of the Southern Ocean).

General reply: We would like to thank the anonymous Referee #2 for her/his positive comments on our manuscript. The reviewer acknowledges the broad scientific interest of our study. She/ he also gives us credit for linking the relative importance of sea ice diatoms in the krill diet to their performance, which she/he sees as a ‘very promising’ step forward.

Action: None.

The authors have looked at several aspects and present many interesting results, but I would say the result section is far too long, including too many results/figures which make it challenging for the readers to follow.

Reply: We agree with the reviewer that our manuscript is complex and potentially challenging for the reader, but so is the matter of our study – sea ice. Our aim was to use a holistic approach looking at different aspects of sea ice (supply of food and conditioning of the environment); and we applied a novel method that is not yet established in the Southern Ocean. We think it is in the interest of the reader that these aspects are comprehensively discussed and that a link to research in the Arctic is established. However, we agree with the reviewer that some shortening and further clarifying of the manuscript could be done and accordingly we have followed this advice.

Action: We use headings throughout Methods, Results and Discussion so that the reader can easily follow certain parts of the study and neglect aspects he/she is less interested in (which will differ depending on the background and research interest of the reader). We have now reduced the number of figures from 11 to 8, shortened the text in ‘Results’ by 20 lines (~20% of the Result text) and removed 20 references.

The result section also includes discussion parts which makes it even longer and hamper the overall structure of the paper.

Reply: We agree that the 'Results' section includes some interpretation of the data. However, we think that in some cases this is inevitable. For instance when presenting stable isotope signal, an interpretation of the values (e.g. sea ice vs. open water origin) needs to follow and this will require a reference. Likewise, when we compare trophic markers in different tissues, explaining the different turnover time of these tissues is essential to understand the results.

Action: We carefully rewrote the 'Results' to keep interpretation of data to the essential minimum. As a consequence the 'Results' text is now shortened by ~20% (see marked up version).

I am positive to the work done. I think it is very promising that the authors bring it one step further by relate the relative importance of sea ice diatoms to the krill performance. The authors have also included copepods performance into the study, but since they did not determine the relative importance of sea ice diatoms for these copepods I will recommend the authors to cut the copepod part in the results and rather bring it in as a "supportive" argument in the discussion instead.

Reply: We would like to keep the copepods as a central part of our study. Firstly, their recruitment data do strongly support our findings on Antarctic krill that the MIZ is an important feeding ground for pelagic grazers. Second, copepods are an essential part of the Southern Ocean food webs and need to be considered alongside krill. Third, copepods are the main overlap between our study and Arctic studies.

Action: We kept the copepods in the 'Results', but reduced the copepod-related figure in the main part of the manuscript. Therefore, we moved 2 of the panels in the original Fig. 11 to 'Supplement' and 2 panels to the new Fig. 8, which now shows body conditions/ fitness of both krill and copepods within one figure.

The main reason for why I recommend major revision is that the authors needs to "trim down" the number of figures to the half and get the manuscript less wordy and more focused on the most important results – the results that address the main aim/research question in this paper.

Reply: We notice that the reviewer's critics on our manuscript are only for presentation/style, not for more substantial issues such as lack, error or inconclusiveness of the data. However, as noticed by Ref. 1, this manuscript has multiple purposes (validating a method, looking at direct and indirect effects of sea ice on food availability, relating the consumer's body conditions to the occurrence of certain trophic markers). We think that all three of these aims are valuable and allow us to reach a broad readership; therefore we are reluctant to cut the text to follow only one of these aims as the reviewer suggests. Moreover, the number of figures and length of text is within the common range for publications in 'Biogeosciences'. For instance, we counted the number of display items in 20 papers recently published in this journal and found a range of 6 to 14 display items, with a mean of 9-10. Our original version of the manuscript had 13 display items, but we have now reduced the number to 10.

Action: We reduced the number of figures from 11 to 8 (3 figures are now in 'Supplement') and the Result part from 128 lines of text to 107 lines.

Specific comments:

Title: replace pelagic grazers with krill.

Reply: As mentioned above we think that copepods are an essential part of our manuscript and that the use of the term 'pelagic grazers', which includes both krill and copepods, is verified by our results. This title will extent the interest in the manuscript beyond the krill community.

Action: None

Keywords: missing?
Reply: We did not find keywords in papers published in Biogeosciences, so assume that keywords are not a feature of this journal.
Action: None

Introduction: Somewhat long, but overall ok. Aim of the study/ research question could potentially be more hypotheses driven. At current very descriptive approach.
Reply: As mentioned above, this manuscript has multiple purposes that cannot be covered by one single hypothesis. We therefore settle with a descriptive approach.
Action: None

Methods (Materials and Methods)
Move the chlorophyll a measurements under Oceanography to 2.1 Phytoplankton bloom development,
Reply: The chlorophyll *a* measurements are part of the sampling activities onboard ship, while the phytoplankton bloom development is based on satellite-derived data.
Action: To clarify this, we changed the headings in the Method sections: '2.1 Phytoplankton bloom development' is now called '2.1 Satellite-derived chlorophyll *a* data' and '2.3 Oceanography' is now called '2.3 Station sampling of oceanographic parameters' with the onboard chl *a* sampling and analysis remaining in the latter section.

Remove 2.8 Copepod abundance and stage composition
Reply: As mentioned above, we would like to keep the copepods as a central part of the manuscript.
Action: None

Results
See my general comments above.
Reply: We agree with the reviewer that some of our figures and their description could be moved to 'Supplementary information'.
Action: We moved the original Fig. 1, Fig. 7 and part of Fig. 11 to 'Supplement' and reduced the text in 'Results' by 20 lines (~20% of total text in 'Results').

Table 1. Please specify in Materials and Methods from how many stations carbon isotopic signatures of krill were analysed. From Table 1 only values from 4 stations are shown, but in the remaining result section the reader get the impression that many more krill samples are analysed, but this may only be the case for IPSO25 and HBI III, shown in Fig. 5D
Reply: We agree.
Action: We now clarified this by inserting the following sentence at the beginning of section '2.7 Stable isotope determination' in the Methods section: 'The stable carbon isotopic compositions ($\delta^{13}C$) of $IPSO_{25}$ and HBI III were determined for krill from 4 sampling locations near the retreating ice edge (Stn. 5, 17, 31 and 47).'

In **Figure 2** the authors could indicate in the station map with colour codes which analyses have been done from which station
Reply: Most of our figures are ODVs (new Figs 1, 2, 3, 4, 7, 8, Fig. S2), where each sampling location is indicated with a dot. Thus, a colour-coding of the overall station map seems not necessary.
Action: None.

Figure 3. Remove text in brackets that already are given in the figure panels.
Reply: We agree.

Action: We removed the text in brackets and rewrote the figure caption to clarify which months had been averaged on each panel.

Figure 6 – is this figure of top relevance? I suggest to cut it or alternatively add to supplementary information. The same for Fig. 7 and Fig. 8

Reply: Fig. 6 shows the physical environment at stations where the ice algae marker occurred in comparison to stations where the MIZ marker occurred. This figure aids our validation of the HBI approach in the Southern Ocean, which has not been done previously. We therefore would like to keep Fig. 6 in the main text. Fig. 7 is of lower importance and can be moved to the 'Supplement'. Fig. 8 shows the relationship between ice cover and vertical stratification of our sampling stations. This role of sea ice; the conditioning of the upper ocean for phytoplankton blooms, is rarely considered when looking at the role of sea ice for pelagic grazers. We therefore think that this figure is important and verifies a place in the main manuscript.

Action: Fig. 7 has been moved to 'Supplement' as Fig. S2.

Figure 9 A bit complicated at first glance but OK. Panel A: check blue colour.

Reply: We agree, it may be 'purple' rather than 'blue'

Action: In the figure caption, we changed the word 'blue' to 'purple'

One question to panel F why haven't the authors performed separate correlations for the three scenarios. At present one correlation for all three combined – please explain. The same question I have for Fig. 10 panel D correlation.

Reply: Presented is the relationship between the trophic marker ratio in krill muscle and their body mass. The overall relationship is well supported by the individual data points from the three different regions, but n-numbers are not in each case sufficient to run individual regressions.

Action: To clarify, we now wrote in the figure caption:'The regression line indicates the overall negative relationship between $I/(I+H)_{Muscle}$ and krill body mass.'

Fig 10. See above for question to panel D.

Reply: Here we presented one regression line because it gives the opportunity to see if a particular sample is above or below average. Also, it shows the overall trend between the residual in the mass-length ratio and food availability.

Action: To clarify, we now wrote in the figure caption:'Overall linear regression between the residuals of the krill mass-length ratio (panel C) and the availability of food, indicated by the integrated chl *a* concentration in the upper 100 m-water column.'

In addition, I would suggest another way of presenting these results since they are difficult to follow/see patterns in the current form. I would suggest a table.

Reply: This figure aims to compare different regions of the Scotia Sea for their suitability as feeding grounds for krill and copepods. Therefore horizontal ODVs seem most appropriate to us. Reviewer 1 confirmed that our figures are 'effective', so we assume that there is no major problem with their understanding and interpretation.

Action: None.

Fig. 11 Remove copepods from results

Reply: As mentioned above, we would like to keep the copepods as a central part of the manuscript.

Action: We kept the copepods in the 'Results', but reduced the copepod-related figure in the main part of the manuscript. Therefore, we moved 2 of the panels in the original Fig. 11 to 'Supplement' and 2

panels to the new Fig. 8, which now shows body conditions/ fitness of both krill and copepods within one figure.

Discussion

I would start the Discussion with the end paragraph (Lines 75-90 on page 16) and down scale a bit the remaining part on the evaluation HBI approach.

Reply: The HBI approach has rarely been used in food web studies in the Southern Ocean, and those few studies that did apply HBIs have rarely been cited. We therefore made a conscious effort to evaluate the method; mention its strengths and limitations, and compare it with other methods more commonly used. Starting with the lines the reviewer suggested would mean to present a conclusion before the reader receives some background information. We therefore did not follow the reviewer's suggestion.

Action: None

Ocean colour data have been used to determine the progress in phytoplankton blooms and I miss some discussion on the "correctness of these data" since deep chlorophyll a max layer can frequently occur and these are not detected by the satellites.

Reply: We agree with the reviewer that satellites likely miss deep chlorophyll maxima (DCM), and that this may be an additional food source for pelagic grazers. However, while we now mention this issue in the revised version, it may be beyond the scope of this manuscript to speculate about DCM at the time of our sampling.

Action: In the Methods section '2.1 Satellite derived chlorophyll *a* data' we have now included the following sentence: 'To gain an overview of phytoplankton development during the year of our field season (2002/2003) and for comparison with other years, we used satellite-derived chlorophyll *a* (chl *a*) data. These provide large-scale, quasi-synoptic coverage of chl *a* concentrations in surface waters, but have the caveat that deep chl *a* maxima are not detected.'

The stage of the bloom/ seasonal progression differs in the study region. Please also discuss if differences in krill performance is likely to level out at the end of the season among the stations/regions sampled.

Reply: It is well known that not all Southern Ocean habitats support the same zooplankton biomass/ production – so across large parts there is no 'levelling-out' towards the end of the season (see for instance Atkinson et al. 2008, Murphy et al. 2017). However, to discuss this in detail seems beyond the scope of this manuscript.

Action: None.

References

I have not checked references in detail in the current form of the manuscript, but most work referred to is peer-reviewed, easy to find papers. The numbers of references are however very high and the authors should consider to reduce the total numbers.

Reply: We agree with the reviewer that the number of our references is high. This is partly because it is a relatively long manuscript and partly due to the combined referencing of Arctic and Antarctic sea ice studies.

Action: We removed 20 references from our text and reference list (see marked up manuscript). We now cited maximal 2-3 papers for each statement and also used the '... and references therein' option.